Historical Biology

An International Journal of Paleobiology

ISSN: 0891-2963 (Print) 1029-2381 (Online) Journal homepage: www.tandfonline.com/journals/ghbi20

The phylogenetic nomenclature of Caimaninae (Crocodylia: Alligatoroidea)

Giovanne M. Cidade, Pedro L. Godoy, Patricia Amavet, Adam Cossette, Andrés Solórzano, Paula Bona, Mónica Angulo-Bedoya, Sergio A. Balaguera-Reina, Márton Rabi, Izeni Pires-Farias, Rodrigo G. Figueiredo, Martin D. Ezcurra, Pedro S. Bittencourt, Christopher A. Brochu & Igor J. Roberto

HISTORICAL BIOLOGY
https://doi.org/10.1080/08912963.2026.2614968

Taylor & Francis
Taylor & Francis Group

RESEARCH ARTICLE

The phylogenetic nomenclature of Caimaninae (Crocodylia: Alligatoroidea)

Giovanne M. Cidade[1], Pedro L. Godoy[2], Patricia Amavet[3,4], Adam Cossette[5], Andrés Solórzano[6], Paula Bona[4,7], Mónica Angulo-Bedoya[8], Sergio A. Balaguera-Reina[9], Márton Rabi[10], Izeni Pires-Farias[11], Rodrigo G. Figueiredo[12], Martin D. Ezcurra[13], Pedro S. Bittencourt[14,*], Christopher A. Brochu[15] and Igor J. Roberto[16]

[1]Laboratório de Pesquisas Paleontológicas, Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Rio Branco, Brazil; [2]Department of Zoology, Institute of Biosciences, Universidade de São Paulo, São Paulo, Brazil; [3]Laboratorio de Genética, Departamento de Ciencias Naturales, Facultad de Humanidades y Ciencias, Universidad Nacional del Litoral, Santa Fe, Argentina; [4]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Ciudad Autónoma de Buenos Aires, Argentina; [5]Department of Anatomy, New York Institute of Technology College of Osteopathic Medicine, Old Westbury, NY, USA; [6]Escuela de Geología, Departamento de Biología y Química, Facultad de Ciencias Básicas, Universidad Católica del Maule, Talca, Chile; [7]División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Ciudad Autónoma de Buenos Aires, Argentina; [8]Escuela de Ciencias Aplicadas e Ingeniería, Grupo de Investigación en Bioingeniería (GIB), Universidad EAFIT, Medellín, Colombia; [9]Department of Wildlife Ecology and Conservation, Fort Lauderdale Research and Education Center, University of Florida, Davie, FL, USA; [10]Department of Geosciences, Eberhard-Karls-Universität Tübingen, Tübingen, Germany; [11]Departamento de Genética, Laboratório de Evolução e Genética Animal (LEGAL), Universidade Federal do Amazonas, Manaus, Brazil; [12] Departamento de Biologia, Universidade Federal do Espírito Santo, Alegre, Brazil; [13]Sección Paleontología de Vertebrados, ONICET–Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; [14]Fundação Espirito-santense de Tecnologia FEST, Ed. América Centro Empresarial, Brazil; [15]School of Earth, Environment, and Sustainability, University of Iowa, Iowa City, IA, USA; [16]Faculdade de Filosofia Dom Aureliano Matos, Departamento de Biologia, Universidade Estadual do Ceará, Limoeiro do Norte, Brazil

ABSTRACT

Caimaninae is one of the main clades within alligatoroid crocodylians. Its extant diversity encompasses six species in three genera – *Caiman*, *Melanosuchus* and *Paleosuchus* – and is largely native to South America; the fossil record, in contrast, reveals a far greater diversity, extending from the Late Cretaceous and, although concentrated in South America, also showing notable fossils from Central America, North America and the Caribbean. Systematic and taxonomic research on Caimaninae began in the 18th century, with phylogenetic-based systematics, taxonomy and nomenclature being applied since the 1980s. Following the publication of the International Code of Phylogenetic Nomenclature (PhyloCode), a cojoined effort by Caimaninae systematists to standardise the phylogenetic systematics and nomenclature of the group was required, which is the objective of this paper. Herein, we provide phylogenetic definitions for seven clade names: Caimaninae, Bottosauria (new clade name), Caimanini (new clade name), Jacarea, Purussauria (new clade name), Purussauridae (new clade name) and Nettosuchidae. Detailed information on each clade is provided, including taxonomic and evolutionary history, composition, fossil record, divergence dates, characteristics and previous phylogenetic studies. Our intention with this effort is to provide a stable framework on which to base further research on the diversity of the group at several levels, and to encourage the use of phylogenetic nomenclature in Crocodylia.

ZooBank ID: http://zoobank.org/urn:lsid:zoobank.org:pub:C348DC54-4017-4B0E-AA6D-A6412553FE9F

ARTICLE HISTORY
Received 22 September 2025
Accepted 5 January 2026

KEYWORDS
Cladistics; Phylocode; phylogenetic systematics; systematics; taxonomy

HANDLING EDITOR
Dr Mark T. Young, University of Edinburgh, UK

Introduction

Living crocodylomorphs are united in the crown-clade Crocodylia. According to most phylogenetic analyses, Crocodylia may be broadly divided into five clades: the two completely extinct *Borealosuchus* and Planocraniidae, and the ones that include extinct and living representatives, Alligatoroidea, Crocodyloidea and Gavialoidea (e.g. Brochu, 1999, 2012). Alligatoroidea has traditionally been broadly divided into two subclades: Alligatorinae, which includes all alligatoroids closer to *Alligator mississippiensis* (Daudin, 1802) than to *Caiman crocodilus* (Linnaeus, 1758), and Caimaninae, which includes all alligatoroids closer to *Caiman crocodilus* than to *Alligator*

CONTACT Giovanne M. Cidade giovannecidade@hotmail.com Laboratório de Pesquisas Paleontológicas, Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, BR 364 Km 04, Rio Branco, Acre 69.915-900, Brazil

*Present affiliation for Pedro S. Bittencourt: Divisão Técnico-Ambiental (Ditec), Superintendência do IBAMA em Roraima (Supes/RR), Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis - IBAMA. Avenida Brigadeiro Eduardo Gomes, nº 4358, Bairro Aeroporto, CEP: 69310-005 - Boa Vista - RR.

Published online 04 Mar 2026

mississippiensis (Brochu, 1999, 2010, 2011; Cossette, 2021; Cossette & Brochu, 2018; Stocker et al., 2021; Walter et al., 2022).

The extant taxonomic diversity of Caimaninae consists of six species distributed among three genera: *Caiman crocodilus*, *C. latirostris* (Daudin, 1802), *C. yacare* (Daudin, 1802), *Melanosuchus niger* (Spix, 1825), *Paleosuchus palpebrosus* (Cuvier, 1807) and *P. trigonatus* (Schneider, 1801; Brochu, 1999; Medem, 1981, 1983). All species are exclusive to South America, except for *C. crocodilus*, which also naturally occurs in Central America, southern Mexico and in Trinidad and Tobago, in the Caribbean (Brochu, 1999; Medem, 1983; Thorbjarnasson, 1992), and it has been introduced in United States (Florida), Cuba and Puerto Rico (Balaguera-Reina & Velasco, 2019; Parks et al., 2023; Roberto et al., 2021). Dating back from the Late Cretaceous, the Caimaninae fossil diversity includes not only forms related to the extant genera, that occur from the Miocene onwards, but also many extinct taxa that are ecologically and morphologically very distinct from the extant diversity, such as the giant predator *Purussaurus* Barbosa-Rodrigues, 1892, the 'gulp-feeder' predator *Mourasuchus* Price, 1964, and a series of taxa that are considered durophagous forms (e.g. Aguilera et al., 2006; Barbosa-Rodrigues, 1892; Bona et al., 2012; Cidade et al., 2017, 2019a; Fortier et al., 2014; Langston, 1965; Price, 1964; Salas-Gismondi et al., 2015; Scheyer et al., 2013). Nevertheless, the extinct diversity of Caimaninae is significantly higher. Although still predominantly South American, an important extinct diversity is also recognised for Central America and especially North America (Bona et al., 2012; Bona, Ezcurra, et al., 2018; Brochu, 1999, 2010, 2011; Cidade et al., 2019a; Cossette & Brochu, 2018; Godoy et al., 2021; Hastings et al., 2013, 2016; Rio & Mannion, 2021; Salas-Gismondi et al., 2015; Stocker et al., 2021; Walter et al., 2022).

Considering the unequivocal records of Caimaninae identifiable to a specific level (see Bona, Ezcurra, et al., 2018; Bona et al., 2022; Brochu, 1999, 2010, 2011; Cidade et al., 2019a; Cossette & Brochu, 2018; Godoy et al., 2021; Hastings et al., 2013, 2016; Rio & Mannion, 2021; Salas-Gismondi et al., 2015; Stocker et al., 2021; Walter et al., 2022), the oldest known record of the clade is *Bottosaurus harlani* Meyer, 1832, from the Upper Cretaceous of the United States (Cossette & Brochu, 2018). However, some Late Cretaceous crocodylian taxa have been recovered as caimanines, such as *Albertochampsa* Erickson, 1972, *Brachychampsa* Gilmore, 1911 and *Stangerochampsa* Wu, Brinkman, and Russell (1996), from North America (Bona, Ezcurra, et al., 2018; Cossette, 2021; Rio & Mannion, 2021; Salas-Gismondi et al., 2015; Stocker et al., 2021), and *Jiangxisuchus* Li et al., 2019, from China (Walter et al., 2022). In the Paleocene, there are further occurrences in North America – *Bottosaurus fustidens* Cossette, 2021, from the United States (Cossette, 2021) – as well as the earliest occurrences in South America: *Eocaiman palaeocenicus* Bona, 2007, *Necrosuchus ionensis* Simpson, 1937 and *Protocaiman peligrensis* Bona, Ezcurra, Barrios and Blanco, 2018 from Argentina (Bona, 2007; Bona, Ezcurra, et al., 2018; Bona et al., 2022; Brochu, 2011; Simpson, 1937), and *Eocaiman itaboraiensis* Pinheiro, Fortier, Pol, Campos and Bergqvist, 2013 from Brazil (Pinheiro et al., 2012). In the Eocene, there are the most recent occurrences of North American fossil caimanines identifiable at a specific level: *Chinatichampsus wilsonorum* Stocker et al., 2021 and *Tsoabichi greenriverensis* Brochu, 2010, both from the United States (Brochu, 2010; Stocker et al., 2021; Walter et al., 2022), whereas the record in South America is limited to *Eocaiman cavernensis* Simpson, 1933 (Godoy et al., 2021; Simpson, 1933). There are no known records at a specific level for Caimaninae in the Oligocene: a species, '*Caiman tremembensis*' Chiappe, 1988, was proposed (Chiappe, 1988), but the incomplete nature of its remains led it to be considered an indeterminate caimanine by Fortier et al. (2014).

During the macroevolutionary history of caimanines, the Miocene is the epoch in which the greatest morphological and taxonomic diversity is recorded, with important occurrences especially in South America (Paiva et al., 2024), but also with the first occurrences of the group in Central America. In South America, there are records of extinct species of extant genera, such as *Caiman australis* (Bravard, 1858), from Argentina (Bona et al., 2012; Bravard, 1858; Rovereto, 1912), *C. brevirostris* Souza-Filho, 1987, from Brazil (Fortier et al., 2014; Souza-Filho, 1987) and *C. wannlangstoni* Salas-Gismondi et al., 2015, from Peru (Salas-Gismondi et al., 2015) and *Melanosuchus latrubessei* Souza-Filho et al., 2020 from Brazil (Souza-Filho et al., 2020). Additionally, there are also fossils identifiable only at a generic level to *Caiman* Spix, 1825 (Bona et al., 2012; Langston, 1965; Scheyer & Delfino, 2016; Solórzano et al., 2018), *Melanosuchus* (Bona, Fernandez-Blanco, et al., 2018; Foth et al., 2018; Medina, 1976) and *Paleosuchus* (Salas-Gismondi et al., 2007). Regarding exclusively extinct taxa, the Miocene fossil record of Caimaninae from South America comprises: the giant predator *Purussaurus* and the 'gulp-feeder' predator *Mourasuchus*, both with occurrences in Argentina, Brazil, Colombia, Peru and Venezuela (Aguilera et al., 2006; Barbosa-Rodrigues, 1892; Bocquentin-Villanueva, 1984; Bona et al., 2012, 2023; Cidade et al., 2017, 2019a, 2019b; Cidade, Fortier, et al., 2019; Langston, 1965; Mook, 1941; Price, 1964; Scheyer et al., 2013), whereas *Mourasuchus* also has records from Bolivia (Cidade, Souza-Filho, et al., 2019b); the durophagous taxa *Globidentosuchus brachyrostris* Scheyer et al., 2013 from Venezuela (Scheyer et al., 2013) and *Gnatusuchus pebasensis* Salas-Gismondi et al., 2015 and *Kuttanacaiman iquitosensis* Salas-Gismondi et al., 2015 from Peru (Salas-Gismondi et al., 2015); the generalist taxa *Acresuchus pachytemporalis* Souza-Filho, Souza, Hsiou, Riff, Guilherme, Negri and Cidade, 2019, from Brazil and Venezuela (Cidade & Rincón, 2021; Souza-Filho et al., 2018) and *Paranasuchus gasparinae* (Bona & Carabajal, 2013) from Argentina (Bona & Carabajal, 2013; Bona et al., 2024); and taxa with unknown feeding habits such as *Paranacaiman bravardi* Bona, Barrios, Ezcurra, Blanco and Cidade, 2024 (Bona et al., 2024). In Central America, the Caimaninae record of the Miocene is comprised of *Culebrasuchus mesoamericanus* Hastings et al., 2013 and *Centenariosuchus gilmorei* Hastings et al., 2013 from Panama (Hastings et al., 2013, 2016). After the Miocene, all fossil occurrences of Caimaninae are assigned to the extant taxa, either at a generic or specific level (Cidade, et al., 2019a; Fortier, 2011; Fortier & Rincón, 2013).

Biogeographical analyses generally suggest that Caimaninae originated in North America during the Late Cretaceous and subsequently dispersed into South America between the Late Cretaceous and the Paleocene (Bona, Ezcurra, et al., 2018; Brochu, 1999, 2010, 2011; Walter et al., 2022). Within this framework, Central American and North American caimanines may represent either relictual populations from before the dispersion into South America or the result of secondary dispersals back to Central and North America from the South American landmass (see Bona, Ezcurra, et al., 2018; Brochu, 1999, 2010, 2011; Hastings et al., 2013; Stocker et al., 2021; Walter et al., 2022). The first scenario is more likely for taxa identified as early-diverging caimanines, such as *Culebrasuchus* from Central America and *Chinatichampsus* from North America (Hastings et al., 2013; Stocker et al., 2021). In contrast, the second scenario is more plausible for taxa found as later divergences within the clade such as *Centenariosuchus* from Central America and *Tsoabichi* from North America (Hastings et al., 2013). Alternatively, multiple Palaeogene dispersals to South America with a secondary northward expansion to Central America during the Neogene have been proposed by Walter et al. (2022). The first comprehensive phylogenetic analysis on caimanines using morphological characters was the PhD thesis of Norell (1988), whereas the first to be formally published was the work of Brochu (1999), which served as the basis for most of the later phylogenetic analyses on the group (Bona et al., 2012; Bona, Ezcurra, et al., 2018; Bona et al., 2022, 2024; Brochu, 2010, 2011; Cidade et al., 2017, 2020; Cossette, 2021; Cossette & Brochu, 2018; Fortier et al., 2014; Godoy et al., 2021; Hastings et al., 2013, 2016; Rio & Mannion, 2021; Salas-Gismondi et al., 2015; Scheyer et al., 2013; Souza-Filho et al., 2018, 2020; Stocker et al., 2021; Walter et al., 2022).

