



Phylogenetic nomenclature of *Notosuchia* (*Crocodylomorpha*; *Crocodyliformes*)

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
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Abstract

Notosuchia is a large and diverse clade of Mesozoic crocodyliforms that thrived in continental environments especially during the Cretaceous of Gondwana. This clade has been the focus of several phylogenetic studies that led to the consensus of two main topological arrangements, mostly differing in the position of the clade *Sebecidae*: the sebecosuchian and sebecian hypotheses. In this manuscript we review the main phylogenetic definitions of several clades of notosuchians in the context of these hypotheses. As a result, besides the clade names previously established under the ICPN/Phylocode (including registration in RegNum) by Ruiz *et al.* (2021) (*Notosuchia*, *Xenodontosuchia*, *Sphagesauria*, *Sphagesauridae*) and Darlim *et al.* (2021a) (*Baurusuchia*, *Baurusuchidae*, *Baurusuchinae*, *Pissarrachampsinae*), eleven clade names have

been registered and are defined in this contribution. Ten of these represent converted clade names (*Uruguaysuchidae*, *Mahajangasuchidae*, *Peirosauridae*, *Itasuchidae*, *Ziphosuchia*, *Sphagesaurinae*, *Caipirasuchinae*, *Sebecia*, *Sebecosuchia*, and *Sebecia*), while one represents a new clade name (*Peirosauria*). Furthermore, the definition of *Xenodontosuchia* is emended (unrestricted emendation) so that the name can be used in the context of a wider array of topologies.

Key words: *Ziphosuchia*, *Sebecia*, *Xenodontosuchia*, *Peirosauria*, *Sphagesauria*, definition, registration

Introduction

Notosuchia is one of the most diverse clades of *Crocodylomorpha*, including more than 90 currently recognized species (see Recognized Species List). This clade of crocodyliforms thrived during the Cretaceous of Gondwana (e.g., Sereno and Larsson 2009; O'Connor *et al.* 2010; Pol *et al.* 2014; Darlim *et al.* 2021a), in particular during the Late Cretaceous of southern Gondwana, where regions of hyperdiversity have been recognized (Pol and Lardi 2015; however, see de Celis *et al.* 2021).

Notosuchia was established in the early contribution of Gasparini (1971) at the rank of Infraorder to include taxa (*Notosuchus terrestris*, *Uruguaysuchus aznarezi*, *Araripesuchus gomesii* and other taxa now considered *nomina dubia*) that differed widely in their anatomy compared to other fossil crocodyliforms. Contributions centered on notosuchians remained few until the early 2000's (e.g., Gasparini 1982; Gasparini *et al.* 1991; Gomani 1997), when there was a great pulse in descriptions of new taxa, many of which had very peculiar morphologies (e.g., Buckley *et al.* 2000; Martinelli 2003). The increased interest in notosuchians was also accompanied by the widespread use of cladistic methods that resulted in several analyses centered on the group (Ortega *et al.* 2000; Sereno *et al.* 2001; Carvalho *et al.* 2004; Pol 2005). These early analyses recognized *Notosuchia* as a monophyletic group, the sister group of *Neosuchia*, with several unique cranial and postcranial synapomorphies. However, there was a certain degree of disagreement about the position of the genus *Araripesuchus*, which was inferred either as a basal neosuchian closely related to *Peirosauridae* (e.g., Turner 2006) or as the sister group of *Ziphosuchia* (e.g., Pol and Apesteguía 2005). The conflict was later settled during the early 2010's, as new analyses consistently inferred both peirosaurids and *Araripesuchus* + allied taxa (*Uruguaysuchus* and *Anatosuchus*) as notosuchians, forming the sister clade of *Ziphosuchia* (e.g., Turner and Sertich 2010; Soto *et al.* 2011; Pol *et al.* 2012).

Subsequent years have been marked by the discovery and description of several new taxa, further expanding our knowledge of the clade (e.g., Sertich and O'Connor 2014; Sellés *et al.* 2020), but the greater increase in number of species has been seen in two particular notosuchian clades: *Sphagesauria* (e.g., Pol *et al.* 2014; Martinelli *et al.* 2018; Pinheiro *et al.* 2021; Ruiz *et al.* 2021) and *Baurusuchia* (e.g., Montefeltro *et al.* 2011; Nascimento and Zaher 2010; Godoy *et al.* 2014; Darlim *et al.* 2021a). The description of new taxa and their incorporation to new or preexisting phylogenetic datasets has led to further consensus on notosuchian phylogenetic hypotheses (e.g., the monophyly of the sphagesaurians, the overall internal topology of *Sphagesauria* and *Baurusuchia*), but has highlighted the major problem among the different studies: the position of *Sebecidae*. As such, two sets of phylogenetic hypotheses for *Notosuchia* can be recognized: the classical "sebecosuchian hypothesis" (Fig. 1), in which sebecids are closely related to baurusuchians and nested within *Ziphosuchia* (e.g., Lardi *et al.* 2018; Sellés *et al.* 2020; Bravo *et al.* 2021), or the "sebecian hypothesis" (Fig. 2), in which sebecids form a clade with peirosaurids and other taxa closely related to them (*Itasuchidae* and *Mahajangasuchidae*) (Fig. 4A, B). In the case of the latter hypothesis, the clade *Sebecia* would also represent the sister group of all remaining notosuchians (Montefeltro *et al.* 2013; Pinheiro *et al.* 2018; Geroto and Bertini 2019; Ruiz *et al.* 2021).

Phylogenetic definitions have been widely used in notosuchian phylogenetics, with the contribution of Sereno *et al.* (2001) being one of the precursors to establishing a definition for *Notosuchia* that has been widely accepted in most subsequent contributions (e.g., Turner and Sertich 2010; Pol *et al.* 2012, 2014; Lardi *et al.* 2015; Godoy *et al.* 2016). Later, Carvalho *et al.* (2004) defined several names as designating nodes on their phylogenetic hypothesis, but their topology has not been corroborated in subsequent works, and as such, most of these definitions were not considered in following works. In spite of the definitions of some names for clades of basal notosuchians by Sereno and Larsson (2009) and for several clades among baurusuchians by Montefeltro *et al.* (2011), most authors have relied on depicting the groups in the cladograms instead of using formal definitions (e.g., Turner and Sertich 2010; Pol *et al.* 2014; Sellés *et al.* 2020).

The recent formal implementation of the *PhyloCode* (Cantino and de Queiroz 2020) and its application on subsequent contributions dealing with notosuchians (Ruiz *et al.* 2021; Darlim *et al.* 2021a) has caused a sudden interest in defining the names of major clades of *Notosuchia*, even though strict terminology related to the *PhyloCode* was not used (Pinheiro *et al.* 2018, 2021; Geroto and Bertini 2019; Fernández Dumont *et al.* 2020). Given this interest, and for the sake of a unified nomenclature for clades among notosuchians, the present contribution focuses on reviewing the best known notosuchian clades and defining their names according to the *PhyloCode* standards. This joint effort intends to reach a certain level of *consensus* when referring to major clades within *Notosuchia* to prevent future misuses.

Methods

The set of rules in the *PhyloCode* (2020) for establishing clade names and their requirements are followed in this paper. However, when a particular point or topic needs to be further explained, it will be done for each clade individually.

Regarding the names for the clades, whenever possible (e.g., *Peirosauridae*) names that have previously been established and widely used in notosuchian literature are adopted here and, if necessary, converted (i.e., establishing a pre-existing name in accordance with the rules of the *PhyloCode*). Although the same rules do not apply in the *PhyloCode* and in the *International Code of Zoological Nomenclature (ICZN)*, if some internal nodes are named within a previously recognized clade, and if that clade has been given a family name (i.e., suffix *-idae*), the successive internal clades are named respecting the root of the Family name and using a less inclusive category suffix (e.g., *-inae*). We are aware that the categories and the names used in the two systems are not equivalent, but the suffixes used by the *ICZN* are widely used for clade names among crocodylomorphs and their use helps the reader to have a general sense of relative inclusiveness among the clades.

When dealing with clade names, if a prior definition exists but it does not conform to the *PhyloCode* standards (e.g., *Ziphosuchia* of Ortega *et al.* 2000), whenever possible that definition and its specifiers are adopted in order to maintain the original clade conceptualization. The selection of specifiers is based on either the historical use of the taxon (e.g., *Uruguaysuchus aznarezi* Rusconi 1933), the relative completeness of fossils (e.g., *Araripesuchus gomesii* Price 1959), or both (e.g., *Notosuchus terrestris* Woodward 1896). When converting or establishing clade names based on the genus names of included species, we follow the Article 11.10 of the *PhyloCode* (Cantino and de Queiroz 2020), which requires the inclusion of the type species of those genera as internal specifiers. However, in some cases those type species are poorly represented by fossil specimens or the fossils are not easily accessible and are thus not optimal specifiers. Therefore, they have been supplemented using proxies, as suggested by the editor (de Queiroz, pers. comm., June 2024). A proxy is not an additional specifier; instead, it can be substituted for the specifier for which it is a proxy (to apply a phylogenetic definition) in the context of phylogenies in which the specifier is absent, provided that the proxy is thought to be more closely related to its specifier than to every other specifier included in the definition. The type species at issue are *Uruguaysuchus aznarezi* Rusconi 1933 (*Uruguaysuchidae*), *Peirosaurus torminni* Price 1955 (*Peirosauria*, *Peirosauridae*), and *Itasuchus jesuinoi* Price 1955 (*Itasuchidae*). The type specimen of *Uruguaysuchus aznarezi* is deposited in a private collection which is difficult to access for its study, an issue that has been partially solved with the report of an incomplete additional specimen (Soto *et al.* 2011). Thus, when this species is used as an internal specifier it will be accompanied by the proxy *Araripesuchus gomesii* Price 1959. This taxon is known from two specimens, housed in recognized institutions, and the referred specimen is represented by an almost complete individual. Similar cases are those of *Peirosaurus torminni* Price 1955 and *Itasuchus jesuinoi* Price 1955. The type specimen of *Peirosaurus* consists of an isolated premaxilla (as the rest of the postcranial skeleton is currently lost) and even has been considered a potential *nomen dubium* (Martinelli *et al.* 2012). When *Peirosaurus* must be included as an internal specifier it will be accompanied by two proxies: *Lomasuchus palpebrosus* Gasparini, Chiappe and Fernández 1991 (the second peirosaurid recognized, represented by a well-preserved skull and included in every phylogenetic study dealing with the group), and *Uberabasuchus terrificus* Carvalho, Ribeiro and Avila 2004 (the type specimen includes a complete skull and well-preserved postcranial skeleton; and it was suggested as putative synonym of *Peirosaurus* [Martinelli *et al.* 2012]). Finally, the type specimen of *Itasuchus jesuinoi* Price 1955 consists only of a partial mandible. Therefore, we accompany the use of *Itasuchus* in most cases with the proxy *Pepesuchus deiseae* Campos, Oliveira, Figueiredo,

Riff, Azevedo, Carvalho and Kellner 2011, which is known from various specimens that include several regions of its anatomy and have been adequately published (Campos *et al* 2011; Geroto and Bertini 2019).

The registration numbers (in RegNum; *PyloCode* 2020, Art. 7.2.e) of all clade names treated in this contribution are provided for both previously established clade names and newly erected ones. When represented graphically (Figs. 1–6) maximum-clade definitions are depicted as rootward-pointing arrows and minimum-clade definitions as dots, according to the conventions proposed by Sereno (2005).

As mentioned above (see Introduction) the main conflict in recent notosuchian phylogenetics is centered around the position of *Sebecidae*, causing two sets of topologies: the sebecian and the sebecosuchian hypotheses (Fig. 1, 2). This means that some definitions are only applicable in one case or the other (but not both). If so, this is explicitly mentioned for such clades, and when establishing a new clade name its use among different sets of topologies is emphasized.

Phylogenetic Nomenclature

Notosuchia Gasparini 1971 [Ruiz *et al.* 2021]

Registration number: 417 (Ruiz *et al.* 2021).

Definition: “The most inclusive clade containing *Notosuchus terrestris* Woodward 1896, but not *Crocodylus niloticus* Laurenti, 1768 (*Crocodylia*). This is a maximum-clade definition” (Ruiz *et al.* 2021: 281).

Etymology: Based on the genus name *Notosuchus* Woodward 1896. Although not specifically stated by Woodward in the original publication, the name *Notosuchus* is based on the ancient Greek words νότος (nótos), which translates as “south”. The second part of the name derives from the word “Σοῦχος” (Soukhos, Souchos), which refers to an Egyptian crocodile-headed god (Sebek or Sobk). However, a recent contribution by Young *et al.* (2024) mentions that the name Suchus might have been derived from a name given to an undivided tamed crocodile (Zouxos).

Reference Phylogeny: Fig. 6 of Ruiz *et al.* (2021), as originally designated. Additional reference phylogenies are Pol *et al.* (2014: Fig. 31) and Fernández Dumont *et al.* (2020: Fig. 7). See also Figs. 1 and 2.

Composition: Based on the reference phylogenies, *Notosuchia* includes *Uruguaysuchidae* Gasparini 1971; *Mahajangasuchidae* Sereno and Larsson 2009; *Peirosauridae* Gasparini 1982; *Sebecidae* Simpson 1937; *Ziphosuchia* Ortega, Gasparini, Buscalioni and Calvo 2000; and some unstable taxa in some of the reference phylogenies (e.g., *Neuquensuchus*, *Candidodon*).

Comments: The name *Notosuchia* was originally used by Gasparini (1971) in her review of the cranial material of *Notosuchus terrestris* to include this species, *Araripesuchus gomesii* Price 1959, *Uruguaysuchus aznarezi* Rusconi 1933, and *Sphagesaurus huenei* Price 1950. However, the composition expanded throughout the years as additional taxa were described. Although Sereno *et al.* (2001) proposed a branch-based (maximum-clade) definition for the group, it was not initially followed by some researchers (e.g., Carvalho *et al.* 2004), whereas others preferred not to label the group on their phylogenetic hypotheses (e.g., Pol 2005; Turner 2006). In particular, hypotheses of the early 2000’s differ from Gasparini’s (1971) original boundaries of the group in that members of the genus *Araripesuchus* Price 1950 and the family *Peirosauridae* were inferred to be members of *Neosuchia* rather than its sister group *Notosuchia* (Pol *et al.* 2004; Pol 2005; Turner 2006; Leardi and Pol 2009). However, Pol and Apesteguía (2005) placed *Araripesuchus* as the most basal notosuchian clade and later Turner and Sertich (2010) placed both peirosaurids and *Araripesuchus* within *Notosuchia* (*sensu* Sereno *et al.* 2001). Turner and Sertich (2010) adopted Sereno *et al.*’s (2001) branch-based definition of *Notosuchia*. These results were consistently inferred in several analyses dealing with notosuchian phylogeny (Pol *et al.* 2012, 2014; Leardi *et al.* 2015; Godoy *et al.* 2016; Fernández Dumont *et al.* 2020; Bravo *et al.* 2021). Despite the different phylogenetic placements of clades such as *Peirosauridae* and *Sebecidae*, a clade including *Notosuchus terrestris* Woodward 1896 and multiple South American and African taxa is consistently inferred in phylogenetic analyses. This led to the formal *PhyloCode* definition of *Notosuchia* by Ruiz *et al.* (2021), converting the original definition by Sereno *et al.* (2001) into a maximum-clade definition.

Diagnostic apomorphies: Gasparini (1971) originally recognized the group and diagnosed them as crocodyliforms with anteroposteriorly short snouts and skulls, laterally placed orbits, terminal nares, hypertrophied teeth (either on the maxilla or premaxilla), and a reduced number of teeth. Most of these characters have been shown to be

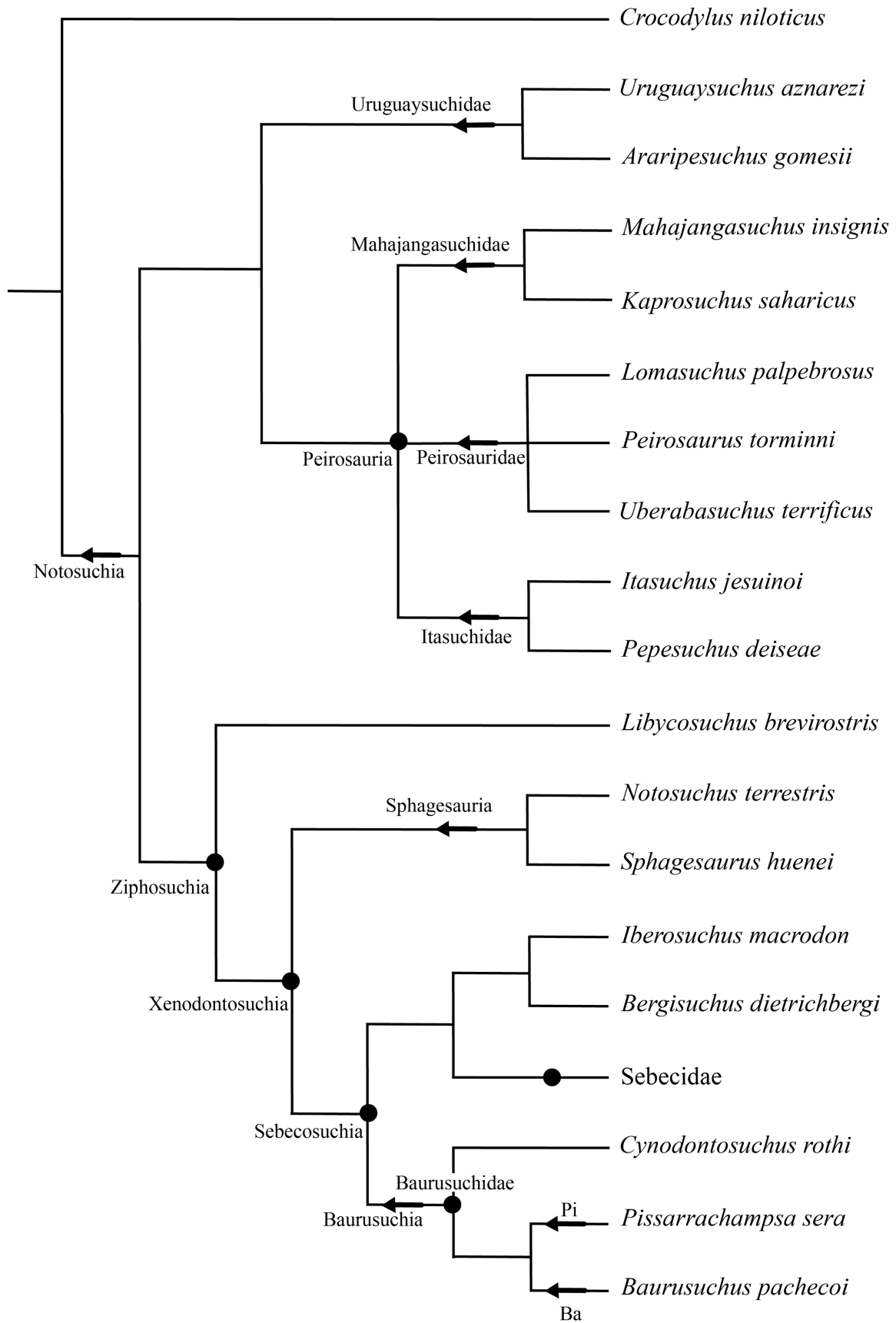


FIGURE 1. Simplified cladogram depicting the major scale phylogenetic relationships and named clades under the sebecosuchian hypothesis *sensu* Pol *et al.* (2014). Abbreviations: Pi, *Pissarrachampsinae*; Ba, *Baurusuchinae*.

distributed among many non-mesoeucrocodylian crocodyliforms (e.g., Clark 1994), but *Notosuchia* has remained monophyletic in most recent analyses (e.g., Sereno *et al.* 2001; Pol 2005; Turner and Sertich 2010). The characters that support *Notosuchia* are variable, depending on the preferred phylogenetic hypothesis some monophyletic groups can be included or excluded from the clade (e.g., Larsson and Sues 2007; Sereno and Larsson 2009) or their phylogenetic positions substantially changed (e.g., Pinheiro *et al.* 2018; Ruiz *et al.* 2021), altering the character optimizations at the base of *Notosuchia*. Despite these differences in phylogenetic hypotheses, *Notosuchia* is a well-supported clade, diagnosed by several cranial and postcranial synapomorphies (Turner and Sertich 2010; Pol *et al.* 2012, 2014; Leardi *et al.* 2015; Pinheiro *et al.* 2018). The most commonly inferred synapomorphies among different studies are: the presence of numerous neurovascular foramina on the lateral surfaces of the premaxilla and maxilla (Turner and Sertich 2010; Pinheiro *et al.* 2018); a rounded, flat and wide retroarticular surface with its surface exposed dorsomedially (Pol and Apesteguía 2005; Turner and Sertich 2010); the insertion area for the *M. pterigoideus* extending onto the lateral surface of the angular (Pol and Apesteguía 2005; Turner and Sertich 2010); major axis of the quadrate oriented vertically (Pol and Apesteguía 2005); rod-like morphology of the neural spines of some cervical vertebrae (Pol 2005); gradual migration of the parapophyses on the anterior dorsal vertebrae (Pol *et al.* 2012; Leardi *et al.* 2015); a wide distal region of the scapular blade (Buckley and Brochu 1999); a deep depression on the posterior surface of the proximal end of the humerus (Pol *et al.* 2012); postacetabular process of the ilium horizontally directed (Pol *et al.* 2012); sigmoidal anterior margin of the femur (Buckley and Brochu 1999); among several others.

