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PALEONTOLOGY

The first notosuchian crocodyliform from the Araçatuba Formation (Bauru Group, Paraná Basin), and diversification of sphagesaurians

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Abstract: The mesoeucrocodylian record from the Bauru Group (Paraná Basin, Brazil) comes from three formations: Adamantina (Late Turonian–Early Maastrichtian), Presidente Prudente (Early Campanian–Early Maastrichtian) and Marília (Maastrichtian). These records are restricted to the Early Coniacian–Early Maastrichtian. Here, we report a new crocodyliform record from the Bauru Group, which was the first of the Araçatuba Formation, from a new locality of Coronel Goulart district, in Álvares Machado municipality. *Coronelsuchus civali* gen. nov. *et* sp. nov. comprises two related specimens - FFP PG 13 and FFP PG 14 recovered close to each other and on the same muddy sandstone level. We perform a phylogenetic analysis with 392 characters (five new added) and 88 taxa. Our analyses supported the new clades: Sphagesauria, Sphagesauriaae and Caipirasuchinae. Our phylogenetic results suggest *C. civali* as a basal Sphagesauria. Regarding the Crocodyliform Assemblage Zones (CAZ), the new species is correlated to the CAZ 1, together with small sphagesaurians, *Caryonosuchus* and itasuchids. The *C. civali* reveals an older appearing (pre-Turonian) and diversification of Sphagesauria. The specimens also expand the stratigraphic range for Notosuchia in the Bauru Group.

Key words: Notosuchia, Sphagesauria, Upper Cretaceous, western São Paulo state, Crocodyliformes Assemblage Zones.

INTRODUCTION

The Bauru Group is the most extensive sedimentary sequence of the Upper Cretaceous in South America (Fernandes & Coimbra 1996a), yielding a diverse and abundant vertebrate fossil content (*e.g.*, Bandeira et al. 2018). Among these, the Mesoeucrocodylia are the most represented vertebrate remains, with three main clades: Notosuchia, Peirosauridae and Itasuchidae (according Pinheiro et al. 2018), mainly coming from three geological unities: Adamantina (Late Turonian–Early Maastrichtian), Presidente Prudente (Early Campanian–Early Maastrichtian) and Marília (Maastrichtian). The diversity of Adamantina Formation to mesoeucrocodylians is remarkable, with 21 among around thirty species to all Bauru Group, corresponding to the second major pulse of notosuchian diversification during Turonian – Santonian (Pol & Leardi 2015, Celis et al. 2020).

Here, we report a sphage saurian (Notosuchia) from Bauru Group, which was found in the top muddy-sandstones sequence of the Araçatuba Formation (Fernandes et al. 2003). This record consists of two specimens - FFP PG 13 and FFP

PG 14. Although they are non-associated, they are probably the same taxon.

GEOLOGICAL CONTEXT

The Bauru Group comprises the Aptian-Maastrichtian (*sensu* Soares et al. 1980, Dias-Brito et al. 2001) of the Paraná Basin (Pinheiro et al. 2018). In a sequence stratigraphic approach, the Bauru is one of the six second-order sequence (Bauru Supersequence) that filled the Paraná Basin (Milani et al. 1998), over the basalts of the Serra Geral Group (*sensu* Rossetti et al. 2018). The Bauru Group is composed of two intervals: a lower one composed of Aptian eolian and fluvial-eolian sandstones; and an upper one composed of Late Cretaceous alluvial and fluvial conglomerates, sandstones and mudstones, with subordinated lacustrine mudstones (*sensu* Fernandes & Coimbra 1996b, 2000).

According to the new stratigraphic framework established by Pinheiro et al. (2018), the Cauiá, Pirapozinho (Lower Cretaceous), Santo Anastácio, Aracatuba, Uberaba, Adamantina, Presidente Prudente and Marília formations (Upper Cretaceous) followed the criteria defined by the Brazilian Code of Stratigraphic Nomenclature (BCSN; Petri et al. 1982, 1986). They also proposed a new stratigraphic chart for the Cretaceous of the Paraná Basin, which improves the stratigraphy of the Bauru Group in a chronostratigraphic approach. They established Crocodyliformes Assemblages Zones (CAZs) based on the high-resolution sequence stratigraphy, which corresponds to the depositional sequences. A similar approach was also performed to the Triassic succession of the Paraná Basin (Zerfass et al. 2003). The Bauru Supersequence was divided by Pinheiro et al. (2018) into two great intervals that were

subdivided into fourth-order depositional sequences.

