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A REVIEW OF SPHAGESAURUS HUENEI AND RELATED SPHAGESAURIDS

UMA REVISÃO DE SPHAGESAURUS HUENEI E ESFEGESAURÍDEOS RELACIONADOS

UNA REVISIÓN DE SPHAGESAURUS HUENEI Y ESFAGOSÁURIDOS RELACIONADOS

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ABSTRACT

Originally described based only on isolated teeth, Sphagesaurus huenei has been subject to successive taxonomic reinterpretations, particularly after descriptions of Armadillosuchus arrudai and Caryonosuchus pricei whose type specimens are now regarded as insufficiently diagnostic within Sphagesauridae. In this article we present a comprehensive inventory of the material attributed to these closely-related sphagesaurids and reassess their diagnostic characters under ICZN guidelines discussing the taxonomic implications and offering provisional recommendations. Based on the available evidence, we consider Armadillosuchus arrudai and Caryonosuchus pricei to represent junior synonyms of Sphagesaurus huenei, as they lack unequivocal and consistently interpretable diagnostic traits distinguishing them from this species. Specimen RCL-100 is herein regarded as referable to Sphagesaurus huenei, following its widespread use in the literature as a reference for the specie's diagnostic features. These interpretations are provisional and may be refined with the discovery of additional, well preserved material, or quantitative morphological analyses.

Keywords: Sphagesauridae. Taxonomy. Bauru Group.

RESUMO

Originalmente descrito com base apenas em dentes isolados, Sphagesaurus huenei foi objeto de sucessivas reinterpretações taxonômicas, particularmente após as descrições de Armadillosuchus arrudai e Caryonosuchus pricei, cujos espécimes-tipo agora são considerados insuficientemente diagnósticos dentro de Sphagesauridae. Neste artigo apresentamos um inventário abrangente do material atribuído a estes sphagesaurídeos proximamente relacionados e reavaliamos seus caracteres diagnósticos sob diretrizes ICZN, discutindo as implicações taxonômicas e oferecendo recomendações provisórias. Com base na evidência disponível, consideramos Armadillosuchus arrudai e Caryonosuchus pricei como sinônimos juniores de Sphagesaurus huenei, pois carecem de características diagnósticas inequívocas e consistentemente interpretáveis que os distingam desta espécie. O espécime RCL-100 é considerado aqui como referível a Sphagesaurus huenei, seguindo

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seu uso generalizado na literatura como referência para os caracteres diagnósticos da espécie. Essas interpretações são provisórias e podem ser refinadas com a descoberta de material adicional bem preservado ou análises morfológicas quantitativas.

Palavras-chave: Sphagesauridae. Taxonomia. Grupo Bauru.

RESUMEN
Originalmente descrito basándose únicamente en dientes aislados, Sphagesaurus huenei ha sido objeto de sucesivas reinterpretaciones taxonómicas, particularmente después de las descripciones de Armadillosuchus arrudai y Caryonosuchus pricei cuyos especímenes tipo ahora se consideran insuficientemente diagnósticos dentro de Sphagesauridae. En este artículo presentamos un inventario exhaustivo del material atribuido a estos esfagesáuridos estrechamente relacionados y reevaluamos sus caracteres diagnósticos bajo directrices ICZN, discutiendo las implicaciones taxonómicas y ofreciendo recomendaciones provisionales. Con base en la evidencia disponible, consideramos que Armadillosuchus arrudai y Caryonosuchus pricei representan sinónimos menores de Sphagesaurus huenei, ya que carecen de características diagnósticas inequívocas e interpretables consistentemente que los distingan de esta especie. El espécimen RCL-100 se considera aquí referible a Sphagesaurus huenei, siguiendo su uso generalizado en la literatura como referencia para los caracteres diagnósticos de la especie. Estas interpretaciones son provisionales y pueden refinarse con el descubrimiento de material adicional bien preservado o análisis morfológicos cuantitativos.

Palabras clave: Sphagesauridae. Taxonomía. Grupo Bauru.

1 INTRODUCTION

Sphagesauridae (Kuhn, 1968) is a Notosuchia (Crocodylomorpha; Crocodyliformes) family ranked clade known for their unique dentition, with three distinct morphologies (incisiform, caniniform and molariform), and a complex pattern of dental occlusion, with a tear shearing mechanism involving propalinal movements (Pol, 2003; Iori & Carvalho, 2011; Ösi, 2013; Iori & Carvalho, 2018; Cunha *et al.,* 2020). Ruiz *et al.* (2021) define Sphagesauridae cladistically as the "the least inclusive clade containing *Sphagesaurus huenei* Price, 1950, *Caipirasuchus* (originally *Sphagesaurus*) *montealtensis* Andrade & Bertini, 2008 and *Yacarenani boliviensis* Novas *et al*., 2009".

