



# A NEW NOMINAL GENUS FOR “*PRESTOSUCHUS*” *CHINIQUENSIS* HUENE, 1938 (TRIASSIC OF SOUTHERN BRAZIL): *HUENESUCHUS*, GENUS NOVUS ET COMBINATIO NOVA

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**ABSTRACT** – The nominal genus *Prestosuchus* Huene was originally proposed comprising two nominal species, but without a valid indication of the type-species. According to the International Code of Zoological Nomenclature, this indication is essential for proposals after the year 1930. Consequently, both nominal species, although valid, have a very uncomfortable situation. Therefore, a new nominal genus, *Huenesuchus*, is here proposed to correct this nomenclatural situation to be used in the new combination *Huenesuchus chiniquensis*. In addition, it is noted that two class-group names that have been used lately in the literature are previously occupied. The first, *Suchia* Krebs, is previously occupied by Simpson. The second, *Loricata* Merrem, is previously occupied by Schumacher. Therefore, two substitute names are here proposed: *Holosuchia* for the first and *Loricatosuchia* for the second.

**Keywords:** Archosauria, *Prestosuchus*, *Huenesuchus*, Santa Maria Formation, Triassic.

**RESUMO** – O gênero nominal *Prestosuchus* Huene foi originalmente proposto compreendendo duas espécies nominais, mas sem indicação válida de espécie-tipo. De acordo com o Código Internacional de Nomenclatura Zoológica, esta indicação é essencial para propostas após o ano de 1930. Como consequência, ambas as espécies nominais, embora válidas, possuem uma situação bastante incômoda. Portanto, é aqui proposto um novo gênero nominal, *Huenesuchus*, para corrigir esta situação nomenclatural, a ser utilizado na nova combinação *Huenesuchus chiniquensis*. Além disso, nota-se que dois nomes de grupo-classe que ultimamente têm sido utilizados na literatura estão previamente ocupados. O primeiro, *Suchia* Krebs, está ocupado pelo de Simpson. O segundo, *Loricata* Merrem, está ocupado pelo de Schumacher. Portanto, são aqui propostos dois nomes substitutos: *Holosuchia* para o primeiro e *Loricatosuchia* para o segundo.

**Palavras-chave:** Archosauria, *Prestosuchus*, *Huenesuchus*, Formação Santa Maria, Triássico.

## INTRODUCTION

Crocodylotarsian archosaurs of the Brazilian Triassic have been the subject of several doctoral/master's theses (Mattar, 1985; Azevedo, 1991; Kischlat, 2003; Mastrantonio, 2010; França, 2011; Lacerda, 2012; Raugust, 2014; Roberto-da-Silva, 2017; Santos, 2017) and articles (Mattar, 1987, 1989; Azevedo, 1995; Kischlat, 2002; França *et al.*, 2011, 2013; Mastrantonio *et al.*, 2013, 2019; Roberto-da-Silva *et al.*, 2016, 2020; Lacerda *et al.*, 2015, 2016, 2018; Desojo *et al.*, 2020) and *Prestosuchus chiniquensis* Huene, 1938a, has been at the center of discussion in the presence of new specimens belonging to this taxon. However, the formal availability of this nominal genus has not been investigated until now. The application of the International Code of Zoological Nomenclature (I.C.Z.N., 1999) shows that *Prestosuchus* Huene, 1938a, is an unavailable genus name. The goal of

this paper is to discuss the nomenclatural validity of the nominal genus *Prestosuchus* Huene, 1938a, as well as some higher order names in the Archosaurian lineage towards the current crocodylians.

## MATERIAL AND METHODS

The anatomical terms follow that proposed by the anatomical committees (Baumel *et al.*, 1993; I.C.V.G.A.N., 2012; F.I.P.A.T., 2019) in place of traditional descriptive ones. Concerning archosaurs, the avian nomenclature (Baumel *et al.*, 1993) occupies a central position. For a comprehensive understanding of general terminology, I suggest Collin (2007).

Throughout the body of this paper, the articles of the International Code of Zoological Nomenclature (I.C.Z.N., 1999, hereinafter referred to as the *Code*) are precisely cited when and where they are relevant. I propose to use the symbol

“G” representing “character”. This symbol was once used for the old Brazilian currency (cruzeiro) and nowadays, this currency is obsolete. Now, this symbol can have a utility.

**Institucional Abbreviations:** **CPEZ**, Coleção de Paleontologia do Museu Paleontológico e Arqueológico Walter Ilha, São Pedro do Sul, Rio Grande do Sul, Brazil; **SNSB-BSPG**, Staatliche Naturwissenschaftliche Sammlungen Bayerns (SNSB), Bayerische Staatssammlung für Paläontologie und Geologie (BSPG), München, Germany; **UFRGS-PV**, Laboratório de Paleovertebrados, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; **ULBRA-PVT**, Coleção de Paleovertebrados, Universidade Luterana do Brasil, Canoas, Rio Grande do Sul, Brazil.

### BACKGROUND: FRIEDRICH VON HUENE AND HIS WORK IN BRAZIL

Huene's (1935–42) book, *Die Fossilen Reptilien des Sudamerikanischen Gondwanalandes*, is the start point of the knowledge of the Brazilian Triassic Paleontology. This work has a Portuguese translation published in 1990 by Carlos Burguer Júnior and revised by M.C. Barberena (see Huene, 1990). Huene's (1935–42) book was published in four parts (*Lieferungen*). The first one (dealing with Anomodontia) was published on December 1<sup>st</sup>, 1935. The second one (Cynodontia) was published on October 26<sup>th</sup>, 1936, and the third and fourth parts (Pseudosuchia and Saurischia, Rhynchosauridae, and the final section – *Schlußabschnitt*) were published in Spring (*Frühjahr*) of 1942 (Huene, 1942: v, 1990:7).

There is a previous report (Huene, 1933a:130) in the journal *Forschungen und Fortschritte* where he introduced three new binomina *Stahleckeria potens*, *Belesodon magnificus*, and *Prestosuchus chiniquensis*. Concerning the binomen *Prestosuchus chiniquensis*, it is a *nomen nudum* (I.C.Z.N., 1999:111) because it was not described nor defined, directly or indirectly by a bibliographic reference (arts. 13.1.1 & 13.1.2).

There is also a *Referate* (report) authored by himself published in 1938a in the journal *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*. In his 1938 *Referate*, he proposed (as a redundant nomenclatural act) the new binomina of the first two parts of his book (Huene, 1935 and 1936) indicating them as new (n. g. and/or n. sp.) and there are no problems concerning priority with those already published, but the new binomina of the yet unpublished third part were published in advance. So, the year of publication of the binomina *Prestosuchus chiniquensis*, *Prestosuchus loricatus*, *Rhadinosuchus gracilis*, *Hoplitosaurus rauli*, *Rauisuchus tiradentes*, *Procerosuchus celer*, and *Spondylosoma absconditum* is 1938a, and not 1942. Concerning the fourth part on Rhynchosauridae there were no new binomina, and all of them were already published earlier in Huene (1926, 1929).

### THE CODE'S “N. G., N. SP.” PAST RULE FOR ORIGINAL TYPE DESIGNATION

Charles W. Stiles proposed (“Opinion 7”) to the International Commission on Zoological Nomenclature (I.C.Z.N., 1910:10) that “if an author publishes a new genus and marks one of the species ‘n. g., n. sp.’, but does not otherwise specifically designate the genotype, such citation (‘n. g., n. sp.’) is to be construed under Art. 30a as type by the original designation” (his italics). It was approved, but the Commission noted that “this method of designating the type species does not [...] represent the best method to adopt; on the contrary” and “urges all authors to state definitely that a certain species is type, regardless of the number of species placed in the genus”.

The “Opinion 7” was expressly included in the 1913 *Code*'s version approved in the Ninth International Congress of Zoology at Monaco (I.C.Z.N., 1914:902) in Art. 30a (“When in the original publication of a genus, one of the species is definitely designated as type, this species shall be accepted as type, regardless of any other considerations. (Type by original Designation)”). In later *Code* versions, this phrasing of Art. 30a continued to be the same (I.C.Z.N., 1958:xix), but in the 1927 Tenth International Congress of Zoology at Budapest, an amendment was included in Art. 25 calling for a “definite unambiguous designation of the type species” (I.C.Z.N., 1945:143) and the “Opinion 7” only “remains valid and binding as respects generic names published in the period from 1st January 1758 up to, and including, 31st December 1930, but it is no longer applicable as respects any generic name published after that date” (I.C.Z.N., 1945:144). This subject was also discussed again at the Thirteenth International Congress of Zoology in Paris in 1948 (I.C.Z.N., 1950:152–153).

In the end, the formula “*gen. n., sp. n.*” (*genus novus, species nova*), was expressly disabled as an original designation for type-species after 1930 in the First Edition of the *Code* [I.C.Z.N., 1961:67, Art. 68(a)(i)], and repeated in the later three editions [I.C.Z.N. 1964:67, Art. 68(a)(i), 1985:129, Art. 68(b)(i), 1999:70, Art. 68.2.1].

### HUENESUCHUS NEW NOMINAL GENUS

Huene (1938a, 1942) introduced the nominal genus *Prestosuchus* including two nominal species: *P. chiniquensis* and *P. loricatus*. He (1938a:146, 1942:161) used the expression “n. g. n. sp.” applied to the first of his two species (*P. chiniquensis*) and, for the second (*P. loricatus*), he used the expression “n. sp.” (Huene, 1938a:147, 1942:185). So, Kuhn (1961a:87) indicated *P. chiniquensis* as the “genotypus” (cf. I.C.Z.N., 1912:45, footnote), followed by Krebs (1976:75, “Typusart”) and Barberena (1978:63, “Type-Species”).

As quoted above, the *Code* (Art. 13.3) asks that “every new genus-group name published after 1930 [...] must [...] be

accompanied by the fixation of a type species in the original publication [...]” and the expressions “gen. n., sp. n.” are only valid as original designation if applied before 1931 (Art. 68.2.1). It should also be noted that any later type fixation likewise only applies to a taxon “established before 1931” (Art. 69). As a consequence, neither Kuhn’s (1961a:87), nor Krebs’ (1976:75), nor Barberena’s (1978:63) type indications can be accepted as subsequent type designations.

The absence of a valid original type-species fixation challenges the availability of *Prestosuchus* as introduced by Huene (1938a, 1942). It is not a matter of invalidity of a name, but a matter of availability, and *Prestosuchus* Huene, 1938a (or 1942) is, today, a *nomen nudum* (I.C.Z.N., 1999:111).

As a *nomen nudum*, *Prestosuchus* is “not an available name, and therefore the same name may be made available later for the same or a different concept” with new authorship and date (I.C.Z.N., 1999:111).

The possibility of understanding a past proposal of a new homonymous substitutive name with the same concept would point again to Kuhn (1961a), but, in this case, it had to “be expressly proposed as a new replacement name (*nomen novum*)” (Arts. 13.3, & 67.8), which is not the case in Kuhn (1961a), nor in any other superfluous type-species indications of Krebs (1976) and Barberena (1978). On the other hand, a formal reintroduction of the new homonymous *Prestosuchus* could also be done here, with the present date and authorship, but it will raise ambiguity and confusion in the literature.

Reintroducing *Prestosuchus* as a new genus will bring some problems because many authors/readers will not understand these nomenclatural meanders in changing, in practice, only the authorship. *Prestosuchus* is the type-genus of the family-group name (Prestosuchidae) and the eponym of the class-group name (Prestosuchia). An unusual situation will happen with *Prestosuchus* Huene, 1838 (*nomen nudum*), and the new homonym because both would be also synonyms in having the same species name *chinquensis* associated. Two names being, at the same time, synonyms, and homonyms of each other will be very confusing. And this would also happen with the coordinated names Prestosuchidae and Prestosuchia.

Nomenclature is “a system of names, and provisions for their formation and use” (I.C.Z.N., 1999:111). On the other hand, Taxonomy is “the theory and practice of classifying organisms” (I.C.Z.N., 1999:119). Therefore, Taxonomy concerns the discovery/recognition of different taxa and their interrelationships, and Nomenclature refers to rules for a name to be applied to each discovered/recognized taxon.

Currently, there is already ambiguity and taxonomic confusion in applying the binomen *Prestosuchus chinquensis* in several recent phylogenetic analyses and this subject should be properly raised. Of special interest are the huge dataset and the phylogenetic analysis presented by Ezcurra (2015, 2016) that was iterated by several authors (see below). His coding sequence for “*Prestosuchus chinquensis*” does not reflect, nor include the type-material and, as consequence, this binomen is applied to a different taxon. Today nearly almost all the information in the literature, except for the description of the type-material of *P. chinquensis* in Desojo *et al.* (2020),

refers to this new taxon named preliminarily by Kischlat & Barberena (in Kischlat, 2002) as “*Karamuru vorax*”. In sum, the binomen *Prestosuchus chinquensis* is currently taxonomically corrupted and this should be properly fixed.