The new specimens were collected in outcrops of the Aracatuba Formation (Late Turonian-Early Coniacian) in the Coronel Goulart district. Álvares Machado municipality. southwestern of São Paulo state (Figure 1). This area was first mapped as Adamantina Formation (Vale do Rio do Peixe Formation by Fernandes & Coimbra 2000, Fernandes & Ribeiro 2015). However, Albarelli et al. (2015) identified lacustrine intervals and correlated them to the Aracatuba Formation. Our detailed geological mapping and correlation of the study area confirmed that the occurrence of this unit is associated with the lower sequences of the Santo Anastácio Formation and upper sequences of the Adamantina Formation (Figure 2). Analyzing the CAZs (Pinheiro et al. 2018), we positioned the new species collected in the lower interval of the CAZ1.

Stratigraphic analysis

The stratigraphic analysis consisted of facies and depositional architecture analysis for fluvial intervals (Miall 1985) and lacustrine delta intervals (Johnson & Graham 2004, Zavala & Pan 2018). The regional (Uberaba, Prata - Campina Verde - Gurinhatã, Monte Alto - Catanduva, Ibirá - São José do Rio Preto, Valparaíso-Mirandópolis, Flórida Paulista - Pacaembu Paulista, Alfredo Marcondes - Presidente Prudente - Álvares Machado, Coronel Goulart - Pirapozinho areas) and the local vertical profiles were carried out and correlated with sequence stratigraphy approach (Catuneanu et al. 2009, 2011), as performed by Pinheiro et al. (2018). We positioned the sphagesaurids species in the depositional sequences in the regional cross-section in a lithostratigraphic framework (Figure 3). The high-resolution cross-section of correlation of the key outcrops in Coronel



Figure 1. Geological map of the Coronel Goulart district. The black dots are outcrops where detailed vertical profiles were carried out for facies analysis and sequence stratigraphy approach; the black star show CG6 site, where the specimens FFP PG 13 and 14 were collected.

Goulart district (Figures 1 and 2), allowed us to define the proper stratigraphic level that yielded the new species at the top of the Araçatuba Formation (CAZ1 *sensu* Pinheiro et al. 2018).

The holotype (FFP PG 13) and paratype (FFP PG 14) materials were discovered in muddy sandstones with some mudstone clasts, convolute lamination that is here interpreted as facies produced by turbulent or hyperpicnal gravity flow with low efficiency (see Zavala & Pan 2018). The facies is associated with fine sandstones with ripples and cross laminations, and mainly interbedded with massive and laminated mudstones (shales) together with subordinated hetherolithic facies of fines and sandstones that are here interpreted as produced by hyperpicnal flows. The architectural elements are tabular, filled with sandstone or mudstone facies. The regional and local stratigraphic correlations (Figure 2) allowed



Figure 2. Cross-section of correlation of vertical profiles of the Coronel Goulart area. The detailed stratigraphic level of the specimens FFP PG 13 and 14 is indicated in the CG6 site profile.

us to interpret that this level belongs to the top of the Aracatuba Formation, close to the contact with the Adamantina Formation. This facies association and depositional architecture are here interpreted as marginal lacustrine prodeltaic complex (see Johnson & Graham 2004). The above Adamantina Formation is marked by the predominant presence of fine to mid sandstone facies with subordinate mudstones. The contact is transitional, marked by a facies change surface, where below there is the facies association with predominant fines, and above there are predominantly sandstone facies. The Adamantina Formation has facies association composed of fine to mid sandstones with ripple and cross laminations, fine to mid sandstones with cross-stratification and horizontal lamination, and massive red to brownish subordinated mudstones. The depositional architecture analysis suggests small channels, lobes and mouth bars linked to tabular elements

filled by normal graded fine sandstones and hetherolithic facies. The facies association and architectural analysis allow us to interpret this lower interval of the Adamantina Formation as delta front. This transitional succession from marginal lacustrine and prodeltaic complex to delta-front systems is rich in paleovertebrate and invertebrate fossils. In the CG2 outcrop, we found undescribed new crocodyliforms, testudines, fishes and other vertebrates in mouth bars elements. In CG1, several fragmented bones occur in muddy sandstones. In CG6 we collected the holotype and paratype specimens of the new crocodyliforms species besides testudines. The higher concentration of remains is in the prodeltaic thicker hiperpycnite facies, which varies in muddy content and sedimentary structures from the eastern outcrop CG2 to the western outcrops CG1 and CG6. This lateral variation is in function to the source area and the incorporation of water, due to the evolution



Figure 3. Cross-section of correlation of vertical profile composites of the Bauru Group. It is showing the lithostratigraphic framework at Formation level of the Bauru Group with the stratigraphic position of the sphagesaurids and more close taxa record (modified from Pinheiro et al 2018). Black star indicates the specimens FFP PG 13 and 14 sites; yellow triangle in the profile of the Uberaba area indicates the possible Sphagesauria record for *Labidiosuchus amicum* Kellner et al 2011).

of the turbulent flow. Some intraclastic conglomerates punctually occur and fill gravel bars of small mouth bar channels. Sometimes, this architectural element provides several fragmented bones and isolated remains.