Cunha *et al.* (2020) subdivide this family in two groups: "large-bodied forms", such as *Sphagesaurus*, *Armadillosuchus* and *Caryonosuchus*; and "small-bodied forms", such as *Adamantinasuchus*, *Caipirasuchus* and *Yacarenani*. Noticing that large-bodied sphagesaurids are often recovered as a monophyletic grouping (Pol *et al*., 2014; Martinelli, 2018; Cunha *et al*., 2020; Pinheiro *et al*., 2021), and recognizing a morphological unity between *Sphagesaurus*, *Armadillosuchus* and *Caryonosuchus*, Pinheiro *et al.* (2021) proposed the Clade Sphagesaurinae, which comprises the last common ancestor of these taxa and all its descendants.

Previously however Kellner *et al.* (2011) noted that the described cranial remains and all the distinct species display basically the same dentition, which is undistinguishable from the type material of *Sphagesaurus huenei*. These authors claimed that one taxonomic revision of the Sphagesauridae was needed, because *Sphagesaurus huenei* might be considered a *nomen dubium*, but this approach might conflict with ICZN guidelines. More than a decade later, no formal revision as such was made. For that matter, this article aims to overview eventual issues in Sphagesaurinae Taxonomy and propose a taxonomical opinion on the matter.

The holotype (DGM 332-R) was found in a railroad cut between Presidente Bernardes and Santo Anastácio; and the paratype (DGM 333-R) was found near Catanduva. Although consisting of such fragmentary material, the uniqueness of these teeth allowed, by that time, the recognition of this taxon and its placement in Crocodyliformes. *Sphagesaurus huenei* was so diagnosed by Price (1950) as teeth with comparatively short crowns and elongated roots, both with some lateral compression; crown covered by a thick layer of dentin; few and prominent carinae, irregularly spaced, arranged longitudinally on the crown; anterior surface of the crown without a keel; posterior surface of the crown with a very prominent keel, with

several tubercles along its length; teeth arranged in a specific and peculiar way, in which occlusion with their complementary teeth results in the use of the posterior keels as cutting margins.

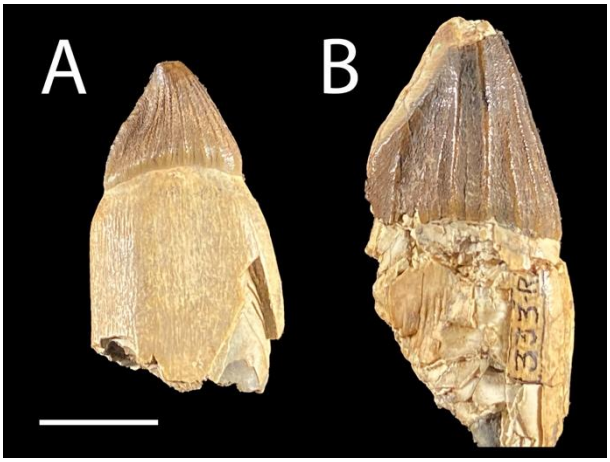
2 HISTORICAL PERSPECTIVE AND TAXONOMIC FRAMEWORK

Prior to its formal description, *Sphagesaurus* was first noticed in 1931 by von Huene, who recorded its existence and identified the fossil teeth as crocodylian, but unfortunately these specimens were considered lost (Andrade & Bertini, 2008).

Price (1950) formally described *Sphagesaurus huenei*, based on two isolated teeth (Figure 1) found in outcrops of the Bauru Group, in São Paulo State, in Brazil. The holotype (DGM 332-R) was found in a railroad cut between Presidente Bernardes and Santo Anastácio; and the paratype (DGM 333-R) was found near Catanduva. Although consisting of such fragmentary material, the uniqueness of these teeth allowed, by that time, the recognition of this taxon and its placement in Crocodyliformes. *Sphagesaurus huenei* was so diagnosed by Price (1950) as teeth with comparatively short crowns and elongated roots, both with some lateral compression; crown covered by a thick layer of dentin; few and prominent carinae, irregularly spaced, arranged longitudinally on the crown; anterior surface of the crown without a keel; posterior surface of the crown with a very prominent keel, with several tubercles along its length; teeth arranged in a specific and peculiar way, in which occlusion with their complementary teeth results in the use of the posterior keels as cutting margins.

Figure 1

Sphagesaurus huenei. A, holotype (DGM 332-R); B, paratype (DGM 333-R). Scale bar = 1cm



Source: prepared by the authors themselves.

Decades later, the description of an almost complete skull, and fragmentary mandible, allowed an emended diagnosis of *Sphagesaurus huenei* by Pol (2003), as maxillary and posterior mandibular tooth crowns with major axis oriented obliquely and disposed like reverse triangles; maxillary teeth with short compressed crowns covered by heavy coat of enamel, the surface of which is coarsely pebbled and possesses few irregularly spaced longitudinal carinae; premaxilla with edentulous region mesial to the caniniforms; maxilla with posterior wall above the anterior margin of the suborbital fenestra that extends dorsally contacting the prefrontal and lacrimal; basioccipital-quadrate contact in occipital area excludes the exoccipital from the ventral margin of the mentioned skull surface.