Evaluating the nomenclatural fault discussed above and the current taxonomic corruption, is, therefore, necessary to propose a new generic name to be used in a binomen with the nominal species *chinquensis* that nowadays only comprises the type-material. Here I propose the new genus name *Huenesuchus* gen. nov., to be used in the new binomen combination *Huenesuchus chinquensis* (Huene, 1938a).

Concerning the species-group name [*Prestosuchus*] *loricatus* originally associated with *Prestosuchus* Huene, 1838 (*nomen nudum*), it was included in its nominal genus *Abaporu* by Kischlat (2002:501).

## SYSTEMATIC PALEONTOLOGY

### ARCHOSAURIA Cope, 1870

**Definition.** “All the descendants of the most recent common ancestor of extant birds and crocodiles” (Gauthier, 1986:8). Recently, Gauthier & Padian (2019:1187) proposed an updated definition as the crown clade containing *Alligator* Cuvier, 1807, and *Compsognathus* Wagner, 1859, but here I continue with my previous definition (Kischlat, 2002:276) as the crown clade containing *Crocodylus* Cuvier, 1807, and *Megalosaurus* Buckland, 1824 (see Appendix 1).

### CROCODYLOTARSI Benton & Clark, 1988

**Definition.** “Crocodiles and archosaurs closer to crocodiles than to birds” (Gauthier & Padian, 1985:189). Here I continue with my previous definition (Kischlat, 2002:277) as the stem containing *Crocodylus* Laurenti, 1768, but not *Vultur* Linnaeus, 1758 (see Appendix 1).

### HOLOSUCHIA (*nomen substitutum*)

**Definition.** Node, the least inclusive clade containing *Aetosaurus* Fraas, 1877, *Rauisuchus* Huene, 1938a, *Huenesuchus* gen. nov., and *Crocodylus* Laurenti, 1768 (updated and simplified from Nesbitt, 2011:195) (see Appendix 1). Suchia Krebs, 1974, is previously occupied by Suchia Simpson, 1937 (Crocodyliformes). Therefore, I propose the substitute class-group name Holosuchia [*cf.* Art. 1.2.2, “Articles (...10.6...) also regulate names of taxa at ranks above the family group” which deals with the invalidity of junior homonyms].

### LORICATOSUCHIA (*nomen substitutum*)

**Definition.** Stem, the most inclusive clade containing *Crocodylus* Laurenti, 1768, but not *Poposaurus* Mehl, 1915, *Ornithosuchus* Newton, 1893, and *Aetosaurus* Fraas, 1877 (simplified from Nesbitt, 2011:200) (see Appendix 1). Loricata Merrem, 1820, is previously occupied by Loricata

Schumacher, 1817 (Mollusca). Therefore, I propose the substitute class-group name *Loricatosuchia* [cf. Art. 1.2.2, “Articles (...10.6...) also regulate names of taxa at ranks above the family group” which deals with the invalidity of junior homonyms].

#### HUENESUCHIA new class-group name

**Definition.** Stem, the most inclusive clade containing *Huenesuchus*, gen. nov., but not *Crocodylus* Laurenti, 1768 (see Appendix 1).

**Eponym.** *Huenesuchus* gen. nov.

**Nomenclatural note.** As *Prestosuchus* Huene, 1938a (also in 1942) is an unavailable name (*nomen nudum*, I.C.Z.N., 1999:111), the obscure class-group name *Prestosuchia* Parrish, 1993 (p. 308; also in Parrish, 1994:204) lost its formal eponym. Therefore, I propose *Huenesuchia* as a new class-group name (cf. analogy to Art. 37.2, which deals with family-group names).

#### HUENESUCHIDAE new family-group name

urn:lsid:zoobank.org:act:AD764DC2-B33C-48BF-AF41-DD2746A1D83D

**Definition.** Node, necessarily including *Huenesuchus* gen. nov. and, today, *Stagonosuchus* Huene, 1938b; to be formally defined in the future when greater diversity is known.

**Type-genus.** *Huenesuchus* gen. nov.

**Diagnosis.** Today, following the present phylogenetic analysis (see ahead), huenesuchids include *Huenesuchus*, gen. nov., and *Stagonosuchus* Huene, 1938b; which share the following unambiguous apomorphies: *Ischium* with *Margo ventralis* with an abrupt change in angle between *Extremitas adacetabularis* and *Scapus* (G296.1); *Fibula* in its *Extremitas distalis*, with a fossa on its *Facies medialis* (G422.1).

**Nomenclatural note.** As *Prestosuchus* Huene, 1938a (also in 1942) is an unavailable name (*nomen nudum*, I.C.Z.N., 1999:111), the family-group name *Prestosuchidae* Romer, 1966 (p. 368), turns also to be unavailable (Art. 37.2).

#### *Huenesuchus* gen. nov.

urn:lsid:zoobank.org:act:E5B41FEA-CF59-4955-9C70-5B72A3CD0792

**Type-species.** *Huenesuchus chiniquensis* (Huene, 1938a), comb. nov.

**Derivatio nominis.** In honor of Friedrich von Huene, who unfortunately proposed the genus-group name *Prestosuchus* in 1938a (repeated in 1942) using a notation for fixation of the type-species that would be suppressed shortly soon, being only valid before the year 1931 (cf. Art. 68.2.1); and *-suchus* (Gr. σοῦχος, *soûchos*: crocodile; Bailly, 2020:2124), the name used by ancient Egyptians from Arsinoë (today el-Fayyūm) for crocodiles (Strábonos [Στράβωνος], ex Jones, 1967:106).

**Included species.** Only the type-species.

**Lectotype.** SNSB-BSPG AS XXV 1~3/5~6/8~12/28~35, designated by Krebs (1976), comprising a complete *Symphysis mandibulae* with most of the left *Ramus mandibulae* preserved with some teeth, right *Os premaxillare* also with some teeth, and an incomplete postcranial skeleton. Desojo *et al.* (2020:8) indicated the number of the lectotype as “1~3/5~11/28~41/49”, but this is not correct because they included #7, #36~#41, and #49, and excluded #12, mixing specimens that are not part of the type-material (see Table 1). According to the SNSB-BSPG catalog (see Supplementary file 1) there are sequential numbers that were here abbreviated as 1~3/5~6/8~12/28~35.

**Paralectotype.** An incomplete sacrum and right ilium, part of the last truncal vertebra, and some sacral osteoderms (SNSB-BSPG AS XXV 7), recently described by Desojo *et al.* (2020).

**Diagnosis.** *Symphysis mandibulae* with both splenials dorsally reaching well rostrally the dental tooth I and, in ventral view, with an extensive *Sutura interspleniales* reaching caudally well the level of the dental tooth V, possibly reaching the dental tooth VI. *Scapula* with the *Acromion* not developed, with a notch (*Incisura acromialis*) cutting the margin of the *Os coracoidale*, forming an uncination in this bone; *Margo medialis* of *Os coracoidale* convexly curved; *Corpus humeri* probably relatively thin. Absence of *Crista supraacetabularis ilii*; *Ischium* with an abrupt change in angle between *Extremitas adacetabularis* and *Scapus*; *Femur* with the *Condylus medialis* (*Norma distalis*) tapering to a point on the medial portion; *Fibula* with a fossa (“lunate fossa”) distally, on *Facies medialis*; *Calcaneus* with a short and wide *Tuber*. The paralectotype shows the transition point of the double row of paramedian pair of osteoderms to only a sagittal pair on the first caudal vertebra. (All updated from both Kischlat, 2002, and Desojo *et al.*, 2020).

**Nomenclatural note.** *Prestosuchus* Huene, 1938a (also in 1942) is an unavailable name (*nomen nudum*, I.C.Z.N., 1999:111), so *Huenesuchus* is not a *nomen novum* because it does not replace any available name (Art. 12.2.3). But, in practice, it works as such because the present type-species (*i.e.*, *Huenesuchus chiniquensis* comb. nov.) has the same name-bearing specimen as for the previously proposed type-species (*i.e.*, “*Prestosuchus chiniquensis*”). As an unavailable name, the nominal genus *Prestosuchus* Huene, 1938a (*nomen nudum*), should be always cited under quotation marks when associated with *chiniquensis* in the binomen “*Prestosuchus chiniquensis*”.

**Stratigraphic precedence.** Pinheiro-Chiniquá Sequence, *Dinodontosaurus* Assemblage Zone, Santa Maria Formation, Ladinian/Carnian (Middle/Upper Triassic) (Schultz *et al.*, 2020:5). The correct name for the locality in the Municipality of Candelária (State of Rio Grande do Sul, Brazil), is Pinheiro (29°47'30”S 52°44'25”W), in singular, and not the plural “Pinheiros”, as expressed by several previous authors (*e.g.*, Barberena, 1978:63; Azevedo, 1991:2; Schultz *et al.*, 2020:6). The Brazilian Code of Stratigraphic Nomenclature (Petri *et al.*, 1986:382) asks for the “immutability of consecrated names”, but the name “Pinheiros” was formally listed twice in the Stratigraphic Lexicon of Brazil (Branco, 1984:317;

**Tabela 1.** Original material of *Huenesuchus chiniquensis* listed in SNSB-BSPG catalogue and/or cited in Huene (1942), comprising the lectotype, paralectotype, and referred ones, compared with material described or indicated in Desojo *et al.* (2020).

Specimen	SNSB-BSPG AS XXV	Material	Huene (1942)	Desojo <i>et al.</i> (2020)
Lectotypus	#1	“Linker Unterkieferast” Left hemimandible	pages 161-163, fig. 28; pl. 18, fig. 3(a-b)	pages 15-17; fig. 5(1-6)
	#2	“Rechte Scapula” Right scapula	page 171; pl. 18, fig. 4	page 22
	#3	“Letzter Sacralwirbel, Schwanzwirbel 1-6, linkes Ilium und beide Ischia” Last sacral vertebrae, caudal vertebrae I-VI, left ilium and both ischia	pages 168-170, 175-176; pl. 18, figs. 1-6; pl. 19, figs. 2, 4	pages 18, 20, 26; figs. 7(6-8), 11(3-5)
	#5(a-d)	“Bauchrippen (4 Teilstücke)” Abdominal ribs (4 sections)	page 168; pl. 19, fig. 1	page 22, fig. 8(1-2)
	#6	“Beide Pubis ohne Proximalende” Both pubis without proximal end	page 176; pl. 19, fig. 3	page 26; fig. 11(1-2)
	#8	“Kopf einer linken mittleren Dorsalrippe ohne Tuberculum” Head of a left middle dorsal rib without a tubercle	pages 167-168; pl. 20, fig. 1	page 22; fig. 8(3, part as #49)
	#9	“Mittleres Dorsalrippenstück” Part of a middle dorsal rib	page 168; pl. 20, fig. 2	page 22, fig. 8(3, part)
	#10	“Linker Femur” Left femur	page 177; pl. 20, fig. 3	pages 26-27; fig. 12(1-6)
	#11(a-l)	“Linke Tibia, Fibula u. Fuß” Left tibia, fibula and foot	pages 177-182, figs. 38-39(a); pl. 20, fig. 4(a-b); pl. 21, fig. 2(a-b)	pages 27-33; figs. 12(7-18), 13(1-8)
	#12	“Brust-Schultergürtel” Chest-shoulder girdle	pages 170-172; pl. 21, fig. 1(a-b)	pages 22-24; fig. 9(1-3)
	#28	“Fragment der rechten Praemaxilla usw.” Fragment of the right premaxilla, etc.	pages 163-164, fig. 29(a-d)	pages 10-15; fig. 4(1-4)
	#29	“Zentrum des letzten Halswirbels” Center of the last cervical vertebra	page 165, fig. 30(a-b)	page 17; fig. 6(1-3)
	#30	“Fragment eines hinteren Halswirbels” Fragment of a posterior cervical vertebra	pages 165-166, fig. 31(a-b)	pages 17-18; fig. 6(4-7)
	#31	“Teile van zwei vorderen Rückenwirbeln” Parts of two anterior vertebrae	pages 166-167, fig. 32	page 18; fig. 6(8-9)
	#32(a-b)	“Zentrum van distalen Schwanzwirbeln mit Haemapophysen, Schwanzwirbel-Zentrum” Centrum of distal caudal vertebrae with haemapophysen, caudal vertebra centrum	page 170, figs. 33-34	pages 20, 22; figs. 6(8-9), 7(6-8)

Tabela 1. Cont.