The Diogenes Almeida Campos contribution to the SW of São Paulo exploration

Although the SW of São Paulo state is widely known for the vertebrate fossils, the extensive report elaborated and organized by DA Campos is paramount. The "Carta Geológica do Brasil ao Milionésimo: Folha Paranapanema" (Campos et al. 1978) is one of the most complete reports upto-date, with identification and mapping of each fossiliferous site, their respective municipalities and fossil occurrences. Circa of 160 locations were mapped and organized by age, fossils, and their proper collectors, with an emphasis on those countryside municipalities of SW of São Paulo state around 1974, as Presidente Prudente, Pirapozinho and Alvares Machado. His paleontological contributions expressively increased the paleovertebrate collection housed at the Museu de Ciências da Terra (MCT, Rio de Janeiro), as well as are a landmark in the Brazilian vertebrate paleontological exploration and research.

MATERIALS AND METHODS

Anatomical abbreviations

an- angular; ant- anterior; awf- apical wear facet; **ax**- axis; **cau**- caudal; **ct**- caniniform tooth; **dc**- distal carina; **f**- frontal; **fom**- foramen occipitale magnum; it- incisiviform teeth; itfinfratemporal fenestra; **j**- jugal; **lab**- labial; lad- labial depression: las- labial surface; ldtlast dentary tooth: **lid**- lingual depression: lin- lingual; mc - mesial carina; mef- external mandibular fenestra: **mt**- molariform teeth **nc**- nuchal crest; **ot**- otoccipital **p**- parietal; **po**postorbital; **porb**- postorbital bar; **pra**- proatlas; *ptf*- posttemporal fenestra; **q**- quadrate; **q**jquadratojugal; **r or**- right orbit; **ros**- rostral; **so**supraoccipital; **sq**- squamosal; **sqp**- squamosal posterior process; **stf**- supratemporal fenestra; **stfo**- supratemporal fossa; **su**- surangular; tof- tempororbital foramen; t- tooth; togtemporoccipital groove; tr- tooth root; tttransitional tooth; **tu**-tubercles.

Institutional Acronyms

CPPLIP- Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Uberaba, Brazil; CPRM-Companhia de Pesquisas e Recursos Minerais, Brasil; **DEGEO**- Departamento de Geologia da UFRJ, Rio de Janeiro, Brazil; DGM- Divisão de Geologia e Mineralogia, extint section of Departamento Nacional de Produção Mineral (DNPM), currently Agência Nacional de Mineração (ANM), Rio de Janeiro, Brazil; **FFP**- Faculdade de Formação de Professores da UERJ Campus São Gonçalo, Rio de Janeiro, Brazil; MCTer- Museu de Ciências da Terra, Rio de Janeiro, Brazil; MN-Museu Nacional da UFRJ, Rio de Janeiro, Brazil; MNK- Museo Noel Kempff Mercado, Santa Cruz de la Sierra, Bolivia; MNN- Musée National Boubou Hama, Niamey, République du Niger; MPMA – Museu de Paleontologia de Monte Alto, São Paulo, Brazil; MUC- Museu de la Universidad

Nacional del Comahue, Neuquén, Argentina; **UA**-Université d'Antananarivo, Madagascar; **UERJ**-Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil; **UFRJ**- Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **UFTM**-Universidade Federal do Triângulo Mineiro, Uberaba, Minas Gerais, Brazil.

Nomenclatural terms

We follow Romer (1956) and Iordansky (1973) for general cranial osteology nomenclature; Iordansky 1964, 2000, Cleuren & De Vree 2000, Holliday & Witmer 2007, Bona & Desojo 2011; and Porter et al. 2016 for cranial myology and vascularity references; Prasad & Broin 2002, Smith & Dodson 2003, Andrade & Bertini 2008a, Lecuona & Pol 2008, and Hendrickx et al. 2015 for dentition terminology and orientation.

Phylogenetic Inference

The memory available for the analysis was 500 MBytes, which enabled to the program hold 450,000 trees. Search for the minimum-length trees (MLTs) was conducted via New Technology using Sectorial Search, Ratchet (parameters: 25 substitutions made, or 99% swapping completed, 8 up-weighting prob., 8 down-weighting prob., and a total number of iterations of 10). Tree fusing, Driven search (15 initial addseqs., 50 times of min. length), random seed equal 0, and without collapsing trees after search. This first analysis aimed for recovering the island with the minimum length. Subsequently, the recovered island was used as starting point for a Traditional Search (TBR swapping algorithm; with starting trees from RAM) and without collapsing trees after search. This second analysis aimed for recovering the maximum number of trees of the island recovered from the first analysis. The MLTs were collapsed using "condense 1; collapse;" and the script "STATS.RUN" was used to retrieve the retention and consistency indexes

(RI and CI respectively). A strict consensus of the recovered MLTs was generated. The command "resols &" was used to explore the polytomies of the consensus. All characters were treated as non-additive.