It also allowed for the first time to evaluate functional aspects of the bizarre dentition, and the phylogenetic relationships of this taxon. Despite not being registered as a type specimen, RCL-100 is the main referred *Sphagesaurus huenei* material in most systematics and taxonomy works (*e.g.,* Andrade, 2005; Andrade *&* Bertini, 2008; Marinho *&* Carvalho, 2009; Kellner *et al.,* 2011; Iori *&* Carvalho, 2011; Iori *et al.,* 2013; Pol *et al*., 2014; Martinelli *et al*., 2018; Ruiz *et al.*, 2021; Pinheiro *et al.*, 2021; Marinho *et al*., 2022; Iori *et al*., 2024; Leardi *et al*., 2024).

While proposing a new species of *Sphagesaurus*, *Sphagesaurus montealtensis* (later reappraised as *Caipirasuchus montealtensis* by Iori *et al*., 2013), Andrade *&* Bertini (2008, p. 107) erected a new diagnosis for the *Sphagesaurus* genus, as:

> […] Skull as high as wide; rostrum slightly elongated; naris anteriorly directed; internarial bar absent; orbits lateral; jugal anterior and posterior rami horizontal and level to each other; jugal foramen single, anteriorly directed, positioned on the lateral surface of the anterior jugal ramus; ascending jugal ramus and postorbital bar inclined posteromedially; triangular antorbital fossa delimited anteriorly by jugal–maxillary and lachrymal crests; elongated supratemporal fenestrae, with parallel main axis coincident with the sagittal axis of the skull; occipital surface exposed posterodorsally (exoccipitals) above, and posteroventrally (basioccipital, basisphenoid) below the foramen magnum; triangular choanae; posterolateral palatine processes present, delimiting anterolateral borders of the choanal opening; palatine and ectopterygoid contact posterior to the suborbital fenestra posterior end; pterygoid and jugal excluded from suborbital fenestra; lachrymal contacting the nasal; edentulous region on the front of the premaxilla; well-developed alveolus, posterior to the hypertrophied caniniform; basioccipital wider than basisphenoid; basioccipital–quadrate contact present, well developed; teeth all single cusped; eight upper and nine lower (mandibulary) teeth; reduced premaxillae, bearing at least one pair of hypertrophied caniniform teeth; six to seven maxillary teeth, all molariform, with a strong oblique implantation (45–90 degrees of paramesial rotation, in respect to the maxillary alveolar surface); symphysis including pairs 1–5, composing a battery of teeth; mandibular pairs 3 and anterior with caniniform–incisiform morphology; at least mandibular pairs 4 and 5 molariform; at least mandibular pair 5 with a strong oblique implantation (45–90 degrees rotation, in respect to the maxillary alveolar surface); mandibular pairs 1–5 increase in size; maxillary molariforms stout, anteriorly rounded and posteriorly compressed, with a teardrop-like cross-section; mandibular molariforms stout, anteriorly compressed and posteriorly more rounded (reverse teardrop-like cross-section); maxillary molariforms with one single posterior carina forming a cutting edge, opposing mandibulary molariforms with an anterior one.

And then, their (Andrade & Bertini, 2008, p. 108) species diagnosis for *Sphagesaurus huenei* is:

> […] antorbital fenestra absent; premaxilla–maxilla suture extending far posteriorly from the hypertrophied caniniform, on the lateral surface of the skull; maxillae forming a posterior wall above the anterior margin of the suborbital fenestra, contacting prefrontal and lachrymal; jugal anterior ramus robust, enlarging progressively towards its contact with the maxilla; palate surface plain; maxillae palatine rami straight and level to each other, not inclined; naso-oral fenestra in premaxilla–maxilla suture; quadrate light, with a trirradiate cross-section; quadrate medial ventral crest thin; quadrate crests reaching from the outer tip of each quadrate, contacting over basisphenoid; pterygoid–basisphenoid surface concave in contact; maxillary dental series forming a straight line in ventral view; two premaxillary and six maxillary teeth; five mandibulary teeth on the symphysis, pairs 1–3 caniniform, at least pairs 4–5 molariform; surface of molariform teeth presenting a thick coarsely pebbled enamel coat.