Specimen	SNSB-BSPG AS XXV	Material	Huene (1942)	Desojo et al. (2020)
Lectotypus	#33	“Oberende des linken Humerus” Upper end of the left humerus	page 173, fig. 35	page 24; fig. 10(1~3)
	#34	“Oberende des rechten Humerus” Upper end of the right humerus	pages 173-174, fig. 36	page 24; fig. 10(5~6, as #33)
	#35	“Distales Fragment des rechten Humerus” Distal fragment of the right humerus	page 174, fig. 37	page 24; fig. 10(4)
	#?, only in text	“Atlas” Atlas	page 164	not cited
	#?, only in text	“Stück des vermutlichen Radius-Distalendes” Piece of the putative radius distal end	page 174	not cited
	#?, only in text	“Eine Handphalange” One hand phalange	page 174	not cited
Paralectotypus	#7	“Oberer Teil des Ilium, beide Sacralrippen, Dornfortsätze beider Sacralwirbel und des letzten Rückenwirbels, dorsale Panzerplatten” Upper part of the ilium, both sacral ribs, spinous processes of both sacral vertebrae and the last dorsal vertebra, dorsal armor plates	pages 183-185; pl. 19, fig. 5 (a~b)	pages 18, 22; figs. 7(1~5), 8(4)
Originally only referred	#36	“eine Klaue [...] dem Fuß” One ungual from foot	page 185	not cited
	#37	“Ein distale Fußphalange” One distal foot phalange	page 185	not cited
	#38	“Das Proximalende einer größeren Phalange” The proximal end of a larger phalange	page 185	not cited
	#39	“gekrümmte Mittelfragment einer Abdominalrippe” Curved middle fragment of an abdominal rib	page 185	not cited
	#40–41, only catalogue	“[2] Abdominalrippen-Fragm.” [2] abdominal rib fragments	page 185 (?) (as indicated in the catalogue)	not cited
Not referred	#49, referred to “ <i>P. loricatus</i> in catalogue	“Dorsalrippenstück” Dorsal rib piece	page not found (not #19, nor #21, both on page 188)	error (see #8)

Hasui & Baptista, 1984:317). Thus, it is convenient to rise this issue for proper evaluation elsewhere.

**Type locality.** “Weg Sanga”, Chiniquá (29°40’1”S 54°22’1”W), Municipality of São Pedro do Sul, west of Santa Maria City, Rio Grande do Sul, Brazil.

## DISCUSSION

Huene (1938a:146) introduced the binomen “*Prestosuchus*” *chiquensis* assembling two specimens from different localities as the hypodigm (*vide* Simpson, 1940:418, 1945:30, 1961:185, for this concept). Later, Krebs (1976:76, repeated in Kischlat & Barberena, 1999:53) designated the first more complete specimen (SNSB-BSPG AS XXV 1~3/5~6/8~12/28~35), that which has the mandible, as the lectotype. Consequently, the second specimen (SNSB-BSPG AS XXV 7) turned out to be the paralectotype (Art. 74.1.3). An extraneous third specimen (from Sanga Pascoal, at Pinheiro, UFRGS-PV 156T), described in Barberena (1978), was once considered as the “type” (Azevedo, 1995:61, “tipo”), but this apparent designation is invalid because this specimen is not part of the original type-material (*cf.* Art. 74.2; Kischlat & Barberena, 1999).

The lectotype has been cited with the number “1~3/5~11/28~41/49” (Nesbitt, 2009:53, 2011:33; Desojo *et al.*, 2020:8), but following the SNSB-BSPG Catalog (Supplementary file 1) this is not correct and should be properly fixed. This Catalog was kindly provided by Dr. Peter Wellnhofer when I visited the Bayerische Staatsammlung in München (November 1997), and it uses the acronym “1933 L” (instead of “AS XXV”) as I have used it before (Kischlat, 2002).

The specimen SNSB-BSPG AS XXV 7 concerns the paralectotype of *Huenesuchus chiquensis*, and the specimens SNSB-BSPG AS XXV 36~41 were only originally referred to *H. chiquensis* with doubts (Huene, 1942:185, 1990:196; “*Prestosuchus chiquensis* (?)”). These are not part of the type-series (*cf.* Art. 72.4.1). Desojo *et al.* (2020:8) also did not expressly include specimen #12 in their full number “1~3/5~11/28~41/49”, but they described it as part of the holotype.

Desojo *et al.* (2020:23, fig. 8.3) figured a proximal rib fragment as being the SNSB-BSPG AS XXV 49. But this same specimen was figured in Huene (1942, 1990, pl. 20, fig. 1) and the SNSB-BSPG Catalog lists it as #8. In this Catalog, the true #49 is indicated as part of a dorsal rib (“dorsalrippenstück”) belonging to “*Prestosuchus loricatus*”, but I didn’t find its description in Huene’s (1942:185–191) text. On the other hand, the description of three rib fragments (#19 and #21a~b) is present (Huene, 1942:188, “Dorsalrippen”).

Huene (1942:186) hypothesized that the type-material of *Prestosuchus loricatus* (SNSB-BSPG AS XXV 13~24/26~27/43~48) belongs to a single individual (“einem einzigen Individuum herrühren”). Thus, all material should be called the holotype and not as syntypes, and only syntypes could become lectotype and paralectotype(s) (*cf.* Art. 73.2.2). Any restriction of this holotype should follow Art. 73.1.5 (“If

a subsequent author finds that a holotype [...] is not derived from an individual animal, the extraneous components may, by appropriate citation, be excluded from the holotype”), and Huene (1942:186) expressly indicated that in case of doubt, the species name should be attached to the presacral vertebral remains (“Im Zweifelsfall soll der Speciesname an den Praesacralwirbelresten hängen”). The composite nature of the holotype is still to be demonstrated (although very probable), but if something is *Prestosuchus loricatus*, the two presacral vertebrae (#13a~b) are the core. Huene (1942:190–191) also referred to additional material (SNSB-BSPG AS XXV 4/25/42) in doubts (“*Prestosuchus loricatus* (?)”) and these specimens are not part of the type-series (*cf.* Art. 72.4.1). I didn’t unequivocally find the citation of specimens #46a~l in Huene’s (1942:185–191) text (“Ein isoliert Dornfortsatz?”, p. 189).

Desojo *et al.* (2020:6) indicated the full number of the “lectotype” (or “holotype”, p. 9) of *Prestosuchus loricatus* as “13–24/26–27/44–48”, excluding specimen #43, which was included in Huene (1942:189). Concerning the purported “paralectotype”, they did not cite expressly any specimen, but according to their dataset it is the additional material (SNSB-BSPG AS XXV 4/25/42) originally referred with doubts to *Prestosuchus loricatus*. Aside from the fault in not following Art. 72.4.1 (exclusion of doubt specimens from type-series) and Art. 73.2.2 (only syntypes could become lecto- and paralectotypes), these lectotype/paralectotype indications were not done as an express statement (*cf.* Art. 74.7) and they are not valid (although repeated in Nesbitt *et al.*, 2020:38; Tolchard *et al.*, 2021:597; Butler *et al.*, 2022:4).

The first mention of the lectotype of *Prestosuchus chiquensis* concerns a short note made by Huene (1929:54) briefly describing a sketch of the mandible (SNSB-BSPG AS XXV 1) sent to him from Brazil and supposedly identified as a probable belodont (“wahrscheinlich Parasuchier”). Later, Huene (1942:164) gave more information about the material assembled under this binomen explaining that the mandible and some bones were collected in 1923 by Vicentino Prestes de Almeida (on whom the name “*Prestosuchus*” was based; Beltrão, 1965:20). In his trip to southern Brazil in 1928 (*vide* Huene, 1930), after some searching, he collected the remaining material. It came from the locality called “Sanga am Wege” or “Weg Sanga” (Huene & Stahlecker, 1931:40, 1968:35; Huene, 1942:161, 1990:171; “Sanga da Estrada” in Portuguese), at the locality of Chiniquá (29°40’1”S 54°22’1”W), Municipality of São Pedro do Sul.

The paralectotype of *Huenesuchus chiquensis* (SNSB-BSPG AS XXV 7) came from an upper layer from a near locality called “Sanga des Theotonio Beles Xavier” (Huene & Stahlecker, 1931:38–39, 1968:34, “Sanga Béles”; Huene, 1942:183). “Cynodontier Sanga” is another name for this locality (Huene, 1935:93, 1942:325, 1990:103, 341, “Sanga dos Cinodontes” in Portuguese) and it was figured in Huene & Stahlecker (1931:38, 1968:34, fig. 17) and Huene (1942:327, 1990:344, fig. 66). The paralectotype was also considered a supposed belodont (“Parasuchier”) in Huene & Stahlecker (1931:39, 1968:34).

Recently, Desojo *et al.* (2020:6–7) redescribed all the type-series of *Huenesuchus chiniquensis* and accepted their conspecificity like Huene (1938a, 1942) originally hypothesized. This approach should be accepted as a hypothesis to be tested in the future when better and more complete material comes to hand. The assumption of this hypothesis implies that both lectotype and paralectotype specimens are closely related, representing the same taxon, and all the remaining available specimens described elsewhere (Barberena, 1978; Azevedo, 1991, 1995; Kischlat, 2002, 2003; Mastrantonio, 2010; França, 2011; França *et al.*, 2011, 2013; Lacerda, 2012; Mastrantonio *et al.*, 2013, 2019; Raugust, 2014; Roberto-da-Silva *et al.*, 2016, 2020; Lacerda *et al.*, 2016; Roberto-da-Silva, 2017; Damke *et al.*, 2022) should be compared to them, chiefly to the lectotype. In this way, the specimen from Sanga Pascoal (UFRGS-PV 156T; Barberena, 1978; Azevedo, 1991, 1995) was recognized as being another taxon (Kischlat, 2002, 2003). On the other hand, *Decuriasuchus* (França, 2011:50; França *et al.*, 2011:391, 2013:474) was mainly compared to the specimen from Sanga Pascoal (UFRGS-PV 156T) that was then identified as *H. chiniquensis*.

The lectotype of *Huenesuchus chiniquensis* was individually scored in Parrish's (1993), Nesbitt's (2009, 2011), and França's (2011) datasets. The paralectotype was individually scored in França (2011) and Desojo *et al.* (2020). The combined type-series (lectotype+paralectotype), as originally proposed by Huene (1938a), was scored in Desojo *et al.* (2020). And the lectotype and the Sanga Pascoal specimen (UFRGS-PV 156T) were combined and scored in the datasets of Benton & Walker (2002), Benton (2004), Nesbitt (2009, 2011), and Brusatte *et al.* (2010).

Benton's (2004) dataset was later iterated by Li *et al.* (2006). Nesbitt's (2011) dataset was later iterated by several authors (Butler *et al.*, 2011, 2014, 2018, 2022; Nesbitt *et al.*, 2011, 2013a, c, 2014, 2017, 2018a, b, 2020; Li *et al.*, 2012, 2016; Langer & Ferigolo, 2013; Lecuona, 2013; Nesbitt & Butler, 2013; Sues & Schoch, 2013; Baczko *et al.*, 2014, 2020; Raugust, 2014; Sookias *et al.*, 2014a, b; Lautenschlager & Rauhut, 2015; Zanno *et al.*, 2015; Cabreira *et al.*, 2016; Lacerda *et al.*, 2016, 2018; Lecuona *et al.*, 2016; Lessner *et al.*, 2016; Niedźwiedzki *et al.*, 2016; Roberto-da-Silva *et al.*, 2016, 2020; Nesbitt & Desojo, 2017; Roberto-da-Silva, 2017; Stocker *et al.*, 2017; Müller *et al.*, 2018; Sarigül *et al.*, 2018; Garcia *et al.*, 2019, 2021; Barrett *et al.*, 2020; Desojo *et al.*, 2020; Kammerer *et al.*, 2020; Marsh *et al.*, 2020; Baron, 2021; DallaVecchia, 2021; Tolchard *et al.*, 2021; Parker *et al.*, 2021; Damke *et al.*, 2022; ) and many of them including modifications/corrections and inserting new taxa. With few exceptions (*e.g.*, Li *et al.*, 2012, 2016; Desojo *et al.*, 2020) the combined score of the lectotype plus the Sanga Pascoal specimen (UFRGS-PV 156T) was the standard sequence used in their phylogenetic analyses for "*Prestosuchus chiniquensis*" terminal. This was also the case in Brusatte's *et al.* (2010) dataset, with the combined lectotype plus UFRGS-PV 156T as the only available sequence and it was later iterated by several authors (Mastrantonio, 2010; Benton & Walker, 2011; Butler *et al.*, 2011; França *et al.*, 2011; Lacerda, 2012;

Lautenschlager & Rauhut, 2015; Nesbitt *et al.*, 2014) also with modifications/corrections and insertions of new taxa.