To perform the phylogenetic analysis on the new taxon we employed a modified character list. data matrix and taxa content from Pinheiro et al. (2018) comprising in our approach 392 characters and 88 taxa; although the character list was originally developed in Pol et al. (2012) and subsequently and progressive expanded and/or modified in some latter works (e.g., Pol et al. 2014, Leardi et al. 2015, Fiorelli et al. 2016, Martinelli et al. 2018, Pinheiro et al. 2018, Cunha et al. 2020). Here we added five characters statements to the list of Pinheiro et al. (2018) and added three taxa (Araripesuchus patagonicus Ortega et al. 2000, Caipirasuchus mineirus Martinelli et al. 2018 and Morrinhosuchus luziae Iori & Carvalho 2009, see **Supplementary Information** for complete phylogenetic dataset).

The **Supplementary Information** is available at: shorturl.at/giDX4

RESULTS

Systematic Paleontology

MESOEUCROCODYLIA Whetstone & Whybrow 1983

ZIPHOSUCHIA modified from Ortega et al. 2000

NOTOSUCHIA Gasparini, 1971; *sensu* Pinheiro et al. 2018

SPHAGESAURIA nom. nov.

Coronelsuchus gen. nov.

Type species: Coronelsuchus civali sp. nov. lsid:zoobank.org:pub:18495748-B2D7 -4C67-8A85-7B64E4D577BE **Genus etymology**: *Coronel*, refers to Coronel Goulart locality, where type specimen was collected, plus the Greek suffix *souchos*, referring to the Egyptian crocodile god.

Diagnosis for genus: mesoeucrocodyliform with follow cranial and dentary characteristics (autapomorphies indicate by asterisk*): circular general outline of supratemporal fossa and fenestra, except by a well-marked anteromedial fronto-postorbital emargination; frontal exposed in supratemporal fossa; large and triangular supraoccipital in skull table, almost entirely excluding the parietal from posterior skull-table edge; squamosal does not contacts supraoccipital in skull table; tempororbital fenestra enclosed by squamosals on supratemporal fossa; presence of vascular temporoccipital groove; posttemporal fenestra obliterated between skull table and occiput (last two features shared with Notosuchus terrestris Woodward 1896); caudal teeth obliguely disposed to sagittal skull axis; * caudal maxillary molariform teeth stout, pointed apices, with lingual surface depressed and labial convex that confers a D-shape morphology for the crown when in occlusal view, presence of big and few basal tubercles in lingual surface, and true serrations on both mesial and distal carinae: * caudal mandibular molariform teeth pointed apices, with compressed crown (narrow D-shape from occlusal view), with labial surface uneven by a radial depression that bears incipient tubercles in the step, and true serrations on both mesial and distal carinae.

Coronelsuchus civali gen. nov. et sp. nov.

Type specimen: FFP PG 13, comprises a partially preserved skull and mandible, proatlas and first three cervical vertebrae, right scapulae partially preserved, and the right forelimb, except metacarpals and digits (Figures 4 and 5 a and b).

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Figure 4. Coronelsuchus civali gen. et sp. nov. FFP PG 13 dorsal view detail. a- dorsal view photo; b- dorsal view outline; cdorso-occipital detail, dventral view of specimen. Scale bar: 10mm each bar. Legends in the text.

Paratype: FFP PG 14, comprises badly preserved skull remains, but some teeth and postcranial remains (postcranial remains under preparation) (Figure 5 c).

Species etymology: *civali*, in honor of Mr. Cival, the landowner where the fossiliferous quarry is located.

Locality, **litology and horizon**: CG6 site of Coronel Goulart district, Álvarez Machado municipality, President Prudente metropolitan region (Figure 1), northwest of São Paulo State, Brazil. The fossil materials were recovered from muddy sandstones packages, from a layer formed by slurry facies and interpreted as being resulted of prodeltaic turbiditic lobes, in a marginal lacustrine context, which is the top of Araçatuba Formation (Turonian; *sensu* Soares et al. 1980). **Diagnosis for species**: same as for the only known species.