The second Sphagesaurinae taxon formally described is *Armadillosuchus arrudai*, by Marinho & Carvalho (2009). It was proposed as a new species in its own genus in Sphagesauridae and was described based on fossil remains from the Adamantina Formation, in the Bauru Group, found in General Salgado, São Paulo State, Brazil. The holotype (UFRJ DG 303-R) consists in an almost complete skull (Figure 2.), with some teeth (Figure 3) embedded in the sediments at the palatal region, complete cervical vertebrae and ribs, dorsal

vertebrae and ribs, scapulae, a partial left coracoid, left humerus displaced anteriorly, left radius and ulna, most of the left manus, and a complete cervical osteoderm shield. The paratype (MPMA 64 0001-04, Figure 4) consists in premaxillae broken at the rostral end and dorsal portion, left maxilla broken after the second left tooth and dorsal portion, right maxilla broken after the fourth tooth and dorsal portion, and lower jaw almost complete at the mandibular symphysis.

Figure 2

Armadillosuchus arrudai. paratype (MPMA 64 0001-04). A, premaxillae and maxillae fragments in palatal view; B, mandibular symphysis in dorsal view. Scale bar = 10cm



Source: Prepared by the authors.

Figure 3

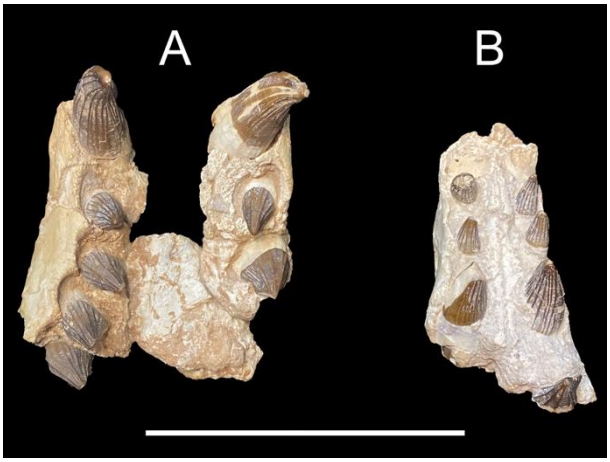
Armadillosuchus arrudai holotype (UFRJ DG 303-R) isolated molariform tooth. Scale bar = 1cm



Source: Prepared by the authors.

Figure 4

Armadillosuchus arrudai holotype in dorsal view (UFRJ DG 303-R) skull, nuchal shield, and anteriorly left displaced humerus. Scale bar = 10cm



Source: Prepared by the authors.

Marinho & Carvalho (2009, p. 39) diagnosed *Armadillosuchus arrudai* as

> […] a Sphagesauridae bearing two premaxillary teeth, the second ones are hypertrophied caniniforms; posterior maxillary teeth present the major crown axis obliquely oriented with few large tubercles disposed in one lingual keel; lower jaw is narrow and elongated at the symphyseal region; the first dentary teeth facing anteriorly; fourth dentary teeth slightly flattened laterally and have anterior keels; the fifth dentary teeth has the major crown axis obliquely oriented with the tuberculated keel facing the labial margin, and occluded behind the third maxillary teeth; basioccipital-basisphenoid suture marginate the foramen intertympanicum posteriorly; foramen intertympanicum in the basisphenoid; basioccipital-basisphenoid suture marginate the lateral Eustachian foramina posteriorly and laterally; lateral Eustachian foramina aligned to the foramen intertympanicum; antorbital depression divided into two parts: a smooth and deeper and an ornamented and shallower one; body armor with two distinct parts: a cervical shield and a banded dorsocervical section; hexagonal osteoderms compose most of the cervical shield.

The third Sphagesaurinae, *Caryonosuchus pricei*, is formally described by Kellner *et al.* (2011) based on the specimen DGM 1411-R, an anterior portion of the rostrum and mandibular symphysis, from Adamantina Formation, in the vicinity of Presidente Prudente, São Paulo State, Brazil, that was originally described as *Sphagesaurus sp.* by Kellner *et al.* (1995).

After Marinho & Carvalho (2009) description of *Armadillosuchus arrudai*, as similar sphagesaurid close to *Sphagesaurus huenei*, but on its own genus and species; and noting that DGM 332-R and DGM 333-R (the isolated teeth that *Sphagesaurus huenei* type material consist of) are indistinguishable from DGM 1411-R, RCL-100 (Pol, 2003 *Sphagesaurus huenei* skull), and UFRJ-303-R (*Armadillosuchus arrudai* holotype) dentition, despite the

cranial differences reported between the later three specimens; Kellner *et al.* (2011) proposed *Caryonosuchus pricei* based on DGM 1411-R, in its own genus and species as well, while suggesting, although not proposing a formal taxonomic revision on Sphagesauridae, that *Sphagesaurus huenei* might be considered a *nomen dubium*.

Kellner *et al.* (2011) diagnosed *Caryonosuchus pricei* as a sphagesaurid bearing first tooth posterior to the premaxillary hypercaniniform supported exclusively by the premaxilla; palatine ramus of maxilla covered by low crests and shallow wrinkles; shallow fossa present at symphysis, medial to the first three teeth. They indicate as autapomorphies: rostrum with horn-like tubercles on the premaxilla and on the maxilla; rostrum showing rough ornamentation with grooves and bony ridges. DGM 1411-R, being the holotype and only *Caryonosuchus* known specimen, was tragically lost during the National Museum of Brazil fire in September 2018, while borrowed at the institution.