Finally the binomen "*Prestosuchus*" *chiniquensis* was used for scoring an assemblage of specimens not including the lectotype (*i.e.*, the name-bearing specimen) by Ezcurra (2015:183, tab. 5.1; 2016:110, tab. 1), which was also later iterated by several authors (Ezcurra *et al.*, 2017, 2019, 2020b, 2021a, b, c, d, 2022; Nesbitt *et al.*, 2017, 2018b; Sengupta *et al.*, 2017, 2022; Stoker *et al.*, 2017; Ezcurra & Butler, 2018; Oliveira *et al.*, 2018; Spiekman, 2018; Butler *et al.*, 2019; Peacock *et al.*, 2019; Baczko *et al.*, 2020; Barrett *et al.*, 2020; Bennett, 2020; Foffa *et al.*, 2020, 2022; Maidment *et al.*, 2020; Müller *et al.*, 2020; Scheyer *et al.*, 2020; Sues *et al.*, 2020, 2021; Troteyn & Ezcurra, 2020; Wynd *et al.*, 2020; DallaVecchia, 2021; Parker *et al.*, 2021; Ezcurra & Sues, 2022; Kellner *et al.*, 2022; Martínez *et al.*, 2022; Müller & Garcia, 2022; Preto *et al.*, 2022; Sengupta & Bandyopadhyay, 2022; Simão-Oliveira *et al.*, 2022; Chen & Liu, 2023). Therefore, these scorings don't reflect, nor include the type-material and, as consequence, they are not representative of *H. chiniquensis*.

As noted above, Kischlat (2002, 2003) considered the Sanga Pascoal specimen (UFRGS-PV 156T) as a different taxon from *Huenesuchus chiniquensis* and the binomen *Karamuru vorax* Kischlat & Barberena in Kischlat, 2002 (*cf.* Code's Recommendation 51E) was preliminarily proposed for this new taxon.

Two new nearly complete specimens were discovered after, the first in March 2003 (UFRGS-PV 629T; Mastrantonio *et al.*, 2009) and the second in May 2010 (ULBRA-PVT 2810; Cabreira *et al.*, 2011). For me, at each time of discovery, both specimens showed marked differences in mandibular morphology with that of the lectotype of *Huenesuchus chiniquensis*, and many similarities with the mandible of the Sanga Pascoal specimen (UFRGS-PV 156T). But, as the specimen from Sanga Pascoal was previously identified as "*Prestosuchus chiniquensis*" (Barberena, 1978; Azevedo, 1991, 1995), an obvious conclusion quickly came, and my previous hypothesis was then rejected by all involved. In the literature this rejection was mainly because of nomenclatural problems rather than the recognition of osteological differences to understand that it represents a new taxon (Mastrantonio, 2010:43; França, 2011:20; Lacerda, 2012:29; Raugust, 2014:1.72; Lacerda *et al.*, 2016:3; Roberto-da-Silva, 2017:40; Roberto-da-Silva *et al.*, 2020:993; Desojo *et al.*, 2020:3). In short, these authors confused Nomenclature with Taxonomy and did not conclude what, to me, was obvious (*i.e.*, the presence of two different taxa whatever the names available). Although the binomen "*Karamuru vorax*" (but see Abdala *et al.*, 2009:84) is not available (*cf.* Arts. 16.1 & 16.4), its formal unavailability does not preclude the discovery/recognition of a new taxon, even if no name was formally proposed. Unfortunately, after 2003 I could not continue my studies on the subject and, with the discovery of these two new specimens (UFRGS-PV 629T and ULBRA-PVT 281), I waited for the conclusions of those involved. Now I feel quite comfortable going back and defending my earlier hypothesis.

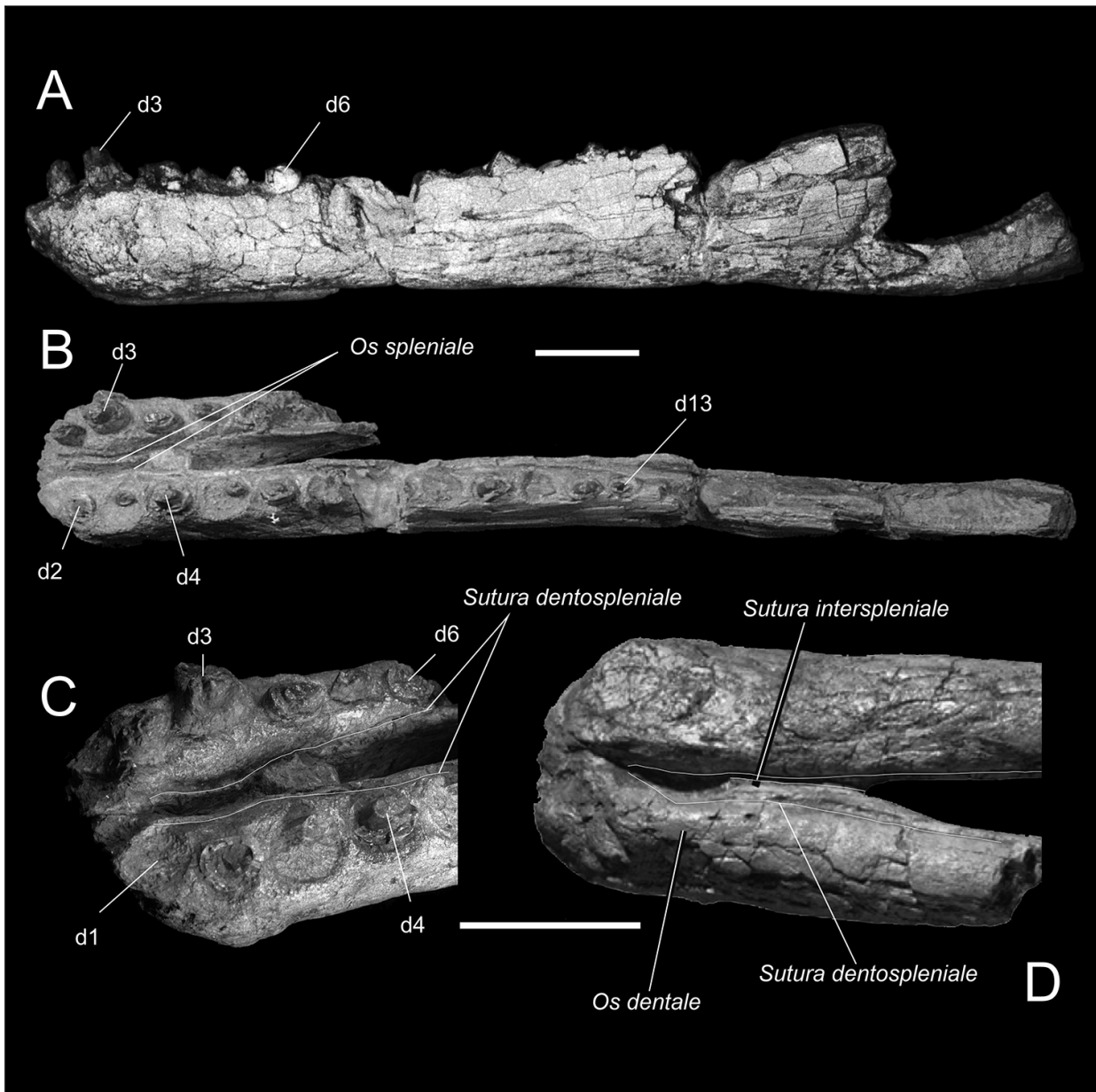


Differences in jaw morphology between the lectotype and the new taxon called “*Karamuru*” are easier to observe using specimen UFRGS-PV 629T than with the others (UFRGS-PV 156T and ULBRA-PVT 281) because in these the mandibles are tightly adpressed to the skulls.

The actual length of the lectotype mandible is unknown because the caudal part is missing, but the preserved part has 49.0 cm (Desojo *et al.*, 2020:11). Otherwise, the complete hemimandible of the specimen UFRGS-PV 629T has 47.19 cm in length (Mastrantonio, 2010:128). Thus, in linear dimensions, the lectotype has a larger mandible and it would represent a larger individual. For comparisons, both mandibles were normalized with the same dimension from the rostral tip of the symphysis to the caudal tip of the ventrocaudal process of the dental bone (Supplementary file 2). The

actual dimension of the lectotype mandible is approximately 150% larger than that of UFRGS-PV 629T, so its apparent slenderness does not correspond to a juvenile condition of the lectotype. Thus, the relative height is shorter and the *Ramus mandibulae* is slenderer. There is a lesser curvature in the *Margo oralis* and the *Eminentia rostralis* is more developed under tooth III. The rostral teeth (II–IV) are relatively procumbent when compared to the highly recumbent ones in UFRGS-PV 629T.

These differences should be added to the most important one in the morphology of mandibular symphysis of the lectotype with both splenials dorsally reaching well rostrally the dental tooth I (Figure 1C) (*cf.* Huene, 1942:161, “Die Splenialia reichen bis an die vordere Spitze der Symphyse”, 1990:171) and, in ventral view, with the *Sutura interspleniales* reaching



**Figure 1.** Mandible of the lectotype of *Huenesuchus chiquensis* (SNSB-BSPG AS XXV 1). **A**, lateral view. **B**, dorsal view. **C-D**, detail of the symphysis in laterorostral and ventral view, respectively. All the pictures from the author except (D) which is modified from Desojo *et al.* (2020). Scale bars = 50 mm.

caudally well the level of the dental tooth V (Figure 1D), possibly reaching the dental tooth VI (*cf.* Desojo *et al.*, 2020:17, fig. 5.1–2; *cf.* Raugust, 2014:44, fig. 21ed). These differences are certainly connected to the mode of prey, and both were carnivorous archosaurs.

Concerning the morphology of an elongated mandibular symphysis of the lectotype, the ventral extension of the intersplenic suture draws attention to the condition found in *Mambawakale* (Butler *et al.*, 2022:15, figs. 10–11), which shows, basically, the same morphology of the mandible of *H. chiniquensis*, with an elongated *Symphysis mandibula* extending up to dental tooth VIII with a clear and elongated *Sutura intersplenicales* rostrally from, at least, tooth II to caudally reaching tooth VIII.

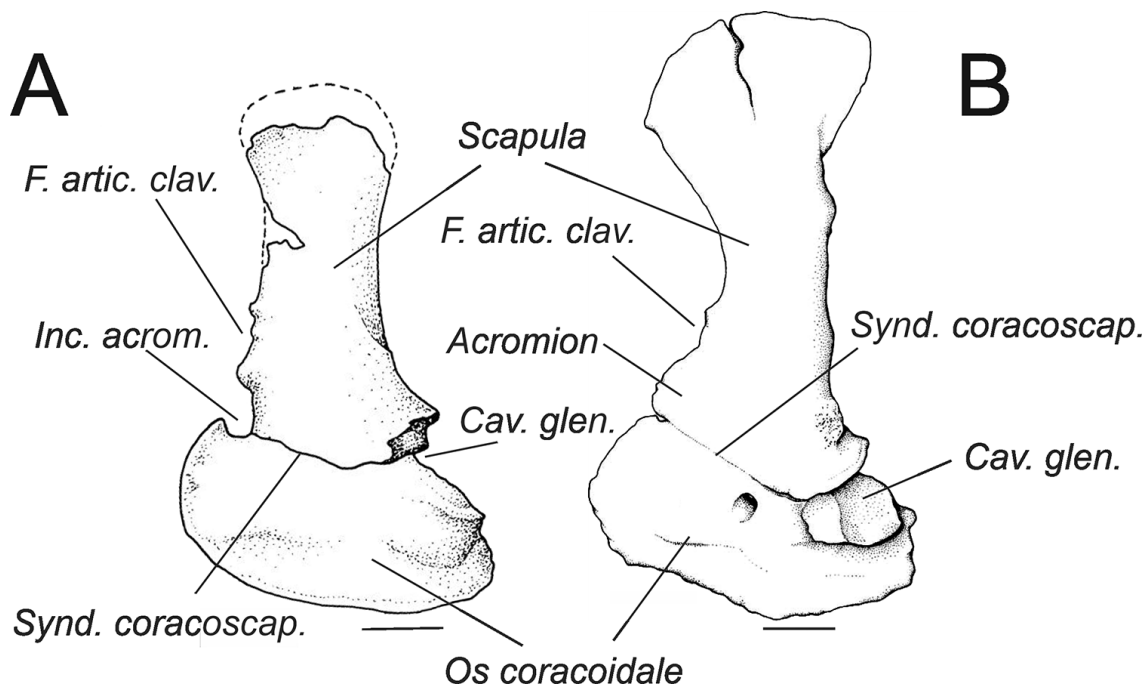
Concerning the *Scapula* (Figures 2A and 3A) of the lectotype, the *Acromion* is not developed, and there is a notch (*Incisura acromialis*) cutting the margin of the *Os coracoidale*, forming an uncination in this bone. In the new taxon, the *Acromion* is well developed and the *Incisura acromialis* is absent (the scapulocoracoid is only preserved in UFRGS-PV 629T and ULBRA-PVT 281; Figures 2B and 3B).