***Uruguaysuchidae* Gasparini 1971 [Leardi *et al.*, this contribution], converted clade name**

Registration number: 986.

Definition: The most inclusive clade containing *Uruguaysuchus aznarezi* Rusconi 1933 (proxy: *Araripesuchus gomesii* Price 1959) but not *Baurusuchus pachecoi* (Price 1945), *Peirosaurus torminni* Price 1955 (proxy: *Lomasuchus palpebrosus* Gasparini, Chiappe and Fernández 1991), *Mahajangasuchus insignis* Buckley and Brochu 1999, *Notosuchus terrestris* Woodward 1896, and *Crocodylus niloticus* Laurenti 1768. This is a maximum-clade definition. The proxies are not specifiers but can be used in place of the specifiers for which they are proxies on phylogenies from which those specifiers are absent (see Methods).

Etymology: The name was proposed by Gasparini (1971), based on that of the included taxon *Uruguaysuchus aznarezi* Rusconi 1933.

Reference phylogeny: Fig. 7 of Fernández Dumont *et al.* (2020) (primary), and Fig. 15 of Soto *et al.* (2011). See also Figs. 1 and 2.

Composition: Based on the reference phylogenies, *Uruguaysuchidae* includes all the species of the genus *Araripesuchus* (i.e., *Araripesuchus gomesii* Price 1959; *Araripesuchus wegneri* Buffetaut and Taquet 1979; *Araripesuchus patagonicus* Ortega, Gasparini, Buscalioni and Calvo 2000; *Araripesuchus buitreaensis* Pol and Apesteguía 2005; *Araripesuchus tsangatsangana* Turner 2006), *Anatosuchus minor* Sereno, Sidor, Larsson and Gado 2003, and *Uruguaysuchus aznarezi* Rusconi 1933. *Araripesuchus rattoides* Sereno and Larsson 2009 has been inferred to be nested in this clade by Sereno and Larsson (2009), but it has not been included in the data matrices of the reference phylogenies.

Comments: The group was originally erected as a family by Gasparini (1971), to include three basal notosuchians: the two species of the genus *Uruguaysuchus* (*U. aznarezi* Rusconi 1933; and *U. terrai* Rusconi 1933, later considered as a junior synonym of *U. aznarezi* by Soto *et al.* [2011]) and *Araripesuchus gomesii* Price 1959. The idea of this group was later abandoned, as in most cladistic analyses of the early 2000s (Pol 2005; Pol and Apesteguía 2005; Turner 2006) members of the genus *Araripesuchus* were found as basal neosuchians and *Uruguaysuchus* was placed as either a basal or stem ziphosuchian. Sereno and Larsson (2009) were the first to infer a sister group relationship between *Uruguaysuchus* and the species of *Araripesuchus* (*Simosuchus clarki* was also included in this group), although they did not use the name *Uruguaysuchidae*. *Uruguaysuchidae* was inferred, but with low support values, and was labeled as such in the contribution of Soto *et al.* (2011), in which they reviewed and described additional material of *Uruguaysuchus aznarezi*. This relationship has been corroborated in several more recent analyses (Pol and Powell 2011; Pol *et al.* 2012, 2014; Leardi *et al.* 2015, 2018; Ruiz *et al.* 2021; Fernández Dumont *et al.* 2020; Pinheiro *et al.* 2018, 2021). It is worth mentioning that the phylogenetic placement of the clade *Uruguaysuchidae* varies among different topologies, as it is found to form a clade with peirosaurids and mahajangasuchids in the

sebecosuchian hypothesis (e.g., Pol *et al.* 2014; Fernández Dumont *et al.* 2020; see Fig. 1) or as the sister group of *Xenodontosuchia* (sphagesaurians, baurusuchians, and some species taxa such as those included in *Simosuchus*, *Libycosuchus*, *Malawisuchus*) in the sebecian hypothesis (e.g., Ruiz *et al.*, 2021; see Fig. 2).

Diagnostic apomorphies: Gasparini (1971) originally characterized uruguaysuchids as crocodyliforms that lacked palatal fenestrae (to separate them from *Notosuchus* and closely related forms) and several other traits that were later found to be widely distributed among crocodyliforms (e.g., anteriorly facing nares, a notch between the premaxilla and maxilla to house a hypertrophied mandibular tooth). Later analyses inferred two unambiguous synapomorphies for *Uruguaysuchidae*: surangular forming one third of the glenoid fossa and a trough-shaped dorsal surface of the mandibular symphysis (Soto *et al.* 2011). Ten years later, Fernández Dumont *et al.* (2021) reviewed the phylogeny of this clade among notosuchians and inferred nine unambiguous synapomorphies, among which those originally listed by Soto *et al.* (2011) were not included.

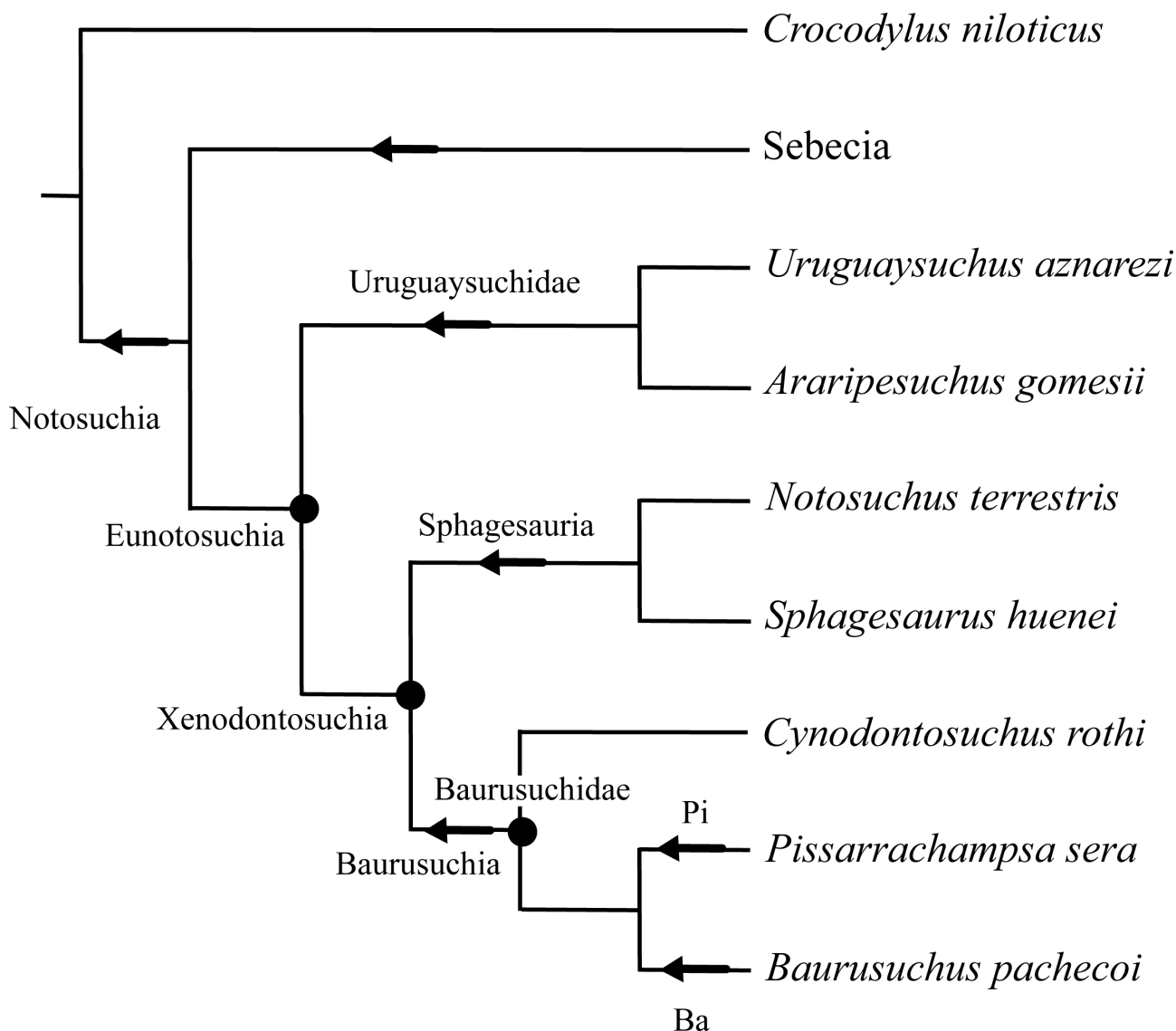


FIGURE 2. Simplified cladogram depicting the major scale phylogenetic relationships and named clades under the sebecian hypothesis *sensu* Ruiz *et al.* (2021). Abbreviations: Pi, *Pissarrachampsinae*; Ba, *Baurusuchinae*.

Peirosauria Leardi *et al.*, this contribution, new clade name

Registration number: 987.

Definition: The least inclusive clade containing *Mahajangasuchus insignis* Buckley and Brochu 1999, *Peirosaurus torminni* Price 1955, *Lomasuchus palpebrosus* Gasparini, Chiappe and Fernández 1991, and *Itasuchus*

jesuinoi Price 1955 provided that it does not include *Sebecus icaeorhinus* Simpson 1937. This is a minimum-clade definition with a qualifying clause.

Etymology: Derived from the clade name *Peirosauridae* (see below), which applies to the most diverse group of crocodyliforms included in *Peirosauria*. Additionally, the suffix “sauria” (from the Ancient Greek “σαῦρος” [sauros] meaning “lizard”) has been used recently to name other notosuchian clades (e.g., *Sphagesauria* [Pinheiro *et al.* 2021; Ruiz *et al.* 2021]).

Reference phylogeny: Fig. 31 of Pol *et al.* (2014) (primary); see also Sertich and O’Connor (2014: Fig. 7) and Fernández Dumont *et al.* (2020: Fig. 7), and Figs 1 and 3. In the reference phylogenies two relevant taxa are not included, *Peirosaurus torminni* Price 1955 and *Itasuchus jesuinoi* Price 1955. *Itasuchus* forms a clade with *Stolokrosuchus* in most recent phylogenetic analyses (Pinheiro *et al.*, 2018, 2023; Ruiz *et al.* 2021; Martins *et al.* 2023, while *Peirosaurus* forms a clade with *Lomasuchus* and other closely related taxa (Geroto and Bertini, 2019).

Composition: Our definition of *Peirosauria* includes three major clades: *Mahajangasuchidae*, *Itasuchidae* and *Peirosauridae*. The placement of the species level taxon *Stolokrosuchus lapparenti* Larsson and Gado 2000 varies among different recent phylogenetic hypothesis, either as the sister group of *Peirosauridae* + *Mahajangasuchidae* (e.g., Pol *et al.* 2014; Leardi *et al.* 2015; Fernández Dumont *et al.* 2020) or among peirosaurids (Sertich and O’Connor 2014).

Comments: *Peirosauria* is a newly erected clade in this contribution that reflects the inferred close relationship between peirosaurids, itasuchids and mahajangasuchids. This sister group relationship was inferred even when these two clades were hypothesized to be outside of *Notosuchia* (e.g., Turner, 2006) and, in the context of *Notosuchia*, was first found by Turner and Sertich (2010) and then in several subsequent studies (e.g., Pol *et al.* 2012; Sertich and O’Connor 2014; Leardi *et al.* 2015). It is worth noting that even though the clade name is only applicable under the sebecosuchian hypothesis, a similar clade is also inferred within the sebecian hypothesis with the difference that the sebecids are also part of the clade (e.g., Sereno and Larsson 2009; Montefeltro *et al.* 2013, Pinheiro *et al.* 2018, Geroto and Bertini 2019; see also Fig. 4). Thus, there is wide consensus on the monophyly of a group including peirosaurids, itasuchids, and mahajangasuchids, but not uruguaysuchids. *Peirosauria* is placed as the sister group of *Uruguaysuchidae* in several analyses. A qualifying clause excluding *Sebecus icaeorhinus* has been added to avoid total or partial overlap with the clade *Sebecia* (as defined below). *Peirosauria* is a useful name for the clade composed of mahajangasuchids, peirosaurids, and itasuchids on phylogenies where sebecids are not part of this clade (see below).

Diagnostic apomorphies: Peirosaurians are diagnosed by several synapomorphies, mostly cranial ones, including: short and broad retroarticular process; deep and anteriorly tapering mandibular symphysis; lack of enlarged maxillary neurovascular foramina; maxillary teeth in discrete alveoli; sculpted region dorsal to the maxillary toothrow; postorbital process of the jugal located in the anteroposterior middle of the jugal body; paroccipital process well-projected laterally to the cranioquadrate passage; quadrate body distinctly projected ventrally to the otoccipital-quadrate suture; a robust splenial posterior to the mandibular symphysis; a complex suture between the surangular and the dentary; among others (see Turner and Sertich 2010 for a more extensive list, including ambiguous synapomorphies).

***Mahajangasuchidae* Sereno and Larsson 2009 [Leardi *et al.*, this contribution], converted clade name**

Registration number: 988.

Definition: The most inclusive clade containing *Mahajangasuchus insignis* Buckley and Brochu 1999 but not *Uruguaysuchus aznarezi* Rusconi 1933 (proxy: *Araripesuchus gomesii* Price 1959), *Peirosaurus torminni* Price 1955 (proxies: *Lomasuchus palpebrosus* Gasparini, Chiappe and Fernández 1991 and *Uberabasuchus terrificus* Carvalho, Ribeiro and Avila 2004), *Itasuchus jesuinoi* Price 1955 (proxy: *Pepesuchus deiseae* Campos, Oliveira, Figueiredo, Riff, Azevedo, Carvalho and Kellner 2011), *Simosuchus clarki* Buckley *et al.* 2000, *Notosuchus terrestris* Woodward 1896, *Baurusuchus pachecoi* Price 1945, and *Sebecus icaeorhinus* Simpson 1937. This is a maximum-clade definition. The proxies are not specifiers but can be used in place of the specifiers for which they are proxies on phylogenies from which those specifiers are absent (see Methods).

Etymology: Based on the name of the first described member of the clade, *Mahajangasuchus insignis* (Sereno and Larsson 2009).

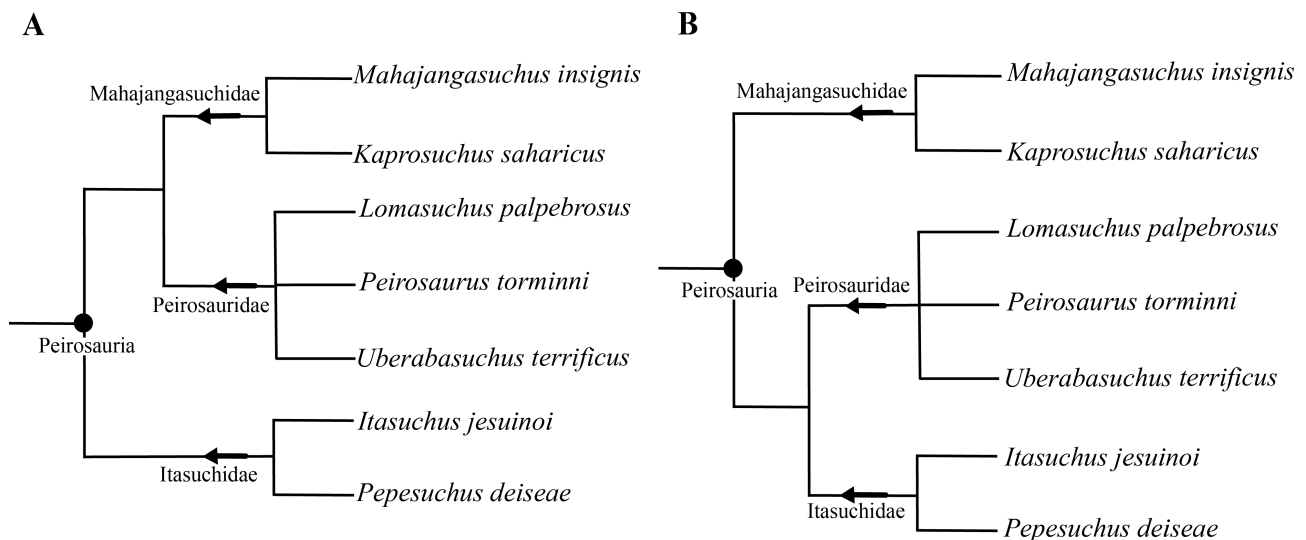


FIGURE 3. Different topological variations within *Peirosauria* (A) *sensu* Pol *et al.* (2014), Fernández Dumont *et al.* (2020) *Peirosauria*; (B) *sensu* Nicholl *et al.* (2021). In these datasets *Itasuchidae* is represented by *Stolokrosuchus* (see *Itasuchidae*).

Reference phylogeny: Fig. 45 of Sereno and Larsson (2009; primary) and in Fig. 11 of Pinheiro *et al.* (2018). See also Figs. 1; 3A, B, and 4A, B.

Composition: *Mahajangasuchus insignis* Brochu and Buckley 1999 and *Kaprosuchus saharicus* Sereno and Larsson 2009. *Anatosuchus minor* may also be part of this clade (see Comments).

Comments: The name *Mahajangasuchidae* was proposed by Sereno and Larsson (2009) for the clade formed by *Mahajangasuchus insignis* Brochu and Buckley 1999 and *Kaprosuchus saharicus* Sereno and Larsson 2009. Sereno and Larsson (2009) established this group with a branch-based definition considering that the relationships of basal metasuchians and notosuchians were poorly established, and the discovery of new taxa could broaden the taxonomic content of the group. Subsequent contributions and analyses (e.g., Turner and Sertich 2010; Pol *et al.* 2012, 2014) did not find any new or known taxa to be included in *Mahajangasuchidae*, thus, it remained a small and distinctive group among notosuchians, including solely *Mahajangasuchus insignis* and *Kaprosuchus saharicus*. Andrade *et al.* (2011) inferred *Anatosuchus minor* as the sister-clade of *Mahajangasuchus insignis* and *Kaprosuchus saharicus*, and as such, under our definition, *Anatosuchus* would be included in *Mahajangasuchidae* under this phylogenetic hypothesis (while it is placed as an uruguaysuchid under phylogenetic analyses).