Description

Cranial elements

Skull Roofing Elements

Frontal

The frontal is hexagonal in upper view and is the most anterior skull bone preserved from FFP PG 13. We cannot determine if *Coronelsuchus civali gen. nov. et sp. nov.* shows a frontal short as *Mariliasuchus amarali* Carvalho & Bertini 1999, or long as sphagesaurids due to the unpreserved its anterior portion. The central region of the frontal is slightly concave and bears a low and robust sagittal crest along its midline that fades to a posteriormost portion of the frontal. A similar crest also occurs in some ziphosuchians (*e.g.*,



Figure 5. Coronelsuchus civali gen. et sp. nov. FFP PG 13. a- right lateral view photo; b- right lateral view outline. c- FFP PG 14: c1- rocky block with cranial, teeth and postcranial remains; c2- fragment with cranial and teeth remains; c3- dentition detail from the skull small fragment; c4-remaining teeth in rocky block and its detail. Black arrows indicate anterior direction. Colored bars indicate dentition morphotypes. Scale bar: 10mm each bar. Legends in the text.

Notosuchus, Comahuesuchus brachybuccalis Bonaparte 1991, Caipirasuchus Iori & Carvalho 2011, Simosuchus clarki Buckley et al. 2000, Anatosuchus minor Sereno et al. 2003, Araripesuchus wegeneri Buffetaut & Taquet 1979, baurusuchids, Kaprosuchus saharicus Sereno & Larsson 2009, sebecids), but is absent in others (e.g., Mariliasuchus Carvalho & Bertini, 1999, Yacarerani boliviensis Novas et al. 2009, Armadillosuchus arrudai Marinho & Carvalho, 2009, Mahajangasuchus insignis Buckley & Brochu 1999, peirosaurids). The lateral edges of the frontal that delimit the orbits are slightly elevated concerning the interorbital plate to forming a discrete periorbital crest on each side.

The frontal contributes with a small part to supratemporal fossa while the parietal and the postorbital do not contact each other on the skull table surface (Figure 4 a to c). Dorsally, the frontoparietal suture (*sutura coronalis*) runs transversally and is slightly convex, being anteromedially and posteriorly located to the anterior edge of the supratemporal fossa. The fronto-postorbital suture is relatively long, oblique and anterolaterally oriented regarding skull sagittal plane.

The frontal is intensely ornamented in its dorsal surface by striations and a fine squamapattern texture radially oriented, that starts at the frontal sagittal crest and runs toward the periphery.

Parietal

They are unpaired, sub-rectangular, shorter and thinner than the frontal. The parietal is densely ornamented by small and large rugosities longitudinally oriented, with the large located more at the center. (Figure 4 a to c). The parietal is constricted by large supratemporal fossae, with a narrow interfenestral plate with minimum width at its middle portion. However, the dorsal surface of the parietal of *Coronelsuchus civali* does not present a marked sagittal crest, as occurs in *Notosuchus* (see Barrios et al. 2017), but a thick, rough and low ridge medially surrounding the supratemporal fossa in parietal's maximum compression.

Anteriorly the parietal is connected to the frontal by a slightly convex frontoparietal suture, and at the other end, in the posterior region of the skull table, it forms a broad and so anteriorly pointed suture with the supraoccipital. The parietal forms the medioposterior portion of supratemporal fossa, being in contact with the frontal anteriorly and with the squamosal posterolaterally.

Postorbitals

The postorbital is a triradiate bone. Its anterior portion expands and contacts frontal anteromedially in skull roof, besides to forms the anterior region of the supratemporal fossa. Its descending branch forms the dorsal half of the postorbital bar; the short posterior branch of this bone contacts squamosal.

The anteromedial process extends obliquely to the longitudinal axis of the skull as in most notosuchians, including peirosaurids and mahajangasuchids (except *Stolokrosuchus lapparenti* Larsson & Gado 2000 [Pol et al. 2014]), and presents the entire dorsal surface heavily ornamented. In the expanded contact with the frontal, the anteromedial process becomes narrow while turns posteriorly to forms the anteromedial edge of the supratemporal fossa; and despite reaches close, the anteromedial process of postorbital do not contacts the parietal (Figure 4 a to c). The contact between the postorbital and jugal in the postorbital bar is not fully preserved, but in the upper portion of the bar the postorbital projects as a compressed lamina from the ventral surface of its main body.

Despite unfortunately no palpebrals were preserved, the facet on the anterolateral corner of the postorbital suggests articulation with a posterior palpebral element.

Concerning the posterior branch of the postorbital, it is short and exhibits coarse ornamentation on its dorsal surface, which is similar to the one found in the squamosal. The suture between postorbital and squamosal is interdigitated and posterolaterally oriented when it's dorsally viewed.