Desojo *et al.* (2020:35) also gave several characters found in the lectotype *Huenesuchus chiniquensis* (and scored in their dataset) that differentiate it from the specimen UFRGS-PV 629T: absence of *Crista supraacetabularis ilii* (G265.0); *Ischium* with an abrupt change in angle between the *Extremitas adacetabularis* and the *Scapus* (G296.1); *Femur* with the *Condylus medialis (Norma distalis)* tapering to a point on the medial portion (G320.0); and, *Fibula* with a fossa (“lunate fossa”) distally on *Facies medialis* (G422.1). All these characters are not preserved in UFRGS-PV 156T,

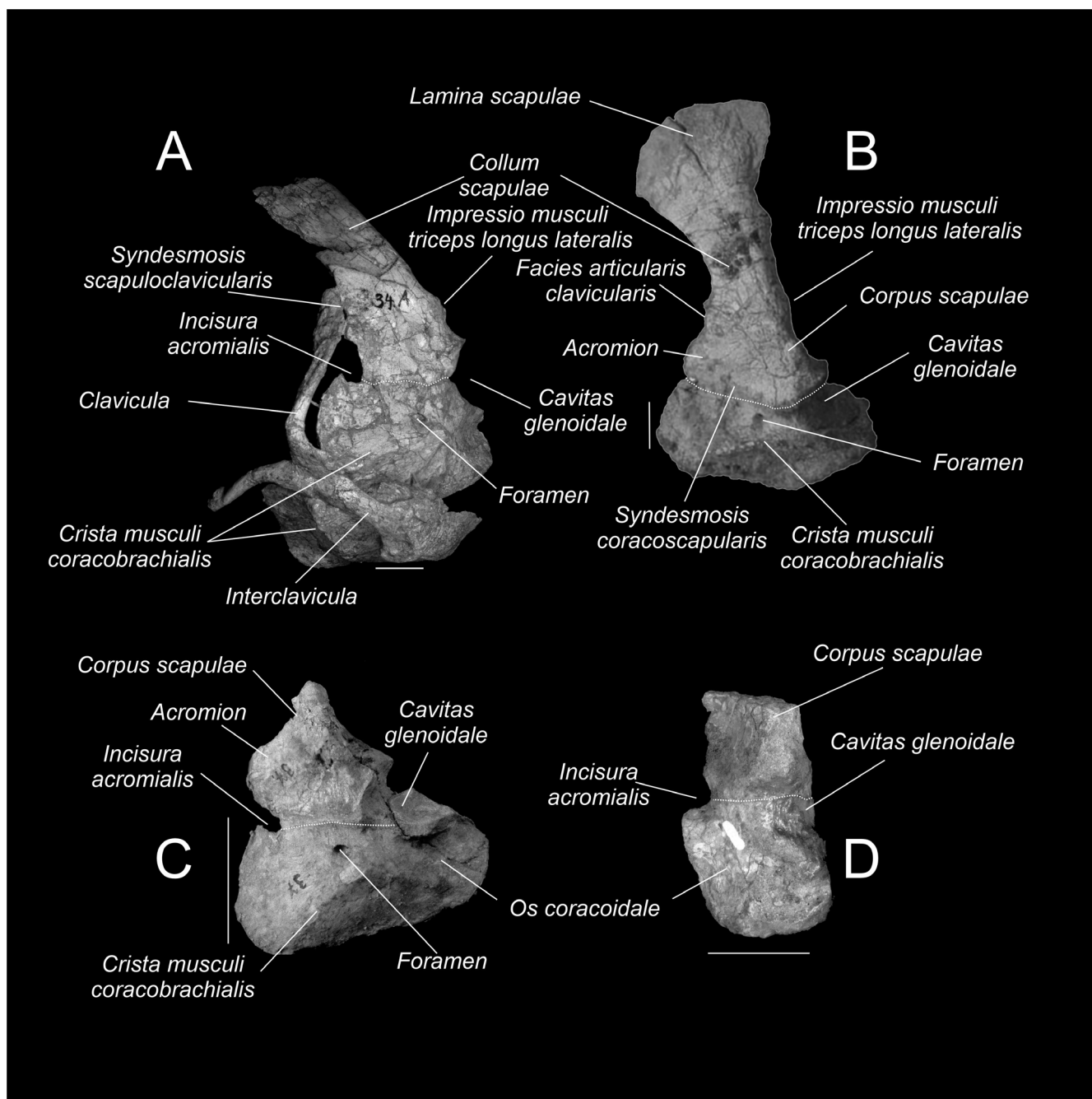
but only in UFRGS-PV 629T (G320 also in ULBRA-PVT 281) and they show a different condition (*cf.* Mastrantonio, 2010; Roberto-da-Silva *et al.*, 2016; Roberto-da-Silva, 2017) from that found in the lectotype of *H. chiniquensis* (*cf.* Desojo *et al.*, 2020).

On the other hand, the paralectotype shows the transition point between the double row of paramedian pair of osteoderms to only a double sagittal row on the first caudal vertebra (Figure 4). This condition is also found in *Decuriasuchus quartacolonia* (França, 2011:142, fig. 35A), *Postosuchus alisonae* (Peyer *et al.*, 2008:373, fig. 6E), and, apparently, also in *Ticinosuchus ferox* (Krebs, 1965:114). Other taxa, such as *Saurosuchus galilei* (Sill, 1974:349, fig. 10) and *Fasolasuchus tenax* (Bonaparte, 1981:74, fig. 20) also show symmetric osteoderms supposed as from the tail, but they are not preserved articulated. The crocodylomorph *Dromicosuchus grallator* has a double row of paired paramedian osteoderms on the first two caudal vertebrae (Sues *et al.*, 2003:330). The condition found in the specimen UFRGS 629T is that double symmetric sagittal osteoderms are found on both sacral vertebrae and the transition point is between the *Vertebra truncalis ultima* (= *truncalis XVII*, = *presacrale XXV*) and *Vertebra sacralis I* (Mastrantonio, 2010:159, figs. 84A and 87C; Raugust, 2014:2.84, fig. 41A).

The dataset of Desojo *et al.* (2020) is an iteration of that of Nesbitt (2019, 2011) plus more characters and taxa. The existence of intersplenic suture is not evaluated and their G160 only concerns its absence or presence rostrally (plesiomorphy) and presence relative to one-third of the lower jaw (apomorphy). This same wording was used by Ezcurra (2015:G251, 2016:G265) and later iterations. The presence



**Figure 2.** Drawline showing the main differences in scapulocoracoids between the (A) lectotype of *Huenesuchus chiniquensis* (SNSB-BSPG AS XXV 12) and the (B) new taxon (UFRGS-PV 629T, reversed). **Abbreviations:** Cav. glen., glenoid cavity (*Cavitas glenoidale*); Inc. acrom., acromial notch (*Incisura acromialis*); Fac. artic. clav., articular surface for clavicle (*Facies articularis clavicularis*); Synd. coracoscap., coracoscapular syndesmosis (*Syndesmosis coracoscapularis*). [A, modified from Parrish (1993), B, modified from Mastrantonio (2010)]. Scale bars = 50 mm.

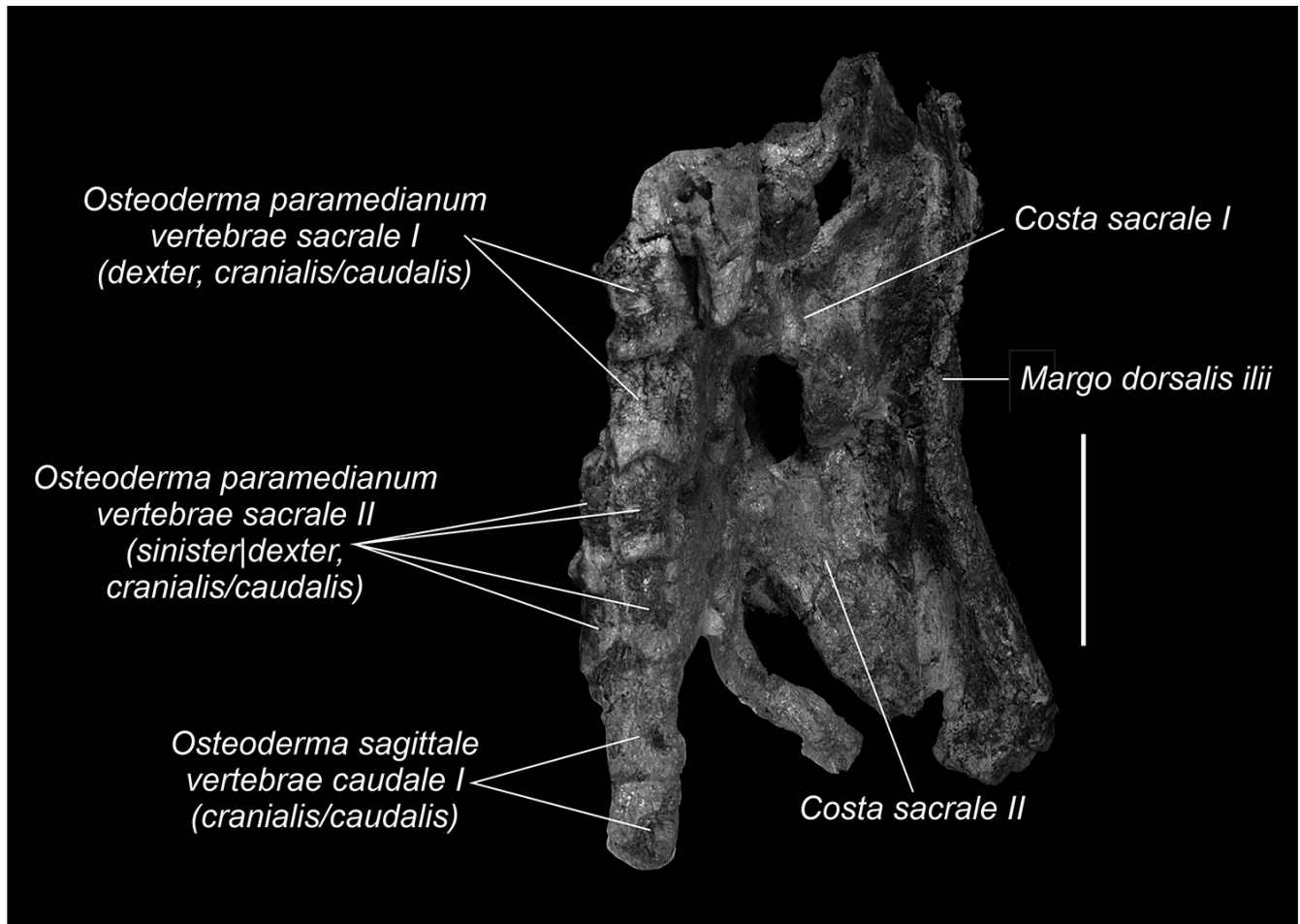


**Figure 3.** Scapulocoracoids of several Brazilian Triassic specimens (left side) normalized with the approximately horizontal coracoscapular syndesmosis. **A**, lectotype of *Huenesuchus chiquensis* (SNSB-BSPG AS XXV 12) comprising both clavicae, interclavicula, both coracoids, and left scapula (with incomplete dorsal *Lamina*). **B**, complete scapula and coracoid of the new taxon (UFRGS-PV 629T). **C**, holotype of *Procerosuchus celer* (SNSB-BSPG AS XXV 134) with the coracoid and the fragmentary scapula (only *Corpus scapulae* preserved). **D**, Baum Sanga specimen (CPEZ 239b, reversed as left) with the coracoid badly preserved attached with only part of the scapular body. [All the pictures from the author except B which is modified from Mastrantonio (2010)]. Scale bars = 50 mm.

of intersplenial suture in the condition of *Huenesuchus* (and *Mambawakale*) was only evaluated in two other expanded iterations of Nesbitt’s (2009, 2011) dataset (Lecuona, 2013:G413.1; Lecuona *et al.*, 2016:G413.1), but the terminal “*Prestosuchus chiquensis*” was coded as “?”. Another dataset concerning only later crocodylomorphs (Leardi *et al.*, 2017:G83.1) also uses this approach. Evaluating all these datasets (and there are differences in codings that should

be investigated), the presence of intersplenial suture was coded for *Euparkeria*, belodonts, aetosaurs, ornithosuchians, *Yonghesuchus* as well in several crocodylomorphs.

Kischlat (2002:291, 2003:263) noted that the condition in UFRGS-PV 156T was different from the lectotype of *Huenesuchus chiquensis*, but the full medial view of the symphysis was precluded for more accurate observations. Otherwise, the condition in UFRGS-PV 629T (Mastrantonio,



**Figure 4.** Dorsal view of the paralectotype of *Huenesuchus chiniquensis* (SNSB-BSPG AS XXV 7) comprising the dorsal margin of the right (*dexter*) iliac blade, both right sacral ribs, and several osteoderms (*Osteoderma paramedianum*), the right double paramedian set of the first sacral vertebra (*Vertebra sacrale I*), both sides of double paramedian set of the second sacral vertebra (*Vertebra sacrale II*), and the sagittal double set (*Osteoderma sagittale*) of the first caudal vertebra (*Vertebra caudale I*). Scale bar = 100 mm.