The definition provided here for *Mahajangasuchidae* differs from previous phylogenetic definitions given for the name (which are not valid under the rules of the ICPN). The original definition (Sereno and Larsson 2009) included several notosuchians (*Notosuchus terrestris*, *Simosuchus clarki*, *Araripesuchus gomesii*, *Baurusuchus pachecoi*, and *Peirosaurus torminni*) along with other neosuchian taxa (*Goniopholis crassidens*, *Pholidosaurus schaubergensis*, *Crocodylus niloticus*) as external specifiers. Turner and Sertich (2010) amended the phylogenetic definition of the clade, adding also *Trematochampsia taqueti* Buffetaut 1974 to the set of external specifiers, given that its relationships were unclear among mesoeucrocodylians. However, based on a re-examination of the materials referred to the taxon, Meunier and Larsson (2018) considered *Trematochampsia taqueti* as a *nomen dubium*. Finally, several recent analyses that support the sebecian hypothesis (Pinheiro *et al.* 2018, 2021; Geroto and Bertini 2019) place *Sebecidae* as the sister group of *Mahajangasuchidae*. Using the original and the amended definition of *Mahajangasuchidae* would include *Sebecidae* in the group under that hypothesis, as no sebecid was included as an external specifier. Thus, to avoid conflict we modified those definitions by: 1) including the proxies *Lomasuchus palpebrosus* and *Uberabasuchus terrificus*, which are included in most recent datasets, for the external specifier *Peirosaurus torminni* and the proxy *Pepesuchus deiseae* for the external specifier *Itasuchus jesuinoi*; 2) removing *Trematochampsia taqueti* Buffetaut 1974 from the list of external specifiers; 3) incorporating *Sebecus icaeorhinus* as an external specifier; and, 4) removing non-notosuchian taxa as external specifiers, as *Mahajangasuchidae* has been consistently inferred as a notosuchian clade.

Diagnostic apomorphies: Mahajangasuchids have some unusual features among crocodyliforms, including: fused nasals; an articular fossa for the posterior palpebral on the posterolateral surface of the postorbital; posterolateral border of the squamosal projected dorsally (“horn-like” projections); posterior process of the jugal steeply projected posteroventrally and bears a fossa at the base of this process; deep mandibular symphysis; and several autapomorphies in the palate (choanal septum with an anterior footplate; pterygoid with its choanal wall evaginated and its ventral edge expanded), among others. Mahajangasuchids are usually very well-supported in most analyses due to their highly modified anatomy, resulting in a large number of both unambiguous and ambiguous synapomorphies (Turner and Sertich 2010).

***Peirosauridae* Gasparini 1982 [Leardi *et al.*, this contribution], converted clade name**

Registration number: 989.

Definition: The most inclusive clade containing *Peirosaurus torminni* Price 1955 (proxies: *Lomasuchus palpebrosus* Gasparini, Chiappe and Fernández 1991 and *Uberabasuchus terrificus* Carvalho, Ribeiro and Avila 2004) but not *Uruguaysuchus aznarezi* Rusconi 1933, *Mahajangasuchus insignis* Buckley and Brochu 1999, *Itasuchus jesuinoi* Price 1955 and *Sebecus icaeorhinus* Simpson 1937. This is a maximum-clade definition. The proxies are not specifiers but can be used in place of the specifier for which they are proxies on phylogenies from which that specifier is absent (see Methods).

Etymology: Based on the name of the type genus *Peirosaurus* Price 1955 (Gasparini 1982).

Reference phylogeny: Fig. 18 of Turner and Sertich (2010; primary); Fig. 24 of Pol *et al.* (2014), Fig. 11 of Pinheiro *et al.* (2018) and Fig. 9 of Geroto and Bertini (2019). See also Figs. 1, 3A, B and 4A, B.

Composition: The name *Peirosauridae* has been variably used in different hypotheses, and in this contribution we propose a definition and reference phylogeny according to which *Peirosauridae* includes a core of several non-ziphsuchian notosuchians that have been inferred in many studies as being closely related (e.g., *Peirosaurus torminni* Price 1955; *Lomasuchus palpebrosus* Gasparini, Chiappe and Fernández 1991; *Uberabasuchus terrificus* Carvalho, Ribeiro and Avila 2004; *Gasparinisuchus peirosauroides* Martinelli, Sertich, Garrido and Pradeiro 2012; *Montealtosuchus arrudacamposi* Carvalho, Vasconcellos and Tavares 2007; *Hamadasuchus rebouli* Buffetaut 1994) but excludes *Mahajangasuchidae* (e.g., *Mahajangasuchus*, *Kaprosuchus*), *Itasuchidae* (e.g., *Itasuchus*, *Pepesuchus*) and *Uruguaysuchidae* (e.g., *Uruguaysuchus*, *Araripesuchus*). Some additional taxa might be included in *Peirosauridae*, such as *Barcinosuchus gradilis* Leardi and Pol 2009 (Leardi and Pol 2009) and *Bayomesasuchus hernandezi* Barrios, Paulina-Carabajal and Bona 2016 (Barrios *et al.* 2016), but they have been included in relatively few datasets. Most results would exclude *Stolokrosuchus* from *Peirosauridae* (as defined in this contribution) except for those of Sertich and O’Connor (2014).

Comments: *Peirosauridae* was erected as a new family by Gasparini (1982) to include the taxon *Peirosaurus torminni* Price 1955 (originally included in *Sebecosuchia* by Price), to which she referred a new specimen from the Late Cretaceous of Argentina. Although it was not strictly named in the cladogram, *Peirosauridae* was first inferred in a phylogenetic analysis by Gasparini *et al.* (1991). Afterwards, *Peirosauridae* was recognized as a clade in several phylogenetic studies (e.g., Gasparini *et al.* 2006; Leardi and Pol 2009; Turner and Sertich 2010). However, no explicit phylogenetic definition was provided until the contribution of Larsson and Sues (2007), which did so in the context of the sebecian hypothesis. They defined *Peirosauridae* as all taxa more closely related to *U. terrificus* and *P. torminni* than to *S. icaeorhinus*, a definition that would expand the composition of the group to include other taxa not considered peirosaurs in the context of the alternative sebecosuchian hypotheses (Pinheiro *et al.* 2018; Ruiz *et al.* 2021). Later, Martinelli *et al.* (2012) redescribed the Argentinean specimen described by Gasparini (1982) and distinguished it taxonomically from *P. torminni*, coining the name *Gasparinisuchus peirosauroides*. Considering the fragmentary nature of the type specimen of *P. torminni*, Martinelli *et al.* (2012) considered a possible synonymy of *P. torminni* with *Uberabasuchus terrificus* based on the morphology and dentition of the premaxilla. Although Martinelli *et al.* (2012) maintained both taxa as valid, this synonymy was followed by some authors in subsequent contributions (Lio *et al.* 2016; Geroto and Bertini 2019). However, despite this possible synonymy (Marinho *et al.*, in prep.), until new information is available both taxa are here considered as valid. Later, Geroto and Bertini (2019) proposed a branch-based definition for a clade of similar composition but with a different name (*Peirosaurinae*) based on *Peirosaurus torminni* as the internal specifier. Geroto and Bertini (2019) justified this decision, instead

of using more complete taxa like *Hamadasuchus* and *Uberabasuchus*, based on the differences between some specimens of *Hamadasuchus* and the proposed synonymy between *Peirosaurus* and *Uberabasuchus*. Despite accepting this synonymy, both taxa were included as separate terminals in their analysis (also see above).

Regarding the definition adopted in this contribution, and considering that no study published in the last 10 years supports the synonymy between *Peirosaurus* and *Uberabasuchus*, the type species of the family is included as an internal specifier (*Phylocode* Art. 11.10). Additionally, considering the fragmentary nature of *Peirosaurus torminni* Price 1955 and the topological variation seen in the relationships of peirosaurids, two well-preserved taxa (*Lomasuchus palpebrosus* Gasparini, Chiappe and Fernández 1991 and *Uberabasuchus terrificus* Carvalho, Ribeiro and Avila 2004) are also listed as proxies (see Methods). These taxa have consistently been inferred as peirosaurids in most phylogenetic studies of Mesozoic crocodyliforms (see Reference Phylogenies). Finally, in order to provide further stability to the definition, taxa from the other closely related clades are included as external specifiers (*Uruguaysuchus aznarezi* Rusconi 1933; *Itasuchus jesuinoi* Price 1955; *Mahajangasuchus insignis* Buckley and Brochu 1999; and *Sebecus icaeorhinus* 1937 for the case of the sebecian hypotheses) and a maximum-clade definition is adopted.

Since its recognition in computer-assisted phylogenetic analyses, the exact composition of *Peirosauridae* has varied (e.g., Turner and Sertich 2010; Pol *et al.* 2012). However, since the recognition of a monophyletic *Mahajangasuchidae* (see above), peirosaurids have been restricted as the sister group of *Mahajangasuchidae* (Turner and Sertich 2010; Pol *et al.* 2012, 2014), *Itasuchidae* (Geroto and Bertini 2019; Ruiz *et al.* 2021) or a clade formed by *Mahajangasuchidae* + *Sebecidae* in some sebecian hypotheses (Pinheiro *et al.* 2018, 2023).

Diagnostic apomorphies: Gasparini (1982) erected the family *Peirosauridae* underscoring the differences between the Argentinean specimen then regarded as *Peirosaurus* (i.e., the holotype of *Gasparinisuchus*) and other Mesozoic crocodyliforms (e.g., five premaxillary teeth; an anteriorly-projecting premaxillary process; wide and relatively long snout; the lack of antorbital fenestra). Subsequently, Gasparini *et al.* (1991) identified derived features of the group, with one of them still being retained as an unambiguous synapomorphy of the group in most analyses (Leardi and Pol 2009; Turner and Sertich 2010; Sertich and O'Connor 2014): a wedge-like process of the maxilla lateral to the premaxilla-maxilla suture. Other unambiguous synapomorphies of the clade include: an enlarged tooth of the dentary that fits in a notch between the premaxilla and maxilla; well-developed perinarial fossa that occupies almost the entire ventral margin of the external nares; posteroventrally oriented quadrates; supraoccipital not exposed in dorsal view; among others (Turner and Sertich 2010; Sertich and O'Connor 2014; Geroto and Bertini 2019).

***Itasuchidae* Carvalho, Ribeiro, and Avila 2004 [Leardi *et al.*, this contribution], converted clade name**

Registration number: 990.

Definition: The most inclusive clade including *Itasuchus jesuinoi* Price 1955 (proxy: *Pepesuchus deiseae* Campos, Oliveira, Figueiredo, Riff, Azevedo, Carvalho and Kellner 2011) but not *Mahajangasuchus insignis* Brochu and Buckley 1999, *Peirosaurus torminni* Price 1955 (proxies: *Lomasuchus palpebrosus* Gasparini, Chiappe and Fernández 1991 and *Uberabasuchus terrificus* Carvalho, Ribeiro and Avila 2004), *Uruguaysuchus aznarezi* Rusconi 1933, and *Sebecus icaeorhinus* Simpson 1937. This is a maximum-clade definition. The proxies are not specifiers but can be used in place of the specifier for which they are proxies on phylogenies from which that specifier is absent (see Methods).

Etymology: Based on the name of the included species *Itasuchus jesuinoi* Price 1955.

Reference phylogeny: Fig. 9 of Geroto and Bertini (2019; primary reference); Fig. 11 of Pinheiro *et al.* (2018). See also Figs. 1, 3A, B, 4A, B.

Composition: Based on the cited phylogenies, some recent studies infer a clade formed by *Itasuchus jesuinoi* Price 1955 and *Pepesuchus deiseae* Campos, Oliveira, Figueiredo, Riff, Azevedo, Carvalho and Kellner 2011; with the potential inclusion of other Brazilian taxa such as *Caririsuchus camposi* (Kellner 1987), *Barreirosuchus franciscoi* Iori and García 2012 and *Roxochampsia paulistanus* (Roxo 1936) (Pinheiro *et al.* 2018, 2021, 2023; Geroto and Bertini 2019). *Stolokrosuchus* could represent the only non-Brazilian itasuchid, as it has been inferred in various analyses as part of the clade (Montefeltro *et al.* 2013; Pinheiro *et al.* 2018).

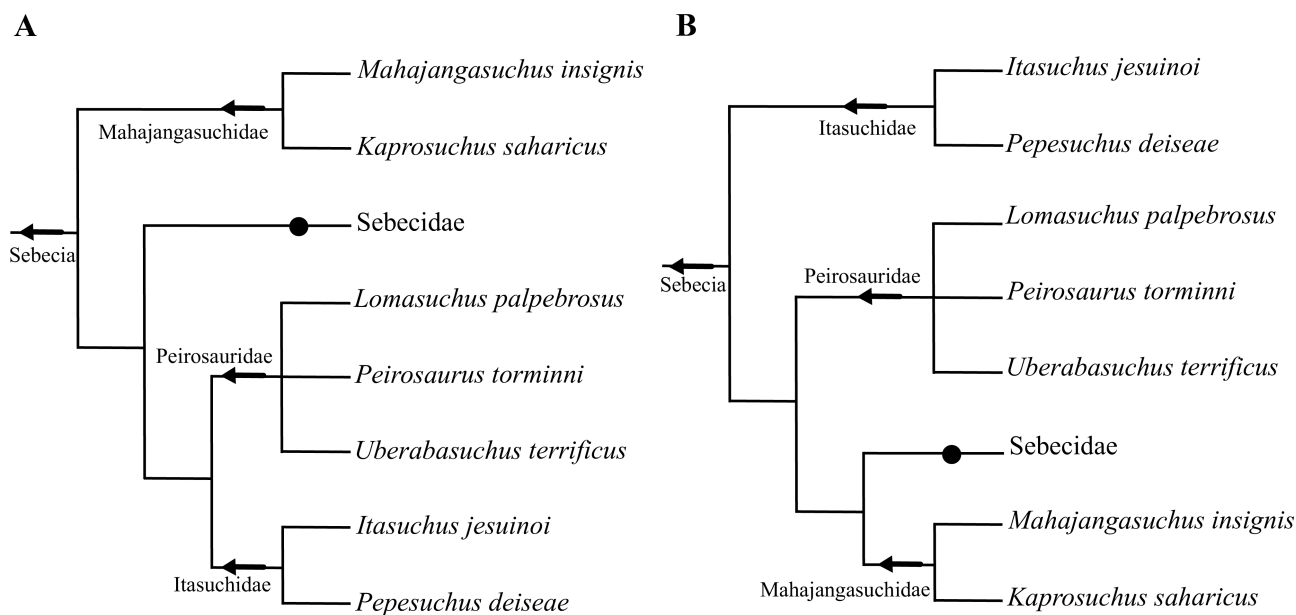


FIGURE 4. Internal topological variations in *Sebecia* (A) sensu Montefeltro *et al.* (2013) and Geroto and Bertini (2019); (B) sensu Pinheiro *et al.* (2018, 2021, 2023).

Comments: The name *Itasuchidae* was originally proposed by Carvalho *et al.* (2004) for a clade including *Malawisuchus* and *Itasuchus*, a relationship that was not found in other studies. Pinheiro *et al.* (2018) later redefined the name, also using a branch-based definition, with *Itasuchus* as the internal specifier and *Barreirosuchus*, *Montealtosuchus*, *Mahajangasuchus*, and *Sebecus icaeorhinus* as external specifiers. Later, Geroto and Bertini (2019) defined a different name (*Pepesuchinae*) for a clade of similar composition using a similar type of definition but using *Pepesuchus deiseae* as the internal specifier. This group includes similar taxa to *Itasuchidae* but excludes the poorly known taxa *Amargasuchus minor* Chiappe 1988, *Miadanosuchus oblita* (Buffetaut and Taquet 1979) and *Stolokrosuchus*, which were placed as non-pepesuchine peirosaurids in their hypothesis. Here, a maximum-clade definition using members of closely related clades as external specifiers (as with *Peirosauridae*) was chosen to avoid synonymies with other clade names ending in *-idae* if different relationships are inferred in future analyses. The study of the interrelationships of both peirosaurids and itasuchids is still in its first steps, and changes regarding some taxa might modify the hypothesized compositions of the named clades. Thus, using maximum-clade definitions for both *Peirosauridae* and *Itasuchidae* provides future stability for the maintenance of both names. However, it is important to note that the use of our maximum-clade definition for *Itasuchidae* results in the inclusion of some taxa that have not been considered as part of the clade in any previous analysis (e.g., *Ayllusuchus*, *Barreirosuchus*, and *Stolokrosuchus*) under some hypotheses (Pinheiro *et al.* 2018, 2021). *Caririsuchus camposi* has been variably inferred as part of *Itasuchidae* (Pinheiro *et al.* 2018, Geroto and Bertini 2019) or closer to mahajangasuchids (Pinheiro *et al.* 2021). Despite the recent inclusion of itasuchids in phylogenetic studies, few species related to *Itasuchus* are currently known (Pinheiro *et al.* 2023). As a result, many contributions that deal with Cretaceous mesoeucrocodylians frequently do not include itasuchid taxa in their datasets (e.g., Fernández Dumont *et al.* 2020; Sellés *et al.* 2020; Bravo *et al.* 2021). *Itasuchidae* is the sister group of *Peirosauridae* (Geroto and Bertini 2019) or of a clade formed by *Peirosauridae* + *Mahajangasuchidae* + *Sebecidae* (Pinheiro *et al.* 2018, 2021, 2023). Datasets that favor the sebecosuchian hypothesis have only included the basal itasuchid (given most hypotheses) *Stolokrosuchus* to represent *Itasuchidae*, where this taxon is placed as the sister group of either the clade formed by *Mahajangasuchidae* + *Peirosauridae* (Fernández Dumont *et al.* 2020; Bravo *et al.* 2021) (Fig. 3A) or *Peirosauridae* (Nicholl *et al.* 2021) (Fig. 3B).

Diagnostic apomorphies: The exact list of synapomorphies varies among different studies, mainly depending on the internal topology of the clade that affects the optimization of the characters. This is most notable in Pinheiro *et al.*'s (2018) analysis, the placement of the fragmentary taxon *Roxochampsia* within this group results in a large internal polytomy. Among the most notable synapomorphies inferred are absence of a notch in the premaxilla on the

lateral edge of the external nares; trapezoidal skull roof; posterolateral process of the nasal that wedges between the prefrontal and lacrimal; rod-shaped jugal ventrally to the infratemporal fenestra; procumbent anterior dentary teeth (Pinheiro *et al.* 2018; Geroto and Bertini 2019).

***Eunotosuchia* Ruiz, Bronzati, Ferreira, Martins, Queiroz, Langer, and Montefeltro 2021**

Registration number: 418.

Definition: “The least inclusive clade containing *Notosuchus terrestris* Woodward, 1896 and *Uruguaysuchus aznarezi* Rusconi, 1933 [proxy: *Araripesuchus gomesii* Price 1959] but not *Crocodylus niloticus* Laurenti 1768 (*Crocodylia*). This is a minimum-clade definition [with an external specifier]” (Ruiz *et al.* 2021: 281).

Etymology: Although the etymology was not specified by Ruiz *et al.* (2021), it is the same as for *Notosuchia*, but with addition of the prefix “Eu”, which comes from the ancient Greek εὖ, often used as “true” (or more appropriately, “core”) in taxonomic names.

Reference phylogeny: Fig. 6 of Ruiz *et al.* (2021), as originally designated. Additional reference phylogenies are Pinheiro *et al.* (2018: Fig. 11; and 2021: Fig. 9). See also Fig. 2.