Methods

This work aims to establish the phylogenetic nomenclature of the clade Caimaninae and less inclusive clades within it according to the set of rules of the International Code of Phylogenetic Nomenclature – PhyloCode (Cantino & de Queiroz, 2020). Within this objective, this paper sought to provide a comprehensive, stable and clear phylogenetic nomenclature for the Caimaninae clade under two general principles: to establish clade names that comprehend the diversity of Caimaninae in a thorough, practical way, and to respect the history of previous systematic and nomenclatural research with the group by preserving preexisting names (either in a context of Linnean systematics or already as phylogenetic nomenclature) and phylogenetic definitions already proposed by the group (see Cantino & de Queiroz, 2020, Art. 6). In cases in which a previously proposed name was not defined phylogenetically, this paper provides a phylogenetic definition. New clade names and definitions are only established when no previous clade names or definitions exist. These guidelines are in accordance with PhyloCode provisions (Cantino & de Queiroz, 2020, Art. 10.1–2).

In this paper, seven clade names are defined: two preexisting names (Caimaninae and Jacarea) that have had phylogenetic definitions proposed previously to the publication of the "Phylonyms: a Companion to the PhyloCode (de Queiroz et al., 2020) and, therefore, are not considered established according to the PhyloCode (2020 Art. 7.1), one preexisting name without a previously proposed phylogenetic definition (Nettosuchidae), and four new names with definitions (Caimanini – the crown-clade, Bottosauria, Purussauria and Purussauridae) (Table 1). The preexisting names that are established in this contribution are 'converted names' (see Cantino & de Queiroz, 2020, Art. 6.3), independently of whether a phylogenetic definition had already been proposed previously (Caimaninae, Jacarea) or not (Nettosuchidae) (Cantino & de Queiroz, 2020; Art. 6.2; see also Joyce et al., 2021). Following PhyloCode dispositions, there are two categories of authors of

Table 1. Clade names and definitions established in this paper, with information on the nominal authorship, type of definition and reference phylogenies.

Clade name	Nominal authorship[1]	Definition type	Definition	Reference phylogeny
Bottosauria	This contribution	Maximum-clade definition	The clade consisting of *Bottosaurus harlani* Agassiz, 1849 and all organisms or species that share a more recent common ancestor with *Bottosaurus harlani* Agassiz, 1849 than with *Caiman crocodilus* (Linnaeus, 1758), *Caiman latirostris* (Daudin, 1802), *Eocaiman cavernensis* Simpson, 1933, *Mourasuchus atopus* (Langston, 1965) and *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892.	Figure 11 of Cossette and Brochu (2018)
Caimaninae	Brochu, 1999	Maximum-total-clade definition	The total clade consisting of *Caiman crocodilus* (Linnaeus, 1758) and all organisms and species that share a more recent common ancestor with *Caiman crocodilus* (Linnaeus, 1758) than with *Alligator mississippiensis* (Daudin, 1802)	Figure 9 of Godoy et al. (2021)
Caimanini	This contribution	Minimum-crown-clade definition	The crown clade originating in the most recent common ancestor of of *Caiman crocodilus* (Linnaeus, 1758), *Caiman latirostris* (Daudin, 1802), *Caiman yacare* (Daudin, 1802), *Melanosuchus niger* (Spix, 1825), *Paleosuchus palpebrosus* (Cuvier, 1807) and *Paleosuchus trigonatus* (Schneider, 1801)	Figure 9 of Godoy et al. (2021)
Jacarea	Gray, 1844	Minimum-clade definition	The clade originating in the most recent common ancestor of *Caiman crocodilus* (Linnaeus, 1758), *C. latirostris* (Daudin, 1802), *C. yacare* (Daudin, 1802) and *Melanosuchus niger* (Spix, 1825)	Figure 9 of Godoy et al. (2021)
Nettosuchidae	Langston, 1965	Maximum-clade definition	The clade consisting of *Mourasuchus atopus* (Langston, 1965) and all organisms or species that share a more recent common ancestor with *Mourasuchus atopus* (Langston, 1965) than with *Bottosaurus harlani* Agassiz, 1849, *Caiman crocodilus* (Linnaeus, 1758), *Caiman latirostris* (Daudin, 1802), *Eocaiman cavernensis* Simpson, 1933, *Paleosuchus palpebrosus* (Cuvier, 1807) and *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892	Figure 9 of Godoy et al. (2021)
Purussauria	This contribution	Minimum-clade definition	The clade originating in the most recent common ancestor of of *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892 and *Mourasuchus atopus* (Langston, 1965)	Figure 2 of Bona et al. (2018)
Purussauridae	This contribution	Maximum-clade definition	The clade consisting of *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892 and all organisms or species that share a more recent common ancestor with *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892 than with *Bottosaurus harlani* Agassiz, 1849, *Caiman crocodilus* (Linnaeus, 1758), *Caiman latirostris* (Daudin, 1802), *Eocaiman cavernensis* Simpson, 1933, *Mourasuchus atopus* (Langston, 1965) and *Paleosuchus palpebrosus* (Cuvier, 1807)	Figure 9 of Godoy et al. (2021)

names: the nominal author (the original author of the name itself) and the definitional author (the author of the phylogenetic definition as recognised by the PhyloCode) (see Joyce et al., 2021; Cantino & de Queiroz, 2020, Art. 19). For preexisting names that are converted in this paper, the nominal authors appear in front of the name followed by the statement 'this contribution' in between brackets, which evidences that the definitional authors are the authors of this paper; for new clade names, the nominal and definitional authors are the same (Cantino & de Queiroz, 2020, Art. 19, Note 19.1.2), with a statement to that effect in between brackets being present after the name.

Caimaninae itself is a total clade, as it 'is composed of a crown clade' (named here as Caimanini, see below) 'and all species that share a more recent common ancestor with that crown clade than with any extant species that are not members of that crown clade' (Cantino & de Queiroz, 2020, Art. 2.2, modified). As Caimaninae is a preexisting name, it is used as a converted clade name for the total clade; because of this a panclade name, with the prefix 'Pan', is not used (Cantino & de Queiroz, 2020, Art. 10.6).

We employ both maximum-clade (formerly named as 'stem-based' or 'branch-based') and minimum-clade (formerly named as 'node-based') definitions. The choice between one of the definitions for each clade name had the aim of providing a thorough nomenclature that respects previously proposed phylogenetic definitions, the traditional content of previously proposed names and their relations to other already proposed names, and that could be able to comprehend as many species as possible within at least one clade. Similarly, the choice of specifiers for all clade names was made to provide the most comprehensive and stable definition for each clade name, to avoid content instability and reduce the possibility of heterodefinitional synonyms (see Cantino & de Queiroz, 2020, Art. 14.1). For this intent, each clade name with a minimum-clade definition has seven specifiers, due to the instability in the phylogenetic placement of some fossil taxa within Caimaninae, such as *Centenariosuchus gilmorei*, *Culebrasuchus mesoamericanus*, *Eocaiman* spp. and *Necrosuchus ionensis*, amongst others (see Bona, Ezcurra, et al., 2018; Bona et al., 2022; Cidade et al., 2020; Cossette, 2021; Cossette & Brochu, 2018; Godoy et al., 2021; Hastings et al., 2013, 2016; Rio & Mannion, 2021; Stocker et al., 2021; Walter et al., 2022).

All clade names proposed in this contribution have been registered at the Registration Database for Phylogenetically Defined Names (RegNum; Cantino & de Queiroz, 2020,

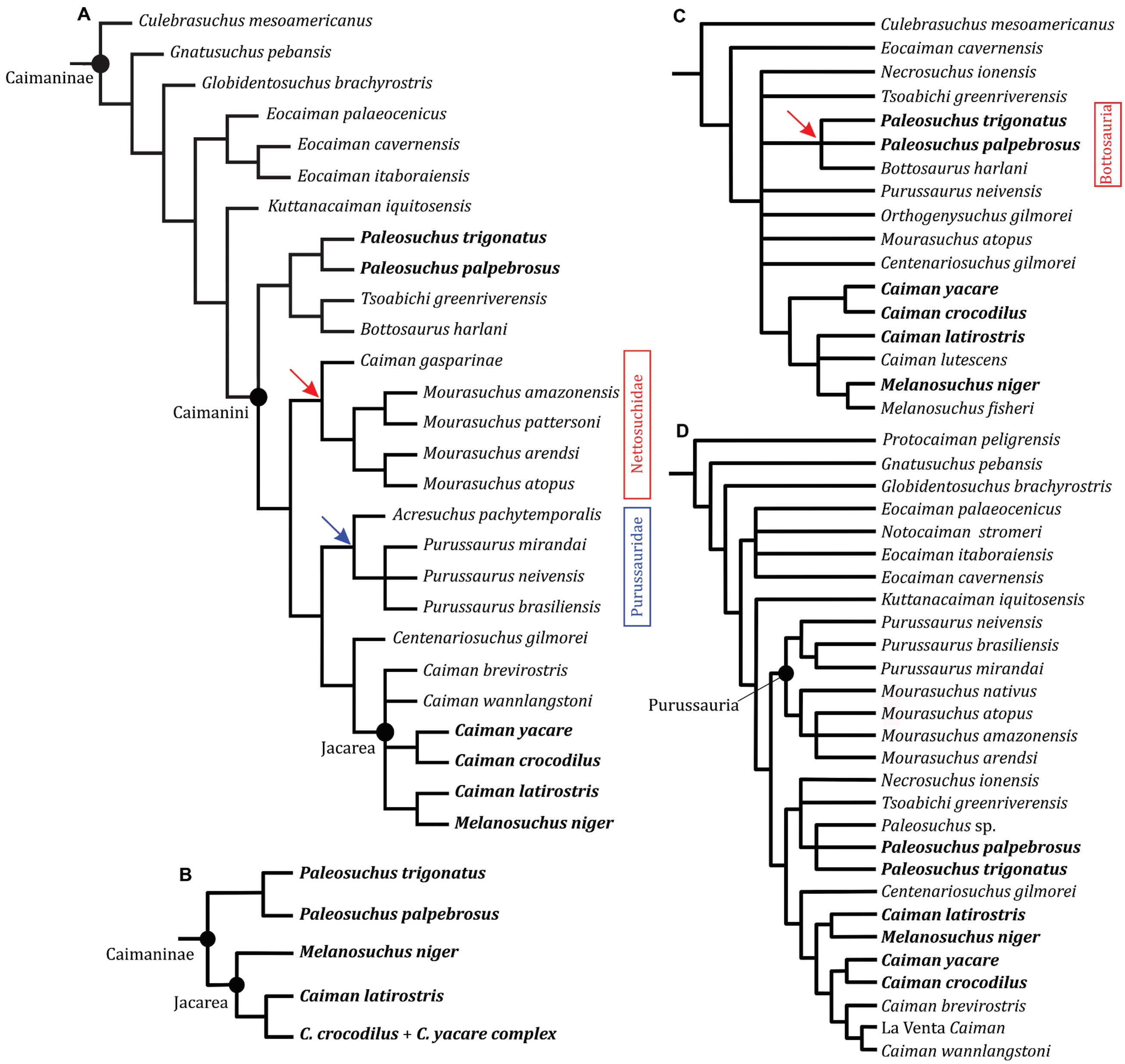

Figure 1. The reference phylogenies for the clade names defined in this paper. (A) Caimaninae topology from Godoy et al. (2021, fig. 9) based on morphological data, which is the reference phylogeny for Caimaninae, Caimanini, Jacarea, Purussauridae and Nettosuchidae. (B) Caimaninae and Jacarea topologies from Pan et al. (2021, fig. 1) based on molecular data. (C) Caimaninae topology from Cossette and Brochu (2018, fig. 11) based on morphological data, which is the reference phylogeny of Bottosauria. (D) Caimaninae topology from Bona, Ezcurra, et al. (2018, fig. 2) based on morphological data, which is the reference phylogeny of Purussauria.

Art. 8.1), which generated the official registration numbers that correspond to each phylogenetic definition and must be displayed alongside them as per the PhyloCode (Cantino & de Queiroz, 2020, Art. 7.2e). If two or more clade names established in this paper are later considered heterodefinitional synonyms, the name associated with the lower registration number will have priority (Cantino & de Queiroz, 2020, Art. 14.3); accordingly, more inclusive clade names are named and registered before less inclusive ones, following the approach of Joyce et al. (2021).

Results

Phylogenetic nomenclature

Caimaninae Brochu, 1999 [this contribution], converted clade name

Definition

The total clade consisting of *Caiman crocodilus* (Linnaeus, 1758) and all organisms and species that share a more recent common ancestor with *Caiman* *crocodilus* (Linnaeus, 1758) than with *Alligator mississippiensis* (Daudin, 1802). This is a maximum-total-clade definition (Registration number: 1145) (Figure 1 (A–B)).

Etymology

The name was proposed by Norell (1988) and refers to the genus *Caiman*, the most speciose of the extant genera of the group. The etymology of *Caiman* is uncertain: it is either from Caribbean indigenous languages words '*cayeman*' or '*acayoúman*' (meaning 'crocodile'), or from the Congo river area in Africa, where '*caiman*' also meant 'crocodile' in the local language, from which the word was brought to the Caribbean by Europeans (Oxford English Dictionary, 2023).

Reference Phylogeny

Phylogenetic hypothesis depicted in figure 9 of Godoy et al. (2021; Figure 1(A–B)).

Composition

Based on the reference phylogenies, Caimaninae includes Bottosauria (new clade name), Caimanini (new clade name), Jacarea Gray, 1844, Purussauria (new clade name), Purussauridae (new clade name) and Nettosuchidae Langston, 1965, as well as some unstable taxa recovered in some of the reference phylogenies.

Synonyms

There are no known synonyms for Caimaninae.

Comments

Content. Caimaninae has historically included the extant and extinct crocodylians commonly known as 'caimans'. Our definition follows Brochu (1999) in conceptualising this clade as a total group. Under the topology of Brochu (1999), Caimaninae included the extant species of the genera *Caiman* – *C. crocodilus, C. latirostris* and *C. yacare* –, *Melanosuchus* – *M. niger* –, *Paleosuchus* – *P. palpebrosus* and *P. trigonatus* – and the extinct taxa *Caiman lutescens* (Rovereto, 1912), *Eocaiman cavernensis*, *Melanosuchus fisheri* Medina, 1976, *Mourasuchus* spp., *Orthogenysuchus olseni* Mook, 1924 and *Purussaurus neivensis* (Mook, 1941).

Regarding extant taxa, recent molecular studies indicate that the extant diversity of this clade is likely underestimated, with cryptic lineages identified in both *Paleosuchus* spp. (Bittencourt et al., 2019; Muniz et al., 2018; Hernández-Rangel et al., 2025; Vasconcelos et al., 2025) and *Caiman* spp. (Amavet et al., 2023; Borges et al., 2018; Roberto et al., 2020; Venegas-Anaya et al., 2008).