2010:135, fig. 72A; Mastrantonio *et al.*, 2019:189, fig. 17) shows that there isn't any clear *Facies articularis dentalis dentale* (dental articular face for the other dental bone). So, the contact between both dental bones was not strong, and this suggests that the symphysis was formed by ligaments in a syndesmosis (*cf.* Holliday *et al.*, 2010:1351; *cf.* Holliday & Nesbitt, 2013:556). The condition in ULBRA-PVT 281 is very similar with the dentals (= dentaries) only attached to each other in a probable syndesmotomic symphysis (Roberto-da-Silva *et al.*, 2016:983, fig. 5; Roberto-da-Silva, 2017:148, fig. 4).

In the classification of symphysis types, the specimen UFRGS-PV 156T was considered by Holliday & Nesbitt (2013:564, tab. 1) as from Class I, characterized by flat symphyseal plates, conspicuous smooth region, and equally high and deep joint. Otherwise, *Huenesuchus chiniquensis*, with an extensive symphysis, although formed largely by the splenials, appears to be near Class II symphysis, a condition also indicated for *Saurosuchus* (Alcober, 2000:315, fig. 10A; Holliday & Nesbitt, 2013:565, fig. 7c).

I noted previously (Kischlat, 2002:290) that the holotype of *Procerosuchus celer* (SNSB-BSPG AS XXV 131~139), could represent a juvenile of *Huenesuchus chiniquensis*

(endorsed by Desojo & Rauhut, 2008:19; and Baczko *et al.*, 2019:14). But I was wrong because there is no evidence that the holotype of *P. celer* could be an ontogenetic miniature of the lectotype of *H. chiniquensis*.

Both the holotype of *Procerosuchus celer* and the lectotype of *Huenesuchus chiniquensis* were found in the same locality ("Weg-Sanga"; Huene & Stahlecker, 1931:40, 1968:35; Huene, 1942:217, 1990:228; "Sanga da Estrada" in Portuguese), but in different places ("Grabung 37" in the former, "Grabung 34" in the latter; Huene, 1942:161, 1990:171). The type-series of the dicynodont *Dinodontosaurus turpior* (Huene, 1935:76, 1990:85) also came from the Weg-Sanga ("Grabung 38").

Three remarkable details are present in the holotype of *Procerosuchus celer*. As noted by Huene (1938a:148, 1942:220, 1990:230) the morphology of the humerus shaft is exceptionally thin, resembling the condition of the additional material recently described (Lacerda, 2012:98, f. 53; Lacerda *et al.*, 2016:30, fig. 19) as *Huenesuchus chiniquensis*. This latter specimen (now CPEZ 239b) I personally partially collected in 1994 (but I didn't find it) in the Baum Sanga locality (Huene & Stahlecker, 1931:39, 1968:35; Beltrão,

1968:86), mixed with the holotype of *Archaeopelta arborensis* Desojo *et al.*, 2011. This is the same locality where the dicynodont *Stahleckeria potens* and the aphanosaur *Spondylosoma absconditum* were found (Huene, 1933a:129, 1933b:129; 1935:1, 1942:326; 1990:11, 342).

The condition of the humerus in the lectotype of *Huenesuchus chiquensis* could not be fully observed because the shaft is not preserved, but it is suggestive of being relatively thin (pers. obs.; Raugust, 2014:104, fig. 52D–E; Desojo *et al.*, 2020:27, fig. 10.4–6).

The second detail is the presence of a notable *Incisura acromialis* with also a uncinated margin of the coracoid at the joint between coracoid and scapula (Huene, 1942:219, 1990:230, pl. 29.1), which is also found in the lectotype of *Huenesuchus chiquensis* (pers. obs.; Huene, 1942:171, pl. 21.1, 1990:182; Raugust, 2014:99, fig. 49, “ent”; Desojo *et al.*, 2020:23, fig. 9, “oi”), but in *Procerosuchus celer* the acromion is well developed (*i.e.*, both margins of scapula and coracoid have similar cranial limits; Figure 3C). An *Incisura acromialis* could be potentially present, although the uncination is not clearly preserved, in the additional material from Baum Sanga (CPEZ 239b; Lacerda, 2012:96, fig. 97; Lacerda *et al.*, 2016:29, fig. 18A, “?coracoid foramen”; Figure 3D). The third detail concerns the medial margin of the coracoids. It is nearly straight in the holotype of *P. celer* and curved in the lectotype of *H. chiquensis* (Figures 2A, 3A, C). In sum, there are notable morphological differences between *H. chiquensis* and *P. celer*, and, as consequence, they represent different taxa, although sharing the slenderness of humeri and the presence of acromial uncinated incisure.

As cited before, critical parts of the lectotype of *Huenesuchus chiquensis* (mandible and trunk plus fore/hindlimbs) were collected on two different occasions. Mixed material is commonly found in Santa Maria Formation, therefore the mixed condition of the lectotype cannot be ruled out. In this hypothetical case, the binomen *H. chiquensis* (Huene, 1938a) should be restricted to the mandible (SNSB-BSPG AS XXV 1) with all the remaining parts having this mandible as the core of the binomen (*cf.* Art. 73.1.5).

## PRELIMINARY PHYLOGENETIC ANALYSIS

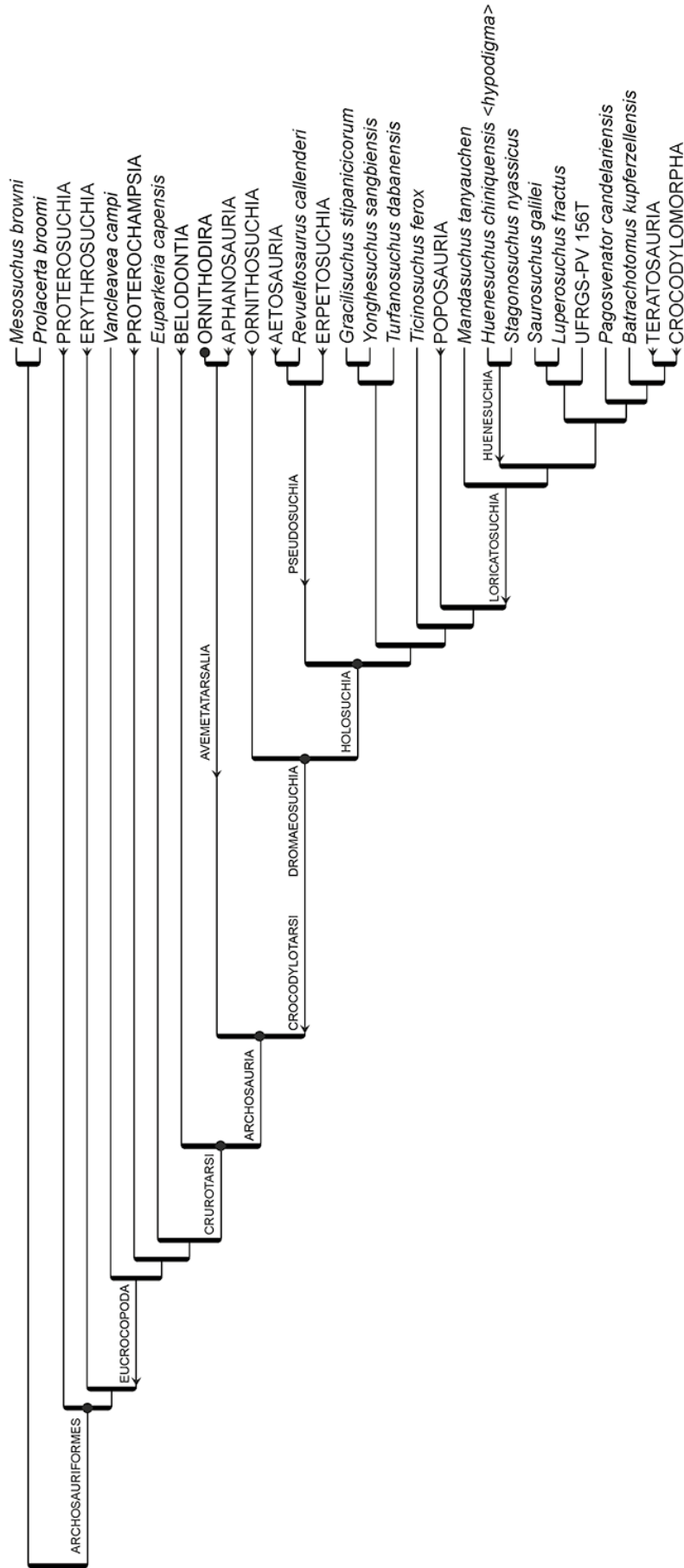
Kischlat (2002, 2003) hypothesized that the Sanga Pascoal specimen (UFRGS-PV 156T) was taxonomically different from *Huenesuchus chiquensis*. To preliminary test the interrelationships of *H. chiquensis* and this possible new taxon, I used Desojo’s *et al.* (2020) modified dataset. This one was initially taken from Nesbitt (2011), modified by Butler *et al.* (2014), and later by Nesbitt & Desojo (2017). As Desojo *et al.* (2020) did not indicate which characters are ordered, I followed Nesbitt & Desojo (2017) ordering characters 32, 52, 121, 137, 139, 156, 168, 188, 223, 247, 258, 269, 271, 291, 297, 328, 356, 399, and 413, with the following modifications: (1) exclusion of the lectotype and paralectotype of *Huenesuchus chiquensis*, but using

Huene’s (1938a) original hypodigm, expressly endorsed by the authors, and using the combined sequence; (2) exclusion of Vale Verde specimen (UFRGS-PV 152T); (3) exclusion of the Baum Sanga specimen (CPEZ 239b); (4) exclusion of the “paralectotype” (*sic!*, probably SNSB-BSPG AS XXV 4/25/42) of “*Prestosuchus*” *loricatus*; (5) exclusion of the individual sequences of *Pseudolagosuchus major* and *Lewisuchus admixtus*, but using their combined sequence, reflecting a new hypodigm comprising both binomina (Ezcurra *et al.*, 2020a; Agnolín *et al.*, 2021); (6) substitution of the sequence of *Rauisuchus tiradentes* in the characters 1–412 by the updated sequence given by Lautenschlager & Rauhut (2015), but changing the G75(3→2); (7) substitution of the sequence of *Parringtonia gracilis* in the characters 1–412 by the updated sequence given by Nesbitt *et al.* (2018a); (8) inclusion of the sequence of *Teratosaurus suevicus* given by Lessner *et al.* (2016) completing characters 413–422 with “?”; and, the most important, (9) the combined sequence of both the lectotype and paralectotype of *Huenesuchus chiquensis*, given by Desojo *et al.* (2020:47), fails in the scores for G412(?→0), G416(?→1), G417(?→1), G418(?→1), G419(?→1), G420(?→0), G421(?→1) and G422(?→1), but all were scored in the lectotype. Except for these modifications, I did not modify/correct any other score. This will be done in an upcoming paper dealing with the proposition of the new taxon using UFRGS-PV 156T as the name-bearing specimen (*cf.* Kischlat, 2002, 2003).

*Mesosuchus browni* and *Prolacerta broomi* were used as outgroups, as originally proposed by Nesbitt (2009:403, 2011:185). Instead, he did not implement this composite outgroup because he used the software TNT 1.0 (Goloboff *et al.*, 2003, 2008) for his phylogenetic analyses. So far as I know, TNT software does not work with a composite outgroup group like PAUP 4.0, but this is possible as recently shown (Goloboff, 2022:154).

The matrix with 91 taxa (two as outgroup) was analyzed under equally weighted parsimony using P.A.U.P. 4.0β10 (Swofford, 2002) and 4.0α (Swofford & Bell, 2017) and the results were the same. I used a heuristic search and 100 replicates, using a batch procedure (see Appendix 2). This resulted in 79,380 maximum parsimony trees (MPTs). When multistate taxa are interpreted as a variable (polymorphisms and uncertainty, see Swofford & Bell, 2017:105 for differences), the length has 1,476 steps (CI = 0.348; RI = 0.754); when interpreted as all uncertainties the length has 1,456 steps (CI = 0.339; RI = 0.754). The strict consensus tree has a good resolution with a polytomy only at basal Avemetatarsalia and Crocodylomorpha+Teratosauria clades (Figure 5). The majority rule tree (50%) shows these clades with a better resolution inside (see Supplementary file 3). Such results are not different from the results achieved by Nesbitt (2009, 2011) and the later iterations.