Composition: Under the *Sebecia* hypothesis, *Eunotosuchia* includes *Baurusuchia sensu* Montefeltro *et al.* 2011, *Sphagesauria* Ruiz *et al.* 2021, and *Uruguaysuchidae* Gasparini 1971, plus some species-level taxa not nested within those groups (Ruiz *et al.* 2021). Under the *Sebecosuchia* hypothesis, *Eunotosuchia* is the minimum clade counterpart to (the maximum clade) *Notosuchia* (see Comments) and thus has the same currently known composition as that clade.

Comments: *Eunotosuchia* is a clade named in the context of the *Sebecia* hypothesis (Fig. 2), particularly when the latter is inferred outside the clade formed by uruguaysuchids, xenodontosuchians, and some monospecific genera (*Simosuchus*, *Libycosuchus*, *Malawisuchus* and *Morrinhosuchus*) (Ruiz *et al.* 2021). Following the definition of Ruiz *et al.* (2021), under alternative phylogenetic hypotheses that find uruguaysuchids closely related to mahajangasuchids + peirosaurids (e.g., Sertich and O’Connor 2014; Pol *et al.* 2014; Lardi *et al.* 2018; Fernández Dumont *et al.* 2020; Bravo *et al.* 2021), this clade would include very similar taxa to *Notosuchia*. This is caused by the conflicting alternative positions found for *Uruguaysuchidae* in the sebecosuchian hypothesis (i.e., closely related to peirosaurians [Fig. 1]) versus the sebecian hypothesis (i.e., more closely related to xenodontosuchians than to peirosaurids and mahajangasuchids [Fig. 2]). Thus, the use of *Eunotosuchia* is recommended when uruguaysuchids are positioned closer to xenodontosuchians (and ziphosuchians) (e.g., under the sebecian hypothesis) than to peirosaurids and mahajangasuchids.

Diagnostic apomorphies: Ruiz *et al.* (2021) cited seven synapomorphies supporting *Eunotosuchia*: external antorbital fenestra about half the diameter of the orbit; a loosely sutured premaxilla anterior to the nares; the absence of dermal bone overhanging the supratemporal fenestra; the presence of a peg in the posterior end of the mandibular symphysis; the absence of a crest and poorly delimited posterior margin on the glenoid fossa of the articular; maxillary teeth located in a groove; and constricted cheek tooth bases.

***Ziphosuchia* Ortega, Gasparini, Buscalioni, and Calvo 2000 [Lardi *et al.*, this contribution], converted clade name**

Registration number: 991.

Definition: The least inclusive clade containing *Notosuchus terrestris* Woodward 1896, *Libycosuchus brevirostris* Stromer 1914, *Sebecus icaeorhinus* Simpson 1937, and *Baurusuchus pachecoi* Price 1945, but not *Lomasuchus palpebrosus* Gasparini, Chiappe, and Fernández 1991. This is a minimum-clade definition with an external specifier.

Reference phylogeny: Fig. 31 of Pol *et al.* (2014, primary). See also Lardi *et al.* (2015: Fig. 23; 2018: 11A), Fernández Dumont *et al.* (2020: Fig. 7) and Bravo *et al.* (2021: Fig. 6) and Fig. 1.

Etymology: Not specified by Ortega *et al.* (2000) but derived from the presence of ziphodont (from the ancient double-edged Greek sword ξίφος [xíphos]) teeth, as it was originally intended to include all crocodyliforms with such tooth morphology.

Composition: Under topologies conforming to the *Sebecosuchia* hypothesis, *Ziphosuchia* includes *Sphagesauria* and *Sebecosuchia* (see below), and some monospecific genera not included in those groups (e.g., *Simosuchus*, *Libycosuchus*, *Comahuesuchus*). Under topologies conforming to the *Sebecia* hypothesis, the name *Ziphosuchia* does not apply to any clade

Comments: Ortega *et al.* (2000) originally inferred *Ziphosuchia* as the sister group of *Neosuchia* (*sensu* Sereno *et al.*, 2001), which also included several taxa now regarded as notosuchians (the peirosaurid *Lomasuchus*, and two species of the genus *Araripesuchus* [*A. gomesii* and *A. patagonicus*]). Thus, under Ortega *et al.*'s (2000) phylogenetic hypothesis, *Ziphosuchia* (as defined by those authors) would have a similar taxonomic content to *Notosuchia* (which was formally defined a year later by Sereno *et al.* [2001]). Later analyses (Turner and Sertich 2010; Pol *et al.* 2012, 2014) placed this clade as a subgroup of *Notosuchia*, including sphagesaurians, baurusuchians + sebecids + some additional taxa, such as *Libycosuchus* and *Malawisuchus*. The Brazilian taxon *Candidodon itapecuruense* Carvalho and Campos, 1988 takes variable positions relevant to its inclusion or exclusion from *Ziphosuchia*: either as the sister group of *Ziphosuchia* (e.g., Pol *et al.* 2014; Leardi *et al.* 2018); or forming a clade with *Malawisuchus*, *Pakasuchus*, and *Lavocatchampsia* that is included within *Ziphosuchia* (Martin and de Broin 2016; Bravo *et al.* 2021). Pinheiro *et al.* (2018, 2021, 2023) used a new concept for *Ziphosuchia* in their phylogenetic hypothesis, which consists of *Sebecia* + *Notosuchia* (reconceptualized and used as an equivalent of *Eunotosuchia*). This modification is not followed here, as it is not in agreement with the original proposal of *Ziphosuchia* by Ortega *et al.* (2000).

The definition proposed in this contribution is an amended conversion of the one stated by Turner and Sertich (2010), which in turn is an amended definition from the one proposed by Carvalho *et al.* (2004, p. 996: “the most recent common ancestor of *Notosuchus*, *Libycosuchus*, and *Baurusuchoidea* and all of their descendants”). The recognition of *Ziphosuchia* is accepted only under those hypotheses in which sebecids are closely related to baurusuchians, forming *Sebecosuchia* (see below). When sebecids form *Sebecia* with peirosaurids and mahajangasuchids, they form the sister group of *Uruguaysuchidae* + *Sphagesauria* + *Baurusuchia* + some species-level taxa (Pinheiro *et al.* 2018, 2021; Ruiz *et al.* 2021). In the context of these phylogenetic hypotheses, *Ziphosuchia* would be similar to *Notosuchia* (its minimum-clade counterpart) if a definition like the one proposed by Turner and Sertich (2010) is used. In order to avoid this conflict, we added an external specifier (the peirosaurid *Lomasuchus*) to make the name *Ziphosuchia* inapplicable in the context of the sebecian hypothesis. On the other hand, it could be argued that a similar clade (included within *Eunotosuchia*) can be recognized on these hypotheses if the position of *S. icaeorhinus* is not considered (Ruiz *et al.* 2021). However, the original conceptualization of the clade, which is followed in this contribution, included *Sebecus* as part of the clade.

Diagnostic apomorphies: Ortega *et al.* (2000) recognized six synapomorphies of the clade (last maxillary tooth anterior to the palatine fenestrae; medial quadrate condyle expanded ventrally; splenial convex in medial view; proximal end of radiale expanded; coracoid rod-like, and pterygoids with a deep parasagittal depression); however, due to the changes in the topology involving non-ziphosuchian taxa, these were not recovered in subsequent studies. Later, Turner and Sertich (2010) recognized three unambiguous synapomorphies for *Ziphosuchia*: no tooth size variation in the maxilla (reversed in baurusuchids and some species-level taxa); unsculpted region of the maxilla dorsally to the alveolar margin (reversed in sebecosuchians); and an extensive perinarial fossa with a concave surface facing anteriorly. Other ambiguous synapomorphies were identified, both cranial (Turner and Sertich 2010) and postcranial (Leardi *et al.* 2015). The large amount of missing data for the postcranial anatomy of some basal ziphosuchians (e.g., *Libycosuchus*) precludes the unambiguous optimization of several postcranial characters, and when these taxa are excluded from the analyses, additional postcranial ziphosuchian apomorphies are inferred (Leardi *et al.* 2015; Godoy *et al.* 2016).

***Xenodontosuchia* Ruiz, Bronzati, Ferreira, Martins, Queiroz, Langer, and Montefeltro 2021 {Leardi *et al.*, this contribution}**

Registration number: 556 (Ruiz *et al.* 2021).

Definition (emended): The least inclusive clade containing *Sphagesaurus huenei* Price 1950 and *Baurusuchus pachecoi* Price 1945 but not *Uruguaysuchus aznarezi* Rusconi 1933, *Araripesuchus gomesii* Price 1959, *Montealtosuchus arrudacamposi* Carvalho *et al.* 2007, and *Crocodylus niloticus* Laurenti 1768 (*Crocodylia*). This is a minimum-clade definition.

Etymology: The name *Xenodontosuchia* derives from the ancient Greek ξένος (xénos) which means “strange”, ὀδούς (odoús), “tooth”, and the suffix “suchia” as commonly used for naming pseudosuchian (pan-crocodylian) clades (see *Notosuchia* for the exact meaning). This name is inspired by the bizarre dentition of sphagesaurians and baurusuchians (Ruiz *et al.* 2021).

Reference phylogeny: Fig. 6 of Ruiz *et al.* (2021). This same topology is also inferred by Pinheiro *et al.* (2018: Fig. 11; 2021: Fig. 9), but the name *Notosuchia* was applied to this clade in that paper. See also Figs. 1 and 2.

Composition: Ruiz *et al.* (2021) established this clade name to include two large clades: *Sphagesauria* and *Baurusuchia*. In hypotheses that find the sebecosuchian topology *Sebecidae* and related taxa are also included (see Fig. 1).

Comments: As mentioned above, this clade was named in the recent contribution by Ruiz *et al.* (2021) to refer to a nested group within *Notosuchia* that includes the two large clades that diversified during the Late Cretaceous of Gondwana, *Sphagesauria* and *Baurusuchia* (see below for the definitions of these names). The close relationship of these two clades has been a common inference amongst notosuchian phylogenetic studies (e.g., Pol 2005; Turner 2006; Turner and Sertich 2010; Pol *et al.* 2012; Leardi *et al.* 2015). However, the original inclusion of *Sebecus icaeorhinus* Simpson 1937 as an external specifier makes this definition applicable only under the sebecian hypothesis, as this species is found as closely related to baurusuchians in other hypotheses (e.g., Pol *et al.* 2012, 2014; Leardi *et al.* 2018). Thus, we propose, as an unrestricted emendation, the removal of this taxon as an external specifier to allow the application of this clade name across a wider range of possible topologies (i.e., those conforming to the sebecosuchian hypothesis).

Diagnostic apomorphies: Xenodontosuchians, as their name implies, are identified by the presence of strongly laterally compressed teeth that is a synapomorphy of the clade (Ruiz *et al.* 2021). This synapomorphy has been recognized under other phylogenetic hypotheses along with additional cranial ones, particularly highlighting a reorganization of several elements in the palate, including laterally diverging and rod-like palatines and an ectopterygoid that extends widely over the lateral half of the ventral surface of the pterygoid wings (Turner and Sertich 2010: Unnamed clade—*Notosuchidae* + *Comahuesuchus* + *Sebecosuchia* + “*Sphagesauridae*”). An additional postcranial synapomorphy has been inferred in the humerus, as its deltopectoral crest is displaced medially leaving an anterolaterally facing surface on the lateral margin of the anterior surface (Pol *et al.* 2012; Leardi *et al.* 2015).

***Sphagesauria* Ruiz, Bronzati, Ferreira, Martins, Queiroz, Langer, and Montefeltro 2021**

Registration number: 419 (Ruiz *et al.* 2021).

Definition: “The most inclusive clade containing *Sphagesaurus huenei* Price 1950, but not *Baurusuchus pachecoi* Price, 1945, *Araripesuchus gomesii* Price, 1959, *Montealtosuchus arrudacamposi* Carvalho *et al.*, 2007, *Sebecus icaeorhinus* Simpson, 1937 [and] *Crocodylus niloticus* Laurenti, 1768 (Crocodylia). This is a maximum-clade definition” (Ruiz *et al.* 2021: 281).

Etymology: Although the etymology was not specified in the contribution that registered the name (Ruiz *et al.* 2021), it was done so by Pinheiro *et al.* (2021). Derived from the type species name *Sphagesaurus huenei* Price 1950, the first species named in this group.

Reference phylogeny: Fig. 6 in Ruiz *et al.* (2021, primary) where *Crocodylus niloticus* is part of *Neosuchia*; see also Pinheiro *et al.* (2021: Fig. 9), Pol *et al.* (2014: Fig. 31), and Figs. 1, 2, and 5.

Composition: Based on the reference phylogeny, *Sphagesauria* includes *Notosuchus terrestris* Woodward 1896, *Mariliasuchus amarali* Carvalho and Bertini 1999 and *Sphagesauridae* Kuhn 1968. It may also include *Morrinhosuchus luziae* Iori and Carvalho 2009 and *Labidiosuchus amicum* Kellner *et al.* 2011 (Pol *et al.* [2014] and derived datasets).

Comments: This clade was originally recognized by Pol *et al.* (2014) who referred to it as the “advanced notosuchians”, recognizing a close relationship between sphagesaurids and several taxa usually inferred as omnivorous or herbivorous (*Notosuchus*, *Mariliasuchus*, *Labidiosuchus*, *Coringasuchus* and *Morrinhosuchus*). This clade was recovered in most subsequent analyses (e.g., Leardi *et al.* 2015, 2018; Fiorelli *et al.* 2016; Godoy *et al.* 2016) and was later named as *Sphagesauria* by both Pinheiro *et al.* (2021) and Ruiz *et al.* (2021). Although different definitions were given in these two contributions, Ruiz *et al.* (2021) registered the name and definition, thus we consider them the nominal and definitional authors.

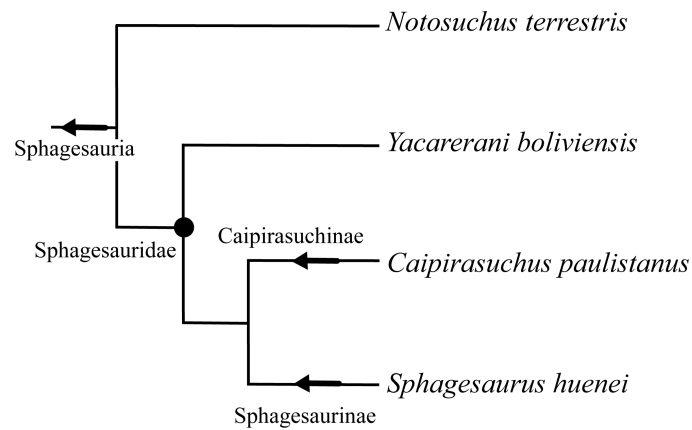


FIGURE 5. Simplified cladogram depicting the internal topology of *Sphagesauria* sensu Pol *et al.* (2014), Leardi *et al.* (2015), and Ruiz *et al.* (2021).

Diagnostic apomorphies: To date, this is an exclusively South American clade of notosuchians with an inferred herbivorous or omnivorous diet, mostly composed of small animals (e.g., Pol 2003; Marinho and Carvalho 2009; Iori *et al.* 2011, 2018; Kellner *et al.* 2011; Fiorelli *et al.* 2016; Martinelli *et al.* 2018). Pol *et al.* (2014) listed three unambiguous synapomorphies supporting the clade (a laterally concave premaxilla-nasal suture; presence of a transitional tooth set in an alveolus formed by both the premaxilla and maxilla; and an anterior process with parallel lateral margins on the anterior region of the mandibular symphysis) as well as eight ambiguous ones (see Pol *et al.* 2014). According to Ruiz *et al.* (2021), *Sphagesauria* is supported by five (six are mentioned but only five are listed) unambiguous synapomorphies: distal hemimandible strongly curved, creating a “Y-shaped” mandible; oblique disposition of the maxillary and posterior dentary teeth in relation to the craniomandibular axis; lateral asymmetry of tooth crowns; presence of ridged ornamentation and apicobasal ridges on the enamel surface of the middle to posterior teeth; and the presence of a transitional tooth in the premaxilla-maxilla contact. Similar character support is mentioned in the diagnosis of the clade by Pinheiro *et al.* (2021), with the addition of an absence of tooth variation in the maxillary tooth row; presence of a broad alveolar shelf on the posterior region of the mandibular tooth row; and the presence of wear facets in the posterior teeth.

Sphagesauridae Kuhn 1968 [Ruiz *et al.*, 2021]

Registration number: 420 (Ruiz *et al.* 2021).

Definition: “The least inclusive clade containing *Sphagesaurus huenei* Price, 1950, *Caipirasuchus* (originally *Sphagesaurus*) *montealtensis* Andrade & Bertini, 2008a and *Yacarerani boliviensis* Novas *et al.*, 2009. This is a minimum-clade definition” (Ruiz *et al.* 2021: 281).

Etymology: Although not specified in the study that defined and registered the name (Ruiz *et al.* 2021), the name is derived from the name of the type genus *Sphagesaurus* Price 1950.

Reference phylogeny: Fig. 6 in Ruiz *et al.* (2021, primary); see also Pinheiro *et al.* (2021: Fig. 9), Pol *et al.* (2014: Fig. 31), and Fig. 5.

Composition: Based on the reference phylogeny, *Sphagesauridae* includes *Sphagesaurus huenei* Price 1950, *Caipirasuchus* Iori and Carvalho 2011, *Caryonosuchus pricei* Campos, Riff, and Andrade 2011, *Armadillosuchus arrudai* Marinho and Carvalho 2009, *Yacarerani boliviensis* Novas *et al.* 2009, and *Adamantinasuchus navae* Nobre and Carvalho 2006. It is formed by three mutually exclusive clades, *Sphagesaurinae* and *Caipirasuchinae* plus an unnamed clade formed by two additional species (*Yacarerani boliviensis* Novas *et al.*, 2009 and *Adamantinasuchus navae* Nobre and Carvalho 2006).

Comments: *Sphagesaurus huenei* was originally described by Price (1950) who recognized its affinities with *Notosuchus*. Later, Kuhn (1968) erected *Sphagesauridae* as a monotypic family to include the species *Sphagesaurus huenei* Price 1950, based on its unique dental morphology. *S. huenei* was first incorporated in phylogenetic datasets

in the early 2000's (e.g., Pol 2003). Andrade and Bertini (2008) inferred a monophyletic *Sphagesauridae*, formed by *S. huenei* and *S. montealtensis* (later moved to the genus *Caipirasuchus* by Iori *et al.* [2013]), results that were not repeated in more inclusive analyses (Turner and Sertich 2010). During the late 2000's and early 2010's, a large number of new species assigned to *Sphagesauridae* were described (e.g., Marinho and Carvalho 2009; Novas *et al.* 2009; Iori and Carvalho 2011; Pol *et al.* 2014; Martinelli *et al.* 2018), which led to the recognition of a monophyletic *Sphagesauridae* in more inclusive datasets (Pol *et al.* 2014). This monophyly has not since been challenged, and sphagesaurids have been corroborated as a monophyletic group in several recent analyses (e.g., Leardi *et al.* 2015; Ruiz *et al.* 2021; Pinheiro *et al.* 2021). As a general consensus, *Sphagesauridae* is formed by three internal groups, *Yacararani* + *Adamantinasuchus*, the sister group of the rest of the clade, and the sister groups *Sphagesaurinae* and *Caipirasuchinae* (Pol *et al.* 2014; Pinheiro *et al.* 2021; see below).