Regarding extinct taxa, concerns about some species included in Caimaninae have been raised, such as whether *M. fisheri* is a valid species (Bona, Fernandez-Blanco, et al., 2018; Foth et al., 2018). Furthermore, the specimen used by Brochu (1999) to score '*C. lutescens*' (a *nomen dubium* according to Bona et al., 2024) in the phylogenetic analysis (UCMP-39978) may not belong to this taxon (Bona & Barrios, 2015; Bona et al., 2024; Cidade et al., 2015; Rio & Mannion, 2021), although possibly representing a distinct caimanine species that effectively belongs to the Jacarea clade (Rio & Mannion, 2021; see also Bona, Ezcurra, et al., 2018; Bona et al., 2022, 2024; Cidade et al., 2020; Fortier et al., 2014; Salas-Gismondi et al., 2015). On whether *Orthogenysuchus* is a caimanine or not, further preparation of its holotype and only known specimen has revealed new information that suggests that this taxon may belong to another clade (Salas-Gismondi et al., 2015). As such data remain unpublished, we refrain from assigning *Orthogenysuchus* to Caimaninae in this paper.

Our understanding of the diversity of fossil caimanines increased steadily from Brochu's original work, including extinct species of *Caiman* – *C. wannlangstoni* Salas-Gismondi et al., 2015 – and *Melanosuchus* – *M. latrubessei* Souza-Filho et al., 2020 –, and new species of *Eocaiman* – *E. palaeocenicus* Bona, 2007 and *E. itaboraiensis* Pinheiro et al., 2013 –, *Mourasuchus* – *M. pattersoni* Cidade et al., 2017 –, and *Purussaurus* – *P. mirandai* Aguilera et al., 2006 –, and new genera and species such as *Acresuchus pachytemporalis, Centenariosuchus gilmorei*, *Chinatichampsus wilsonorum*, *Culebrasuchus mesoamericanus*, *Gnatusuchus pebasensis*, *Globidentosuchus brachyrostris*, *Kuttanacaiman iquitosensis*, *Protocaiman peligrensis* Bona, Ezcurra et al., 2018, *Tsoabichi greenriverensis*, *Paranacaiman bravardi* and *Paranasuchus gasparinae* (Bona & Carabajal, 2013). Additionally, other fossil taxa described before Brochu's study (Brochu, 1999) have been recovered as caimanines in later analyses. These include not only species belonging to genera that had already been recovered within Caimaninae, such as *Caiman brevirostris* (Fortier et al., 2014), *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892 (Salas-Gismondi et al., 2015), but also other genera such as *Bottosaurus* – with the species *B. harlani* (von Meyer, 1832) (Cossette & Brochu, 2018), and then a new species, *B. fustidens* Cossette, 2021 – and *Necrosuchus ionensis* (Brochu, 2011). These are the taxa that have comprised the Caimaninae clade in most analyses (Bona, Ezcurra, et al., 2018; Bona et al., 2022; Brochu, 1999, 2010, 2011; Cidade et al., 2017, 2020; Cossette, 2021; Cossette & Brochu, 2018; Fortier et al., 2014; Godoy et al., 2021; Hastings et al., 2013, 2016; Rio & Mannion, 2021; Scheyer et al., 2013; Stocker et al., 2021; Walter et al., 2022)

The inclusion of other taxa within Caimaninae may be more contentious. Some analyses have recovered taxa typically placed as stem alligatorids (Norell et al., 1994; Brochu, 1999, 2004) such as *Albertochampsa langstoni*, *Brachychampsa* spp. and *Stangerochampsa mccabei* at the base of Caimaninae (Bona, Ezcurra, et al., 2018; Cossette, 2021; Rio & Mannion, 2021; Salas-Gismondi et al., 2015; Stocker et al., 2021). This question has been addressed in detail by Walter et al. (2022) who found the caimanine affinities of these taxa to be controversial. Rio and Mannion (2021, fig. 12) also include the traditionally non-caimanine alligatoroids *Ceratosuchus burdoshi* Schmidt, 1928 and *Wannaganosuchus brachymanus* Erickson, 1982 within Caimaninae, forming a clade with *Brachychampsa montana* Gilmore, 1911 and *Stangerochampsa mccabei*, whereas two species of the traditional caimanine genus *Eocaiman* (*E. cavernensis* and *E. palaeocenicus*) were recovered as early-diverging alligatoroids. Walter et al. (2022) recovered representatives of the Asian Cretaceous-Palaeogene clade Orientalosuchina, including *Jiangxisuchus nankangensis* and *Orientalosuchus naduongensis* Massone, Vasilyan, Rabi and Böhme, 2019, as early diverging caimanines but considered the character support dubious. Previous analyses had placed these taxa as crocodyloids (Li et al., 2019; Rio & Mannion, 2021) or early diverging alligatoroids (Massonne et al., 2019).

Prior definitions. Norell (1988), in his unpublished PhD thesis, was the first author to use the name Caimaninae, referring to it as the clade that including the extant taxa *Paleosuchus trigonatus*, *Paleosuchus palpebrosus*, *Melanosuchus niger*, *Caiman latirostris* and *Caiman crocodilus*, but without providing a phylogenetic definition. As it is an unpublished PhD thesis, Norell (1988) is not considered the nominal author of the 'Caimaninae' name according to Chapter 3 of the International Code of Zoological Nomenclature (ICZN [ICNZ], 1999) and, if a phylogenetic definition had been provided, it would likewise not considered according to Article 4.6 of the PhyloCode (Cantino & de Queiroz, 2020). Brochu (1999), following the name first coined by Norell, 1988) provided the first phylogenetic definition of Caimaninae: a stem-based group including *Caiman crocodilus* and all crocodylians more closely related to it than to *Alligator mississippiensis*. As it is a published paper, Brochu (1999) is considered the nominal authors of Caimaninae but not its definitional author, as it was published before the 'Phylonyms' (Cantino & de Queiroz, 2020, Preamble 6 and Art. 7.1). The definition of Brochu (1999) might, therefore, be more inclusive than the concept of Norell (1988) and has been consistently followed by most later work (see Walter et al., 2022 for a recent review). An alternative, non-established definition was proposed by Hastings et al. (2013): a minimum-clade stemming from the common ancestor of *Culebrasuchus mesoamericanus* and *Caiman crocodilus*.

Characteristics. Brochu (1999, 2010) found the following four unambiguous synapomorphies for Caimaninae: splenial excluded from mandibular symphysis and anterior tip of splenial passes dorsal to Meckelian groove (Character 43, state 2 of his analysis), angular-surangular suture passes broadly along ventral margin of external mandibular fenestra late in ontogeny (48–1), parietal excluded from posterior edge of skull table (82–3), exoccipitals with slender processes ventral to the basioccipital tubera (151–2). Brochu (1999) also found the following 17 ambiguous synapomorphies: atlantal ribs with very thin medial laminae (16–1), scapulocoracoid synchondrosis closes early in ontogeny (24–1), dorsal margin of iliac blade narrow with dorsal indentation (28–3), six nuchal osteoderms with four central and two lateral (38–2), ventral osteoderms consist of paired ossifications (39–2), splenial lacks anterior perforation for mandibular ramus of cranial nerve V (41–1), coronoid completely surrounds foramen intermandibularis medius at maturity (46–1), surangular extends to posterior end of retroarticular process (51–0), inferior process of coronoid remains largely on medial surface of the mandible (55–1), dorsal projection of hyoid cornu flared (58–1), surangular-angular suture lingually meets articular dorsal to ventral tip (67–1), quadrato-jugal does not extend to superior angle of infratemporal fenestra (80–1), frontoparietal suture linear (86–1), dorsal edges of orbits upturned (103–1), medial parietal wall of supratemporal fenestra bearing foramina (104–1), posterior rim of internal choana deeply notched (107–1), anterior face of palatine process invaginate (108–1).

Hastings et al. (2013), following their alternative definition of Caimaninae, found two traits characterising the group, which had already been recovered by Brochu (1999): splenial excluded from the mandibular symphysis and anterior tip of splenial passing dorsal to Meckelian groove, and the parietal excluded from posterior edge of skull table.

Scheyer et al. (2013) found a single potential unambiguous and unequivocal synapomorphy of Caimaninae: the surangular – angular suture lingually meeting articular dorsal to tip (Character 66, state 1 of their analysis).

Salas-Gismondi et al. (2015) found five synapomorphies supporting Caimaninae: small supratemporal fenestrae with overhanging rims (Character 152, state 1 of their analysis), surangular extending to the posterior end of retroarticular process (72–0), maxilla with a broad shelf extending into the suborbital fenestra (-112–1), parietal excluded from posterior edge of skull table (160–4) and exoccipitals with slender processes ventral to the basioccipital tubera (176–2).

Hastings et al. (2016) found only a single character to be distinctive of the Caimaninae clade: parietal excluded from the posterior edge of the skull table (Character 159–3 in Godoy et al., 2021).

Cidade et al. (2017) found two synapomorphies supporting Caimaninae: the third maxillary alveolus as the largest one in the maxilla (Character 93, state 0 of their analysis) and parietal excluded from the posterior edge of the skull table (Character 159–3). Furthermore, their analysis found several synapomorphies supporting the clade formed by all caimanines except *Culebrasuchus*: dermal bones of skull roof overhanging rim of supratemporal fenestra near maturity, with the fenestrae being small, with a circular or nearly circular shape (Character 151–1); medial parietal wall of supratemporal fenestrae bearing foramina (Character 153–1); exoccipitals with slender processes ventral to the basioccipital tubera (Character 175–2; a synapomorphy of Caimaninae according to Brochu, 1999); and anterior extremity of the frontal short, not reaching the anterior margins of the orbits (Character 184–1). These authors also found synapomorphies for a clade uniting all caimanines except *Culebrasuchus* and *Gnatusuchus*: surangular – angular suture lingually meeting the articular dorsal to the ventral tip of the articular (Character 66–1) and by the prefrontals meeting medially (Character 128–1). *Culebrasuchus* and *Gnatusuchus* are recovered as caimanines in most analyses; nevertheless, these characters that unite clades not including these two taxa may be useful in a less strict understanding of the morphological characteristics of the Caimaninae clade.

Bona, Ezcurra, et al. (2018) list two synapomorphies for Caimaninae: proatlas without an anterior process (Character 3, state 1 in their analysis) and an angular not extended dorsally beyond the anterior end of the foramen intermandibularis caudalis (Character 65–1). Additionally, this study mentions that a dorsally facing external nares (Character 81–1) is a Caimaninae synapomorphy in some of its trees. These synapomorphies are different from those of other analyses due to their recovery of the genera *Brachychampsa*, *Albertochampsa* and *Stangerochampsa* at the base of Caimaninae. Furthermore, this analysis recovers the clade formed by all caimanines except *Brachychampsa*, *Albertochampsa* and *Stangerochampsa* sustained by two synapomorphies – presence of dermal bones of skull roof overhanging the rim of the external supratemporal fenestrae (Character 152–1) and medial parietal wall of external supratemporal fenestra bearing foramina (Character 154–1) – and a clade formed by all caimanines except *Protocaiman*, *Brachychampsa*, *Albertochampsa* and *Stangerochampsa* sustained by the parietal excluded from the posterior edge of the skull table (Character 160–4). As in the case of Cidade et al. (2017), these characters that unite clades not including some of the taxa may be useful in a less strict understanding of the morphological characteristics of the Caimaninae clade.

Cossette and Brochu (2018) noted that depending on topology within Globidonta, two or three character states unambiguously diagnosed Caimaninae: the splenials do not meet at the midline and their anterior tips pass dorsal to the Meckelian groove (Character 34, state 2 in their analysis); the frontoparietal suture is linear between the supratemporal fenestrae (Character 95–1); and supraoccipital exposure on the dorsal skull table is large and excludes the parietal from reaching the posterior edge of the skull table (Character 101–3). In their analysis, all shortest trees included the first two character states and a subset of the trees, which recovered Cretaceous globidontans at the base of Caimaninae, included the third character state.

Massonne et al. (2019) found four synapomorphies for Caimaninae: inferior process of coronoid remaining largely on medial surface of mandible (Character 57, state 1 of their analysis); surangular-angular suture lingually meeting articular dorsal to tip (66–1); (72) surangular extending to the posterior end of retroarticular process (72–0); and supraoccipital large such that parietal is excluded from posterior edge of table (160–3).

Cossette (2021) diagnosed Caimaninae based on three character states. The author noted that plesiomorphically, caimans have splenials that do not meet at the midline and whose anterior tips pass dorsal to the Meckelian groove (Character 50, state 2 of his analysis). Additionally, the frontoparietal suture is linear between the supratemporal fenestrae (Character 139–1). Cossette (2021), also noted that large exposures of the supraoccipital on the skull table that exclude the parietal from touching the posterior margin of the skull table (Character 147–3) were an autapomorphy for the group. Like Bona, Ezcurra, et al. (2018), the author recovers the Cretaceous globidontans *Albertochampsa langstoni, Stangerochampsa mccabei* and species of *Brachychampsa* as the basalmost members of Caimaninae. The Cretaceous globidontans + Caimaninae clade was diagnosed by two characters in their analysis: the angular does not extend dorsally beyond the anterior end of the foramen intermandibularis caudalis, while the anterior tip is blunt (Character 61–1); and the naris projecting dorsally (Character 75–1). The former character state was autapomorphic for the clade, in agreement with the strict consensus tree of Bona, Ezcurra, et al. (2018). Consistent with a subset of trees from Bona, Ezcurra, et al. (2018), the strict consensus tree presented here reveals that the latter character state used to diagnose the group is homoplastic and shared with several other clades, including derived alligatorines.

Godoy et al. (2021) recovered only the same character found by Hastings et al. (2016) to be distinctive of the Caimaninae clade: parietal excluded from posterior edge of skull table (Character 159–3 in Godoy et al., 2021). In the analysis done by Godoy et al. (2021), other features that may be relevant as characteristics of the Caimaninae clade are the synapomorphies recovered for the clade uniting all caimanines except *Culebrasuchus* – dermal bones of skull roof overhanging rim of the supratemporal fenestrae near maturity, with the fenestrae small, with a circular or nearly circular shape (Character 151–1); medial parietal wall of supratemporal fenestra bearing foramina (Character 153–1); exoccipitals with slender processes ventral to the basioccipital tubera (Character 175–2); anterior extremity of the frontal short, not reaching the anterior margins of the orbits (Character 184–1) – and for the clade uniting all caimanines except *Culebrasuchus* and *Gnatusuchus* – surangular-angular suture lingually meeting articular dorsal to tip (Character 66–1); prefrontals meeting medially (Character 128–1).

Stocker et al. (2021) found two unambiguous and four ambiguous synapomorphies for Caimanae. The two unambiguous synapomorphies are the presence of an angular that does not extend dorsally beyond the anterior end of the foramen intermandibularis caudalis and has a very blunt anterior tip (character 65, state 1 of their analysis) and a naris that projects dorsally (81–1). The four ambiguous synapomorphies are a proatlas that lacks an anterior process (3–1), a splenial that lacks an anterior perforation for the mandibular ramus of cranial nerve V (52–1), an inferior process of the coronoid that remains largely on the medial surface of the mandible (57–1) and a maxilla with the posterior process between the lacrimal and the prefrontal (128–2).

Walter et al. (2022) found the following unique synapomorphies of Caimaninae: posterior rim of internal choana is deeply notched; exoccipitals with slender processes ventral to the basioccipital tubera; parietal, squamosal and postorbital overhang the rim of supratemporal fenestra near maturity; and medial parietal wall of the supratemporal fenestra bears foramina.