The result shows the original hypodigm of *Huenesuchus chiquensis* nested with *Stagonosuchus nyassicus*, and, higher in the next clade, the specimen UFRGS-PV 156T nested with *Luperosuchus fractus* and *Saurosuchus galilei*.



**Figure 5.** Phylogenetic relationships of *Hueneosuchus chiniquensis* and the new taxon (Sanga Pascoal specimen, UFRGS-PV 156T) among loricatosuchians archosaurs. Strict consensus tree (some taxa collapsed into larger clades) based on the analysis of Desojo *et al.* (2020) with the modifications explained in the text. The use and definitions of class-group names are also explained in the text. Tree constructed using TreeGraph 2 (Stöwer & Müller, 2010).

This preliminary result shows that the specimen UFRGS-PV 156T is a different taxon from *Huenesuchus chiniquensis* contradicting the opinion of many researchers and supporting my previous hypothesis (Kischlat, 2002, 2003). *Huenesuchus chiniquensis* is related to *Stagonosuchus nyassicus*, a result virtually achieved by Desojo *et al.* (2020). But UFRGS-PV 156T is closer to *Luperosuchus fractus* and *Saurosuchus galilei*, as well as all the remaining teratosaurs and crocodylomorphs.

### FINAL REMARKS

Unfortunately, the universally used nominal genus *Prestosuchus* Huene, 1938a (*nomen nudum*), is not available in the light of the *Code*. As such, the specific name *chiniquensis*, part of the original Huene’s (1938a, 1942) binomen “*Prestosuchus*” *chiniquensis*, turned out to be an orphan. This awkward nomenclatural situation was fixed here.

*Huenesuchus chiniquensis* was a taxon that reached a large size with a mandible exceeding 50 cm and with a huge femur measuring nearly 45 centimeters. “*Prestosuchus*” *chiniquensis*” has been used as the iconic taxon representative for Brazilian Triassic, but the specimen usually figured (UFRGS-PV 156T) is not *Huenesuchus chiniquensis* but represents a new taxon, as noted before (Kischlat, 2002, 2003).

Past errors in the literature were corrected here and I hope that this present contribution can provide a new nomenclatural and taxonomic understanding of the hypercarnivorous crocodylotarsans archosaurs of the Triassic fauna of Rio Grande do Sul (Brazil). The choice of honoring Friedrich von Huene, and his seminal work, introducing the new nominal genus *Huenesuchus*, should be considered as a tribute that I could not avoid doing, literally calling this already long-known taxon paronomastically as “Huene’s *suchus* from Chiquá”.

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I am especially grateful to my former advisor (deceased), Dr. Mario C. Barberena, who from our first conversation in 1994 alerted me about the nomenclatural problems of *Prestosuchus* and the large skull described by him in 1978 (“I stuck it in *Prestosuchus*, but it’s not *Prestosuchus*!”). I wish to thank many colleagues that helped me on my trip to Germany (land of my grandfather Ernst-Wilhelm Kischlat) in late 1997: D.J. Gower (British Museum, Natural History, London), E.S. Gafney (American Museum of Natural History, New York), M.W. Maisch (Institut und Museum für Geologie und Paläontologie, Eberhard-Karls-Universität, Tübingen), P. Wellnhöfer (Bayerische Staatssammlung für Paläontologie und Geologie, München), R. Wild and R. Schoch (Staatliches Museum für Naturkunde, Stuttgart). Several papers were downloaded from the Wikipaleo community and R. Guzmán-Gutiérrez (Universidad Humanista de las Américas, Monterey, Mexico) helped me many times. B.L. Horn (project manager here in Serviço Geológico do Brasil, Porto Alegre) and the

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**Appendix 1.** Nomenclatural remarks on binomina and some class-group names.

**Binomina used as terminals in the phylogenetic analysis.**

*Proterosuchus fergusi* used by Nesbitt (2009:21, 2011:17) includes three type-specimens which now comprise three (*Proterosuchus fergusi*, *P. alexanderi*, and *P. goweri*) different taxa (Ezcurra & Butler, 2015). So, here it was renamed as *Proterosuchus* spp.

*Lagosuchus talampayensis* Romer, 1971, and *Marasuchus lilloensis* (Romer, 1972b) are now considered as representing the same taxon (Agnolín & Ezcurra, 2019), which the former binomen has a preference (cf. Art. 23.1).

*Lewisuchus admixtus* Romer, 1972a, and *Pseudolagosuchus major* Arcucci, 1987, were suspected as representing the same taxon (Arcucci, 1997, 1998, 2005), and this hypothesis gained support. Today they are now considered (Ezcurra *et al.*, 2020a; Agnolín *et al.*, 2021) as representing the same taxon, which the former binomen has a preference (cf. Art. 23.1).

Nesbitt (2009:95, 2011:54) noted that the type-material of *Plateosaurus engelhardti* Meyer, 1837, is not diagnostic and indicated the specimens from Trossingen (SMNS 13200 and AMNH FR 6810) as the source of his codings. A recent decision of I.C.Z.N. (2019) designated *Plateosaurus trossingensis* Fraas, 1913, as the type-species of the nominal genus *Plateosaurus* Meyer, 1837. As SMNS 13200 is the holotype of *Plateosaurus trossingensis* Fraas, 1913 (Galton, 2012:205) and AMNH FR 6810 was referred to this species (Fernández & Werneburg, 2022:775, although improperly calling it as “syntype”), the valid name for the taxon is *Plateosaurus trossingensis* Fraas, 1913.

*Ornithosuchus woodwardi* Newton, 1893, was resurrected by Baczko & Ezcurra (2016:203) from its junior synonym with *Dasygnathus* (= *Dasygnathoides* Kuhn, 1961b:79) *longidens* Huxley, 1877. As noted by Baczko & Ezcurra (2016:204), Nesbitt’s (2009, 2011) scorings were based on the type-material of *Ornithosuchus woodwardi*.

The nominal genus *Lagerpeton* Romer, 1971, came from Ἐρπετόν (*herpetón*, reptile; Bailly, 2020:1011) which has neuter gender. In gender agreement (Arts. 31.2, 34.2, & 50.3.2) the correct spelling will be *Lagerpeton chanarensis* (not “*chanarensis*”, as originally in Romer, 1971:1).

The original binomina *Baroqueosuchus haughtoni* Busbey & Gow, 1984, and *Stagonosuchus nyassicus* Huene, 1938b, were used instead of *Protosuchus haughtoni* and “*Prestosuchus*” *nyassicus*. A genus, as a taxon *per se*, is only a mental construction (Hennig, 1966:78) and not a natural entity, and two paleospecies sharing the same genus is a subjective convenience, based on the shared morphology and an alleged some kind of stratigraphic correlation/continuation. A genus name is only part of a Latin binomen, which is a tradition in Nomenclature (I.C.Z.N., 1999).

**Class-group names used in Figure 5.**

Every nominal genus has type-species, there is no need to repeat the species name. Any phylogenetic definition could be simplified with this in mind.

In the past, the genus-name *Crocodylus* Cuvier, 1807 (type-species *C. vulgaris* Cuvier, 1807, cf. Fitzinger, 1843:35), was widely used instead of *Crocodylus* Laurenti, 1768 (type-species *C. niloticus* Laurenti, 1768; cf. Hay, 1902:512), which has the preference, and this is implicit in the usage of the class-group names *Crocodylia* Owen, 1842, and *Crocodylia* Loveridge, 1946. But in the following definitions, I preserved the original nomenclatural context of usage of *Crocodylus* Cuvier, 1807, as a specifier, in analogy to Art. 67.1.2 (Recommendation 67B).

“*Passer domesticus* Linnaeus, 1758” has been used as a reference taxon in phylogenetic definitions (*e.g.*, Nesbitt, 2011:191; Ezcurra, 2016:293). Actually, Linnaeus (1758:183) introduced *Fringilla domestica*, and Brisson (1760:72) transferred the species name to the nominal genus *Passer* Brisson, 1760, which has *Fringilla domestica* Linnaeus, 1758, as the type-species (cf. Amadon *et al.*, 1962:8). According to Art. 51.3 this binomen should be written as *Passer domesticus* (Linnaeus, 1758), but this can be abbreviated as only *Passer* Brisson, 1760, in phylogenetic definitions without losing the information. On the other hand, the first avian nominal genus introduced by Linnaeus (1758:86) is *Vultur*, which the type-species is *V. gryphus* Linnaeus, 1758 (cf. Peters, 1931:189).

As explained above, I simplified all phylogenetic definitions using only nominal genera (see ahead a synopsis) and I also applied the historical nomenclatural context of usage of *Crocodylus* Cuvier, 1807, instead of *Crocodylus* Laurenti, 1768, in correcting the previous definitions of *Aetosauria* Marsh, 1884 (Nesbitt, 2011:196), *Belodontia* Brauns, 1890 (Kischlat, 2002:283), *Erythrosuchia* Watson, 1957 (Kischlat, 2002:279), *Suchia* Krebs, 1974 (Nesbitt, 2011:195), *Loricata* Merrem, 1820 (Nesbitt, 2011:200), *Ornithosuchia* Huene, 1908 (Kischlat, 2002:285), *Proterochampsia* Bonaparte, 1971 (Kischlat, 2002:279), *Proterosuchia* Broom, 1906 (Kischlat, 2002:278), and *Rauisuchia* Bonaparte, 1975 (Nesbitt *et al.*, 2013b:245).

Archosauriformes Gauthier *et al.*, 1988, was defined with *Crocodylus* Cuvier, 1807, as a specifier because I assume the coordination with *Archosauria* Cope, 1870.

Eucrocopoda Ezcurra, 2016, should be a subset of *Crocopoda* Ezcurra, 2016, which means “crocodile-foot” (Ezcurra, 2016:385). Eucrocopods are the “noble crocops” (Gr. εὖ, *eû*: noble, well; Bailly, 2020:1208). If anyone owns a typical crocodile-foot, this certainly is *Crocodylus*. So, both names are coordinated with each other and should have *Crocodylus* Laurenti, 1768, as a primary specifier in their definitions. Although Ezcurra (2016:293) used *Crocodylus* Laurenti, 1768, in the definition of his Eucrocopoda, this was not the case in the definition of *Crocopoda* (p. 284).

I used *Vultur* Linnaeus, 1758, instead of *Passer* Brisson, 1760, in Ornithodira Gauthier, 1986 (Nesbitt, 2011:206) and corrected my previous mistake (Kischlat, 2002:278) in using the fake eponym *Pterosaurus* Fitzinger, 1843, a squamate agamidae (= *Draco* Linnaeus, 1758), as a pterosaurian name.

Benton & Clark (1988:315, fig. 8.1) when converting Crocodylomorpha Walker, 1970, to a clade name, did not include *Postosuchus* Chatterjee, 1985, but Nesbitt's (2011:203) stem definition and phylogenetic context included it. Thus, I prefer my previous sense excluding *Postosuchus* (Kischlat, 2002:277).

Rauisuchia Bonaparte, 1975, has been the name used variably for the group composed of hypercanivorous crocodylotarsans archosaurs with recurved serrated teeth that have not been clearly referable to aetosaurs, belodonts, ornithosuchians, and crocodylomorphs (Nesbitt *et al.*, 2013b:241). It was recently phylogenetically defined (Nesbitt *et al.*, 2013b:245) as the node comprising the least inclusive clade containing *Poposaurus* Mehl, 1915; *Batrachotomus* Gower, 1999; "*Prestosuchus*" Huene 1938a, and *Rauisuchus* Huene 1938a; but not *Crocodylus* Laurenti, 1768; *Ornithosuchus* Newton, 1893; and *Aetosaurus* Fraas, 1877.

In Nesbitt's (2009, 2011) matrix and later derivative iterations, Rauisuchia is always paraphyletic. A monophyletic Rauisuchia was only recovered in Brusatte *et al.* (2010) and later derivative iterations (see Tolchard *et al.*, 2019). In the present phylogenetic hypothesis (Figure 4), which is very similar to that original in Nesbitt (2009, 2011) and in all derivative iterations, this definition results in a paraphyletic assemblage. On the other hand, there are several older class-group names available to be used instead of Rauisuchia Bonaparte, 1975, which is the youngest of all of them. Although Rauisuchia has potential redundancy with the older Teratosauria (see next), it might have some utility if applied in a broad, informal sense ("rauisuchians").

Teratosauria Colbert, 1970, can be applied to *Teratosaurus* Meyer, 1861, and its kins (*Rauisuchus* Huene, 1838a, and *Postosuchus* Chatterjee, 1985), defined as the stem comprising all taxa more related to *Teratosaurus* Meyer, 1861, than to *Crocodylus* Cuvier, 1807.