Diagnostic apomorphies: Kuhn (1968) placed *S. huenei* in its own family based on the differences between its teeth (the only known elements at that time) and those of other crocodylomorph taxa (triangular in cross section with prominent, coarse denticles on their carinae and a “pebbled-like” enamel). Pol (2003) reported a nearly complete skull of this taxon and identified additional autapomorphies (e.g., edentulous anterior region of the premaxillae mesially to the hypertrophied premaxillary teeth; maxilla with posterior wall above the anterior margin of the suborbital fenestra that extends dorsally contacting the prefrontal and lacrimal; exoccipital excluded from the ventral margin of the occipital surface). As a consequence of the discovery and description of a plethora of sphagesaurids (see above), the anatomical knowledge of this clade has been significantly increased. Sphagesaurids are a unique group of notosuchians, characterized by their distinctive heterodont dentition and additional craniomandibular adaptations to herbivory (e.g., compressed and elongated mandibular teeth forming a battery [*sensu* Andrade and Bertini 2008]). Pol *et al.* (2014) and Ruiz *et al.* (2021) found *Sphagesauridae* supported by seven and eight synapomorphies, respectively. Besides the aforementioned features of their dentition, the following synapomorphies can be highlighted: a gap between the anterior and posterior series of aligned neurovascular foramina of the lateral surface of maxilla; the presence of large (as long as an alveolus) neurovascular foramina on the mid to posterior region of the alveolar edge of the dentary; the quadrate processes of pterygoids are extremely short and fail to extend along the lateral margins of the basisphenoid, ending far away from the level of the lateral eustachian openings; the anterior process of quadratojugal forms the posterior third of the ventral margin of the infratemporal fenestra; a continuous lachrymal-jugal contact; elongated prefrontals anterior to the orbit and aligned with the major axis of the skull; and, an anteriorly convex postorbital-squamosal suture in lateral view; supraoccipital exposed in the dorsal aspect of the skull.

***Sphagesaurinae* Pinheiro *et al.* 2021 [Leardi *et al.*, this contribution], converted clade name**

Registration number: 992.

Definition: The most inclusive clade within *Sphagesauridae* including *Sphagesaurus huenei* Price 1950 but not *Notosuchus terrestris* Woodward 1896, *Caipirasuchus paulistanus* Iori and Carvalho 2011, and *Yacararani boliviensis* Novas *et al.* 2009. This is a maximum-clade definition.

Etymology: Based on the name of the type genus, *Sphagesaurus* Price 1950.

Reference phylogeny: Fig. 9 in Pinheiro *et al.* (2021, primary); see also Ruiz *et al.* (2021: Fig. 6), Pol *et al.* (2014: Fig. 31), and Fig. 5.

Composition: Based on the reference phylogenies, *Sphagesaurinae* includes three species: *Sphagesaurus huenei* Price 1950, *Armadillosuchus arrudai* Marinho and Carvalho 2009, and *Caryonosuchus pricei* Kellner *et al.* 2011.

Comments: *Sphagesaurinae* was first proposed (but not registered) by Pinheiro *et al.* (2021) as a node-based name for a clade that includes the large-bodied sphagesaurids *Sphagesaurus*, *Armadillosuchus*, *Caryonosuchus*, and all their descendants. *Sphagesaurinae* is the sister group of *Caipirasuchinae* (see below). A similar topology was also inferred by Pol *et al.* (2014) and Ruiz *et al.* (2021). However, we propose a change in the type of definition, compared that of Pinheiro *et al.* (2021). In order to retain mutual exclusivity between the subfamilies, a maximum-clade definition is chosen using a member of *Caipirasuchinae* as external specifier. Additional external specifiers within *Sphagesauridae* (*Yacararani boliviensis*, which is found as the sister group of *Caipirasuchinae* + *Sphagesaurinae* in most recent analyses; *Caipirasuchus paulistanus*, which is the found as a member of its sister

group, *Caipirasuchinae*) and outside *Sphagesauridae* (*Notosuchus terrestris*, a non sphagesaurid sphagesaurian) are also included to promote stability in terms of composition (see reference phylogenies).

Diagnostic apomorphies: Pinheiro *et al.* (2021) suggest that members of *Sphagesaurinae* are diagnosed by having two premaxillary teeth; dorsal border of the external nares formed by the nasals and premaxillae; an anteriorly placed postorbital process of the jugal; maxillary dental implantation in isolated alveoli; well-developed medial crest of the quadrate meeting the basioccipital on the occipital surface of the skull, excluding the otoccipital from the ventral margin of the occipital surface. However, Iori *et al.* (2011) described the dental pattern of sphagesaurids and showed that at least *Armadillosuchus arrudai* (UFRJ DG 380-R) has three premaxillary teeth and that *Caipirasuchus* species also have maxillary dental implantation in isolated alveoli (as do most notosuchians). These observations, not considered by Pinheiro *et al.* (2021), point out that the two putative synapomorphies originally used to diagnose the clade represent plesiomorphies for the clade as they are present in a more inclusive group of sphagesaurids.

***Caipirasuchinae* Pinheiro *et al.* 2021 [Leardi *et al.*, this contribution], converted clade name**

Registration number: 993.

Definition: The most inclusive clade within *Sphagesauridae* that includes *Caipirasuchus paulistanus* Iori and Carvalho 2011 but not *Notosuchus terrestris* Woodward 1896, *Sphagesaurus huenei* Price 1950, and *Yacarerani boliviensis* Novas *et al.* 2009. This is a maximum-clade definition.

Etymology: Based on the name of the type genus, *Caipirasuchus* Iori and Carvalho 2011.

Reference phylogeny: Ruiz *et al.* (2021: Fig. 6) (primary); see also Pinheiro *et al.* (2021: Fig. 9A, B), Pol *et al.* (2014: Fig. 31), and Fig. 5.

Composition: Based on the reference phylogenies, *Caipirasuchinae* includes all the species of the genus *Caipirasuchus* (*C. stenognathus* Pol *et al.* 2014; *C. paulistanus* Iori and Carvalho 2011; *C. montealtensis* Andrade and Bertini 2008; *C. mineirus* Martinelli *et al.* 2018; *C. attenboroughi* Ruiz *et al.* 2021). In one of the reference phylogenies (Pinheiro *et al.* 2021), *Morrinhosuchus luziae* Iori and Carvalho 2009 is included in *Caipirasuchinae*, representing the only potential caipirasuchine that is not a species of *Caipirasuchus*.

Comments: In the primary reference phylogeny for the group (Ruiz *et al.* 2021), *Caipirasuchinae* comprises the five *Caipirasuchus* species, with the clade *C. paulistanus* + *C. montealtensis*, being the sister group of a group formed by *C. attenboroughi*, *C. stenognathus*, and *C. mineirus*. This topology is largely congruent with that of Pol *et al.* (2014) and subsequent studies based on this dataset (e.g., Leardi *et al.* 2015; Martinelli *et al.* 2018). The analysis of Marinho *et al.* (2022), however, challenged the monophyly of *Caipirasuchus*. This study found a paraphyletic *Caipirasuchus* in which only *C. paulistanus* + *C. montealtensis* form a monophyletic group, and *C. mineirus* and *C. stenognathus* were placed as the consecutive outgroups to *Sphagesauridae*. Within the context of this topology, *Caipirasuchinae* would be limited to the clade formed by *C. paulistanus* and *C. montealtensis*.

The name *Caipirasuchinae* was coined by Pinheiro *et al.* (2021) who proposed this clade as a subfamily, with *Morrinhosuchus luziae* nested within the *Caipirasuchus* species. It is worth noting that *Morrinhosuchus luziae* has a “V-shaped” mandible in dorsal and ventral views (lacking the distinctive “Y-shaped” mandible that is synapomorphic of *Sphagesauria*; see Iori *et al.* 2018) and has not been placed close to (or within) *Caipirasuchinae* in any other phylogenetic studies.

In this contribution, a similar approach to that for its sister-group (see *Sphagesaurinae*) was taken for the definition of *Caipirasuchinae*.

Diagnostic apomorphies: As proposed by Pinheiro *et al.* (2021), caipirasuchines are smaller than the sphagesaurines. These authors diagnose *Caipirasuchinae* by the presence of small antorbital fenestra with less than half the diameter of the orbit; dorsal edge of dentary straight with an abrupt dorsal expansion, being straight posteriorly; jugal anteroventral process between the maxilla and ectopterygoid extending anteriorly as a short triangular process that wedges between the ectopterygoid; and maxilla on the ventrolateral surface of the skull at the level of the orbits with a “sickle-like medial process present on the ventral surface of the anterior jugal ramus” (*sensu* Andrade and Bertini 2008).

Sebecia Larsson and Sues 2007 [Leardi *et al.*, this contribution], converted clade name

Registration number: 997.

Definition: The most inclusive clade including *Sebecus icaeorhinus* Simpson 1937 and *Lomasuchus palpebrosus* Gasparini, Chiappe, and Fernández 1991 but not *Baurusuchus pachecoi* Price 1945, *Notosuchus terrestris* Woodward 1896, and *Crocodylus niloticus* Laurenti 1768. This is a maximum-clade definition.

Etymology: Based on the family name *Sebecidae* Simpson 1937 (Larsson and Sues 2007).

Reference phylogeny: Pinheiro *et al.* (2018: Fig. 11) (primary); see also Larsson and Sues (2007: Fig. 8C), Ruiz *et al.* (2021: Fig. 6), and Fig. 2 and 4A, B.

Composition: *Sebecia* is a clade that includes *Sebecidae*, *Mahajangasuchidae*, *Peirosauridae* and *Itasuchidae* (Montefeltro *et al.* 2013; Pinheiro *et al.* 2018; Geroto and Bertini 2019). However, the internal topology has seen some variation, mostly involving the relative placement of *Sebecidae* as the sister group of either *Mahajangasuchidae* (Pinheiro *et al.* 2018; Geroto and Bertini 2019; Fig. 4B) or *Peirosauridae* + *Itasuchidae* (*sensu* this contribution, see above; Ruiz *et al.* 2021; Fig. 4A).

Comments: *Sebecia* was a clade named by Larsson and Sues (2007) for a group composed of peirosaurids (including *Stolokrosuchus*), sebecids, and *Pabwehshi*; it was originally defined as “all crocodyliforms more closely related to *S. icaeorhinus* than to *C. niloticus*” and was considered to exclude *Baurusuchus*. This clade was inferred by the authors as the sister group of *Neosuchia*. The decision to name this clade was based on the fact that *Baurusuchus pachecoi* was not included in it, thus it did not correspond to the traditional *Sebecosuchia*. Under this hypothesis (*Sebecia*), similarities among sebecids and baurusuchids (see *Sebecosuchia*) are considered as widely distributed among crocodyliforms, and topologies grouping these crocodyliforms are strongly suboptimal (Larsson and Sues 2007). In a later iteration of the dataset, Sereno and Larsson (2009) inferred a monophyletic *Sebecia* placed within *Neosuchia* as the sister group of the rest of the members of the clade (which also included mahajangasuchids) (Sereno and Larsson 2009: Fig. 43). Afterwards, Montefeltro *et al.* (2013) compiled an extensive dataset that included a large sample of crocodyliforms. The study inferred a monophyletic *Sebecia* within *Notosuchia*, as the sister group of *Eunotosuchia* (see *Eunotosuchia* above), a topology also recovered by other studies using variations of this dataset (Pinheiro *et al.* 2018, 2021; Geroto and Bertini 2019; Ruiz *et al.* 2021). In this hypothesis, *Sebecia* has low support values and places the European taxon *Doratodon carcharidens* as the basal-most sebecian, whilst mahajangasuchids are found to be the sister group of a clade formed by *Peirosauridae* + *Sebecidae* (Montefeltro *et al.* 2013: Figs. S4, S5).

Montefeltro *et al.*'s (2013) dataset has been modified for several subsequent analyses (Geroto and Bertini 2019; Ruiz *et al.* 2021) and similar results were obtained. However, some internal variations regarding the relationships of sebecians were found, especially in the results of Pinheiro *et al.* (2018, 2021, 2023), which place *Itasuchidae* as the sister taxon of the clade with the topology (*Peirosauridae* (*Mahajangasuchidae* + *Sebecidae*)).

It is important to note that under the definition proposed in this contribution, *Sebecia* will only be applied to a clade under phylogenies in which sebecids are more closely related to peirosaurids than to baurusuchids, sphagesaurians, and neosuchians (sebecian hypothesis; Figs. 2, 4). By contrast, *Sebecia* will not apply to any clade under phylogenies in which sebecids are closer to one or more of those taxa than they are to peirosaurids (sebecosuchian hypothesis; Fig. 1).

Diagnostic apomorphies: Larsson and Sues (2007) found three unambiguous synapomorphies diagnosing *Sebecia*: a large neurovascular foramen on the palatal processes at the premaxilla-maxilla contact; premaxillae not meeting posteriorly at the palatal surface; and a sagittal torus on the maxillary palatal shelves. Also, considering the ambiguous optimizations caused by the position of the highly incomplete *Pabwehshi*, which was placed at the base of *Sebecia*, two unambiguous synapomorphies (presence of a large and elongated incisive foramen; and the posterior premaxillary alveolus being posteriorly excavated by a lateral fossa on the premaxilla and maxilla) and seven ambiguous synapomorphies (e.g., a deep fossa between, and posterior to, the first two premaxillary alveoli; an accessory condyle on the quadratojugal that articulates with the glenoid fossa) were also found to diagnose the clade formed by sebecids + peirosaurids (Larsson and Sues 2007). Similar synapomorphies were inferred by Sereno and Larsson (2009) supporting *Sebecia*, with the addition of the presence of a circumnarial fossa and a posterodorsally projected retroarticular process.

On the other hand, Montefeltro *et al.* (2013) and later iterations of this dataset (e.g., Ruiz *et al.* 2021) found two synapomorphies for *Sebecia*: distinctly raised borders of the supratemporal fenestrae; and a complex surangular-

dentary suture that bears several interlocked prongs from each of these bones. Pinheiro *et al.* (2018) found eleven unambiguous synapomorphies diagnosing *Sebecia* (e.g., a deep longitudinal groove on the lateral surface of the surangular and dentaries; a broad splenial posterior to the symphysis; first and second premaxillary teeth nearly confluent; among others).

***Sebecosuchia* Simpson 1937 [Leardi *et al.*, this contribution], converted clade name**

Registration number: 994.

Definition: The least inclusive clade containing *Sebecus icaeorhinus* Simpson 1937 and *Baurusuchus pachecoi* Price 1945 but not *Araripesuchus gomesii* Price 1959 or *Montealtosuchus arrudacamposi* Carvalho *et al.* 2007 or *Crocodylus niloticus* Laurenti 1768 (*Crocodylia*). This is a minimum-clade definition with external specifiers.

Etymology: Based on the stem of the name of the family *Sebecidae* (Simpson 1937; Colbert, 1946) with the addition of the suffix “suchia”, usually used to name pseudosuchian (pan-crocodylian) taxa (see *Notosuchia* for the exact derivation).

Reference phylogeny: Fig. 31 in Pol *et al.* (2014) (primary); see also Pol *et al.* (2012: Fig. 24), Leardi *et al.* (2018: Fig. 11), Bravo *et al.* (2021: Fig. 6), and Fig. 1.

Composition: *Sebecosuchia* is a clade that includes two distinct subclades of predatory terrestrial crocodyliforms: *Baurusuchidae* and *Sebecidae*. *Sebecidae* and some allied taxa (*Bergisuchus*, *Iberosuchus*, *Dentaneosuchus*) form the sister group of *Baurusuchidae* (Bravo *et al.* 2021; Martin *et al.* 2023). Additional species-level taxa (*Comahuesuchus brachybuccalis* Bonaparte 1991; *Chimaerasuchus paradoxus* Wu and Sues 1996; *Pabwehshi pakistanensis* Wilson *et al.* 2001; and *Pehuenchesuchus enderi* Turner and Calvo 2005) are found more closely related to *Sebecosuchia* than to *Sphagesauria* in some phylogenetic hypotheses (e.g., Pol *et al.* 2012, 2014; Leardi *et al.* 2018; Bravo *et al.* 2021), but are not included in *Sebecosuchia* as they form successive outgroups to the clade. *Sebecosuchia*, and the taxa mentioned above, are the sister group of *Sphagesauria* (Fig. 1; see the reference phylogeny).

Comments: Turner and Calvo (2005) and Turner and Sertich (2010) attributed the name *Sebecosuchia* to Colbert (1946). However, the name *Sebecosuchia* first used by Simpson (1937) to include solely *Sebecidae* as a suborder or order outside of *Mesosuchia* (then considered valid). This idea was followed by Colbert (1946), but he added *Baurusuchidae* to *Sebecosuchia*, noting similarities in the snout (i.e., narrow and high snout) and in the dentition (reduced number of maxillary teeth that are compressed labiolingually and serrated) with the then recently described *Baurusuchus pachecoi* (Price 1945). Subsequently, Price (1955) added *Peirosaurus torminni* to *Sebecosuchia*. The author did not provide an extensive explanation for this inclusion, but it was likely due to the presence of a ziphodont dentition, and this idea was not followed by subsequent authors. Gasparini (1972) considered *Sebecosuchia* as a subgroup of mesoeucrocodylians (i.e., *Mesosuchia* at that time), based on the anatomy of the vertebrae (amphicoelous), choanae (without pterygoid participation) and other regions of the skull (snout, mandibular articulation) of both baurusuchians and sebecids. Although the sister-group relationship between *Baurusuchus* and *Sebecus* (and allies) was inferred for the first time by Ortega *et al.* (2000) and was recognized as such in many phylogenetic analyses in the following years (Pol 2003; Pol and Apesteguía 2005; Company *et al.* 2005), the monophyly and history of the clade was first discussed in detail within a phylogenetic context by Turner and Calvo (2005). In their contribution, they referred to *Sebecosuchia* (graphically in their Fig. 5) using a maximum-clade concept, as they included *Pehuenchesuchus enderi* in the clade. *Sebecosuchia* was corroborated in most subsequent phylogenetic analyses, with some authors restricting it to the group formed by *Baurusuchus* + *Sebecus* (Turner and Sertich 2010), whilst others used the maximum-clade concept (Pol and Powell 2011; Pol *et al.* 2012). Due to the uncertainty about the phylogenetic affinities of *Pehuenchesuchus enderi*, the use of *Sebecosuchia* subsequently became restricted to the minimum-clade concept—that is, the least inclusive clade containing both *Baurusuchus pachecoi* and *Sebecus icaeorhinus* (e.g., Pol *et al.* 2014; Leardi *et al.* 2015, 2018; Bravo *et al.* 2021). Despite its wide use in several cladograms, *Sebecosuchia* lacked a formal phylogenetic definition until this contribution. Here we adopt the most commonly employed concept (and therefore a minimum-clade definition), with the inclusion of external specifiers to make it inapplicable in the context of the *Sebecia* hypothesis (see Definition above).

Diagnostic apomorphies: Sebecosuchians were originally grouped by Colbert (1946) due to the presence of a narrow oreinirostral snout, laterally placed orbits, a reduced number of teeth, and labiolingually compressed teeth with serrated carinae that made them almost indistinguishable from those of theropod dinosaurs. In the 21st century,

phylogenetic analyses inferred these traits as synapomorphic (except for the lateral placement of the orbits, which is widely present in most non-neosuchian crocodyliforms) with the addition of several other characters (more than ten by Turner and Sertich 2010). Among these, the following can be highlighted (Turner and Sertich 2010; Pol *et al.* 2012): large ventrally-open notch on the premaxilla-maxilla contact; presence of a hypertrophied mandibular tooth opposite to the premaxilla-maxilla contact; absence of sculpture dorsally to the tooth row on the maxilla; a longitudinal depression on the anterior region of the surangular and posterior region of the dentary; lateral edges of the nasals nearly parallel to each other; unsculptured region on the dentary ventrally to the toothrow; dentary with a lateral concavity for reception of an enlarged maxillary tooth; splenial-dentary suture V-shaped in ventral view at the symphysis; evaginated maxillary alveolar edges present as a continuous sheet; paroccipital process elongated exceeding the lateral edge of the cranioquadrate passage; a distinct bulge at the midpoint of the prezygapophyseal process; absence of ventral keels on the cervical vertebrae; well-developed prespinal fossae on the dorsal surface of the neural arches of the anterior dorsal vertebrae; vertical orientation of the insertion area of the *M. subscapularis* dorsal to the internal tuberosity of the humerus; and the distal end of the deltopectoral crest exceeding medially the midpoint of the humeral shaft (Turner and Sertich 2010; Pol *et al.* 2012; Leardi *et al.* 2015). Under the sebecian hypothesis (see *Sebecia*), many of the classical sebecosuchian synapomorphies are deemed as convergences due to the predatory habits of baurusuchians and sebecids (Larsson and Sues 2007).