Squamosals

As a triradiate bone the anterior branch of the squamosal contacts the postorbital, the medial branch reaches the parietal, and the posterolateral branch contacts the otoccipital and quadrate. Similar to *Caipirasuchus mineirus* but distinct from some advanced notosuchians, as *Notosuchus*, and living crocodylian forms, the squamosal of *Coronelsuchus civali* does not reach the supraoccipital bone in the skull table (Figure 4 a to c). We could not observe the suture between squamosal and quadrate in FFP PG 13.

The anterior branch of the squamosal forms most of the supratemporal lateral bar, with its dorsal surface well ornamented by rugosities and deep sulci. Along the outer surface of the lateral edge of the supratemporal lateral bar the squamosal presents a longitudinal smooth and laterodorsally oriented upper earlid attachment groove. The lateral margin of the postorbital and squamosal, overhangs quadratojugal and quadrate elements in the otic region, forming a deep meatal chamber (according to Montefeltro et al 2016) - partially crushed in FFP PG 13 (Figure 4 a to c). Posterior in the skull table, the posterior margin of the supratemporal fossa and the coarse dorsal ornamentation surround it are abruptly interrupted at the squamosal medial branch to giving passage to the temporo-orbital vessels, which form a conspicuous groove; a shared characteristic with *Notosuchus* and *Morrinhosuchus*. This feature - *temporoccipital* groove, is less marked in *Caipirasuchus mineirus* and absent among others notosuchians (Pol et al. 2014, Barrios et al. 2017, Martinelli et al. 2018).

Dorsally the medial branch of the squamosal is thin and posteromedially forms the temporoccipital groove, with a rough and small elevated process that barely makes contacts with the parietal in the mid-posterior skull table. Near the parietal-squamosal contact and together otoccipital, the posterior margin of the squamosal medial branch form most of the strangled (or compressed) postemporal foramen. Within the supratemporal fossa the squamosal contacts the parietal posteriorly and totally encloses the tempororbital foramen (Figure 4 a to c). From a dorsoposterior view, a low and sharp mediodorsal crest runs longitudinally along with squamosal medial and posterior processes, and produces in the occiput a narrow and smooth mediodorsal surface near the skull roof posterior edge.

The posterolateral branch of the squamosal exhibits an extended posterior projection, forming a slender and non-ornamented process that slightly bends downward. The non-ornamented posterior process is present in *Libycosuchus brevirostris* Stromer 1914, *Simosuchus*, and advanced notosuchians (*sensu* Pol et al. 2014), as *Notosuchus*, *Morrinhosuchus*, *Mariliasuchus amarali*, and sphagesaurids (Barrios et al. 2017). The sharp and arched posterior edge of the squamosal separates the posterior process into a dorsolateral ornamented surface, and a non-ornamented occipital surface. Such a feature is similar to *Mariliasuchus* (see Zaher et al. 2006).

Temporal Region

Jugal

The jugal is also a triradiated bone with anterior ramus forming the ventral wall of the orbit and contacts the maxilla and ectopterygoid; the ascending process is posterodorsally projected to form the postorbital bar, and the posterior ramus forms the infratemporal bar and contacts quadratojugal (Figure 5 a and b).

Only the most posterior portion of the anterior ramus of FFP PG 13 is preserved. The anterior ramus is vertically oriented (ellipsoid cross-section), slightly broader than the jugal's infratemporal bar and shows external ornamentations with rugosities.

Despite broken in FFP PG13 and badly preserved in FFP PG14, the ascending process of jugal in the postorbital bar of *Coronelsuchus civali* is cylindrical, not ornamented and emerges confluent with the dorsolateral margin of the jugal plate (as in derived notosuchians and metriorhynchids neosuchians). Such condition differs from the subdermal condition found in eusuchians, uruguaysuchids notosuchians, and many sebecians (*e.g.*, peirosaurids and sebecids). The contact at the postorbital bar is uncertain.

The posterior ramus of the jugal is dorsoventrally compressed, laterally projected (condition shared with *Araripesuchus* Price 1959, *Notosuchus* and *Mariliasuchus*), and appears to exhibit a uniform width in the infratemporal bar extension (Figure 5a and b). It overlaps the quadratojugal in the infratemporal bar and closes to the posterior corner of the infratemporal fenestra.

Quadratojugal

The quadratojugal of FFP PG 13 is a wedged element in the posterior of the temporal region. at the corner of the infratemporal fenestra. Overlapped by the jugal forming a posterolaterally directed suture, the small anterior guadratojugal branch forms the infratemporal bar last portion, being slightly ornamented at its base. (Figure 5a and b). The guadratojugal projects a laminar and unsculptured anterodorsally ascending process that forms the posterior corner (with no spina quadratojugalis) and the posterodorsal border of the infratemporal fenestra. It broadly contacts the quadrate dorsally and meets the postorbital bone close to the superior corner of the fenestra, a shared feature with others notosuchians (e.g., uruguaysuchids, Simosuchus, Notosuchus, Mariliasuchus and Sphagesaurus Price 1950).