3 MATERIALS AND METHODS

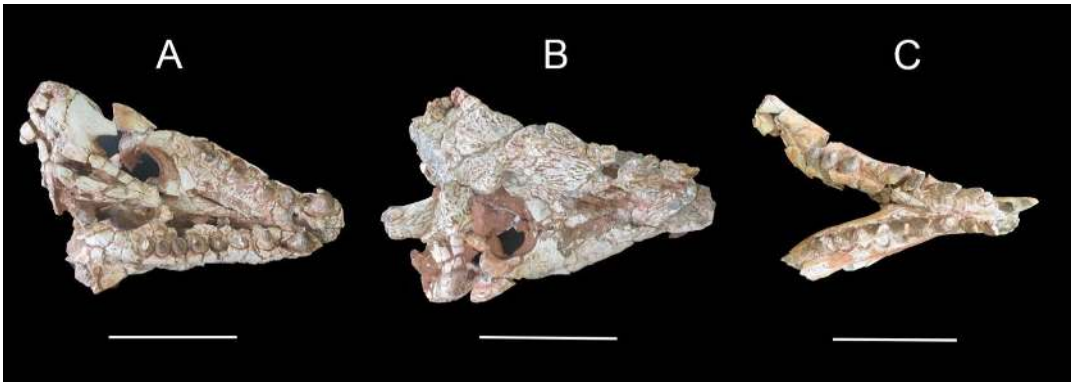
For this study, the analyses were based on direct examination of the original fossil specimens: DGM 332-R, DGM 333-R, URC R-92, UFRJ DG 303-R, MPMA 64 0001 04; housed in the following institutions: Serviço Geológico do Brasil (SGB / RJ), Museu de Paleontologia e Estratigrafia Prof. Dr. Paulo Milton Barbosa Landim (UNESP / SP), Coleção de Macrofósseis da Universidade Federal do Rio de Janeiro (UFRJ / RJ), and Museu de Paleontologia de Monte Alto (MPMA/SP). Additional comparative information was obtained from literature, including information about RCL-100 and DGM 1411-R.

Referred specimens of fossil sphagesaurids used for comparisons are listed in Table 1, which includes *Sphagesaurus huenei*, *Armadillosuchus arrudai* and *Caryonosuchus pricei* type specimens. It also includes the *Sphagesaurus* specimens RCL-100, which is widely used as referred specimen in most contributions regarding Notosuchia systematics after Pol (2003) (*e.g.,* Andrade, 2005; Andrade & Bertini, 2008; Marinho & Carvalho, 2009; Kellner *et al.,* 2011; Iori & Carvalho, 2011; Iori *et al.,* 2013; Pol *et al*., 2014; Martinelli *et al*., 2018; Ruiz *et al.*, 2021; Pinheiro *et al.*, 2021; Marinho *et al*., 2022; Iori *et al*., 2024; Leardi *et al*., 2024); and URC-R-92 (Figure 5), a *Sphagesaurus* skull reported in Bertini *et al*. (2006), later described in Agostinho (2009), which provides additional elements for known *Sphagesaurus* Anatomy. The diagnostic traits of each proposed taxa were observed (if verifiable) in each specimen from their respective published descriptive work, and direct observation whenever it was timely available (DGM 332-R; DGM 333-R; URC-R-92; UFRJ DG 303-R; MPMA 64 0001-

04). Observations and measurements related to RCL-100 were made on a cast (URC-without number).

Figure 5

Sphagesaurus huenei. URC-92-R. A, skull in palatal view; B, skull in dorsal view; C, mandible in dorsal view. Scale bar = 10 cm



Source: Prepared by the authors.

4 RESULTS AND DISCUSSION

4.1 GENERAL SKULL FEATURES

Aspects such as skull general shape and texture are observable in specimens RCL-100, URC-R-92 and UFRJ DG 303-R; while some of its texture is observable at the rostral region preserved in DGM 1411-R and MPMA 64 0001-04. The skull length of RCL-100 is about 20 cm (from broken anterior tip of premaxillae to occipital posterior end); URC-R-92 skull is 27 cm (Agostinho, 2009); and in UFRJ DG 303-R is 26 cm. Regarding its shape, Pol (2003) reported that RCL-100 has a short and high snout (compared to living crocodyliforms) and anterior facing external nares that characterize supposedly terrestrial habits. Marinho & Carvalho (2009) claimed that UFRJ DG 303-R snout is proportionally wider and longer than RCL-100, even though the specimen seems more flattened. On the other hand, URC-92-R skull looks higher than both, but there is a severe oblique deformation from the left-side, making the skull notably crooked. The skull width (measured between squamosal lateral ends) in UFRJ DG 303-R is 22,4 cm. Andrade (2005) noted missing parts and some crushing deformation on the posterior region of RCL-100 skull, making it difficult to infer the real specimen width, and preservation on URC-92-R posterior region of the skull is even worse.