Molecular data (mitochondrial and nuclear genes) also support the recognition of this clade. The only difference is the recognition of *Melanosuchus* as a separate genus from *Caiman*, with high probabilistic support (Gatesy et al., 2003; Oaks, 2011; Pan et al., 2021). Instead, the morphological data recovers *Melanosuchus* as closely related to *Caiman latirostris*, inside *Caiman* (Brochu, 1999, 2011; Hastings et al., 2016; Poe, 1996; Salas-Gismondi et al., 2015; Souza-Filho et al., 2020).

Divergence times for and within Caimaninae have been estimated using both molecular data, with fossils as calibration points (Darlim & Höhna, 2024; Oaks, 2011; Pan et al., 2021; for a review, see Walter et al., 2022), and with topological information from morphology, including fossils as tips (Darlim et al., 2022; Godoy et al., 2021). Explicit and up to date calibration points following best practices (Parham et al., 2012) are provided in Walter et al. (2022) with *Necrosuchus ionensis* and *Protocaiman peligrensis* justifying a hard minimum fossil age of 63.5 Ma and *Brachychampsa sealeyi* a conservative soft maximum of 83 Ma for Caimaninae (divergence of Alligatorinae and Caimaninae). For crown-group Caimaninae (named here as Caimanini), 18.06 Ma has been proposed as a minimum age fossil calibration justified by *Centanariosuchus gilmorei* and a soft maximum age of 66 Ma (Walter et al., 2022). Using molecular data, several studies seem to agree on a latest Cretaceous/early Cenozoic age for Caimaninae (Darlim & Höhna, 2024; Oaks, 2011; Pan et al., 2021). Using the age information of fossils as tips, Godoy et al. (2021) estimated a Late Cretaceous age for the group (between 83.86 and 70.34 million years ago [Ma]), but it is worth mentioning that this kind of analysis is sensitive to change in topology and taxonomic content of clades. Therefore, focusing on the divergence times between living genera, using solely molecular data, the divergence between *Paleosuchus* and the Jacarea clade (*Caiman* + *Melanosuchus*) was estimated as ranging from the Oligocene to the Late Miocene, between 20.4 and 38.2 Ma (Oaks, 2011; Pan et al., 2021). The dichotomy between *Melanosuchus* and *Caiman* was dated to the Middle-

Late Miocene (10.3–18.4 Ma), similarly to the divergence between the *Paleosuchus* species (5.7–17.4 Ma). The divergence among the *Caiman* species was estimated to have occurred from the Middle Miocene to the Pleistocene (6.7–16.9 Ma) (Darlim & Höhna, 2024; Oaks, 2011; Pan et al., 2021). Most of the divergence between the cryptic lineages of *Caiman* and *Paleosuchus* would have occurred during the Late Miocene to Pleistocene (Darlim & Höhna, 2025). For a summary of divergence time estimates, see Walter et al. (2022).

Bottosauria [this contribution], new clade name

Definition

The clade consisting of *Bottosaurus harlani* Agassiz, 1849 and all organisms or species that share a more recent common ancestor with *Bottosaurus harlani* Agassiz, 1849 than with *Caiman crocodilus* (Linnaeus, 1758), *Caiman latirostris* (Daudin, 1802), *Eocaiman cavernensis* Simpson, 1933, *Mourasuchus atopus* (Langston, 1965) or *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892. This is a maximum-clade definition (Registration number: 1146) (Figure 1(C)).

Etymology

Derived from the genus *Bottosaurus*, whose own etymology was not detailed upon its erection (Agassiz, 1849). It is likely a corruption of *boto* (Latin for 'button'), which likely refers to the blunt, button-like teeth seen in the taxon (A. Cossette, personal observation, 2024), whereas the suffix 'sauria' (from the Ancient Greek 'σαῦρος' [saurus]) means 'lizard' but has been used for various names within Crocodylomorpha).

Reference Phylogeny

Phylogenetic hypothesis depicted in figure 11 of Cossette and Brochu (2018; Figure 1(C)).

Composition

Based on the reference phylogeny, Bottosauria includes *Bottosaurus harlani, B.fustidens Paleosuchus trigonatous*, *P. palpebrosus* with some phylogenies also recovering the taxa *Necrosuchus ionensis* and *Protocaiman peligrensis* (Rio & Mannion, 2021) and *Tsoabichi greenriverensis* (Cidade, 2019; Cossette, 2021; Godoy et al., 2021) within the clade.

Comments

Content. The concept behind Bottosauria is to provide a name for the clade formed around Bottosaurus harlani, but also as a possible stem lineage of crown-group *Paleosuchus* as some topologies recovered a monophyletic clade consisting of the extinct North American *Bottosaurus harlani* and *B. fustidens* as well as the extant South American caimanines *P. palpebrosus* and *P. trigonatus* – (Cossette, 2021; Cossette & Brochu, 2018). Other work furthermore included the North American Eocene taxon *Tsoabichi greenriverensis* within this clade (Cidade, 2019; Cossette, 2021; Godoy et al., 2021), and Rio and Mannion (2021, fig. 10) recovered *Necrosuchus ionensis* and *Protocaiman peligrensis* within the clade. On the other hand, the placement of *Bottosaurus harlani* as a crown-caimanine is contentious as not reproduced by other analyses (Walter et al., 2022) and previous work noting the low nodal support, homoplastic or ambiguous synapomorphies and poor stratigraphic-spatial fit of the inferred close relationship between *Paleosuchus* spp., *Bottosaurus* spp. and *Tsoabichi greenriverensis* (Cossette, 2021; Cossette & Brochu, 2018; Massonne et al., 2019; Stocker et al., 2021; Walter et al., 2022). The uncertainty around the placement of *Bottosaurus harlani* as a representative of Caimaninae or crown-group Caimaninae (named here as Caimanini) has been summarised in Walter et al. (2022). Molecular studies have recently identified greater lineage diversity within *Paleosuchus* spp., with lineages separated by major hydrographic basins in South America (Bittencourt et al., 2019; Hernández-Rangel et al., 2024; Muniz et al., 2018, 2022; Vasconcelos et al., 2025). These findings suggest the presence of cryptic diversity and highlight the need for a taxonomic review of the genus.

Characteristics. Cossette and Brochu (2018) recovered *Bottosaurus harlani* as a member of Caimaninae due to the possession of a linear frontoparietal suture (Character 95, state 1 of their analysis). Additionally, *B. harlani* was recovered in a polytomy with species of *Paleosuchus* but with low character support for the grouping. The species share compressed posterior teeth and alveoli of the maxilla and dentary (Character 52–1). However, this character state is also shared with the alligatorines *Procaimanoidea utahensis* Gilmore, 1946 and *Procaimanoidea kayi* (Mook, 1941) from the Eocene of Wyoming and *Arambourgia gaudryi* from the Eocene of France. The authors note that the posterior teeth of species of *Paleosuchus* are not an exact match to those of *B. harlani*, except for labiolingual compression. Relative to species of *Paleosuchus*, the posterior mandibular and maxillary teeth of *B. harlani* exhibit less acute apices and look bulbous in lateral view. The unexpected phylogenetic placement of the Upper Cretaceous – Paleocene North American *B. harlani* close to species of *Paleosuchus*, which are first known from the Miocene of South America, could reflect a true relationship or be the product of convergent evolution. The authors state that the large stratigraphic gap and low character and nodal support for the *B. harlani* + *Paleosuchus* clade suggest that the phylogenetic relationship recovered in this analysis is unlikely.

Cidade (2019) recovered *B. harlani* as sister to *Tsoabichi greenriverensis* and this group as sister to the species of *Paleosuchus*, but no synapomorphies are provided for this topology or the subgroups within.

Cossette (2021) named a new species of *Bottosaurus* – *Bottosaurus fustidens* Cossette, 2021 – and recovered the species of *Bottosaurus* in a sister group relationship based upon the preservation of three character states: surangular – articular suture bowed strongly laterally within the glenoid fossa (Character 68, state 1 of his analysis); a large medial jugal foramen (Character 94–1); and the presence of a U-shaped depression at the point of greatest mediolateral constriction between the orbits (Character 170–1). The last character state was an autapomorphy for the *Bottosaurus* clade. A subset of the shortest trees in the analysis recovered a clade including species of *Bottosaurus* and *Paleosuchus*, which was unambiguously diagnosed by labiolingually compressed posterior teeth and alveoli of the maxilla and dentary (Character 73–1). However, this character was homoplasious and was shared with a number of alligatorines in the analysis. A subset of shortest trees that recovered the *Bottosaurus* + *Paleosuchus* sister-group relationship also recovered *Tsoabichi greenriverensis*, a caimanine from the Lower Eocene of Wyoming, as the successive outgroup to the clade. In this analysis, the *Tsoabichi* + *Paleosuchus* + *Bottosaurus* clade was unambiguously diagnosed by a large exposure of the supraoccipital on the dorsal skull table (Character 147–2). In agreement with Cossette and Brochu (2018), this was the only character state unambiguously diagnosing the clade and was found in all trees that recovered *T. greenriverensis* as sister to the *Bottosaurus* + *Paleosuchus* clade.

Godoy et al. (2021) recovered the following synapomorphies for Bottosauria: lacrimal making broad contact with nasal, with no posterior process of maxilla (Character 127, state 0 of their analysis); prefrontals separated by frontals and nasals (Character 128–0); large exposure of the supraoccipital on dorsal skull table (Character 159–2); and anterior extremity of the frontal long and reaching or exceeding the anterior margins of the orbits (Character 184–0). Their analysis also recovered a single synapomorphy for the clade formed by *Bottosaurus harlani* and *Tsoabichi greenriverensis*: external naris projecting anterodorsally (Character 81–0).

In contrast, using modified datasets of Bona, Ezcurra, et al. (2018) and Massonne et al. (2019), Walter et al. (2022) found *Bottosaurus harlani* as an early diverging caimanine but noted that the synapomorphies supporting inclusion into Caimaninae are predominantly lower jaw traits unknown in or not shared by other early diverging caimanines (*Eocaiman* spp., *Protocaiman peligrensis* and *Chinatichampsus wilsonoroum* (splenial lacks an anterior perforation for mandibular ramus of cranial nerve V; dentary symphysis extends to forth or fifth alveolus; surangular/angular suture meets the articular dorsal to tip; and surangular extends to posterior end of retroarticular process).

Caimanini [this contribution], new clade name

Definition

The crown clade originating in the most recent common ancestor of *Caiman crocodilus* (Linnaeus, 1758), *Caiman latirostris* (Daudin, 1802), *Caiman yacare* (Daudin, 1802), *Melanosuchus niger* (Spix, 1825), *Paleosuchus palpebrosus* (Cuvier, 1807) and *Paleosuchus trigonatus* (Schneider, 1801). This is a minimum-crown-clade definition. (Registration number: 1147) (Figure 1(A)).

Etymology

Refers to the genus *Caiman*, the most speciose of the extant genera of the group. For the etymology of 'caiman', see the etymology section of the Caimaninae clade.

Reference Phylogeny

Phylogenetic hypothesis depicted in figure 9 of Godoy et al. (2021; Figure 1(A)).

Composition

Based on the reference phylogenies, Caimanini includes Bottosauria (new clade name), Jacarea Gray, 1844, Purussauria (new clade name), Purussauridae (new clade name) and Nettosuchidae Langston, 1965.

Comments

Content. This clade name is of relevance for molecular divergence dating studies as it allows explicit distinction between total (Caimaninae) and crown clade (Caimanini).

In the analysis of Brochu (1999), Caimanini included, aside from its specifiers *Caiman crocodilus*, *C. latirostris*, *C. yacare*, *Melanosuchus niger*, *Paleosuchus palpebrosus* and *P. trigonatus*, two extinct species assigned to extant genera, '*Caiman lutescens*' and '*Melanosuchus fisheri*', and the extinct taxa *Orthogenysuchus olseni*, *Purussaurus neivensis* and *Mourasuchus* spp. Caimanini also included the clade Jacarea in the analysis of Brochu (1999), a relationship also recovered in all later analyses within the clade except Rio and Mannion (2021), which found crown-group Caimaninae and Jacarea as synonyms.

Later analyses revealed several other clades within Caimanini which are now recognised in this paper: Bottosauria (Cossette, 2021; Cossette & Brochu, 2018), Purussauria (Walter et al., 2022), Purussauridae (Cidade et al., 2020; Godoy et al., 2021; Souza-Filho et al., 2018) and Nettosuchidae (Bona et al., 2012, 2022; Cidade et al., 2017, 2020; Godoy et al., 2021; Stocker et al., 2021). The specific contents of each of these clades are detailed subsequently.

Extinct species consistently recovered as belonging to Caimanini, in addition to those recovered by Brochu (1999), include: *Acresuchus pachytemporalis* (Bona et al., 2024; Cidade et al., 2020; Godoy et al., 2021; Rio & Mannion, 2021; Souza-Filho et al., 2018); *Bottosaurus fustidens* (Cossette, 2021) and *B. harlani* (Bona, Ezcurra, et al., 2018; Bona et al., 2022; Cidade et al., 2020; Cossette, 2021; Cossette & Brochu, 2018; Godoy et al., 2021; Rio & Mannion, 2021; Stocker et al., 2021); *Caiman brevirostris* (Bona, Ezcurra, et al., 2018; Bona et al., 2022; Cidade et al., 2017, 2020; Fortier et al., 2014; Godoy et al., 2021; Rio & Mannion, 2021; Salas-Gismondi et al., 2015; Stocker et al., 2021; Walter et al., 2022) and *C. wannlangstoni* (Bona, Ezcurra, et al., 2018; Bona et al., 2022; Cidade et al., 2017, 2020; Godoy et al., 2021; Rio & Mannion, 2021; Salas-Gismondi et al., 2015; Stocker et al., 2021; Walter et al., 2022); *Centenariosuchus gilmorei* (Bona, Ezcurra, et al., 2018; Bona et al., 2022; Cidade et al., 2017, 2020; Cossette, 2021; Cossette & Brochu, 2018; Godoy et al., 2021; Hastings et al., 2013, Hastings et al., 2016; Salas-Gismondi et al., 2015; Stocker et al., 2021; Walter et al., 2022); the species of *Mourasuchus* as separate operational taxonomic units (Bona et al., 2012, 2022; Cidade et al., 2017, 2020, Godoy et al. 2021; Stocker et al., 2021); *Necrosuchus ionensis* (Bona et al., 2018; Brochu, 2010, 2011; Cidade et al., 2020; Cossette, 2021; Cossette & Brochu, 2018; Hastings et al., 2016; Rio & Mannion, 2021; Salas-Gismondi et al., 2015; Stocker et al., 2021; Walter et al., 2022); *Paranasuchus gasparinae* (Bona et al., 2012; Cidade et al., 2020; Godoy et al. 2021); *Purussaurus brasiliensis* (Bona et al., 2022; Cidade et al., 2020; Godoy et al., 2021; Rio & Mannion, 2021; Stocker et al., 2021; Walter et al., 2022) and *P. mirandai* (Bona et al., 2012, 2022; Brochu, 2010, 2011; Cidade et al., 2017, 2020; Fortier et al., 2014; Godoy et al., 2021; Rio & Mannion, 2021; Stocker et al., 2021; Walter et al., 2022); and *Tsoabichi greenriverensis* (Bona, Ezcurra, et al., 2018; Bona et al., 2022; Brochu, 2010, 2011; Cidade et al., 2017, 2020; Cossette, 2021; Cossette & Brochu, 2018; Fortier et al., 2014; Godoy et al., 2021; Hastings et al., 2016; Rio & Mannion, 2021; Salas-Gismondi et al., 2015; Scheyer et al., 2013; Stocker et al., 2021). Extinct species occasionally recovered within Caimanini include *Globidentosuchus brahcyrostris* (Walter et al., 2022), *Kuttanacaiman iquitosensis* (Cidade et al., 2017; Walter et al., 2022) and *Protocaiman peligrensis* (Rio & Mannion, 2021). Walter et al. (2022) cast doubt on the placement of *T. greenriverensis* as a crown-group caimanine and recognises *Gnatusuchus pebasensis* as a potential representative of the crown clade.