The posteroventral tip of the quadratojugal does not reach the lateral articular condyle of the quadrate, not contributing to the craniomandibular articulation.

Occipital and Braincase

Supraoccipital

From a dorsal view, the supraoccipital appears as a single diamond-shaped element, which in the skull table contacts the parietal by a broad and anteriorly pointed triangular suture. In occiput, the supraoccipital contacts ventrally with otoccipital, and laterally with squamosal in the low postoccipital process. In the posterior margin of the skull table, the supraoccipital presents a flat but rugous edge that separates the skull table from the occiput (Figure 4 a to c).

The supraoccipital is well exposed in the skull table as a broad triangular element, wedging anteriorly between parietal. The ornamentation of the supraoccipital is rough but thinner and softer when compared to any skull table elements (Figure 4 a to c). The posterior margin is straight and possesses a small caudal projection connected to the nuchal crest.

On the occiput the supraoccipital is broadly exposed, most then in the skull table, which in morphology appears as a wide inverted triangle that contacts ventrally the otoccipitals by a non-serrated wedge. The occipital surface is smooth and bears a central nuchal crest along half of its dorsoventral extension. In occiput the supraoccipital forms the medial portion of the low and robust postoccipital process of Coronelsuchus civali. Also, the supraoccipital comprises half of the posterior margin of the posttemporal fenestra, which is narrow and slitlike compressed, that opens dorsally instead on the occiput surface (Figure 4 a to c); a characteristic shared with Notosuchus at moment (see Barrios et al. 2017). The supraoccipital ventral border is excluded from the dorsal edge of the foramen magnum by the otoccipitals, an apomorphy for the crocodyliforms according to Benton & Clark (1988).

Otoccipitals

The exoccipital and opisthotic are indistinguishably fused into an otoccipital element, wich in each side forms large portions of the occiput of *Coronelsuchus civali* as well for the others mesoeucrocodylians (Iordansky 1973, Benton & Clark 1988). The otoccipitals meet each other in occiput midline forming a bony shelf over the foramen magnum, which slightly compress the mid-region of such foramen as a wedge and ventrally pointed structure. (Figure 4 a to c).

The otoccipital forms two distinct surfaces in occiput, divided by a transversal crest: one posterodorsal facing and above the magnum foramen level, and another posteroventrally exposed and below the magnum foramen level; being the posterodorsal surface much broader than the posteroventral one. This condition is found in other derived notosuchians nonsphagesaurids (e.g., Araripesuchus patagonicus, Simosuchus, Malawisuchus mwakasyungutiensis Gomani 1997, Comahuesuchus, Morrinhosuchus, Notosuchus, Mariliasuchus amarali, baurusuchids). Dorsally, the posterodorsal surface forms two-third of the blunt and short postoccipital process - marked by the insertion area for M. transversospinalis capitis (Cleuren & de Vree 2000), and makes the posterior corner of posttemporal fenestra at its lateral portion. The posterodorsal surface of the otoccipital is broad and concave and extends laterally as a well-developed paraoccipital process, an area for cervical muscles, as *M. epistroheo-capitis*, *M.* spinalis capitis posticus, M. longissimus capitis superficialis and M. ilio-costalis capitis (Cleuren & De Vree 2000, Iordansky 2000). The squamosal borders the otoccipital in its dorsal and lateral portions to makes a posteroventral oriented suture of irregular profile (Figure 4 b and c).

Unfortunatelly, due to the preservational conditions we could not access the cranioquadrate passage and other foramina for cranial nerves exit (*i.e.*, CN IX, X, XI and XII) as well as the entry for the internal carotid artery.

Suspensorium

Quadrate

Due to preservational conditions, the otic notch and anterodorsal branch of quadrate are unfortunately obliterated. The distal body of the quadrate is short and well ventrally directed, as most notosuchians (*e.g.*, uruguaysuchids, *Notosuchus*, *Mariliasuchus*, *Simosuchus*, sphagesaurids and baurusuchids) but differently than found in neosuchian and sebecian taxa, besides presents a low and smooth ridge on its laterodorsal surface, that runs from the lateral condyle towards otic recess.

Mandibular elements

Surangular

The surangular of FFP PG 13 comprises most of the hemimandibular structure preserved, and contacts the angular ventrally, the splenial medially, and the articular posteromedially. Anteroposteriorly long, the surangular does not carry ornamentation on its external surface.