All specimens in which skull texture is observable showed some degree of skull ornamentation, including DGM 1411-R (reported in Kellner *et al.*, 2011) and MPMA 64 0001-04. In literature, skull ornamentation is considered lower in *Sphagesaurus huenei*, higher in

Armadillosuchus arrudai (Marinho & Carvalho, 2009) and bearing “horn-like” tubercles in *Caryonosuchus pricei* (Kellner *et al*., 2011). Some skull ornamentation is visible in RCL-100, despite dorsal rostral surface being considerably worn out, and as observed by Andrade (2005) it follows a similar pattern as in *Notosuchus terrestris* and *Mariliasuchus amarali*, with general thickening of rostral bony elements and jugal, bearing scattered shallow and narrow grooves. UFRJ DG 303-R shows a denser ornamentation of pits and grooves on the surface of snout, jugal, and skull roof. URC-92-R has a heavier ornamentation, marked by deep ridges and grooves, especially on rostrum top surface, jugal, skull table, and dentary lower medial surface. Kellner *et al.* (2011) reported a very conspicuous rostral surface ornamentation composed of a series of wrinkles, furrows, and sulci that changes to a pattern of deep pits and grooves in DGM 1411-R and drew attention to “horn-like” tuberosities on premaxilla and maxilla. Such tuberosities were hard to spot from the article figures, but it would probably be more remarkable from direct observation if the specimen was still available.

All observable specimens exhibit skull ornamentation patterns in varying degrees, but not too distant from each other. Degrees of skull ornamentation is commonly variable intraspecifically in Crocodylomorpha, such as *Mariliasuchus amarali* and *Caiman latirostris*, observed by Augusta (2013). This trait is more discrepant between juveniles and sub-adults/adults from a same species, but as bone ornamentation is related to dynamic remodeling processes occurring during most of the course of postnatal skeletal growth, at least potentially indefinite in crocodylians (Buffrenil *et al.*, 2015), the differences observable between the specimens should not be considered as distinguishable as a polarizing diagnostic trait.

4.2 DENTITION

Although being the most remarkable and diagnostic Sphagesauridae set of traits, dentition morphology preservation varies between specimens. DGM 332-R and DGM 333-R are both single isolated teeth; with molariform morphology; bearing a short crown, with some lateral compression, thick layer of tooth enamel, longitudinal ridges, and a single lingually oriented keel. In DGM-332-R, several denticules (*i.e*., tubercles *sensu* Price, 1950) are visible along the keel length, while in DGM-333-R keel and apex are severely worn. Whole molariform teeth crowns with exact same morphology are observable in maxillary dentition in URC-R-92, MPMA 64 0001-04, DGM 1411-R, and in isolated tooth from UFRJ DG 303-R.

Damaged crowns in RCL-100 maxillae suggest a compatible molariform morphology as well, and its oblique disposition, also observable in URC-92-R, MPMA 64 0001-04 and DGM 1411-R, confirms the keels poster-lingual position. Complementary lower molariforms with antero-labial faced keels are preserved in URC-92-R and MPMA 64 0001-04. This matching contact in occlusion, and its effect in keel worn surfaces, is noticeable in URC-92-R and supports Price (1950) tear-shearing mechanism proposal, in propalinal occlusion (Pol, 2003).

Only two premaxillary teeth/alveoli are present in RCL-100, MPMA 64 0001-04 and DGM 1411-R, corresponding to a hypertrophied caniniform followed by a smaller with a "transitional" morphology toward the molariforms. In URC-92-R there is an additional premaxillary alveolus before the caniniform. This and the uneven anterior surface of preserved premaxillary portion, in RCL-100, MPMA 64-0001-04 and DGM 1411-R, suggest that these specimens may originally had an additional tooth in their anterior most portion of premaxilla with an incisiform morphology, which has broken apart in, as already showed in Iori *et al.* (2011), based on the assigned *Armadillosuchus arrudai* specimen UFRJ DG 380-R. This detail alarms to characters from lists and diagnoses that relies on teeth number and series position that may not be updated, regarding the hypertrophied caniniform as the first premaxillary teeth, or misplacing subsequent teeth ordinals of the series.