Most of these species are usually recovered as belonging to one of the clades within Caimanini (Jacarea, Nettosuchidae, Purusauria or Purusauridae, see below), with some exceptions such as *Centenariosuchus gilmorei* (Bona et al., 2018; Cidade et al., 2017; Cossette, 2021; Cossette & Brochu, 2018; Godoy et al., 2021; Hastings et al., 2013, 2016; Salas-Gismondi et al., 2015; Stocker et al., 2021; Walter et al., 2022), *Globidentosuchus brahcyrostris* (Walter et al., 2022), *Kuttanacaiman iquitosensis* (Cidade et al., 2017; Walter et al., 2022), *Necrosuchus ionensis* (Bona et al., 2018; Brochu, 2010, 2011; Cossette, 2021; Cossette & Brochu, 2018; Hastings et al., 2016; Salas-Gismondi et al., 2015; Stocker et al., 2021; Walter et al., 2022), *Protocaiman peligrensis* (Rio & Mannion, 2021), *Tsoabichi greenriverensis* (Bona et al., 2018, 2022; Brochu, 2010, 2011; Cidade et al., 2017, 2020; Cossette, 2021; Cossette & Brochu, 2018; Fortier et al., 2014; Godoy et al., 2021; Hastings et al., 2016; Salas-Gismondi et al., 2015; Scheyer et al., 2013; Stocker et al., 2021). *Caiman wannlangstoni* is also recovered within Caimanini but not within Jacarea, in some analyses (Cidade et al., 2017; Stocker et al., 2021; Walter et al., 2022).

Prior definitions. None. Prior to the definition provided here, this clade has been referred to as and cited in previous work under various appellations, including 'crown group Caimans', 'crown caimans', 'crown group Caimaninae' or 'crown caimanines', among others (e.g (Bona et al., 2022; Brochu, 1999, 2011; Cidade et al., 2020; Cossette, 2021; Fortier et al., 2014; Godoy et al., 2021; Hastings et al., 2013; Rio & Mannion, 2021; Salas-Gismondi et al., 2015; Souza-Filho et al., 2018; Stocker et al., 2021; Walter et al., 2022).

Characteristics. Brochu (1999) found both unambiguous and ambiguous synapomorphies for Caimanini. The unambiguous are: dermal bones of skull roof overhang rim of supratemporal fenestra near maturity (Character 87, state 1 of his analysis) and ectopterygoid-pterygoid flexure remaining throughout ontogeny (116–1). The ambiguous are: ribs with very thin medial laminae (16–1); scapulocoracoid synchondrosis closes early in ontogeny (24–1); dorsal margin of iliac blade narrow with dorsal indentation (28–3); ventral osteoderms consist of paired ossifications (39–2); splenial lacks anterior perforation for mandibular ramus of cranial nerve V (41–1); surangular extends to posterior end of retroarticular process (51–0); inferior process of coronoid largely on medial surface of mandible (55–1); dorsal projection of hyoid cornu flared (58–1); angular does not extend dorsally beyond anterior end of foramen intermandibularis caudalis (66–1); surangular-angular suture lingually meets articular dorsal to ventral tip (67–1); dorsal edges of orbits upturned (103–1) and posterior rim of internal choana deeply notched (107–1).

Godoy et al. (2021) recovered three synapomorphies supporting Caimanini: dentary symphysis extending to fourth or fifth alveolus (Character 49, state 0 of their analysis); maxilla with linear medial margin adjacent to suborbital fenestra (111–0); upturned dorsal edges of orbits (136–1).

Walter et al. (2022) found two synapomorphies of Caimanini: articular-surangular suture, articular bears an anterior lamina ventral to lingual foramen; and ectopterygoid-pterygoid flexure retained during ontogeny.

Jacarea Gray, 1844 [this contribution], converted clade name

Definition

The clade originating in the most recent common ancestor of *Caiman crocodilus* (Linnaeus, 1758), *C. latirostris* (Daudin, 1802), *C. yacare* (Daudin, 1802) and *Melanosuchus niger* (Spix, 1825). This is a minimum-clade definition. (Registration number: 1148) (Figure 1(A–B)).

Etymology

Jacarea comes from 'Jacare', a genus proposed by Gray (1844) that included the species *Caiman crocodilus*, *C. latirostris* and *Melanosuchus niger*. 'Jacare' itself comes from the Portuguese 'jacaré' and Spanish 'yacare', names used in Latin America to refer to extant caimanines. The two terms originate from the ancient Tupi (indigenous language of South America) word 'îakaré', which was used to refer to all alligatorid crocodylians (Navarro, 2013).

Reference Phylogeny

Phylogenetic hypothesis depicted in figure 9 of Godoy et al. (2021; Figure 1(A–B)).

Composition

Based on the reference phylogenies, Jacarea is mainly comprised of *Caiman crocodilus*, *C. latirostris*, *C. yacare* and *Melanosuchus niger*, as well as extinct taxa occasionally recovered in the clade (see below).

Comments

Content. Since its original definition by Brochu (1999), the clade Jacarea has predominantly encompassed species of the genera *Caiman* and *Melanosuchus*. These include not only the extant species of both genera, which are the specifiers of the clade name (*Caiman crocodilus*, *C. latirostris*, *C. yacare* and *Melanosuchus niger*), as well also several extinct species that have been recovered within the clade by distinct analyses performed through the years. Brochu (1999) recovered two fossil species within Jacarea: '*Caiman lutescens*' (Rovereto, 1912) and '*Melanosuchus fisheri*' Medina, 1976 – both later considered *nomina dubia* (Bona et al., 2017, 2024; Souza-Filho et al., 2020). Later, other species were commonly recovered in Jacarea: *C. brevirostris* (Bona, Ezcurra, et al., 2018; Bona et al., 2022; Cidade et al., 2017, Cidade et al., 2020; Fortier et al., 2014; Godoy et al., 2021; Rio & Mannion, 2021), *C. wannlangstoni* (Bona, Ezcurra, et al., 2018; Bona et al., 2022; Cidade et al., 2020; Godoy et al., 2021; Rio & Mannion, 2021; Salas-Gismondi et al., 2015; Walter et al., 2022) and *Paranasuchus gasparinae* (Bona et al., 2012). *P. gasparinae*, however, has also been recovered outside Jacarea, in the Nettosuchidae clade (Bona et al., 2024; Cidade et al., 2020; Godoy et al., 2021).

Other fossil species have appeared less frequently inside Jacarea. Cidade et al. (2020) recovered *Centenariosuchus gilmorei*, *Necrosuchus ionensis* and the clade formed by *Acresuchus* and *Purussaurus* (Purussauridae) as part of the clade. Bona et al. (2022) recovered *Centenariosuchus gilmorei* and a clade formed by *Mourasuchus* and *Purussaurus* within Jacarea, whereas Bona et al. (2024) recovered only *Centenariosuchus* within Jacarea. Rio and Mannion (2021) recovered Jacarea as the same clade as

Caimanini, which led many taxa that were not commonly recovered within Jacarea to be in the clade in their analysis: Purussauridae, Bottosauria and a clade formed by *Tsoabichi greenriverensis* as the sister-taxon of the two species of *Paleosuchus*.

Recently, molecular data and advances in species discovery methods have revealed a higher diversity of genetic lineages within the Jacarea clade. Within the *Caiman crocodilus/yacare* complex (Roberto et al., 2020), subspecies such as *Caiman c. fuscus* (Cope, 1868) (Central America and trans-Andean Colombia) and *C. c. chiapasius* (Bocourt, 1876) (Mexico) have been recovered as distinct candidate species (Amavet et al., 2023; Roberto et al., 2020; Venegas-Anaya et al., 2008). Additionally, cryptic lineages have been identified within this species complex, including a lineage tentatively assigned as *Caiman crocodilus* sensu stricto, which exhibits genetic diversity in the Upper Branco River basin, Southwest Amazon, the Amazon River basin, the Brazilian craton, and the Orinoco River. Furthermore, two distinct genetic lineages have been found within *Caiman yacare*: one in the Paraguay River basin (sensu stricto) and another in the Madeira-Bolivia River basins; the latter of which is also considered a hybridisation zone between *C. crocodilus* and *C. yacare* (Brazaitis et al., 1998; Hrbek et al., 2008; Medem, 1983). Moreover, Amavet et al. (2023) identified an additional lineage in the Argentine Chaco region.

Conversely, *Caiman c. apaporiensis* Medem, 1955, despite exhibiting distinct morphological differences in the skull shape (Angulo-Bedoya et al., 2019; Escobedo-Galvan et al., 2011), has not been recovered as a separate lineage using mitochondrial gene analysis (Balaguera-Reina et al., 2020, 2022). The phylogenetic relationships among the lineages within this species complex remain unresolved (Amavet et al., 2023; Roberto et al., 2020), and ongoing genomic research is expected to provide further insights (Roberto, I.J., personal observation, 2025).

Caiman latirostris also possesses three distinct genetic lineages: one in the Pilcomayo and Paraná rivers, a second in the São Francisco River and northeastern coastal drainages of Brazil, and a third lineage, designated as *C. latirostris* sensu strict, in the Doce River and southeastern coastal drainages of Brazil (Amavet et al., 2023; Borges et al., 2018; Roberto et al., 2020). Pacheco-Sierra et al. (2025) found an introgressive hybridisation pattern in Argentina between *C. latirostris* and *C. yacare*. A comprehensive taxonomic revision is required to elucidate the true species diversity within the genus *Caiman*.

Prior definitions. Brochu (1999) originally defined Jacarea as 'a node-based group comprising the last common ancestor of *Caiman crocodilus*, *C. latirostris*, *C. yacare* and *Melanosuchus niger* and all of its descendants' (not established). This concept is retained in the present contribution, but with a revised definition. Since the Phylocode is not retroactive and only recognises the phylogenetic definition of a name if published in the 'Phylonyms' (de Queiroz et al., 2020) or in a work published after it (Cantino & de Queiroz, 2020, Preamble 6 and Art. 7.1), the definitional authors of Jacarea are the authors of this paper, and not Brochu (1999).

Characteristics. Brochu (1999) found the following unambiguous synapomorphies for Jacarea: half of axis neural spine slopes anteriorly (Character 11, state 1 of his analysis), iliac blade rounded with modest dorsal indentation (28–1), 3) articular-surangular suture with anterior process ventral to lingual foramen (44–2), 4) lateral edge of suborbital fenestra bowed medially (105–1); and the following ambiguous synapomorphies: edges of scapular blade subparallel (22–1), six nuchal osteoderms with four central and two lateral (38–2), medial parietal wall of supratemporal fenestra bearing foramina (104–1), anterior face of palatine process rounded or pointed anteriorly (108–0), median pelvic keel scales form single row along tail (157–1).

Fortier et al. (2014) found three synapomorphies of Jacarea: the anterior half of the axial neural spine sloping anteriorly (character 8, state 1 of their analysis), the articular bearing an anterior lamina ventral to the lingual foramen (54–2) and the prefrontal pillar with a large pneumatic recess (82–1).

Godoy et al. (2021) found one synapomorphy supporting Jacarea: maxilla with a broad shelf extending into the suborbital fenestra, making the lateral margin concave (Character 111, state 1 of their analysis).

Purussauria [this contribution], new clade name

Definition

The clade originating in the most recent common ancestor of *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892 and *Mourasuchus atopus* (Langston, 1965). This is a minimum-clade definition. (Registration number: 1149) (Figure 1D).

Etymology

The name comes from the genus *Purussaurus*, which in turn means 'lizard from the Purus', referring to the Purus River in Brazil where remains of the taxon have been found. The suffix 'sauria' (from the Ancient Greek 'σαῦρος' [saurus]) means 'lizard' but has been used for various names within Crocodylomorpha.

Reference Phylogeny

Phylogenetic hypothesis depicted in fig. 2 of Bona, Ezcurra et al. (2018; Figure 1(D)).

Composition

Based on the reference phylogeny, Purussauria includes Purussauridae (new clade name) and Nettosuchidae Langston, 1965.

Comments

Content. Brochu (1999, 2011), Bona et al. (2012), Scheyer et al. (2013) and Fortier et al. (2014) recovered *Purussaurus* (Purussauridae) and *Mourasuchus* (Nettosuchidae) forming a clade with *Orthogenysuchus*. Most analyses (Bona et al., 2012; Brochu, 1999; Fortier et al., 2014; Scheyer et al., 2013) also recovered the latter two as sister-taxa (for the systematic issue regarding *Orthogenysuchus*, see 'Caimaninae' above). Later, Purussauridae and Nettosuchidae were also recovered as a clade in successive studies (Bona, Ezcurra, et al., 2018; Bona et al., 2022, 2024; Cidade et al., 2017; Salas-Gismondi et al., 2015; Stocker et al., 2021; Walter et al., 2022), with Bona et al. (2024) recovering *Paranasuchus gasparinae* and *Paranacaiman bravardi* within Nettosuchidae.

Characteristics. Brochu (1999) found the following unambiguous synapomorphies for a clade formed by *Purussaurus* as the sister-taxon of *Orthogenyuchus* and *Mourasuchus*: scapulocoracoid facet anterior to glenoid fossa uniformly narrow (Character 25, state 0 of his analysis), prefrontals meet medially (100–1), prefrontalonger than lacrymal (117–1); and the following ambiguous synapomorphies: dorsal margin of atlantal rib generally smooth with modest dorsal process (14–0), axial hypapophysis with deep fork (19–0).

Purussauridae [this contribution], new clade name

Definition

The clade consisting of *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892 and all organisms or species that share a more recent common ancestor with *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892 than with *Bottosaurus harlani* Agassiz, 1849, *Caiman crocodilus* (Linnaeus, 1758), *Caiman latirostris* (Daudin, 1802), *Eocaiman cavernensis* Simpson, 1933, *Mourasuchus atopus* (Langston, 1965) and *Paleosuchus palpebrosus* (Cuvier, 1807). This is a maximum-clade definition (Registration number: 1150) (Figure 1(A)).

Etymology

The name comes from the genus *Purussaurus*, which in turn means 'lizard from the Purus', referring to the Purus River in Brazil where remains of the taxon have been found. The suffix 'sauria' (from the Ancient Greek 'σαῦρος' [saurus]) means 'lizard' but has been used for various names within Crocodylomorpha.

Reference Phylogeny

Phylogenetic hypothesis depicted in fig. 9 of Godoy et al. (2021; Figure 1(A)).

Composition

Based on the reference phylogenies, Purussauridae includes the genera *Acresuchus* Souza-Filho et al., 2018 and *Purussaurus* Barbosa-Rodrigues, 1892.