***Sebecidae* Simpson 1937 [Leardi *et al.*, this contribution], converted clade name**

Registration number: 995.

Definition: The least inclusive clade that contains *Sebecus icaeorhinus* Simpson 1937, *Bretesuchus bonapartei* Gasparini *et al.* 1993, *Barinasuchus arveloi* Paolillo and Linares 2007 and *Sahitisuchus fluminensis* Kellner *et al.* 2014. This is a minimum clade definition.

Etymology: Although Simpson (1937) did not explain the *derivatio nominis* of either the genus or the family, this topic was later tackled by Colbert (1946). Derived from the name of the type genus, *Sebecus* Simpson 1937.

Reference phylogeny: Fig. 24 in Pol *et al.* (2012) (primary); see also Kellner *et al.* (2014), Sellés *et al.* (2020: Fig. 3), Bravo *et al.* (2021: Fig. 6), and Fig. 6.

Composition: *Sebecidae* includes the species of the genus *Sebecus* (*S. icaeorhinus* Simpson, 1937, *S. huilensis* Langston 1965, *S. querejazus* Buffetaut and Marshall 1991, *S. ayrampu* Bravo *et al.* 2021, an unnamed taxon from the Lumbrera Formation [Lumbrera form, see Pol and Powell 2011]), and at least five additional species-level taxa (*Ogresuchus furatus* Sellés *et al.* 2020, *Sahitisuchus fluminensis* Kellner *et al.* 2014, *Bretesuchus bonapartei* Gasparini *et al.* 1993, *Ayllusuchus fernandezi* Gasparini 1984, and *Barinasuchus arveloi* Paolillo and Linares 2007). Some European taxa (*Iberosuchus*, *Bergisuchus*, *Dentaneosuchus*) have been placed as successive outgroups to *Sebecidae* in multiple recent studies (Pol *et al.* 2012, 2014; Sellés *et al.* 2020; Bravo *et al.* 2021; Nicholl *et al.* 2021), while others even considered them to be sebecids (Martin *et al.* 2023). In this contribution, we restrict the usage of *Sebecidae* to the clade formed by the South American taxa.

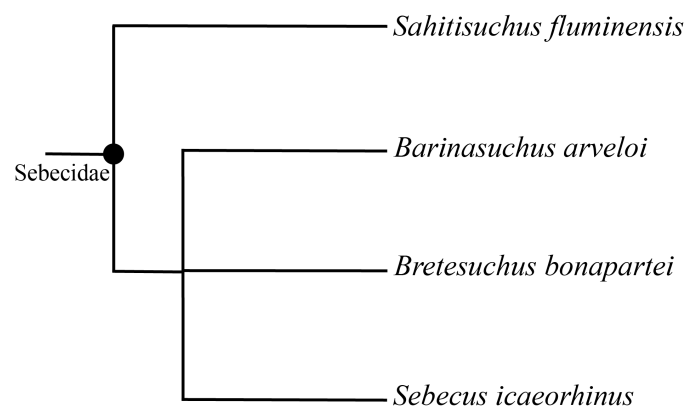


FIGURE 6. Simplified cladogram depicting the topology of *Sebecidae* *sensu* Pinheiro *et al.* (2018) and Bravo *et al.* (2021) (see *Sebecidae*).

Additionally, some taxa have been recognized as problematic as they have been placed in different positions by different authors. In some analyses, *Bergisuchus dietrichbergi* Kuhn 1968 is placed within *Sebecidae* (e.g., Montefeltro *et al.* 2013). *Lorosuchus nodosus* Pol and Powell 2011 has been included as a member of the clade (e.g., Pol *et al.* 2011, 2012; Kellner *et al.* 2014), but a recent study noted it can be positioned outside of *Sebecidae* under a parsimony analysis using implied weights (Bravo *et al.* 2021). *Sebecidae* has two different positions among notosuchian phylogenetic hypotheses: closer to *Baurusuchia* than to other notosuchian clades (sebecosuchian hypothesis), or closer to *Mahajangasuchidae* or *Peirosauridae* than to other notosuchian clades (sebecian hypothesis).

Comments: *Sebecidae* was created as a family in the same contribution in which Simpson (1937) created the suborder *Sebecosuchia*. Both taxa were erected to include *Sebecus icaeorhinus* Simpson 1937. Over the years, the taxonomic composition of *Sebecidae* has been augmented by the discovery of several other taxa, including several species of the genus *Sebecus*, as well as other new monotypic genera (see above). In more recent analyses, *Sebecidae* has been restricted almost exclusively to a group of South American forms, excluding European taxa such as *Bergisuchus dietrichbergi* Kuhn 1968, *Iberosuchus macrodon* Antunes 1975, and some species of the genus *Doratodon* Seeley 1881 (Company *et al.* 2005; Pol and Powell 2011; Pol *et al.* 2012; Kellner *et al.* 2014; Bravo *et al.* 2021). The recent discovery of the taxon *Ogresuchus furatus* Sellés *et al.* 2020 from the Cretaceous of Spain highlighted a European taxon that was inferred to be nested within *Sebecidae* (Sellés *et al.* 2020). Furthermore, some studies have also placed other European taxa (*Bergisuchus* in Montefeltro *et al.* 2013 and Geroto and Bertini 2013; *Bergisuchus* and *Iberosuchus* in Pinheiro *et al.* 2018) deeply nested within *Sebecidae*. Thus, there is some uncertainty regarding the possible geographic distribution of the clade *Sebecidae* outside South America.

The only definition available for the clade is the one given by Larsson and Sues (2007), which defined *Sebecidae* as all taxa more closely related to *Sebecus icaeorhinus* than to *Uberabasuchus terrificus* and *Peirosaurus torminni*. This definition is useful in the context of the phylogenetic hypothesis where *Sebecidae* is nested within *Sebecia*; however, under the sebecosuchian hypothesis this definition would make *Sebecidae* almost synonymous with (but more inclusive than) *Ziphsuchia* and would include forms never included in the family before (e.g., *Notosuchus terrestris*, sphagesaurids, baurusuchians). Thus, in order to avoid such conflict, a minimum-clade definition is chosen, using representative members of the main clades of *Sebecidae* as internal specifiers (i.e., *Bretesuchus*, *S. icaeorhinus*, *Barinasuchus*). Also, given that *Sahitisuchus* is placed near the base of the clade and has been considered a sebecid (Kellner *et al.* 2014; Pinheiro *et al.* 2018), it is also included as an internal specifier. Finally, an additional rationale to prefer the minimum-clade definition is the recognition of some species-level taxa (e.g., *Iberosuchus macrodon*, *Bergisuchus dietrichbergi*, *Dentaneosuchus crassiproratus*) which are not nested among sebecids but closely related to them in recent publications (e.g., Rabi and Sebök 2015; Sellés *et al.* 2020; Martin *et al.* 2023).

The phylogenetic position of *Sebecidae* remains one of the major issues in mesoeucrocodylian phylogenetics (Pol and Powell 2011). During the early 2000's, although only represented by few species, sebecids (*Bretesuchus*) were inferred as nested in *Notosuchia*, closely related to baurusuchians (e.g., Ortega *et al.* 2000; Buckley and Brochu 2000; Pol 2003; Pol *et al.* 2004; Pol and Apesteguia 2005; Turner and Calvo 2005). However, Larsson and Sues (2007) found *Sebecidae* closely related to *Peirosauridae*, near the base of *Neosuchia*, and proposed the clade *Sebecia*. This topic has since been tackled in several studies, which have agreed on a placement of *Sebecidae* within *Notosuchia*, but with differing ideas on the position of sebecids within the diverse array of notosuchians. Pol and Powell (2011) inferred sebecids as closely related to baurusuchians, forming a monophyletic *Sebecosuchia*, a result that was also obtained in other studies derived from this same dataset, either centered on sebecids (e.g., Pol *et al.* 2012; Kellner *et al.* 2014; Bravo *et al.* 2021) or notosuchians in general (Pol *et al.* 2014; Leardi *et al.* 2015, 2018; Godoy *et al.* 2016). On the other hand, Montefeltro *et al.* (2013) found sebecids to be the sister group of *Peirosauridae*, which was also inferred in other analyses that modified this dataset (Geroto and Bertini 2019). Considering that both of these competing hypotheses have incorporated several sebecid taxa in their datasets (see Pinheiro *et al.* 2018 and Bravo *et al.* 2021) there is still a considerable uncertainty and lack of consensus about the phylogenetic affinities of *Sebecidae* and future integrative studies are needed.

Diagnostic apomorphies: Simpson (1937) diagnosed *Sebecidae*, solely based on *S. icaeorhinus*, as having narrow oreinirostral snouts, a primitive secondary palate (i.e., without participation of the pterygoids in the secondary choana) and double-jaw articulation (i.e., participation of the quadratojugal in the mandibular condyles and of the surangular in the glenoid cavity). Colbert (1946) added additional characteristics to Simpson's diagnosis, including

the presence of laterally compressed and serrated maxillary teeth. Sebecids were diagnosed phylogenetically as additional members of the clade were included in the datasets. Pol and Powell (2011) found that *Sebecidae* was diagnosed by seven synapomorphies: palatal parts of the premaxillae meet posteriorly to the incisive foramen; absence of an antorbital fenestra; flat lateral surface of the jugal, lacking a broad shelf anteriorly; absence of small neurovascular foramina on the lateral surface of the premaxilla-maxilla suture; the base of the postorbital process of the jugal is directed dorsally; surangular forms at least one-third of the glenoid fossa for an articulation for an additional condyle on the quadratojugal; and perinarial fossa with restricted extension. The lack of several of these features in taxa closely related to *Sebecidae*, due to their fragmentary nature, causes these synapomorphies to be ambiguous (Pol and Powell 2011).

***Baurusuchia* Walker 1968 [Darlim *et al.* 2021a]**

Registration number: 410 (Darlim *et al.* 2021a).

Definition (emended): “The most inclusive clade containing *Baurusuchus pachecoi* Price, 1945, but not *Sebecus icaeorhinus* Simpson 1937 (*Sebecidae*), *Sphagesaurus huenei* Price 1950 (*Sphagesauridae*), *Araripesuchus gomesii* Price 1959 (*Uruguaysuchidae*), *Montealtosuchus arrudacamposi* Carvalho, Vasconcellos & Tavares 2007 (*Peirosauridae*), [and] *Crocodylus niloticus* Laurenti 1768 (*Crocodylia*). This is a maximum-clade definition” (Darlim *et al.* 2021a:625).

Etymology: The name was proposed originally by Walker (1968) without specific explanation about the derivation of the name. Presumably the name is derived from the name of the included genus *Baurusuchus* Price 1945.

Reference phylogeny: Fig. 11 in Pinheiro *et al.* (2018), as originally designated by Darlim *et al.* (2021a); see also Figs. 1 and 2.

Composition: Based on the reference phylogeny, *Baurusuchia* includes *Cynodontosuchus*, *Baurusuchus*, *Stratiotosuchus*, *Pissarrachampsa*, *Campinasuchus*, and *Pabwehshi* (Darlim *et al.* 2021a). However, depending on the topology, *Baurusuchia* also includes other notosuchians that might be closer to baurusuchids than to other named clades, such as *Pakasuchus kapilimai* O’Connor *et al.* 2010, *Comahuesuchus brachybuccalis* Bonaparte 1991, *Chimaerasuchus paradoxus* Wu and Sues 1995, *Razanandrongobe sakalavae* Maganuco *et al.* 2016, and *Ogresuchus furatus* Sellés *et al.* 2020 (O’Connor *et al.* 2010, Montefeltro *et al.* 2013, Martin and de Broin 2016, Ruiz *et al.* 2021; Martins *et al.* 2023).

Comments: *Baurusuchia* was a taxon originally created by Walker (1968) as an infraorder, which was included in the suborder *Paracrocodylia*. This suborder constituted a separate suborder from the suborder *Crocodylia*, which included the traditional groups (then infraorders) such as *Mesosuchia* and *Eusuchia* (Walker 1968). *Baurusuchia* was abandoned in subsequent publications, and a less inclusive taxon (*Baurusuchidae*) was preferred (e.g., Gasparini 1972). The use of the name *Baurusuchia*, this time for a clade, was revived by Montefeltro *et al.* (2011) who defined it with a branch-based definition that only includes *Baurusuchidae* as currently recognized. Despite including the same taxa as the family, Montefeltro *et al.* (2011) defined the name based on the large morphological gap between baurusuchians and their closest relatives, and to give a stable phylogenetic framework for the group. Later, Darlim *et al.* (2021a) took the *Baurusuchia* definition of Montefeltro *et al.* (2011) and converted it according to the *PhyloCode* regulations. That definition, composition of the group, and reference phylogeny are followed in this contribution, although the operator “or” in the definition of Darlim *et al.* (2021a) has been replaced with “and” as an unrestricted emendation.

Diagnostic apomorphies: Given the same inclusion of taxa as *Baurusuchidae* (see below), this clade is currently diagnosed by the same traits (Montefeltro *et al.* 2011).

***Baurusuchidae* Price 1945 [Darlim *et al.* 2021a]**

Registration number: 411 (Darlim *et al.* 2021a).

Definition: “The least inclusive clade containing *Cynodontosuchus rothi* Woodward 1896, *Pissarrachampsa sera* Montefeltro, Larsson & Langer, 2011, and *Baurusuchus pachecoi* Price, 1945. This is a minimum-clade definition” (Darlim *et al.* 2021a:625).

Etymology: The name is derived from that of the type genus, *Baurusuchus* Price 1945, which was named after the Bauru Basin of Brazil, where it comes from (Price 1945).

Reference phylogeny: Fig. 47 in Darlim *et al.* (2021a), as originally designated by those authors; see also Figs. 1 and 2.

Composition: Based on the reference phylogeny, *Baurusuchidae* includes two putative basal *Baurusuchidae* (*Cynodontosuchus rothi* and *Gondwanasuchus scabrosus* Marinho *et al.* 2013), three pissarrachampsines (*Wargosuchus australis* Martinelli and Pais 2008, *Campinasuchus dinizi* Carvalho *et al.* 2011, and *Pissarrachampsia sera* Montefeltro *et al.* 2011), and six baurusuchines (*Baurusuchus pachecoi*, *Stratiotosuchus maxhechti*, *Baurusuchus salgadoensis* Carvalho *et al.* 2005, *Baurusuchus albertoi* Nascimento and Zaher 2010, *Aplestosuchus sordidus* Godoy *et al.* 2014, and *Aphaurosuchus escharafacies*, Darlim *et al.* 2021a).

Comments: *Baurusuchidae* was erected by Price (1945) to include *Baurusuchus pachecoi*. Afterwards, *Cynodontosuchus rothi* Woodward 1896 was assigned to the family (Price 1959). For the next five decades, two fragmentary taxa from Cenozoic European deposits (*Iberosuchus marcodon* and *Bergisuchus dietrichbergi*) were tentatively included in *Baurusuchidae* (Antunes 1975; Steel 1973; Molnar 1978), as well as taxa from the Cretaceous of South America (*Stratiotosuchus maxhechti* Campos *et al.* 2001 and *Pehuenchesuchus enderi* Turner and Calvo 2005) and Pakistan (*Pabwehshi pakistanensis* Wilson *et al.* 2001). At that time, the definitions and diagnostic features associated with *Baurusuchidae*, *Sebecidae*, and *Sebecosuchia* were unclear, and several taxa were alternatively placed in these groups by different authors.

More recent descriptions of taxa from the Late Cretaceous of Argentina and Brazil, together with the systematic framework presented by Montefeltro *et al.* (2011), helped to identify of a morphological gestalt that limited *Baurusuchidae* to South American Late Cretaceous taxa (Montefeltro *et al.* 2011, Godoy *et al.* 2014, Darlim *et al.* 2021a). *Baurusuchidae* has repeatedly been separated into two main groups, *Pissarrachampsinae* and *Baurusuchinae*, as well as taxa outside this dichotomy. The internal phylogenetic structure of *Baurusuchidae* was firstly identified by Montefeltro *et al.* (2011), and confirmed by Godoy *et al.* (2014), Darlim *et al.* (2021a) and Martins *et al.* (2023), as well as other phylogenies with broader scope with slightly different arrangements among the taxa (Geroto and Bertini 2019; Leardi *et al.* 2018; Ruiz *et al.* 2021).

Diagnostic apomorphies: The original description of *B. pachecoi* highlighted the divergent morphology relative to other crocodyliforms known at that time, such as the presence of a laterally compressed rostrum, absence of antorbital fenestrae, notch in the rostrum for reception of the hypertrophied dentary tooth, approximation of prefrontals, well-developed palatine bar, ectopterygoids forming the choanal border, quadratojugal extending dorsally as broad sheet contacting most of postorbital portion of postorbital bar, vertical quadrate, reduced number of teeth, hypertrophied maxillary tooth and ziphodont dentition. Later, some of the general traits recognized in *B. pachecoi* were also identified in *Sebecus icaeorhinus*, and other more distantly related taxa (Colbert 1946; Price 1955; Berg 1966; Buffetaut 1989), which blurred the clear-cut, differentiated morphology of baurusuchids with respect to other crocodyliform taxa.

In the early application of the phylogenetic systematics in crocodyliforms (e.g., Benton and Clark 1988; Clark 1994; Ortega *et al.* 2000), *B. pachecoi* played a central role in interpreting basal crocodyliform evolutionary patterns. Although *B. pachecoi* is present in nearly every phylogenetic analysis of *Crocodyliformes*, the growing diversity of baurusuchids was not promptly included in phylogenetic analyses. Montefeltro *et al.* (2011) were the first to investigate the synapomorphies of *Baurusuchidae*, leading to expanded taxonomic and character sampling in more recent analyses (Godoy *et al.* 2014; Darlim *et al.* 2021a). The identification of the synapomorphies at the baurusuchid node is obscured by the fragmentary nature of the fossils of the basal-most taxa *Cynodontosuchus* and *Gondwanasuchus*. Darlim *et al.* (2021a) recognized two common synapomorphies of baurusuchids: the premaxilla-maxilla suture being internalized in a notch for the reception of lower caniniform, and the serrated mesial and distal carinae of the teeth. However, when the ambiguous optimizations are considered, the number of baurusuchid synapomorphies could be increased considerably (alveolar margin of maxilla in lateral view arched anterior to enlarged caniniform tooth; anterior extension of palatines not reaching the level of the anterior margin of suborbital fenestrae; presence of posteroventral depressions in the mandibular symphysis; and the orientation of terminus of mandibular symphysis anterodorsal, at approximately 45 degrees to the jaw line) (Montefeltro *et al.* 2011).

***Baurusuchinae* Montefeltro, Larsson, and Langer 2011 [Darlim *et al.* 2021a]**

Registration number: 412 (Darlim *et al.* 2021a).

Definition: “The most inclusive clade containing *Baurusuchus pachecoi* Price, 1945, but not *Pissarrachampsasera* Montefeltro, Larsson & Langer, 2011 (Pissarrachampsinae). This is a maximum-clade definition” (Darlim *et al.* 2021a:625).

Etymology: As for the names of the more inclusive clades (see *Baurusuchia* and *Baurusuchidae*), the name is derived from that of the included genus *Baurusuchus* Price 1945.

Reference phylogeny: Fig. 47 in Darlim *et al.* (2021a), as originally designated by those authors; see also Figs. 1 and 2.