Three anterior conical teeth are present on dentary symphyseal region in RCL-100, URC-92-R, MPMA 64 0001-04 and DGM 1411-R. In RCL-100, URC-92-R and MPMA 64 001-04 their apex is antero-dorsally faced, although in MPMA 64 001-04 it is regarded just as anterior faced by Marinho *&* Carvalho (2009) or procumbent by Iori *et al.* (2011). In RCL-100 it is regarded as procumbent by Andrade *&* Bertini (2008) and, contradictorily, as dorsal-oriented by Iori *et al.* (2011). However, in neither three specimens the first dentary teeth are completely dorsally or anteriorly oriented, while in DGM 1411-R it is completely collapsed. Not only this trait was ambiguously interpreted between different observers, but it also does not qualify as surely diagnostic feature because teeth protrusion is a common type of malocclusion widely present (but not exclusively) in modern mammals (Tinaw *et al.*, 2003), which heterodont dentition is analogous to notosuchids. Another evidence of malocclusion in Sphagesaurids is some asymmetrical mismatching in dental wear between left and right maxillae and dentaries in URC-92-R, and its right caniniform visibly larger than the left one.

4.3 ROSTRAL REGION

Morphology does not vary significantly between specimens in which this is mostly preserved (RCL-100, URC-92-R, UFRJ DG 303-R, DGM 1411-R). There is some dorsoventral flattening deformation in RCL-100 and UFRJ DG 303-R, while URC-100 is obliquely flattened on the right and crushed on the left, and DGM 1411-R skull was flatteringly crushed (Kellner *et al*., 1995). The absence of antorbital fenestrae is accordingly observable in RCL-100, URC-92-R and UFRJ 303-R.

4.4 ORBITAL/POSTORBITAL REGION

Partially preserved in RCL-100, severely damaged in URC-92-R, and almost complete in UFRJ DG 303-R. The skull roof is wide, and supraorbital fenestrae are large in UFRJ DG 303-R. Jugal expands laterally beyond skull roof and orbits both in RCL-100 and UFRJ DG 303-R.

4.5 OCCIPITAL REGION

Partially preserved in RCL-100, and UFRJ DG 303-R, is postero-ventrally oriented. The basioccipital-quadrate contact in occipital area excluding the exoccipital from the ventral margin of skull surface, observed in RCL-100 by Pol (2003) is also an observable feature in UFRJ DG 303-R; while traits observed in UFRJ DG 303-R observed by Marinho & Carvalho (2009), such as basioccipital-basisphenoid suture posteriorly marginating intertympanic foramen, basioccipital-basisphenoid suture marginating the lateral Eustachian foramina posteriorly and laterally, and lateral Eustachian foramina alignment to the intertympanic foramen, are also observable features in RCL-100.

4.6 PALATAL REGION

Preserved remains consist in partially preserved palate and damaged choanal region in RCL-100; crushed and partially preserved palate and choanal region in URC-92-R; and a medial maxillary fragment in MPMA 64 0001-04. In RCL-100, Andrade & Bertini (2008) observed a plain and straight palate surface; a naso-oral fenestra in premaxilla-maxilla suture; thin quadrate medial crests reaching from the outer tip of each quadrate, contacting over the basisphenoid; and a concave surface in pterygoid-basisphenoid contact.

4.7 MANDIBULAR REGION

The symphysis is preserved in RCL-100, URC-92-R, MPMA 64 0001-04 and DGM 1411-R. Although cracked, the mid portion of URC-92-R is also preserved, showing its complete dentary teeth series, and confirms the predicted “Y” shaped lower jaw in Sphagesauridae. Kellner *et al.* (2011) observed a shallow fossa present at symphysis, medial to the first three teeth in DGM 1411-R.

4.8 POSTCRANIUM REMAINS

Preserved in URC-92-R and UFRJ DG 303-R. Agostinho (2009) described a set of three thoracic vertebrae; and a right ulna, radius and humerus from URC-92-R. Marinho *&* Carvalho (2009) described a body armor with two distinct parts: a cervical shield and a banded dorsocervical section; and hexagonal osteoderms composing most of the cervical shield in UFRJ DG 303-R. This specimen also has an anteriorly displaced left humerus, left radius and ulna, and almost complete manus. The specimen humerus, radius and ulna are similar in size and morphology.

4.9 TAXONOMICAL NOMENCLATURE REMARKS

The advent of Molecular Biology and genetics from the last few decades has led to the increasing recognition of cryptic species complexes in extant Crocodylia, which may suggest an underestimate of potentially distinct different fossil Crocodylomorpha species under overlooked subtle morphological variation (Brochu *&* Sumrall, 2020). However, is worth noting that proper adoption of a stated species concept relies deeply on specimen data availability and applicability of the taxonomical study for its operability.

The “Biological Species Concept” (BSC), as proposed by Mayr (1942), is the most influential (although not universal) species concept. Stating that “species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups”. It contraposes the traditional “Typological Species Concept” (TSC), based on degree of morphological difference, deeply rooted in Platonic Idealism, and deemed as “subjective” by Mayr (19142).

This view already conflicts with Paleontology, which heavily draws on TSC since sexual reproduction is unobservable in extinct lineages, and fossil taxa description relies almost exclusively on Morphology observations from incomplete specimens, being closer to a morphospecies concept as framed by Ruse (1969).