Comments

Content. The giant caimanine genus *Purussaurus* is certainly the most well-known component of Purussauridae. First described in the 19th century (Barbosa-Rodrigues, 1892; Gervais, 1876), *Purussaurus* is currently represented by three species: *P. brasiliensis*, *P. neivensis* and *P. mirandai*. These species are distributed across various Lower to Upper Miocene localities in central and northern South America, including Bolivia, Brazil, Colombia, Peru and Venezuela (Cidade et al., 2019a; Solórzano et al., 2018). The largest species, *P. brasiliensis*, has been estimated between 7.99 and 10.0 metres in body length (Paiva et al., 2022), with some estimates extending up to 12.5 metres (Aureliano et al., 2015). As one of the largest known crocodylomorphs, *Purussaurus* has been the subject of extensive discussion regarding its role as an apex predator in Cenozoic South American ecosystems (Aureliano et al., 2015; Cidade, et al., 2019a; Pujos & Salas-Gismondi, 2020; Scheyer et al., 2019).

Acresuchus has been recently described. Its original description is based on specimens from the Brazilian state of Acre (Souza-Filho et al., 2018), with a subsequent occurrence in Venezuela (Cidade & Rincón, 2021). In contrast to *Purussaurus*, *Acresuchus* was a medium-sized taxon, likely occupying an ecological niche similar to that of the extant *Melanosuchus niger* (Souza-Filho et al., 2018). Despite these differences, *Acresuchus* and *Purussaurus* have been recovered as a clade (Souza-Filho et al., 2018). The synapomorphies supporting this clade are presented below ('Characteristics').

Characteristics. Souza-Filho et al. (2018) and Godoy et al. (2021) have identified three synapomorphies for Purussauridae: external mandibular fenestra present and very large, with most of the foramen inter- mandibularis caudalis visible in lateral view (Character 63, state 2 of both analysis); anterior tip of frontal forming simple acute point (130–0); dermal bones of the skull roof overhanging the rims of the supratemporal fenestrae near maturity, with the fenestrae large, significantly longer than wide and with an oval shape (151–3).

Additionally, Souza-Filho et al. (2018) and Godoy et al. (2021) list the following synapomorphies for *Purussaurus*: an external naris that is longer than wide (Character 83, state 2 of their analysis); orbits equal to or subequal in size to the infratemporal fenestrae (181–0); and a posterior margin of the skull table that is deeply concave (185–1). Souza-Filho et al. (2018) list the following characteristic as being diagnostic of *Acresuchus pachytemporalis*: 'a caimanine with a medium-sized body; teeth with smooth (non-serrated) carinae; orbits large in comparison with other caimanines, having roughly straight margins that are larger than the infratemporal fenestrae; circular external naris; posterior margin of the skull table transversely straight to slightly concave, posterolateral margin of squamosal upturned throughout the entire dorsal lateral margin with a dorsoventral expansion in the posterior portion of the eminence' – this last feature being an autapomorphy of the species within Caimaninae (Souza-Filho et al., 2018, p. 3).

Nettosuchidae Langston, 1965 [this contribution], converted clade name

Definition. The clade consisting of *Mourasuchus atopus* (Langston, 1965) and all organisms or species that share a more recent common ancestor with *Mourasuchus atopus* (Langston, 1965) than with *Bottosaurus harlani* Agassiz, 1849, *Caiman crocodilus* (Linnaeus, 1758), *Caiman latirostris* (Daudin, 1802), *Eocaiman cavernensis* Simpson, 1933, *Paleosuchus palpebrosus* (Cuvier, 1807) and *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892. This is a maximum-clade definition (Registration number: 1151) (Figure 1(A)).

Etymology

Derived from *Nettosuchus*, the type genus of the Nettosuchidae family name as proposed by Langston (1965). *Nettosuchus* derives from 'netta', which means 'duck' in Ancient Greek, in reference to the wide snout of the fossil, and 'suchus' ('Σοῦχος', or Soukhos/Souchos), which is the Greek word for the Egyptian crocodile-headed god (Sebek or Sobk) and has been widely used as a suffix for several crocodylomorph genera.

Reference Phylogeny

Phylogenetic hypothesis depicted in fig. 9 of Godoy et al. (2021; Figure 1(A)).

Composition

Based on the reference phylogeny, Nettosuchidae includes the genus *Mourasuchus*, as well as *Paranasuchus gasparinae* and *Paranacaiman bravardi*.

Synonyms

There are no known synonyms for Nettosuchidae.

Comments

Content. *Mourasuchus*, the senior synonym of *Nettosuchus* Langston, 1965, is the taxon most traditionally associated with Nettosuchidae. *Mourasuchus* is a large-sized caimanine, with body length estimations for the largest species, *M. amazonensis*, between 5.27 m and 7.67 m (Paiva et al., 2022) to up to 9.4 metres (Cidade, Rincón, & Solórzano, 2021). This genus is characterised by its long, wide, dorsoventrally flattened, 'duck-like' rostrum (Bona et al., 2012; Cidade et al., 2017, 2019a; Langston, 1965) classified by Busbey (1994) as 'platyrostral-broad'. The distinctive cranial morphology, alongside some postcranial characters, has led some authors to propose that *Mourasuchus* employed unique feeding strategies, which led the taxon to be characterised as a 'filter-feeder' or 'gulp-feeder' (Bona et al., 2012; Cidade, et al., 2019c; Langston, 1965, 2008; Riff et al., 2010). These feeding strategies would be significantly different from those of most other crocodylomorphs, both extinct and extant, with the possible exception of *Stomatosuchus* Stromer, 1925, *Laganosuchus* Sereno & Larsson, 2009 and possibly also *Aegyptosuchus* Stromer, 1933 and *Aegisuchus* Holliday & Gardner, 2012 (all crocodyliforms from the Cretaceous of northern Africa), which also exhibit a platyrostral-broad morphology (Cidade et al., 2019c; Holliday & Gardner, 2012; Sereno & Larsson, 2009).

Other species that may belong to Nettosuchidae are *Paranasuchus gasparinae*, which has been recovered as sister-taxon to *Mourasuchus* in recent phylogenies

(Bona et al., 2024; Cidade et al., 2020; Godoy et al., 2021), and *Paranacaiman bravardi* (type specimen MACN-PV-13551, formerly considered a '*Caiman lutescens*' specimen – see Bona et al. (2024) and comments about '*C. lutescens*' in the 'Caimaninae' section above), which appeared as the sister-taxon to the clade formed by *Paranasuchus gasparinae* and *Mourasuchus* in the analysis of Rio and Mannion (2021), and as part of a polytomy with *P. gasparinae* and *Mourasuchus* and Bona et al. (2024).

Prior definitions. The name Nettosuchidae was erected by Langston (1965) as a family name within the traditional Linnean system, with *Nettosuchus* as the type genus. Later, Langston (1966) recognised that *Nettosuchus* was a junior synonym of *Mourasuchus*, which had been described by Price (1964). This synonymy, however, does not invalidate Nettosuchidae as a valid family name according to Article 40.1 of the International Code of Zoological Nomenclature (ICNZ, 1999). This justifies the use of the name Nettosuchidae for a clade that primarily involves *Mourasuchus*, which is the case of the clade name here defined.

There has never been a phylogenetic definition of Nettosuchidae. Brochu (1999) discussed the possible use of this name for a clade uniting *Mourasuchus* and *Orthogenysuchus olseni*, a crocodylian from the Eocene of the United States, but did not explicitly name the clade as such. On whether *Orthogenysuchus* is a nettosuchid, ongoing preparation of its holotype and only known specimen has significantly revealed new information that might change the systematic position of the taxon (Salas-Gismondi et al., 2015). As such data remains unpublished, we refrain from assigning *Orthogenysuchus* to Nettosuchidae in this paper.

Characteristics. Godoy et al. (2021) recover one synapomorphy for Nettosuchidae: nasals excluded, at least externally, from naris, with the nasals and the premaxillae still in contact (Character 82, state 2 of their analysis). This analysis also recovers one synapomorphy for *Mourasuchus*: long dorsal premaxillary processes, extending beyond the third maxillary alveolus (90–1). Additionally, Cidade et al. (2017) provide the following characters as diagnostic for *Mourasuchus*: 'dentary symphysis very short, extending only to the level of the first alveolous; orbits smaller than infratemporal fenestrae; prefrontal and frontal thickened, forming a marked knob at the anteromedial margin of the orbits; dentary linear between fourth and tenth alveoli; posterior teeth and alveoli of maxilla and/or dentary laterally compressed; nasals excluded, at least externally, from the naris, with premaxillae and nasals still in contact; dorsal premaxillary processes long, extending beyond the level of the third maxillary alveolus; frontoparietal suture linear between supratemporal fenestrae; an extremely wide, compressed and long rostrum related with a very small skull table; lateral border of rostrum without festooning; prefrontals contacting at the midline, so that nasals do not contact the frontal in dorsal view; slender U-shaped mandibles that curve from first to fifth alveoli and then are straight posteriorly to sixth alveolus; upper and lower tooth rows with more than 40 teeth; osteoderms with conspicuous spines on the dorsal surface' (Cidade et al., 2017, pp. 8–9).

Discussion

Perspectives on phylogenetic nomenclature of Caimaninae after this article

The standardisation of the phylogenetic nomenclature for Caimaninae established in this contribution (summarized in Table 1) should not be regarded as a conclusive framework but as a foundational basis for future research. As our understanding of the Caimaninae group inevitably evolves, this nomenclature will serve as a reference point for subsequent investigations into its phylogeny, systematics and taxonomy. There are several unresolved issues concerning the phylogeny of Caimaninae and its various subclades, involving both extant and extinct taxa, that may necessitate modifications, refinements or updates to the phylogenetic nomenclature.

Perspectives on the phylogeny of Caimaninae concerning fossil forms include several unresolved issues. These issues involve the following key points:

(1) Taxonomic assignments: The placement of taxa such as *Albertochampsa*, *Brachychampsa* and *Stangerochampsa* within Caimaninae remains uncertain (Bona, et al., 2018; Cossette, 2021; Rio & Mannion, 2021; Salas-Gismondi et al., 2015; Stocker et al., 2021; Walter et al., 2022).
(2) Early-diverging caimanines: The placement of taxa such as *Culebrasuchus*, *Globidentosuchus* and *Gnatusuchus* relative to the crown-group (Caimanini) requires further investigation. They have been predominantly identified as early-diverging caimanines (Hastings et al., 2013; Salas-Gismondi et al., 2015; Scheyer et al., 2013; Stocker et al., 2021) but several of these taxa may belong to Caimanini (Walter et al., 2022), with secondary adaptations for durophagy (Cidade et al., 2019a; Salas-Gismondi et al., 2015; Scheyer

et al., 2013) potentially complicating their placement.

(3) Phylogeny of Paleocene–Eocene caimanines: There is no consensus on the exact phylogenetic positions of the early-diverging caimaninies *Tsoabichi*, *Chinatichampsus*, *Eocaiman*, *Necrosuchus* and *Protocaiman* (Bona, et al., 2018; Brochu, 2011; Cidade et al., 2020; Godoy et al., 2021; Walter et al., 2022).

(4) Relationships of *Bottosaurus*: The relationship of this taxon with extant *Paleosuchus*, the extinct *Tsoabichi* and Caimaninae in general (Cidade, 2019; Cossette, 2021; Cossette & Brochu, 2018; Rio & Mannion, 2021; Walter et al., 2022) remain uncertain.

(5) Affinities of *Centenariosuchus*: whether *Centenariosuchus* is a member of or closely related to Jacarea, or represents a more early-diverging crown-group (Caimanini) taxon requires further clarification (Bona et al., 2022; Cidade et al., 2020; Walter et al., 2022).

(6) Nettosuchidae and Caimaninae: whether the species *Paranasuchus gasparinae* and *Paranacaiman bravardi* belong to Nettosuchidae or can be placed elsewhere along the Caimaninae clade is an issue that must be addressed by further studies (Bona et al., 2024; Cidade et al., 2020; Godoy et al., 2021; Rio & Mannion, 2021).

(7) Extant genera in the fossil record: The taxonomic implications of assigning generic names with extant representatives (e.g. *Caiman*, *Melanosuchus*, and *Paleosuchus*) to fossil taxa within the clade defined by the extant representatives of each genus (crown-groups) requires further investigation.

The integration of molecular data from extant taxa with morphological data from both fossil and extant Caimaninae representatives may offer new insights and raise additional questions about the phylogenetic nomenclature of extinct taxa. These issues will need to be addressed as new data emerge.

The extant diversity of Caimaninae species is likely underestimated. An integrative taxonomic review is required to analyse the mitochondrial molecular lineages within *Caiman crocodilus/yacare* complex and *Paleosuchus* spp. (see Amavet et al., 2023; Balaguera-Reina et al., 2022, 2024; Bittencourt et al., 2019; Díaz-Moreno et al., 2021; Hernández-Rangel et al., 2024; Jiménez-Alonso et al., 2023; Muniz et al., 2018; Roberto et al., 2020; Venegas-Anaya et al., 2008). Both genera have a complex taxonomic and nomenclature history, with numerous names available for various lineages (Medem, 1983; Mook & Mook, 1940; Roberto et al., 2022; Schmidt, 1928). Studies utilising skull geometric morphometrics have demonstrated shape differences among the delimited lineages and subspecies of *Caiman crocodilus* (Angulo-Bedoya et al., 2019). However, the case of *C. crocodilus apaporiensis*, a subspecies with a slender snout within the *C. crocodilus* complex (Escobedo-Galván et al., 2015; Medem, 1955), but that was not recovered as a distinct evolutionary lineage in mitochondrial analysis (Balaguera-Reina et al., 2020, 2022). Phylogenomic studies incorporating nuclear genes are also necessary to properly delimit these molecular evolutionary units and resolve the relationships within the species.

Conclusions

This effort represents the establishment of a standard phylogenetic nomenclature of the crocodylian alligatoroid clade Caimaninae under the rules of the recently published International Code of Phylogenetic Nomenclature, the PhyloCode. The phylogenetic definitions of seven clade names are established: Caimaninae, Bottosauria, Caimanini, Jacarea, Purussauria, Purussauridae and Nettosuchidae. Four of these are new names (Bottosauria, Caimanini, Purussauria and Purussauridae), one is an established name to which a phylogenetic definition is first given (Nettosuchidae), and two are established names and definitions that are conserved in this paper (converted clade names; Caimaninae and Jacarea).

While this contribution aims to establish a phylogenetic nomenclature system that is clear, direct, reasonable and enduring, we acknowledge that evolutionary, phylogenetic and systematic studies are inherently dynamic. Thus, our current understanding of caimanine phylogenetics, which forms the basis of this nomenclature, is expected to undergo inevitable revisions in the future. This evolution will result from advancements in analytical tools, changes in the sampling of both extant and extinct taxa, shifts in taxonomic and nomenclatural perspectives and evolving philosophical approaches to systematics. Therefore, this proposal should be viewed as a collective effort that provides an initial, foundational step – rather than an attempt to establish definitive names and rules – towards implementing phylogenetic nomenclature in the systematics and taxonomy of Caimaninae. It is intended as a basis upon which future research can build, refine, modify and improve. While the primary objective of this contribution is the definition of the phylogenetic nomenclature for the Caimaninae clade, we also aim to encourage the adoption of phylogenetic nomenclature in other biological groups, particularly among other crocodylians and crocodylomorphs. This nomenclature system has demonstrated greater alignment with our current understanding of the dynamics and complexities inherent to the systematisation of the different forms of life as they have evolved – and continue to evolve.