Composition: Based on the reference phylogeny, *Baurusuchinae* includes *Baurusuchus*, *Stratiosuchus*, *Aplestosuchus*, and *Aphaurosuchus* (Darlim *et al.* 2021a). *Baurusuchinae* was first proposed by Montefeltro *et al.* (2011) and has been recovered in the successive expansions of the original data matrix (Godoy *et al.* 2014; Darlim *et al.* 2021a). This clade encompasses most of the diversity of baurusuchids, including the three species in the genus *Baurusuchus* (*B. pachecoi*, *B. salgadoensis*, and *B. albertoi*), *Stratiosuchus*, *Aplestosuchus*, and *Aphaurosuchus*. At present, known baurusuchine occurrences are limited to the Adamantina Formation (Late Cretaceous, Bauru Basin) in state of São Paulo, Brazil (Montefeltro *et al.* 2011; Darlim *et al.* 2021b).

Diagnostic apomorphies: Baurusuchines are characterized by a relatively straight dorsal skull profile; the medial contact for the prefrontals occurring along most of their dorsal medial edge; broad frontals, about twice the width of nasals; jugal with the antorbital portion deeper than the infraorbital one; row of foramina dorsal to ectopterygoid-jugal suture; quadrate fenestrae internalized in otic notch; muscle scar in the medial surface of quadrate almost straight to curved (Darlim *et al.* 2021a).

***Pissarrachampsinae* Montefeltro, Larsson, and Langer 2011 [Darlim *et al.* 2021a]**

Registration number: 413 (Darlim *et al.* 2021a).

Definition: “The most inclusive clade containing *Pissarrachampsasera* Montefeltro, Larsson & Langer, 2011, but not *Baurusuchus pachecoi* Price, 1945 (Baurusuchinae). This is a maximum-clade definition” (Darlim *et al.* 2021a:625).

Etymology: Not stated by Darlim *et al.* (2021a), but presumably derived from the name of the type genus, *Pissarrachampsasera* Montefeltro, Larsson, and Langer 2011.

Reference phylogeny: Fig. 47 in Darlim *et al.* (2021a), as originally designated by those authors; see also Figs. 1 and 2.

Composition: Based on the reference phylogeny, *Pissarrachampsinae* includes *Pissarrachampsasera*, *Campinasuchus*, and *Wargosuchus* (Darlim *et al.* 2021a).

Comments: *Pissarrachampsinae* was first erected by Montefeltro *et al.* (2011) to include the baurusuchids closer to the then recently discovered *Pissarrachampsasera* than to *Baurusuchus pachecoi*. In addition to *P. sera*, the clade includes only *Campinasuchus dinizi* and *Wargosuchus australis* (Martinelli and Pais 2008) and was recovered in the successive expansions of the original matrix (Godoy *et al.* 2014; Darlim *et al.* 2021a). Pissarrachampsines were mostly recovered from outcrops of the Adamantina Formation (Upper Cretaceous, Bauru Basin) in Minas Gerais, Brazil (Montefeltro *et al.* 2011; Darlim *et al.* 2021b), and additionally the taxon *W. australis* from the Bajo de la Carpa formation (Santonian, Neuquén Basin, Martinelli and Pais 2008; Leardi *et al.* 2018). Only recently, the clade has been identified in other deposits of the Bauru Basin, in the state of São Paulo, Brazil (Darlim *et al.* 2021b). The possible geographical distribution of the clade was expanded with the inclusion of the Pakistani *Pabwehshi pakistanensis* (Wilson *et al.* 2001) within *Pissarrachampsinae* in a phylogenetic analysis conducted by Martins *et al.* (2023).

Diagnostic apomorphies: *Pissarrachampsinae* is characterized by a posterior portion of the dorsal surface of the nasal bearing a rugose broad depression; approximation of prefrontals along their medial edges anteriorly; presence of a midline longitudinal depression on the anterior portion of the frontal; a frontal longitudinal ridge extending anteriorly to the frontal mid-length; sculpture on the outer surface of the dentary and the splenial; and a rounded dorsal margin of the mandibular fenestra (Darlim *et al.* 2021a).

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Appendix 1: Valid species.

Here we provide a list of the valid species up to the date of the present article. The taxa are arranged following an indented list, to reflect their inclusion in the relevant clades, e.g.:

Clade 1 (more inclusive)

Clade 2 (less inclusive, included in 1)

Species 1

Species 2

Clade 3 (less inclusive, included in 1)

Clade 4 (less inclusive, included in 1 and in 3)

Species 3

Species 4

Species and clades involved in the conflict between the hypotheses named here as *Sebecosuchia* and *Sebecia* are nested (indented) only within *Notosuchia*. The phylogenetic placement of each species is based on the original publication; however, if additional information is available, it is provided along with citations of the relevant studies. Each of the species is presented with information regarding its provenance, stratigraphic units where fossils have been recovered, and the age of those units. That information is based on the references cited for those taxa.

Finally, some taxa have uncertain relationships. This can be caused by unstable placement among different phylogenetic hypotheses or, in a few cases, by other means (e.g., considered a *nomen dubium* in recent studies or materials have been lost). The specific causes of this uncertainty are described in those cases.

Notosuchia

Uruguaysuchidae

Anatosuchus minor Sereno, Sidor, Larsson, and Gado 2003—Elrhaz Formation, Tegama Series (Lower Cretaceous: Aptian–Albian), Gadoufaoua, Agadez District, Niger Republic (Sereno *et al.* 2003; Sereno and Larsson 2009).

Araripesuchus wegneri Buffetaut and Taquet 1979—Elrhaz Formation, Tegama Series (Lower Cretaceous: Aptian–Albian), Gadoufaoua, Agadez District, Niger Republic (Sereno and Larsson 2009)

Araripesuchus gomesii Price 1959—Romualdo Member, Santana Formation (Lower Cretaceous: Middle Albian), Araripe Basin, Northeastern Brazil.

Uruguaysuchus aznarezi Rusconi 1933—Guichón Formation (Hauterivian–Campanian), Paysandú Province, Uruguay (Rusconi 1933; Soto *et al.* 2011). Rusconi (1933) originally recognized an additional species of the genus *Uruguaysuchus* (*U. terrai*), but the name has since been treated as a junior synonym (Andrade and Bertini, 2005; Soto *et al.*, 2011).

Araripesuchus patagonicus Ortega, Gasparini, Buscalioni, and Calvo 2000—Candeleros Formation (Upper Cretaceous: lower Cenomanian), Río Limay Subgroup, Neuquén Group, Neuquén Province, Argentina (Ortega *et al.* 2000; Garrido 2010).

Araripesuchus buitreaensis Pol and Apesteguía 2005—Candeleros Formation (Upper Cretaceous: lower Cenomanian), Río Limay Subgroup, Neuquén Group, “La Buitrera” locality, Neuquén Province, Argentina (Pol and Apesteguía 2005; Garrido 2010; Fernández Dumont *et al.* 2020).

Araripesuchus rattoides Sereno and Larsson 2009—Kem Kem Beds (Upper Cretaceous: Cenomanian), Er Rachidia District, eastern Morocco. Exact provenance is unknown as it was recovered from the surface of a small wash at Darelkarib (Sereno and Larsson 2009).

Araripesuchus tsangatsangana Turner 2006—Anembalemba Member, Maevarano Formation (Upper Cretaceous: Campanian?–Maastrichtian), Mahajanga Basin, Madagascar (Turner 2006).

Mahajangasuchidae

Kaprosuchus saharicus Sereno and Larsson 2009—Echkar Formation, Tegama Series (Upper Cretaceous: Cenomanian), Iguidi, Agadez District, Niger Republic (Sereno and Larsson 2009).

Mahajangasuchus insignis Buckley and Brochu 1999—Upper part of the Anembalemba Member, Maevarano Formation (Upper Cretaceous: Campanian?–Maastrichtian), Mahajanga Basin, northwestern Madagascar (Buckley and Brochu 1999; Turner and Buckley 2008).

Peirosauridae

Amargasuchus minor Chiappe 1998—La Amarga Formation (Barremian–Early Aptian), southern Neuquén Province, Argentina (Chiappe 1998; Leanza *et al.* 2004).

Miadasuchus oblita (Buffetaut and Taquet 1979)—near contact between the Anembalemba and Miadana members, Maevarano Formation (Upper Cretaceous: Maastrichtian), Mahajanga Basin, Breviotra, Madagascar (Rasmussen, Simons, and Buckley 2009). Originally assigned to the problematic genus *Trematochampsia* (Buffetaut and Taquet 1979), but new materials and the uncertain nature of the genus *Trematochampsia* led to the recognition of a new genus (Rasmussen, Simons, and Buckley 2009).

Barcosuchus gradilis Lardi and Pol 2009—Cerro Castaño Member, Cerro Barco Formation (Lower Cretaceous: latest Albian), Chubut Group, Chubut, Argentina (Lardi and Pol 2009; Carballido *et al.* 2017).

Hamadasuchus rebouli Buffetaut 1994—Kem Kem beds (Upper Cretaceous: Cenomanian), south-eastern Morocco (Larsson and Sues 2007).

Antaeusuchus taozensis Nicholl, Hunt, Ouarhache, and Mannion 2021—Kem Kem Group (Upper Cretaceous: Cenomanian), Taouz township, Errachida Province, eastern Morocco (Nicholl *et al.* 2021).

Rukwasuchus yajabelijekundu Sertich and O'Connor 2014—Namba Member, Galula Formation (Aptian–Cenomanian), Red Sandstone Group, Rukwa Rift Basin, southwestern Tanzania (Sertich and O'Connor 2014).

Bayomesasuchus hernandezi Barrios, Paulina-Carabajal, and Bona 2016—Cerro Lisandro Formation (middle–late Turonian), Río Neuquén Subgroup, Neuquén Group, Cerro Bayo Mesa, Neuquén, Argentina (Barrios *et al.* 2016).

Lomasuchus palpebrosus Gasparini, Chiappe, and Fernández 1991—Portezuelo Formation (late Turonian–early Coniacian), Río Neuquén Subgroup, Neuquén Group, Department of Confluencia, Neuquén, Argentina (Gasparini *et al.* 1991; Garrido 2010).

Gasparinisuchus peirosauroides Martinelli, Sertich, Garrido, and Pradeiro 2012—Bajo de la Carpa Formation (Upper Cretaceous: Santonian), Neuquén Group, Neuquén Province, Argentina and Anacleto Formation (Upper Cretaceous: early Campanian), south of Malargüe, Mendoza Province, Argentina (Martinelli *et al.* 2012). The holotype of *Gasparinisuchus* was previously assigned to *Peirosaurus torminni* (Gasparini 1982) but later was considered a different taxon (Martinelli *et al.* 2012). The referred specimen was also originally assigned to *P. torminni* (Pradeiro *et al.* 2009) but was subsequently referred to *Gasparinisuchus* due to similarities in the maxilla (Martinelli *et al.* 2012).

Barrosasuchus neuquenianus Coria, Ortega, Arcucci, and Currie 2019—Bajo de La Carpa Formation (Upper Cretaceous: Santonian), Río Colorado Subgroup, Neuquén Group, Neuquén, Argentina (Coria *et al.* 2019).

Uberabasuchus terrificus Carvalho, Ribeiro, and Avila 2004—Serra da Galga Formation (Upper Cretaceous: Maastrichtian *sensu* Soares *et al.* 2021), Bauru Group, “Ponto 1 do Price”, Peirópolis rural neighborhood, Uberaba municipality, Minas Gerais State, Brazil (Carvalho *et al.* 2004).

Montealtosuchus arrudacamposi Carvalho, Vasconcellos, and Tavares 2007—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Bauru Basin, Monte Alto, São Paulo State, Brazil (Carvalho *et al.* 2007).

Peirosaurus torminni Price 1955—Serra da Galga Formation (Upper Cretaceous: Maastrichtian *sensu* Soares *et al.* 2021), Bauru Group, “Ponto 2 do Price”, Peirópolis rural neighborhood, Uberaba County, Minas Gerais State, Brazil. Only known from a single specimen that is limited to an isolated premaxilla, teeth, and postcranial bones (Martinelli *et al.* 2012). The taxon was originally included in *Sebecosuchia* by Price (1955) but was moved to a new family (*Peirosauridae*) by Gasparini (1982). Larsson and Sues (2007) suggested a possible synonymy with *Uberabasuchus*, an idea rejected by Martinelli *et al.* (2012) due to the presence of denticulate carinae in *Peirosaurus* but not in *Uberabasuchus*.

Taxa tentatively assigned to *Peirosauridae*

The following taxa have not been included in phylogenetic datasets to date but have been considered members of *Peirosauridae*.

Kinesuchus overoi Filippi, Barrios, and Garrido 2018—Bajo de la Carpa Formation (Upper Cretaceous: Santonian), Río Colorado Subgroup, Neuquén Group, Neuquén Province, Argentina (Filippi *et al.* 2018).

Patagosuchus anieliensis Lio, Agnolín, Juárez Valeri, Filipi, and Rosales 2016—Portezuelo Formation (late Turonian–early Coniacian), Río Neuquén Subgroup, Neuquén Group, Lago Los Barreales, Neuquén Province, Argentina (Lio *et al.* 2015).

Colhuehuapisuchus lunai Lamanna, Casal, Ibiricu, and Martínez 2019—Lago Colhué Huapi Formation (Upper Cretaceous: Campanian–?lower Maastrichtian), Chubut Group, southern Chubut, Argentina (Lamanna *et al.* 2019).

Itasuchidae

Stolokrosuchus lapparenti Larsson and Gado 2000—Elrhaz Formation, Tegama Series (Lower Cretaceous: Aptian–Albian), Gadoufaoua, Agadez District, Niger Republic (Larsson and Gado 2000; Sereno and Larsson 2009).

Caririsuchus camposi (Kellner 1987)—Romualdo Member, Santana Formation (Lower Cretaceous: middle Albian), Araripe Basin, NE Brazil. Originally erected as a species of a new genus (*Caririsuchus camposi*) but later was referred to the genus *Itasuchus* (Buffetaut 1991). Most analyses consider it an independent taxon and place it as a basal peirosaurid (e.g., Pinheiro *et al.* 2018; Geroto and Bertini, 2019).

Barreirosuchus franciscoi Iori and Garcia 2012—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Bauru Basin, Monte Alto, São Paulo State, Brazil (Iori and Garcia 2012).

Pepesuchus deiseae Campos, Oliveira, Figueirido, Riff, Azevedo, Carvalho, and Kellner 2011—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Bauru Group, Presidente Prudente, São Paulo State, Brazil (Campos *et al.* 2011; Geroto and Bertini 2018).

Roxochampsia paulistanus (Roxo 1936)—Adamantina (Upper Cretaceous: Turonian–Campanian) and Presidente Prudente (Upper Cretaceous: late Campanian–early Maastrichtian) formations, Bauru Group, Alfredo Marcondes municipality, southwestern São Paulo State, Brazil (Pinheiro *et al.* 2018). Originally named

Gonipholis paulistanus (Roxo 1936), that name was later considered a *nomen dubium*. Pinheiro *et al.* (2018) restudied the material and resurrected this taxon as an itasuchid.

Itasuchus jesuinoi Price 1955—Serra da Galga Formation (Upper Cretaceous: Maastrichtian *sensu* Soares *et al.* 2021), Bauru basin, Peirópolis rural neighborhood, Uberaba County, Minas Gerais State, Brazil and Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Bauru Group, São Paulo State, Brazil (Price 1955; Mezzalana 1989; Geroto and Bertini 2018). *Itasuchus jesuinoi* was originally considered a goniopholidid (Price 1955), but later was restudied and assigned as a peirosaurid (Buffetaut 1991; Pinheiro *et al.* 2018; Geroto and Bertini 2019).

***Sebecidae* + allied taxa (unnamed clade)**

Bergisuchus dietrichbergi Kuhn 1968—Messel Formation, Messel, Hessen, Germany (Kuhn 1968; Ortega 1996; Rossmann *et al.* 2000). Carroll (1988) included *Bergisuchus dietrichbergi* within *Baurusuchidae*. Currently, numerous phylogenetic analyses support the close relationship of this species with *Sebecidae* (Pol and Powell 2011; Pol *et al.* 2014; Godoy *et al.* 2016; Sellés *et al.* 2020; Bravo *et al.* 2021).

Iberosuchus macrodon Antunes 1975—Felgueira Grande Formation (middle Eocene), Vale Furado, Pataias, Leiria, Portugal (Antunes 1975; Ortega 1996). Numerous phylogenetic analyses support the close relationship of this species with *Sebecidae* (Pol and Powell 2011; Pol *et al.* 2014; Godoy *et al.* 2016; Sellés *et al.* 2020; Bravo *et al.* 2021).

Dentaneosuchus crassiproratus Martin, Pochat-Coutilloux, Laurent, Perrier, Robert, and Antoine 2023—La Vernières fossiliferous locality (Eocene, Bartonian), Réalmont, Tarn, France. This species was previously assigned to the genus *Atacisaurus* (former type specimen of the species of *Atacisaurus crassiproratus* Astre 1931), but prior analyses considered the genus *Atacisaurus* a *nomen dubium* (Jouve, 2016). Thus a new combination was proposed (*Dentaneosuchus crassiproratus*), and new materials were assigned to it based on mandibular similarities (Martin *et al.* 2023).

Sebecidae

Ogresuchus furatus Sellés, Blanco, Vila, Marmi, López-Soriano, Llácer, Frigola, Canals, and Galobart 2020—Trempe Formation (upper Cretaceous), El Mirador, Lleida, Catalonia, Spain (Sellés *et al.* 2020).

Sahitisuchus fluminensis Kellner, Pinheiro, and Campos 2014—São José Form (middle–upper Paleocene), São José de Itaboraí, Rio de Janeiro, Brazil (Kellner *et al.* 2014).

Sebecus ayrampu Bravo, Pol, and García-López 2021—Mealla Formation (middle Paleocene), Mina Aguilar, Jujuy, Argentina (Bravo *et al.* 2021).

Sebecus querejazus Buffetaut and Marshal 1991—Santa Lucía Formation (late Paleocene), Vila Vila, Mizque, Cochabamba, Bolivia (Buffetaut and Marshal 1991; Pochat-Cottilloux *et al.* 2022). Paolillo and Linares (2007) proposed the name *Zulmasuchus querejazus* for this taxon, but the results of most phylogenetic analyses so far are compatible with the original referral of this species to *Sebecus* (Pol and Powell 2011; Pol *et al.* 2012, 2014; Leardi *et al.* 2018; Sellés *et al.* 2020; Bravo *et al.* 2021). Gasparini *et al.* (1993) referred to this species as *Sebecus carajazus*, *lapsus calami* for *Sebecus querejazus*.

Sebecus icaeorhinus Simpson 1937—Sarmiento Formation (middle Eocene), Bird Clay, Cañadón Hondo, Chubut, Argentina (Simpson 1937; Colbert 1946; Gasparini 1982; Pol *et al.* 2012; Bravo *et al.* 2022).

Sebecus huilensis Langston 1965—Formación Villa Vieja (middle Miocene), Monkey Beds, Huila, Colombia (Langston 1965; Busbey 1986; Paolillo and Linares 2007). Paolillo and Linares (2007) proposed the name *Langstonia huilensis* for this taxon, but the results of most phylogenetic analyses so far are compatible with the original referral of this species to *Sebecus* (Pol and Powell 2011; Pol *et al.* 2012, 2014; Leardi *et al.* 2018; Sellés *et al.* 2020; Bravo *et al.* 2021).

Bretesuchus bonapartei Gasparini, Fernandez, and Powell 1993—Maíz Gordo Formation (middle Eocene), El Brete, Salta, Argentina (Gasparini *et al.* 1993).

Ayllusuchus fernandesi Gasparini 1984—Lumbrera inferior Formation (middle Eocene), Mina Aguilar, Jujuy, Argentina (Gasparini 1984).