As cladistics gained popularity and became favored in Systematic Taxonomy, it saw the rise of “Phylogenetic Species Concept” (PSC), in which “a species is the smallest diagnosable cluster of organism within which there is a parental pattern of ancestry and descent” (Cracraft, 1983), expanded as “the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of characters of comparable individuals (semaphoronts)” (Nixon & Wheeler, 1990). The PSC became widely adopted by zoologists, and collaterally paleozoologists might be leaning towards it as well. In Conservation Biology, the switch from BSC to PSC often represents a challenge to document species lists, which Macroecology studies and conservation efforts relies on, due to “taxonomy inflation” (Isaac *et al*., 2004).

In Paleontology, PSC approach might be useful in some cases to better understand the evolutionary history of past biodiversity. However, it must be faced with extreme caution due to the intrinsic nature of most fossil data: mostly incomplete specimens; taxa represented generally by few specimens (or even a monotypic one); and extremely limited molecular data (if existent at all).

Despite the importance of phylogenetic studies and nomenclature to the evolutionary understanding of Mesozoic Crocodylomorpha, fossil notosuchids species proposal and description studies, while attempt to place fossil taxa (represented by few scattered remains) in a PSC framework, still employ TSC Methodology, relying solely in morphological evidence centered on type material as “platonically ideal specimens”, potentially leading to unverifiable taxonomical splits. This issue can be included alongside poor stratigraphical constraints of fossil specimens, and unknown morphological variance between semaphoronts, as limitations for the applicability of a phylogenetic species concept in sphagesaurids. Given the constraints imposed by incompleteness of data, paleozoological nomenclature must remain deliberately conservative, while bearing in mind the limitations of such approach compared to current extant taxa nomenclature.

Although probable, the occurrence of two or more remarkably similar distinct species (or even cryptic species complexes) in the geological past, a taxonomical split based on a small set of subtle morphological differences between similar fossil specimens, is not verifiable unless there is statistical consistency between distinct morphotypes. For the sake of nomenclatural stability, we advocate that given a newer similar specimen, without conspicuously unambiguous autapomorphic traits, it must be (if diagnostic) inferred as

belonging to a previous described species until there is enough samples (Sokal & Rohlf, 1995 suggest $n \geq 30$) to make a trait analysis study statistically viable.

Regarding the diagnosability of sphagesaurid fossil remains, Kellner *et al.* (2011) fairly addressed that DGM-332-R, being an isolated tooth, was problematic as a holotype, not being diagnosable enough after later advancements in Sphagesauridae known morphology. For that, we propose a neotype designation in conformity with ICZN (1999) Art. 75.3.2.("a statement of the characters that the author regards as differentiating from other taxa the nominal species-group taxon for which the neotype is designated, or a bibliographic reference to such a statement"), the statement of characters being the ones from Pol (2003) and Andrade & Bertini (2008) *Sphagesaurus huenei* emended diagnosis.

In this work we interpret the previous listed as autapomorphic traits in *Armadillosuchus arrudai* and *Caryonosuchus pricei* as within expected *Sphagesaurus huenei* degrees of morphological variation. As the firstly formally described species, *Sphagesaurus huenei* is favored against *Armadillosuchus arrudai* and *Caryonosuchus pricei* under the Principle of Priority from ICZN (1999) Art. 23. – "The valid name of a taxon is the oldest available name applied to it, unless that name has been invalidated or another name is given precedence by any provision of the Code or by any ruling of the Commission. For this reason, priority applies to the validity of synonyms [Art. 23.3], to the relative precedence of homonyms [Arts. 53-60], the correctness or otherwise of spellings [Arts. 24, 32], and to the validity of nomenclatural acts (such as acts taken under the Principle of the First Reviser [Art. 24.2] and the fixation of name-bearing types [Arts. 68, 69, 74.1.3, 75.4]". The treatment of *Armadillosuchus arrudai* and *Caryonosuchus pricei* as *Sphagesaurus huenei* junior synonyms is so predicted in Art. 23.3 – "The Principle of Priority requires that a taxon formed by bringing together into a single taxon at one rank two or more previously established nominal taxa within the family group, genus group or species group takes as its valid name the name, determined in accordance with the Principle of Priority [Art. 23.1] and its Purpose [Art. 23.2], with change of suffix if required in the case of a family-group name [Art. 34]".

5 CONCLUSION

Considering the historical perspective of Sphagesaurid taxonomy and the diagnostic traits present in the specimens, RCL-100 is regarded as referable to *Sphagesaurus huenei*, and for its widespread use in the literature as a reference for the specie's diagnostic features, it is a reliable neotype candidate. On the other hand, UFRJ DG 303-R, MPMA 64 0001-04,

and DGM 1411-R should be, in a more carefully approach, addressed as *Sphagesaurus huenei*, making *Armadillosuchus arrudai* and *Caryonosuchus pricei* junior synonyms of *Sphagesaurus huenei*.

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