Acknowledgments

This work is dedicated to the memory of Mark Norell (1957–2025), a distinguished vertebrate paleontologist who worked with several groups, including crocodylians, and who created the name "Caimaninae". We would like to thank Daniel Madzia and one anonymous reviewer for valuable comments that greatly improved the manuscript. We would like to extend our appreciation to all systematists that studied Caimaninae, both extant and extinct, until the publication of this paper: Carolus Linnaeus, Augusto Bravard, Paul Gervais, Cayetano Rovereto, Hermann Burmeister, João Barbosa-Rodrigues, Charles Mook, Carlos Rusconi, George G. Simpson, Bryan Patterson, Llewellyn I. Price, Wann Langston, Jr., Jean Bocquentin-Villanueva, Zulma Gasparini, Carmen Medina, Jonas Pereira de Souza-Filho, Orangel Aguilera, Alexander Hastings, Torsten Scheyer, André Piacentini Pinheiro, Daniel Fortier, Ascánio Rincón, Rodolfo Salas-Gismondi, Francisco Barrios, Tobias Massonne, Lucy Souza, Jonathan Rio, Phillip Mannion, Michelle Stocker, Jules Walter, Gustavo Darlim, Federico Medem, Karl Schmidt, Lou Desmore III, Tomas Hrbek, Miryam Venegas-Anaya, Sandra M. Hernández-Rangel, Fabio Muniz, Peter Brazaitis, Robert Godshalk, Heinz Wermuth. We deeply apologize for any omission. This study was funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) grants 2021/02199-5 and 2023/05433-4 to GMC and grant 2024/09825-7 to PLG, by Coordenação de Aperfeiçoamento de Pessoal de Níve Superior (CAPES) grant (88882.156872/2016-01, finance code: 001), by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) fellowship (SWE 22/2018) and by International Union for Conservation of Nature (IUCN) Crocodile Specialist Group Student Research Assistance grant to IJR.

Author contributions

CRediT: **Giovanne M. Cidade**: Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing; **Pedro L. Godoy**: Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing; **Patricia Amavet**: Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing; **Adam Cossette**: Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing; **Andrés Solórzano**: Validation, Visualization, Writing – original draft, Writing – review & editing; **Paula Bona**: Validation, Visualization, Writing – review & editing; **Mónica Angulo-Bedoya**: Validation, Visualization, Writing – review & editing; **Sergio A. Balaguera-Reina**: Validation, Visualization, Writing – review & editing; **Márton Rabi**: Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing; **Izeni Pires-Farias**: Validation, Visualization, Writing – review & editing; **Rodrigo G. Figueiredo**: Validation, Visualization, Writing – review & editing; **Martin D. Ezcurra**: Validation, Visualization, Writing – review & editing; **Pedro S. Bittencourt**: Validation, Visualization, Writing – review & editing; **Christopher A. Brochu**: Conceptualization, Validation, Visualization, Writing – review & editing; **Igor J. Roberto**: Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This study was funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) grants 2021/02199-5 and 2023/05433-4 to GMC and grant 2024/09825-7 to PLG, by Deutsche Forschungs Gemeinschaft grant 417629144 to MR, by Coordenação de Aperfeiçoamento de Pessoal de Níve Superior (CAPES) grant (88882.156872/2016-01, finance code: 001), by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) fellowship (SWE 22/2018) and by International Union for Conservation of Nature (IUCN) Crocodile Specialist Group Student Research Assistance grant to IJR.

ORCID

Giovanne M. Cidade http://orcid.org/0000-0001-8621-5122
Pedro L. Godoy http://orcid.org/0000-0003-4519-5094
Patricia Amavet http://orcid.org/0000-0001-8143-7498
Adam Cossette http://orcid.org/0000-0002-8030-0112
Andrés Solórzano http://orcid.org/0000-0003-1862-2724
Paula Bona http://orcid.org/0000-0001-7782-855X
Mónica Angulo-Bedoya http://orcid.org/0000-0001-7580-0502
Sergio A. Balaguera-Reina http://orcid.org/0000-0002-5153-0031
Márton Rabi http://orcid.org/0009-0005-8929-3106
Izeni Pires-Farias http://orcid.org/0000-0002-1416-4351
Rodrigo G. Figueiredo http://orcid.org/0000-0002-4304-6434
Martin D. Ezcurra http://orcid.org/0000-0002-6000-6450
Pedro S. Bittencourt http://orcid.org/0000-0002-4074-3541
Christopher A. Brochu http://orcid.org/0000-0003-4044-8371
Igor J. Roberto http://orcid.org/0000-0003-3268-9597

Data availability statement

The authors confirm that the data supporting the findings of this study are available within the article.

References

Agassiz, L. (1849). On the distinction between the fossil Crocodiles of the green sand of New Jersey. *Academy of Natural Sciences of Philadelphia*, *4*, 169.

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.

Amavet, P. S., Pacheco-Sierra, G., Uhart, M. M., Prado, W. S., & Siroski, P. A. (2023). Phylogeographical analysis and phylogenetic inference based on the cytochrome b gene in the genus *Caiman* (Crocodylia: Alligatoridae) in Central and South America. *Biological Journal of the Linnean Society*, *138*(3), 289–303. https://doi.org/10.1093/biolinnean/blac145

Angulo-Bedoya, M., Correa, S., & Benítez, H. A. (2019). Unveiling the cryptic morphology and ontogeny of the Colombian *Caiman crocodilus*: A geometric morphometric approach. *Zoomorphology*, *138*, 387–397. https://doi.org/10.1007/s00435-019-00448-2

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. https://doi.org/10.1371/journal.pone.0117944

Balaguera-Reina, S. A., & Velasco, A. (2019). *Caiman crocodilus*. The IUCN Red List of Threatened Species 2019, e. T46584A3009688. https://doi.org/10.2305/IUCN.UK.2019-1.RLTS.T46584A3009688.en (Accessed 25 July 2025)

Balaguera-Reina, S. A., Angulo-Bedoya, M., Moncada-Jiménez, J. F., Webster, M., Roberto, I. J., & Mazzotti, F. J. (2022). Update: Assessing the evolutionary trajectory of the Apaporis caiman (*Caiman crocodilus apaporiensis*, Medem 1955) via mitochondrial molecular markers. *Biological Journal of the Linnean Society*, *137*, 700–710.

Balaguera-Reina, S. A., Vargas-Ramírez, M., Ordóñez-Garza, N., Hernández-Gonzalez, F., & Densmore, L. D. (2020). Unveiling the mystery: assessing the evolutionary trajectory of the Apaporis caiman population (*Caiman crocodilus apaporiensis*, Medem 1955) via mitochondrial molecular markers. *Biological Journal of the Linnean Society*, *131*, 163–171.

Barbosa-Rodrigues, B. (1892). Les reptiles fossiles de la vallée de l'Amazone. *Vellosia*, *2*, 41–46.

Bittencourt, P. S., Campos, Z., de Lima Muniz, F., Marioni, B., Campos Souza, B., Da Silveira, R., de Thoisy, B., Hrbek, T., & Pires-Farias, I. P. (2019). Evidence of cryptic lineages within a small South American crocodilian: the Schneider's dwarf caiman *Paleosuchus trigonatus* (Alligatoridae: Caimaninae). *PeerJ*, *7*, e6580.

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

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. In M. Fernández & Y. Herrera (Eds.), *Reptiles Extintos - Volumen en Homenaje a Zulma Gasparini* (pp. 143–158). 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. https://doi.org/10.1017/S175569101300042X

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. https://doi.org/10.1098/rspb.2018.0843

Bona, P., Fernandez-Blanco, M. V., Scheyer, T. M., & Foth, C. (2018). 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., Barrios, F., Ezcurra, M. D., & Fernandez-Blanco, M. V. (2022). The taxonomic status of *Notocaiman stromeri* (Crocodylia, Alligatoroidea) and the Early diversity of South American caimanines. *Ameghiniana*, *59*(3), 210–220. https://doi.org/10.5710/AMGH.27.02.2022.3470

Bona, P., Pol, D., Pérez, L. M., Tineo, D. E., Brandoni, D., & Noriega, J. I. (2023). The first record of *Purussaurus* (Crocodylia, Alligatoridae) in the Late Miocene of Argentina. *Revista del Museo Argentino de Ciencias Naturales, Nueva Serie*, *25*(1), 71–84. https://doi.org/10.22179/REVMACN.25.797

Bona, P., Barrios, F., Ezcurra, M. D., Fernandez Blanco, M. V., & Cidade, G. M. (2024). New taxa of giant caimans from the southernmost hyperdiverse wetlands of the South American late Miocene. *Journal of Systematic Palaeontology*, *22*(1). https://doi.org/10.1080/14772019.2024.2375027

Borges, V. S., Santiago, P. C., Lima, N. G. S., Coutinho, M. E., Eterovick, P. C., & Carvalho, D. C. (2018). Evolutionary significant units within populations of neotropical broad-snouted caimans (*Caiman latirostris*, Daudin, 1802). *Journal of Herpetology*, *52*, 282–288. https://doi.org/10.1670/17-074

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.

Brazaitis, P., Rebêlo, G. H., & Yamashita, C. (1998). The distribution of *Caiman crocodilus crocodilus* and *Caiman yacare* populations in Brazil. *Amphibia-Reptilia*, *19*(2), 193–201. https://doi.org/10.1163/156853898X00476

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

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*(Suppl_1), S228–S256.

Brochu, C. A. (2012). 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.

Busbey A. B. (1994). In J. J. Thomason (Ed.), *The structural consequences of skull flattening in crocodilians The structural consequences of skull flattening in crocodilians* (pp. 173–192). Cambridge University Press.

Cope, E. D. (1868). On the Crocodilian Genus *Perosuchus*. *Proceedings of the Academy of Natural Sciences of Philadelphia* (pp. 203).

Cantino, P. D., & de Queiroz, K. (2020). *International Code of Phylogenetic Nomenclature (PhyloCode)*. CRC Press.

Chiappe, L. (1988). Un nuevo *Caiman* (Crocodylia, Alligatoridae) de la Formación Tremembé (Oligoceno), Estado de São Paulo, Brasil, y su significado paleoclimático. *Paula-Coutiana*, *3*, 49–66.

Cidade, G. M. (2019). *Phylogenetic review of Alligatoridea (Crocodylia) and taxonomic review of the species of the Caimaninae clade* (Doctoral thesis, Universidade de São Paulo).

Cidade, G. M., & Rincón, A. D. (2021). The first occurrence of *Acresuchus* (Alligatoroidea, Caimaninae) from the Urumaco Formation of Venezuela and the late Miocene crocodylian fauna of northern South America. *Journal of South American Earth Sciences*, *110*, 103344. https://doi.org/10.1016/j.jsames.2021.103344

Cidade, G. M., Barrios, F., Souza, R. G., & Bona, P. (2015). A new diagnosis, phylogenetic relationships and taxonomy of *Caiman lutescens* (Rovereto, 1912), Late Miocene, Argentina. In *V Congreso Latinoamericano de Paleontologia Vertebrados* (p. 81).

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. https://doi.org/10.7717/peerj.3056

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. https://doi.org/10.1016/j.jsames.2018.12.026

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

Cidade, G. M., Riff, D., & Hsiou, A. S. (2019c). The feeding habits of the strange crocodylian *Mourasuchus* (Alligatoroidea, Caimaninae): A review, new hypotheses and perspectives. *Revista Brasileira de Paleontologia*, *22*(2), 106–119. https://doi.org/10.4072/rbp.2019.2.03

Cidade, G. M., Fortier, D., & Hsiou, A. S. (2020). Taxonomic and phylogenetic review of *Necrosuchus ionensis* (Alligatoroidea: Caimaninae) and the early evolution and radiation of caimanines. *Zoological Journal of the Linnean Society*, *189*(2), 657–669. https://doi.org/10.1093/zoolinnean/zlz051

Cidade, G. M., Rincón, A. D., & Solórzano, A. (2021). New cranial and postcranial elements of *Mourasuchus* (Alligatoroidea: Caimaninae) from the late Miocene of Venezuela and their palaeobiological implications. *Historical Biology*, *33*(10), 2387–2399. https://doi.org/10.1080/08912963.2020.1795844

Cossette, A. P. (2021). A new species of *Bottosaurus* (Alligatoroidea: Caimaninae) from the Black Peaks Formation (Palaeocene) of Texas indicates an early radiation of North American caimanines. *Zoological Journal of the Linnean Society*, *191*(1), 276–301. https://doi.org/10.1093/zoolinnean/zlz178

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), e1486321. https://doi.org/10.1080/02724634.2018.1486321

Cuvier, G. L. (1807). Sur les différentes espèces de crocodiles vivants et sur leur caractères distinctifs. *Annales du Museum d'Histoire Naturelle*, *10*, 8–66.

Daudin, F. M. (1802). *Histoire Naturelle, Générale et Particulière des Reptiles; Ouvrage faisant suite à l'Histoire Naturelle générale et particulière, composée par Leclerc de Buffon; et rédigée par C.S. Sonnini, membre de plusieurs sociétés savantes*. Tome second. F. Dufart.

Darlim, G., Lee, M. S., Walter, J., & Rabi, M. (2022). The impact of molecular data on the phylogenetic position of the putative oldest crown crocodilian and the age of the clade. *Biology Letters*, *18*(2), 20210603.

Darlim, G., & Höhna, S. (2025). The effects of cryptic diversity on diversification dynamics analyses in Crocodylia. *Proceedings of the Royal Society B*, *292*, 20250091. https://doi.org/10.1098/rspb.2025.0091

Darlim, G., & Höhna, S. (2024). Mixture models for dating with confidence. *bioRxiv*. https://doi.org/10.1101/2024.09.25.614964

de Queiroz, K., Cantino, P.D. & Gauthier, J.A. (2020). *Phylonyms: A Companion to the PhyloCode*. CRC Press.

Díaz-Moreno, D. M., Hernández-Gonzalez, F., Moncada-Jimenez, J. F., Mora, C., Prada, C., Jiménez-Alonso, G., & Balaguera-Reina, S. A. (2021). Molecular characterization of the spectacled caiman (*Caiman crocodilus*) in the upper Magdalena River basin, Colombia: Demographic and phylogeographic insights. *Systematics and Biodiversity*, *19*(8), 1040–1048. https://doi.org/10.1080/14772000.2021.1892224

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*(1), 66–68. https://doi.org/10.11646/zootaxa.3015.1.7

Escobedo-Galván, A. H., Velasco, J., Gonzalez-Maya, J. F., & Resetar, A. (2015). Morphometric analysis of the Rio Apaporis *Caiman* (Reptilia, Crocodylia, Alligatoridae).