Barinasuchus arveloi Paolillo and Linares 2007—Parángula Formation (middle Miocene), Quebrada Socó, Barinas, Venezuela (Paolillo and Linares 2007).

***Ziphosuchia* / *Eunotosuchia* (not including *Uruguaysuchidae*)**

Libycosuchus brevirostris Stromer 1914—Bahariya Formation (Upper Cretaceous: early Cenomanian), Bahariya Oasis, Egypt (Stromer 1914; Buffetaut 1976a; Tumarkin-Deratzian *et al.* 2004).

Simosuchus clarki Buckley, Brochu, Krause, and Pol 2000—Maevarano Formation (Upper Cretaceous: Maastrichtian), southeast of the village of Berivotra, Mahajanga Basin, northwestern Madagascar (Buckley *et al.* 2000; Turner and Sertich 2010).

Malawisuchus mwakasyungutiensis Gomani 1997—Dinosaur Beds (Lower Cretaceous: probably Aptian), Mwakasyunguti area, Karonga District, Malawi (Gomani 1997).

Pakasuchus kapilimai O'Connor, Sertich, Stevens, Roberts, Gottfried, Hieronymus, Jinnah, Ridgely, Ngasala, and Temba 2010—Namba member of the Galula Formation (Upper Cretaceous: Cenomanian–Campanian), south of Lake Rukwa, Rukwa Rift Basin, Tanzania (O'Connor *et al.* 2010).

Lavocatchampsia sigogneaurusselae Martin and de Broin 2016—Kem Kem Beds (Cretaceous: late Albian–early Cenomanian), OuedTal locality, east of Erfoud city, Errachidia Province, Morocco (Martin and de Broin 2016).

Xenodontosuchia

Baurusuchia

Baurusuchidae

Cynodontosuchus rothi Woodward 1896—Bajo de La Carpa Formation (Santonian), “Paso del Sapo”, Neuquén City, Neuquén Province, Argentina (Woodward 1896; Gasparini 1972).

Pabwehshi pakistanensis Wilson, Malkani, and Gingerich 2001—Pab Formation (Maastrichtian), Vitakri village, eastern Balochistan Province, Pakistan (Wilson *et al.* 2001).

Gondwanasuchus scabrosus Marinho, Iori, Carvalho, and Vasconcellos 2013—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Fazenda Buriti, General Salgado municipality, São Paulo State, Brazil (Marinho *et al.* 2013).

Baurusuchinae

Baurusuchus pachecoi Price 1945—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Vila do Veado, Paulo de Faria municipality, São Paulo State, Brazil (Price 1945).

Baurusuchus salgadoensis Carvalho, Campos, and Nobre 2005—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Fazenda Buriti, General Salgado municipality, São Paulo State, Brazil (Carvalho *et al.* 2005).

Stratiosuchus maxhechti Campos, Suarez, Riff, and Kellner 2001—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Irapuru municipality, São Paulo State, Brazil (Campos *et al.* 2001; Riff 2003).

Aplestosuchus sordidus Godoy, Montefeltro, Norell, and Langer 2014—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Fazenda Buriti, General Salgado municipality, São Paulo State, Brazil (Godoy *et al.* 2014).

Aphaurosuchus escharaphacies Darlim, Montefeltro, and Langer 2021—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Furnas farm, Jales municipality, São Paulo State, Brazil (Darlim *et al.* 2021).

Aphaurosuchus kaiju Martins, Queiroz, Ruiz, Langer, and Montefeltro 2023—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Roadside outcrop at 9.6 km south of Jales, Jales municipality, São Paulo State, Brazil (Martins *et al.* 2023).

Pissarrachampsinae

Pissarrachampsia sera Montefeltro, Larsson, and Langer 2011—Adamantina (Upper Cretaceous: Turonian–Campanian), Inhaumas-Arantes Farm, Campina Verde municipality, Minas Gerais State, Brazil (Montefeltro *et al.* 2011).

Campinasuchus dinizi Carvalho, Teixeira, Ferraz, Ribeiro, Martinelli, Neto, Sertich, Cunha, Cunha, and Ferraz 2011—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Três Antas Farm, Campina Verde Municipality, Minas Gerais State, Brazil (Carvalho *et al.* 2011).

Wargosuchus australis Martinelli and Pais 2008—Bajo de La Carpa Formation (Santonian), vicinity of Neuquén city, Neuquén Province (Martinelli and Pais 2008).

Sphagesauria

Morrinhosuchus luziae Iori and Carvalho 2009—Adamantina Formation (Upper Cretaceous: Turonian–Santonian), Bauru Group, Monte Alto and Cândido Rodrigues municipalities, São Paulo State, Brazil (Iori and Carvalho 2009; Iori *et al.* 2018).

Notosuchus terrestris Woodward 1896—Bajo de La Carpa Formation (Santonian); Boca del Sapo, Neuquén City, Neuquén Province, Argentina; and Paso Córdoba, Río Negro Province, Argentina (Woodward 1896; Andrade and Bertini 2008b; Fiorelli and Calvo 2008; Barrios *et al.* 2018).

Llanosuchus tamaensis Fiorelli, Leardi, Hechenleitner, Pol, Basilici, and Grellet-Tinner 2016—Los Llanos Formation (Upper Cretaceous: Campanian?), Colozacan valley, 4 km south of Tama village, La Rioja Province, Argentina (Fiorelli *et al.* 2016).

Mariliasuchus amarali Carvalho and Bertini 1999—Adamantina/Araçatuba Formation (Upper Cretaceous: Turonian–Campanian), vicinities of Marília city, São Paulo State, Brazil (Carvalho and Bertini 1999; Zaher *et al.* 2006; Andrade and Bertini 2008b).

Mariliasuchus robustus Nobre, Carvalho, Vasconcellos, and Nava, 2007—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), vicinity of Marília city, São Paulo State, Brazil (Nobre *et al.* 2007).

Coronelsuchus civali Pinheiro, Souza, Bandeira, Brum, Pereira, Castro, Ramos, and Simbra 2021—Araçatuba Formation (Upper Cretaceous, Turonian), CG6 site of Coronel Goulart district, Álvarez Machado municipality, São Paulo State, Brazil (Pinheiro *et al.* 2021).

Labidiosuchus amicum Kellner, Figueiredo, Azevedo, and Campos 2011b—Serra da Galga Formation (Upper Cretaceous: Maastrichtian *sensu* Soares *et al.*, 2021), Bauru Group, Peirópolis rural neighborhood, Uberaba municipality, Minas Gerais State, Brazil (Kellner *et al.* 2011b).

Eptalofosuchus viridi Marinho, Martinelli, Basilici, Soares, Marconato, Ribeiro, and Iori 2022—Uberaba Formation (Upper Cretaceous: Campanian?), Bauru Group, Uberaba municipality, Minas Gerais State, Brazil (Marinho *et al.* 2022).

Sphagesauridae

Adamantinasuchus navae Nobre and Carvalho 2006—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), 25 km southwest of Marília city, São Paulo State, Brazil (Nobre and Carvalho 2006).

Yacarerani boliviensis Novas, Pais, Pol, Carvalho, Scanferla, Mones, and Riglos 2009—Cajones Formation (Upper Cretaceous: Turonian–Santonian), Amboro National Park, Santa Cruz de la Sierra, Bolivia (Novas *et al.* 2009; Leardi *et al.* 2015b).

Caipirasuchinae

Caipirasuchus paulistanus Iori and Carvalho 2011—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), São Francisco Farm, Monte Alto city, São Paulo State, Brazil (Iori and Carvalho 2011).

Caipirasuchus montealtensis (Andrade and Bertini 2008)—Adamantina Formation (Upper Cretaceous), Bauru Group, Monte Alto municipality, São Paulo State, Brazil. Previously, the species was named *Sphagesaurus montealtensis* (Andrade and Bertini 2008), but it was reallocated to the genus *Caipirasuchus* by Iori *et al.* (2013).

Caipirasuchus stenognathus Pol, Nascimento, Carvalho, Riccomini, Pires-Domingues, and Zaher 2014—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Boa Esperança Farm, General Salgado municipality, São Paulo State, Brazil (Pol *et al.* 2014).

Caipirasuchus attenboroughi Ruiz, Bronzati, Ferreira, Martins, Queiroz, Langer, and Montefeltro 2021—Santo Anastácio Formation (Upper Cretaceous: Turonian–Campanian), 111 km on SP-463 highway, General Salgado municipality, São Paulo state, Brazil (Ruiz *et al.* 2021).

Caipirasuchus mineirus Martinelli, Marinho, Iori, and Ribeiro 2018—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), “Fazenda Três Antas” site, Campina Verde municipality, Minas Gerais State, Brazil (Martinelli *et al.* 2018).

Sphagesaurinae

Sphagesaurus huenei Price 1950—Adamantina Formation (Upper Cretaceous), Bauru Group. The holotype (DGM 332-R) was found in a railroad cut between Presidente Bernardes and Santo Anastácio in São Paulo State, Brazil; the paratype (DGM 333-R) was found near Catanduva, also in São Paulo State. Both DGM 332-R and DGM 333-R are isolated sphagesaurid molariforms, but Pol (2003) described an almost complete skull and fragmentary mandible (RCL-100) referred to *Sphagesaurus huenei*, from an unknown locality in the São Paulo State called “Buenópolis”. Even though the precise locality could not be properly identified, the sediment around the fossil matches that observed in several outcrops of the Adamantina Formation, especially from the Catanduva area, and the teeth are very similar to those of *Sphagesaurus huenei* (DGM 332-R and DGM 333-R), at this point, the only known sphagesaurid taxon, and hence justifying the referral of RCL-100 to this taxon.

Armadillosuchus arrudai Marinho and Carvalho 2009—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Fazenda Rao X, General Salgado municipality, São Paulo State, Brazil (Carvalho *et al.* 2005).

Caryonosuchus pricei Kellner, Campos, Riff, and Andrade 2011a—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), vicinity of Presidente Prudente municipality, São Paulo State, Brazil. Originally described as *Sphagesaurus* sp. by Kellner *et al.* (1995); assigned to the new genus *Caryonosuchus* by Kellner *et al.* (2011a).

Notosuchian? taxa with uncertain relationships

Taxa are included in this category if their phylogenetic position has varied among studies. Taxonomic issues have been recognized for some of these taxa (e.g., *Trematochampsia taqueti*) or the material has been lost (e.g., *Brasileirosaurus pachecoi*).

Fortignathus felixi (Lapparent de Broin 2002)—Echkar Formation, Tegama Series (Upper Cretaceous: Cenomanian), west of In Abangharit, Agadez District, Niger (Lapparent de Broin 2002; Sereno and Larsson 2009; Young *et al.* 2016). Lapparent de Broin (2002) recognized this taxon as an additional species of the genus *Elosuchus*. Young *et al.* (2016) reevaluated this taxon as a tethysuchian and erected a new genus for it, *Fortignathus*. However, Jouve and Jalil (2020) criticized some of the characters used by Young *et al.* (2016) and consider *Fortignathus* a peirosaurid.

Trematochampsia taqueti Buffetaut 1974—In Becten Formation (Upper Cretaceous: Turonian–Coniacian), Niger (Buffetaut 1974; Meunier and Larsson 2018). *Trematochampsia* was described by Buffetaut in several contributions (Buffetaut 1974, 1976b) based on fragmentary but well-preserved isolated bones. The validity of the taxon has been questioned several times (e.g., Gasparini *et al.* 1991; Larsson and Sues 2007; Larsson and Sereno 2009) and the name has been considered a *nomen dubium* due to the lack of diagnostic features on the holotype (a lacrimal) and the recognition of several morphotypes among the referred materials (Meunier and Larsson 2018).

Microsuchus schilleri Dolgopol de Saez 1922—Bajo de La Carpa Formation (Upper Cretaceous: Santonian), Río Colorado Subgroup, Neuquén Group, Neuquén, Argentina (Leardi *et al.* 2015). Dolgopol de Saez (1922) studied *Microsuchus* and placed the taxon as a new species of the genus *Goniopholis* based on the vertebral and ostederm anatomy. Leardi *et al.* (2015a) placed it as a basal member of either *Notosuchia* or *Neosuchia*.

Neuquensuchus universitas Fiorelli and Calvo 2007—Bajo de La Carpa Formation (Upper Cretaceous: Santonian), Río Colorado Subgroup, Neuquén Group, Neuquén, Argentina (Fiorelli and Calvo 2007; Lio *et al.* 2018). Fiorelli and Calvo (2007) published on the holotype specimen and considered the taxon a non-mesoeucrocodylian crocodyliform. This view was challenged by Leardi *et al.* (2015) who found it nested within *Ziphosuchia*; however, in a review based on additional material Lio *et al.* (2018) found it in a large polytomy taking positions as either a non-mesoeucrocodylian crocodyliform or at the base of *Notosuchia*.

Brasileosaurus pachecoi Huene 1931—Adamantina Formation, near Presidente Prudente. Initially described as a “small coelurosaurian” (Huene 1931). Huene (1933) suggested a close similarity, or even conspecificity, to *Uruguaysuchus aznarezi*.

Candidodon itapecuruense Carvalho and Santos 1988—Itapecuru Formation (Lower Cretaceous: Albian), Itapecuru-Mirim municipality, Maranhão State, Brazil. Described as a mammal by Carvalho and Campos (1988), recognized as a notosuchian by Carvalho (1994) and assigned to a new clade, *Candidodontidae*, by Carvalho *et al.* (2004). Montefeltro *et al.* (2009) reviewed *Candidodontidae* and proposed a branch-based definition for it. In a comprehensive phylogenetic analysis, *Candidodon* is placed in its own clade, nested within *Ziphosuchia*, by Martin and de Broin (2016), as a sister-taxon to *Ziphosuchia* (Pol *et al.* 2014), as a member of *Uruguaysuchidae* (Pinheiro *et al.* 2018), or as a basal member of *Notosuchia* (Pinheiro *et al.* 2021).

Chimaerasuchus paradoxus Wu, Sues, and Sun 1995—Wulong Formation (Lower Cretaceous: Aptian–Albian), small hill on the south bank of the Yangtze River, opposite Yichang, Hubei Province, China (Wu and Sues 1996). Originally described as a member of *Notosuchidae*, with affinities to *Notosuchus* and *Malawisuchus* (Wu and Sues 1996), in recent analysis it was placed as the sister-clade of *Sebecosuchia* or *Comahuesuchus* + *Sebecosuchia* (Pol *et al.* 2014 and subsequent works with the same dataset).

Comahuesuchus brachybuccalis Bonaparte 1991—Bajo de La Carpa Formation (Santonian), northern Neuquén city, Neuquén Province, Argentina (Bonaparte 1991; Martinelli 2003). It was placed as the sister-clade of *Sebecosuchia* (Pol *et al.* 2014 and subsequent works with the same dataset), as a basal member of *Baurusuchia* (Ruiz *et al.* 2021), and as a basal member of *Sphagesauria* (Pinheiro *et al.* 2018, 2021).

Comahuesuchus bonapartei Kellner, Figueiredo, and Calvo 2023—upper part of the Portezuelo Formation or middle portion of the Sierra Barrosa Formation (upper Turonian–lower Coniacian), northwest of Neuquén city, Neuquén Province, Argentina (Kellner *et al.* 2023). It was incorporated into Pinheiro *et al.*'s (2021) dataset and placed in a group with *C. brachybuccalis* at the base of *Sphagesauria*.

Razanandrongobesakalavae Maganuco, Dal Sasso, and Pasini 2006—Mahajanga Basin, Isalo IIIb subunit, ‘Facies Mixte Dinosauriens’ (Middle Jurassic: Bathonian), vicinities of the cities of Ambondromamy and Andranomamy, Mahajanga Province, Madagascar (Maganuco *et al.* 2006; Dal Sasso *et al.* 2017). Originally assigned only to *Archosauria*, because its phylogenetic position was either basal within *Theropoda* or basal within *Crocodylomorpha* (Maganuco *et al.* 2006). New material allowed to Dal Sasso *et al.* (2017) and, subsequently, Sellés *et al.* (2020) to place it as a sebecosuchian, using the dataset of Figueirido *et al.* (2016) and Pol *et al.* (2014), respectively.

Pehuenchesuchus enderi Turner and Calvo 2005—Río Neuquén Formation (Upper Cretaceous: Turonian–Santonian), Cañadón Río Seco site, north of Rincón de los Sauces, Neuquén Province, Argentina (Turner and Calvo 2005). Described as a basal sebecosuchian by Turner and Calvo (2005), an inference also seen in the results of other analyses (Pol and Powell 2011; Leardi *et al.* 2018). Pinheiro *et al.* (2018) placed this species as a member of *Sebecidae*.

Eremosuchus elkoholicus Buffetaut 1982—(Eocene), El Kohol locality, western Algeria (Buffetaut 1989; Turner and Calvo 2005). Described as a member of *Trematochampsidae* (Buffetaut 1989), this species was placed in different positions within *Sebecosuchia* in distinct analysis since that of Ortega *et al.* (1996); additionally, Montefeltro (2013) assigned it to *Baurusuchidae*.

Lorosuchus nodosus Pol and Powell 2011—Río Loro Formation (?upper Paleocene), Aguas Chiquitas, Tucumán, Argentina (Pol and Powell 2011; Bravo *et al.* 2021). The taxon was included originally in *Sebecidae* by Pol and Powell (2011). However, the results of the phylogenetic analysis under implied weights made by Bravo *et al.* (2021) open the possibility of considering this taxon outside the *Sebecidae*: as a basal sebecosuchian, or allied to *Mahajangasuchidae*, or together with *Stolokrosuchus* as a basal notosuchian.

Ilchunaia parca Rusconi 1946—Divisadero Largo Formation (upper Eocene), Mina Atala, Mendoza, Argentina (Rusconi 1946; Langston 1956; Gasparini 1972). This taxon was originally described by Rusconi (1946) as a neosuchian. Langston (1956) transferred it into *Sebecosuchia*, and later, Gasparini (1972) reclassified *Ilchunaia parca* as a potential sebecid. Currently the holotype is missing (Gasparini *et al.* 1993).

Baurusuchus albertoi Nascimento and Zaher 2010—Adamantina Formation (Upper Cretaceous: Turonian–Campanian), Boa Esperança farm, General Salgado municipality, São Paulo State, Brazil (Nascimento and Zaher 2010, 2011). Godoy *et al.* (2014) placed this species as a close relative of *Aplestosuchus sordidus*.

Coringasuchus anisodontis Kellner, Pinheiro, Azevedo, Henriques, Carvalho, and Oliveira 2009—Alcântara Formation (Upper Cretaceous: early Cenomanian), Laje do Coringa, Cajual Island, Maranhão State, Brazil (Kellner *et al.* 2009). Pol *et al.* (2014) performed the most comprehensive analysis of the phylogenetic position of *Coringasuchus*, placing it as a member of *Sphagesauridae* or as a non-sphagesaurid sphagesaurian.

Doratodon carcharidens Bunzel 1871—Grünbach Formation (early Campanian), Gosau Group, Muthmannsdorf, Austria (Bunzel 1871; Company *et al.* 2005) and Csehbánya Formation (Santonian), Bakony Mountains, Veszprém County, Hungary (Rabi and Sebök 2015). Rabi and Sebök (2015) placed this taxon within *Sebecosuchia*, whereas Ruiz *et al.* (2023) inferred a sister relationship with *Sebecia*.

Doratodon ibericus Company, Suberbiola, Ruiz-Omeñaca, and Buscalioni 2005—Sierra Perenchiza Formation (Campanian), Valencia, Spain (Company *et al.* 2005). The species has never been included independently in a phylogenetic analysis, rather it has been combined with *Doratodon carcharidens* into a single OTU. *Doratodon* (including *D. ibericus* and *D. carcharidens*) has been placed as the sister taxon to *Sebecosuchia* by Company *et al.* (2005); however, it has since been frequently excluded from phylogenetic analyses.