Poposauria Nopcsa, 1923, can well be applied and defined as the stem comprising all taxa more related to *Poposaurus* Mehl, 1915, than to *Crocodylus* Cuvier, 1807. Of course, the usage of class-group names instead of family-group names (*e.g.*, Poposauroida Nopcsa, 1928) is a personal choice (see Nesbitt *et al.*, 2013b:244).

Belodontia Brauns, 1890, discussed in Kischlat (2022a), should be used instead of Parasuchia Huxley, 1875, and Phytosauria Baur, 1894. It was defined as a stem including *Belodon* Meyer, 1842, in the exclusion of *Crocodylus* Laurenti, 1768. Now I correct this definition using *Crocodylus* Cuvier, 1807.

Aetosauria Marsh, 1884, was defined (simplified herein) by Nesbitt (2011:196) as a stem including *Aetosaurus* Fraas, 1877, in the exclusion of *Revueltosaurus* Hunt, 1989, and *Crocodylus* Cuvier, 1807.

Erpetosuchia was introduced by Walker (1968:13) to accommodate *Erpetosuchus* Newton, 1893, and *Dyoplax* Fraas, 1867, and this class-group name could be well defined as a stem including *Erpetosuchus* Newton, 1893, in the exclusion of *Aetosaurus* Fraas, 1877, and *Crocodylus* Cuvier, 1807.

Gauthier & Padian (1985:189) noted the "corruption" of the original sense of the class-group name Pseudosuchia Zittel, 1890 (*cf.* Woodward, 1891, for publication year), and defined it as a stem comprising "the crocodiles and all archosaurs closer to crocodiles than to birds". Later, Benton & Clark (1988:307) proposed Crocodylotarsi to receive this definition. It is not a substitutive name for Pseudosuchia Zittel, 1890, as considered by Brochu (1997:448), but a new name to receive Gauthier & Padian's (1985) stem definition in the corrupted sense.

Pseudosuchia was introduced by Zittel (1890:644) including two aetosaurians (*Aetosaurus* Fraas, 1877; and *Typhorax* Cope, 1875) and *Dyoplax* Fraas, 1867, which has been considered as related to *Erpetosuchus* (Huene, 1920:484; Walker, 1961:183, 1968:13; Maisch *et al.*, 2013:360). Recently this kinship was positively tested (Ezcurra *et al.*, 2017:1480, fig. 3). Thus, the original Zittel's (1890) sense, Pseudosuchia can be now recovered with Aetosauria and Erpetosuchia as sister clades. Thus, I propose to use Pseudosuchia Zittel, 1890, in the original sense, tied to a phylogenetic hypothesis comprising the lineage of aetosaurians and erpetosuchians in the exclusion of the lineage towards crocodiles ("the Pseudosuchian Hypothesis"). I define this clade as a stem comprising *Aetosaurus* Fraas, 1877, and *Dyoplax* Fraas, 1867, in the exclusion of *Crocodylus* Cuvier, 1807. This definition also recovers the etymology of Pseudosuchia (Gr. ψευδής, *pseudēs*: false; Bailly, 2020:2573) which means false suchians, which should not include the true suchians (*e.g.*, *Crocodylus* Cuvier, 1807).

Suchia Krebs, 1974, was defined as a node by Nesbitt (2011:195). As it is previously occupied by Suchia Simpson, 1937, I propose Holosuchia (Gr. ὅλος, *hólos*: whole, entire, complete; Bailly, 2020:1661; "all the suchians") as a substitute name (Art. 1.2.2).

Loricata Merrem, 1820, was defined as a stem by Nesbitt (2011:200). As it is previously occupied by Loricata Schumacher, 1817, I propose Loricatosuchia as a substitute name (Art. 1.2.2).

### Definition synopsis.

Aetosauria Marsh, 1884:69. Stem, the most inclusive clade containing *Aetosaurus* Fraas, 1877, but not *Revueltosaurus* Hunt, 1989 [nor *Rutiodon* Emmons, 1856; nor *Gracilisuchus*

- Romer, 1972a; nor *Poposaurus* Mehl, 1915; nor *Huenesuchus* *gen. nov.*; nor *Postosuchus* Chatterjee, 1985]; nor *Crocodylus* Cuvier, 1807 (simplified, updated, and corrected from Nesbitt, 2011:196).
- Aphanosauria Nesbitt *et al.*, 2017:485. Stem, the most inclusive clade containing *Teleocrater* Nesbitt *et al.*, 2017 [and *Yarasuchus* Sen, 2005], but not *Passer* Brisson, 1760, nor *Crocodylus* Laurenti, 1768 (simplified from Nesbitt *et al.*, 2018b:143).
- Archosauria Cope, 1870:30. Node, containing *Crocodylus* Cuvier, 1807, and *Megalosaurus* Buckland, 1824 (Gauthier & Padian, 1985:187; updated by Kischlat, 2002:276).
- Archosauriformes Gauthier *et al.*, 1988:204. Node, containing *Crocodylus* Cuvier, 1807, and *Proterosuchus* Broom, 1903 (Gauthier, 1994:148, updated by Kischlat, 2002:276).
- Avemetatarsalia Benton, 1999:1440. Stem, the most inclusive clade containing *Vultur* Linnaeus, 1758, but not *Crocodylus* Laurenti, 1768 (Benton, 1999:1440; updated by Kischlat, 2002:277).
- Belodontia Brauns, 1890:202. Stem, the most inclusive clade containing *Belodon* Meyer, 1842, but not *Aetosaurus* Fraas, 1877, nor *Crocodylus* Cuvier, 1807 (corrected from Kischlat, 2002:283).
- Crocodylomorpha Walker, 1970:368. Stem, the most inclusive clade containing *Crocodylus* Laurenti, 1768, but not *Postosuchus* Chatterjee, 1985 (Kischlat, 2002:277, *cf.* Benton & Clark, 1988:315, fig. 8.1).
- Crocodylotarsi Benton & Clark, 1988:307. Stem, the most inclusive clade containing *Crocodylus* Laurenti, 1768, but not *Vultur* Linnaeus, 1758 (Kischlat, 2002:276).
- Crurotarsi Sereno & Arcucci, 1990:41. Node, containing *Crocodylus* Laurenti, 1768, and *Rutiodon* Emmons, 1856 (simplified from Nesbitt, 2011:192).
- Dromaeosuchia Juul, 1994:23. Node, containing *Crocodylus* Laurenti, 1768, and *Ornithosuchus* Newton, 1893 (Jull, 1994:23, updated by Kischlat, 2002:277).
- Erpetosuchia Walker, 1968:13. Stem, the most inclusive clade containing *Erpetosuchus* Newton, 1893; but not *Aetosaurus* Fraas, 1877, nor *Crocodylus* Cuvier, 1807 (herein).
- Erythrosuchia Watson, 1957:379. Stem, the most inclusive clade containing *Erythrosuchus* Broom, 1905; but not *Crocodylus* Cuvier, 1807 (corrected from Kischlat, 2002:279).
- Eucrocopoda Ezcurra, 2016:293. Stem, the most inclusive clade containing *Crocodylus* Laurenti, 1768; but not *Proterosuchus* Broom, 1903, nor *Erythrosuchus* Broom, 1905 (simplified from Ezcurra, 2016:293).
- Holosuchia, *nomen substitutum pro* Suchia Krebs, 1974:21 (*non* Simpson, 1937:16). Node, *Aetosaurus*, Fraas, 1877, [and *Huenesuchus* *gen. nov.*, and *Rauisuchus* Huene, 1838a] and *Crocodylus* Cuvier, 1807 (simplified and corrected from Nesbitt, 2011:195).
- Huenesuchia (new class-group name). Stem, the most inclusive clade containing *Huenesuchus*, *gen. nov.*, but not *Crocodylus* Laurenti, 1768 (herein).
- Loricatosuchia, *nomen substitutum pro* Loricata Merrem, 1820:34 (*non* Schumacher, 1817:35). Stem, the most inclusive clade containing *Crocodylus* Cuvier, 1807, but not *Poposaurus* Mehl, 1915 [nor *Ornithosuchus* Newton, 1893; nor *Aetosaurus* Fraas, 1877] (simplified and corrected from Nesbitt, 2011:200).
- Ornithodira Gauthier, 1986:47. Node, containing *Vultur* Linnaeus, 1758, and *Pterodactylus* Rafinesque, 1815 (corrected from Kischlat, 2002:278; and from Nesbitt, 2011:206).
- Ornithosuchia Huene, 1908:395. Stem, the most inclusive clade containing *Ornithosuchus* Newton, 1893; but not *Crocodylus* Cuvier, 1807 (corrected from Kischlat, 2002:285).
- Poposauria Nopcsa, 1923:126. Stem, the most inclusive clade containing *Poposaurus* Mehl, 1915; but not *Crocodylus* Cuvier, 1807 (herein).
- Proterochampsia Bonaparte, 1971:420. Stem, the most inclusive clade containing *Proterochampsia* Reig, 1958, but not *Crocodylus* Cuvier, 1807 (corrected from Kischlat, 2002:279).
- Proterosuchia Broom, 1906:600. Stem, the most inclusive clade containing *Proterosuchus* Broom, 1903, but not *Crocodylus* Cuvier, 1807 (corrected from Kischlat, 2002:278).
- Pseudosuchia Zittel, 1890:644. Stem, the most inclusive clade containing *Aetosaurus* Fraas, 1877, and *Dyoplax* Fraas, 1867; but not *Crocodylus* Cuvier, 1807 (herein, the “Pseudosuchian Hypothesis”).
- Rauisuchia Bonaparte, 1975:63. Node, *Poposaurus* Mehl, 1915; *Batrachotomus* Gower, 1999; *Huenesuchus* *gen. nov.*; *Rauisuchus* Huene, 1938a; but not *Crocodylus* Cuvier, 1807; [nor *Ornithosuchus* Newton, 1893; nor *Aetosaurus* Fraas, 1877] (corrected and updated from Nesbitt *et al.*, 2013:245).
- Teratosauria Colbert, 1970:26. Stem, the most inclusive clade containing *Teratosaurus* Meyer, 1861; but not *Crocodylus* Cuvier, 1807 (herein).

**Appendix 2.** The following batch was introduced in Kischlat (2022b) and it is slightly modified here. It is inserted in the PAUP BLOCK of the nexus file for the phylogenetic analysis. The “K:\Matrix\Output\” string must be changed accordingly to each user’s path (see Swofford, 2002:9).

```
BEGIN PAUP;
log /replace=yes file=K:\Matrix\Output\HuenesuchusMatrix.
paup.log;
log start;
set autoclose=yes;
set outroot=monophyl;
set taxlabels=full;
set InitSeeds=1;
set increase=auto [no];
set mstaxa=variable;
assume ancstates=standard;
outgroup 1-2 /only;
constraints ANCESTOR=((1,2));
```

```
hsearch enforce=yes nchuck=1 chuckscore=1477
addseq=random nreps=100 swap=tbr;
savetrees /replace=yes file=K:\Matrix\Output\
HuenesuchusMatrix.paup.trees;
gettrees /mode=3 warntree=no storeBrlens=no file=K:\
Matrix\Output\HuenesuchusMatrix.paup.trees;
pscores 1 /TL CI RI RC HI;
set mstaxa=uncertain;
pscores 1 /TL CI RI RC HI;
set mstaxa=variable;
showmatrix;
contree /replace=yes majrule=yes treefile=K:\Matrix\
Output\HuenesuchusMatrix.paup.tre;
gettrees /mode=3 warntree=no file=K:\Matrix\Output\
HuenesuchusMatrix.paup.tre;
describetrees 1 /apolist=yes opt=acctrans;
describetrees 1 /apolist=yes opt=deltran;
log stop;
ENDBLOCK;
```

## SUPPLEMENTARY FILES

### Supplementary file 1.

SNSB-BSPG Catalog.pdf

### Supplementary file 2.

Comparisons between the mandibles (left side, lateral view) of the new taxon, represented by the specimen UFRGS-PV 0169T (above, from Mastrantonio *et al.*, 2019), and the lectotype of *Huenesuchus chiniquensis* SNSB-BSPG AS XXV 1 (below, from Desojo *et al.*, 2020). Both mandibles normalized to the same dimension, from the rostral symphyseal tip to the caudal tip of the ventrocaudal

process of the dental bone. Abbreviations: **an**, *Os angulare*; **d**, *Os dentale*; **dIII**, **dVII**, **dXI**, dental teeth 3, 7 and 11; **fo**, foramen; **pvc den**, *Processus ventrocaudalis dentale*; **sa**, *Os supraangulare*. Scale bar equals 5 cm.

### Supplementary file 3.

Dataset.rar

Nexus input data file: HuenesuchusMatrix.paup.nex

Output text file: HuenesuchusMatrix.paup.log

Annotated pdf from the above: HuenesuchusMatrix.paup.log.pdf

Output strict consensus plus majority rule trees: HuenesuchusMatrix.paup.tre