Zootaxa, *4059*(3), 541–554. https://doi.org/10.11646/zootaxa.4059.3.6
Erickson, B. R. (1972). *Albertochampsa 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.
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.
Fortier, D., & Rincón, A. (2013). Pleistocene crocodylians from Venezuela, and the description of a new species of *Caiman*. *Quaternary International*, *305*, 141–148. https://doi.org/10.1016/j.quaint.2012.03.018
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. https://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. https://doi.org/10.1002/jmor.20769
Gatesy, J., Amato, G., Norell, M., DeSalle, R., & Hayashi, C. (2003). Combined support for taxic wholesale taxic atavism in gavialine crocodilians. *Systematic Biology*, *52*(3), 403–422. https://doi.org/10.1080/10635150390192783
Gervais, P. (1876). Crocodile gigantesque fossile du Brésil. *Journal of Zoology*, *5*, 232–236.
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).
Godoy, P. L., Cidade, G. M., Montefeltro, F. C., Langer, M. C., & Norell, M. A. (2021). Redescription and phylogenetic affinities of the caimanine *Eocaiman cavernensis* (Crocodylia, Alligatoroidea) from the Eocene of Argentina. *Papers in Palaeontology*, *7*(3), 1205–1231. https://doi.org/10.1002/spp2.1392
Gray, J. E. (1844). *Catalogue of tortoises, crocodilians, and amphisbaenians in the collection of the British Museum*. British Museum (Natural History).
Gray, J. E. (1862). A synopsis of the species of alligators. *Annals and Magazine of Natural History*, *10*, 327–331.
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. https://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*(2), 317–332. https://doi.org/10.1017/jpa.2015.102
Hernández-Rangel, S. M., Morales-Betancourt, M. A., Muniz, F. L., Vargas-Ramírez, M., Rojas-Runjaic, F. J. M., Lasso, C. A., & Caballero, S. (2024). Phylogenetic identity and population structure of the dwarf caimans *Paleosuchus* spp. in the Orinoco basin of Colombia and Venezuela: Filling gaps. *Biological Journal of the Linnean Society*, *142* (1), 68–80. https://doi.org/10.1093/biolinnean/blad061
Holliday, C. M., & Gardner, N. M. (2012). A new eusuchian crocodyliform with novel cranial integument and its significance for the origin and evolution of Crocodylia. *PLoS One*, *7*(1), e30471. https://doi.org/10.1371/journal.pone.0030471
Hrbek, T., Vasconcelos, W. R., Rebelo, G., & Farias, I. P. (2008). Phylogenetic relationships of South American alligatorids and the Caiman of Madeira river. *Journal of Experimental Zoology Part A*, *309*(10), 588–599. https://doi.org/10.1002/jez.430
ICZN. (1999). *International Code of Zoological Nomenclature* (4th ed.). The International Trust for Zoological Nomenclature.
Jiménez-Alonso, G., Balaguera-Reina, S. A., Hoyos, M., Ibáñez, C., Hernández-Rangel, S. M., Useche, C. M. V., Moncada, J. F., & Bloor, P. (2023). Phylogenetic and phylogeographic insights on Trans-Andean spectacled caiman populations in Colombia. *Marine and Freshwater Research*, *74*(12), 1071–1080. https://doi.org/10.1071/MF22245
Joyce, W. G., Anquetin, J., Cadena, E.-A., Claude, J., Danilov, I. G., Evers, S. W., Ferreira, G. S., Gentry, A. D., Georgalis, G. L., Lyson, T. R., Pérez-García, A., Rabi, M., Sterli, J., Vitek, N. S., & Parham, J. F. (2021). A nomenclature for fossil and living turtles using phylogenetically defined clade names. *Swiss Journal of Palaeontology*, *140*(5). https://doi.org/10.1186/s13358-020-00211-x
Langston, W. (1965). *Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia in South America* (University of California Publications in Geological Sciences, Vol. *52*). University of California Press.
Langston, W. (1966). *Mourasuchus* Price, *Nettosuchus* Langston, and the family Nettosuchidae (Reptilia: Crocodilia). *Copeia*, *1966*(4), 882–885. https://doi.org/10.2307/1442020
Langston, W. (2008). Notes on a partial skeleton of *Mourasuchus* (Crocodylia, Nettosuchidae) from the Upper Miocene of Venezuela. *Arquivos do Museu Nacional*, *66*(3), 125–143.
Li, C., Wu, X. C., & Rufolo, S. J. (2019). A new crocodyloid (Eusuchia: Crocodylia) from the Upper Cretaceous of China. *Cretaceous Research*, *94*, 25–39. https://doi.org/10.1016/j.cretres.2018.09.015
Linnaeus, C. (1758). *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (10th ed., Tomus I). Laurentius Salvius.
Massonne, T., Vasilyan, D., Rabi, M., & Böhme, M. (2019). A new alligatoroid from the Eocene of Vietnam highlights an extinct Asian clade independent from extant *Alligator sinensis*. *PeerJ*, *7*, e7562. https://doi.org/10.7717/peerj.7562
Medem, F. (1955) A new subspecies of *Caiman sclerops* from Colombia. *Fieldiana Zoology*, *37*, 339–344.
Medem, F. (1981). *Los Crocodylia de Sur America*, Volume *1*: Los Crocodylia de Colombia. Universidad Nacional de Colombia.
Medem, F. (1983). *Los Crocodylia de Sur America*, Volume *2*. Universidad Nacional de Colombia.
Medina, C. J. (1976). Crocodilians from the Late Tertiary of Northwestern Venezuela: *Melanosuchus fisheri* sp. nov. *Breviora*, *438*, 1–14.
Meyer, H. von. (1832). *Paleologica zur Geshichte der Erde und irher Geschöpfe*. S. Schmerber.

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

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

Mook, C. C., & Mook, G. E. (1940). Some problems in crocodilian nomenclature. *American Museum Novitates*, *1098*, 1–10.

Muniz, F. L., Campos, Z., Hernández-Rangel, S. M., Martínez, J. G., Souza, B. C., De Thoisy, B., Botero-Arias, R., Hrbek, T., & Farias, I. P. (2018). Delimitation of evolutionary units in Cuvier's dwarf caiman, *Paleosuchus palpebrosus* (Cuvier, 1807): Insights from conservation of a broadly distributed species. *Conservation Genetics*, *19*, 599–610. https://doi.org/10.1007/s10592-017-1035-6

Muniz, F. L., Bittencourt, P. S., Hernández-Rangel, S. M., Roberto, I. J., Farias, I. P., & Hrbek, T. (2022). Biogeography and comparative phylogeography of New-World crocodylians. In R. B. Zucoloto, P. S. Amavet, L. M. Verdade, & I. P. Farias (Eds.), *Conservation genetics of New World crocodilians* (pp. 95–122). Springer. https://doi.org/10.1007/978-3-030-56383-7_4

Navarro, E. A. (2013). *Dicionário de Tupi antigo: A língua indígena clássica do Brasil*. Global.

Norell, M. A. (1988). *Cladistic approaches to paleobiology as applied to the phylogeny of alligatorids* (PhD dissertation). Yale University.

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*(11), 3285–3297. https://doi.org/10.1111/j.1558-5646.2011.01373.x

Oxford English Dictionary. (2023). Cayman | caiman (n.). In *Oxford English Dictionary*. https://doi.org/10.1093/OED/8414912758

Pacheco-Sierra, G., Amavet, P., Siroski, P., Piña, C., Patrón-Rivero, C., & Yáñez-Arenas, C. (2025). Hybridization patterns and evolutionary clues in broad-snouted caiman and yacare caiman: Insights from phylogeographic and ecological analysis. *Journal of Zoology*, *326*(3), 214–230. https://doi.org/10.1111/jzo.70013

Paiva, A. L. S., Godoy, P. L., Souza, R. B. B., Klein, W., & Hsiou, A. S. (2022). Body size estimation of Caimaninae specimens from the Miocene of South America. *Journal of South American Earth Sciences*, *118*, 103970. https://doi.org/10.1016/j.jsames.2022.103970

Paiva, A. L. S., Godoy, P. L., Dunne, E. M., Farnsworth, A., Valdes, P. J., Lunt, D. J., Klein, W., Langer, M. C., & Hsiou, A. S. (2024). The role of climate on the emergence of giant caimanines (Crocodylia, Alligatoroidea) from the Miocene western Amazonian region. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *656*, 112582. https://doi.org/10.1016/j.palaeo.2024.112582

Pan, T., Miao, J.-H., Zhang, H.-B., Yan, P., Lee, P.-S., Jiang, X.-Y., Ouyang, J.-H., Deng, Y.-P., Zhang, B.-W., & Wu, X.-B. (2021). Near-complete phylogeny of extant Crocodylia (Reptilia) using mitogenome-based data. *Zoological Journal of the Linnean Society*, *191*, 1075–1089. https://doi.org/10.1093/zoolinnean/zlab018

Parham, J. F., Donoghue, P. C., Bell, C. J., Calway, T. D., Head, J. J., Holroyd, P. A., & Benton, M. J. (2012). Best practices for justifying fossil calibrations. *Systematic Biology*, *61*(2), 346–359.

Parks, A. J., Godfrey, S. T., Gross, B. A., Balaguera-Reina, S. A., Smith, N. G., Mazzotti, F. J., & Desmore III, L. D. (2023). Not one but two: Examining the genetic origin and characterization of the non-native spectacled caiman (*Caiman crocodilus*) in Florida. *Biological Invasions*, *26*, 779–795. https://doi.org/10.1007/s10530-023-03059-4

Pinheiro, A. E. P., Fortier, D. C., Pol, D., Campos, D. A., & Bergqvist, L. P. (2012). A new Eocaiman (Alligatoridae, Crocodylia) from the Itaboraí Basin, Paleogene of Rio de Janeiro, Brazil. *Historical Biology*, *25*(3), 327–337. https://doi.org/10.1080/08912963.2012.705838

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. https://doi.org/10.1080/08912963.2012.705838

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.

Poe, S. (1996). Data set incongruence and the phylogeny of crocodilians. *Systematic Biology*, *45*(4), 393–414. https://doi.org/10.1093/sysbio/45.4.393

Pujos, F., & Salas-Gismondi, R. (2020). Predation of the giant Miocene caiman *Purussaurus* on a mylodontid ground sloth in the wetlands of proto-Amazonia. *Biology Letters*, *16*, 20200239. https://doi.org/10.1098/rsbl.2020.0239

Riff, D., Romano, P. S. R., Oliveira, G. R., & Aguilera, O. A. (2010). Neogene crocodile and turtle fauna in northern South America. In C. Hoorn & F. Wesselingh (Eds.), *Amazonia, landscape and species evolution: A look into the past* (pp. 259–280). Wiley-Blackwell.

Rio, J. P., & Mannion, P. D. (2021). Phylogenetic analysis of a new morphological dataset elucidates the evolutionary history of Crocodylia and resolves the long-standing gharial problem. *PeerJ*, *9*, e12094. https://doi.org/10.7717/peerj.12094

Roberto, J. I., Bittencourt, P. S., Muniz, F. L., Hernández-Rangel, S. M., Nóbrega, Y. C., Ávila, R. W., Souza, B. C., Alvarez, G., Miranda-Chumacero, G., Campos, Z., Farias, I. P., & Hrbek, T. (2020). Unexpected but unsurprising lineage diversity within the most widespread Neotropical crocodilian genus *Caiman* (Crocodylia, Alligatoridae). *Systematics and Biodiversity*, *18*(4), 377–395. https://doi.org/10.1080/14772000.2020.1769222

Roberto, I. J., Bittencourt, P. S., & Hernández-Rangel, S. M. (2022). Taxonomia e biologia geral dos crocodilianos do Brasil. In A. F. Barreto-Lima, M. R. D. Santos & Y. C. Nóbrega (Eds.), *Tratado de Crocodilianos do Brasil* (pp. 60–93). Instituto Marcos Daniel.

Roberto, I. J., Fedler, M. T., Hrbek, T., Farias, I. P., & Blackburn, D. C. (2021). The taxonomic status of Florida *Caiman*: A molecular reappraisal. *Journal of Herpetology*, *55*(3), 279–284.

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

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. https://doi.org/10.1098/rspb.2014.2490

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. https://doi.org/10.26879/657

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. https://doi.org/10.1038/ncomms2940

Scheyer, T. M., Hutchinson, J. R., Strauss, O., Delfino, M., Carrillo-Briceño, J. D., Sánchez, R., & Sánchez-Villagra, M. R. (2019). Giant extinct caiman breaks constraint on the axial skeleton of extant crocodylians. *eLife*, *8*, e49972. https://doi.org/10.7554/eLife.49972

Schmidt, K. P. (1928). Notes on South American caimans. *Field Museum of Natural History, Zoological Series*, *12*, 205–231.

Schneider, J. G. (1801). *Historiae Amphibiorum naturalis et literariae. Fasciculus secundus continens Crocodilos, Scincos, Chamaesauras, Boas. Pseudoboas, Elapes, Angues. Amphisbaenas et Caecilias*. Frommanni.

Sereno, P. C., & Larsson, H. C. E. (2009). Cretaceous crocodyliforms from the Sahara. *ZooKeys*, *28*, 1–143. https://doi.org/10.3897/zookeys.28.325

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.

Spix, J. B. von. (1825). *Animalia nova sive species nova lacertarum quas in itinere per Brasiliam annis MDCCCXVII-MDCCCXX jussu et auspicius Maximiliani Josephi I Bavariae Regis suscepto collegit et descripsit Dr. J. B. de Spix*. T. O. Weigel; F. S. Hübschmanni.

Solórzano, A., Rincón, A. D., Cidade, G. M., Núñez–Flores, M., & Sánchez, L. (2018). Early Miocene alligatoroids (Crocodylia) from the Castillo Formation, northwestern Venezuela. *Paleobiodiversity and Paleoenvironments*, *99*, 241–259. https://doi.org/10.1007/s12549-018-0332-5

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

Souza-Filho, J. P., Souza, R. G., Hsiou, A. S., Riff, D., Guilherme, E., Negri, F. R., & Cidade, G. M. (2018). A new caimanine (Crocodylia, Alligatoroidea) species from the Solimões Formation of Brazil and the phylogeny of Caimaninae. *Journal of Vertebrate Paleontology*, *38*(5), e1528450. https://doi.org/10.1080/02724634.2018.1528450

Souza-Filho, J. P., Guilherme, E., Toledo, P. M., Carvalho, I. S., Negri, F. R., Maciente, A. A. R., Cidade, G. M., Lacerda, M. B. S., & Souza, L. G. (2020). On a new *Melanosuchus* species (Alligatoroidea: Caimaninae) from Solimões Formation (Eocene–Pliocene), northern Brazil, and evolution of Caimaninae. *Zootaxa*, *4894*(4), 561–593. https://doi.org/10.11646/zootaxa.4894.4.5

Stocker, M. R., Brochu, C. A., & Kirk, E. C. (2021). A new caimanine alligatorid from the Middle Eocene of Southwest Texas and implications for spatial and temporal shifts in Paleogene crocodyliform diversity. *PeerJ*, *9*, e10665. https://doi.org/10.7717/peerj.10665

Thorbjarnarson, J. (1992). *Crocodiles: An action plan for their conservation* (p. 136). IUCN.

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 Part A: Ecological Genetics and Physiology*, *309A*, 614–627. https://doi.org/10.1002/jez.492

Vasconcelos, B. D., Camurugi, F., Mudrek, J. R., Brandão, R. A., & Santana, D. J. (2025). Rivers and spatial distance are drivers of genetic diversity in the South American dwarf caiman (*Paleosuchus palpebrosus*). *Journal of Zoology*, *325*(1), 36–48. https://doi.org/10.1111/jzo.13226

Walter, J., Darlim, G., Massonne, T., Aase, A., Frey, E., & Rabi, M. (2022). On the origin of Caimaninae: Insights from new fossils of *Tsoabichi greenriverensis* and a review of the evidence. *Historical Biology*, *34*(4), 580–595. https://doi.org/10.1080/08912963.2021.1938563

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*, *3*(4), 3–595