The dorsal margin of the surangular over the external mandibular fenestra is flat, being slightly convex after that, gently and ventrally deflecting near the hemimandibular end (Figure 5 a and b). The dorsolateral surface of surangular does not have any marked crest for M. depressor mandibulae (MDM [Iordansky 2000, Holliday & Witmer 2007, Bona & Desojo 2011]) as seen in Crocodylus Laurenti, 1768 and some sebecians (e.g., peirosauroids, Bretesuchus bonapartei Gasparini, Fernandez & Powell, 1993 and Sahitisuchus fluminensis Kellner, Pinheiro & Campos 2014), but there is a smooth dorsal crest that dorsolaterally borders this bone at its final portion close to articular (Figure 5 a and b). From a dorsal view, the surangular is laterally projected at the glenoid fossa and retroarticular process level. From the posterior corner of the external mandibular fenestra, the surangularangular contact is made by a long and irregular subhorizontal suture that runs to the posterior region of hemimandible, being the surangular in this region slightly higher compared to the angular height (Figure 5a and b).

Angular

The angular is elongated and forms the ventral margin of the postdentary ramus of

the hemimandible. It also forms the entire ventral and half of the posterior margin of the mandibular external fenestra. The lateral lamina of angular presents a gentle concavity and is ornamented by some striations. The posterior end of the angular is dorsoventrally tall, a similar condition observed in *Notosuchus*, *Mariliasuchus* and *Baurusuchus* Price 1945 (Figure 5 a and b).

Articular

The right and partially preserved articular bone of FFP PG 13 appears as a wedge-shaped element, with a long anterior process inserted medially and contacting angular throughout of a *sutura harmonica*. In the ventral view, the articular seems weakly twisted to forming a longitudinal crest, close to the angular contact.

Despite partially preserved in FFP PG 13, the retroarticular process appears as a spatulated and medially sloped structure, as occur with

FFP PG 14 С m

Figure 6. Dentition of *Coronelsuchus civali gen. et sp. nov.* FFP PG 14. a- incisiviforms in lingual view; btransitional tooth (tt) and poorly remains and cast of caniniform tooth (ct) in lingual view; c- last two molariform teeth (mt) in lingual view. Scale bar for FFP PG 14 equal 10mm each bar, being to other bars A,B and C equals 2mm. other notosuchians (e.g., Malawisuchus, Mariliasuchus and Notosuchus).

Dentition

The most informative specimen of *Coronelsuchus civali* – FFP PG 13, does not preserve the *rostrum* and teeth. However, FFP PG 14 exhibits some preserved teeth on the left maxillary row and those correspond in the left hemimandible, unfortunately in a badly preserved cranium.

Coronelsuchus civali exhibits a specialized dentition with heterodont tooth series, sharing with most notosuchians the presence of three main crown morphologies: incisiviforms, caniniforms, and monocuspided molariforms (Andrade & Bertini 2008a, Lecuona & Pol 2008, Soto et al. 2011, Pol et al. 2014) (Figures 5 c, 6, 7 and 8).

Therearetwopartiallypreservedincisiviforms teeth from premaxillar, which have subcircular section and are straight and cone-shaped. Both teeth are displaced from their natural position, but appear to be implanted close to each other. The first incisiviform exhibits distal and serrated carina by fine six denticles in a millimetre (Figure 6a). The denticles are low, well-spaced, not inclined, feeble bilobated opercula, weakly marked interdenticular diaphysis and without interdenticular sulci (according to Hendrickx et al. 2015). Gentle and low apicobasal crests mark the crown of incisiviform teeth (Figure 6a).

Following the premaxillary incisiviforms the two recognizing teeth that remain from the upper jaw can be respectively assigned to a transitional tooth (according to Lecuona & Pol 2008) followed by a hypertrophied "caniniform" (Figure 6b). The transitional tooth is smaller than the big "caniniform" and presents a distally curved and serrated carina.

The caniniform is very damaged and majorly lost, but through its remains and mold, it is about a hypertrophied tooth with a pointed apex and distally recurved crown (Figure 6b). Unfortunately, the preservational condition of



Figure 7. Dentition of *Coronelsuchus civali gen. et sp. nov*. FFP PG 14. **a**- the rostralmost molariform tooth preserved from maxillary row; **b**- occlusal view of molariform teeth showing oblique orientation of the crown. Scale bar equals 1mm.

FFP PG 14 unable us to assign if such caniniform corresponds to premaxilla or maxilla toothrow. For *Mariliasuchus* and *Notosuchus* the hypertrophied anterior tooth corresponds to the last premaxillary (Zaher et al. 2006, Lecuona & Pol 2008); however, for *Morrinhosuchus* and sphagesaurids *stricto sensu*, it can be the last or the penultimate premaxillary tooth (Pol 2003, Andrade & Bertini 2008b, Marinho & Carvalho 2009, Iori et al. 2018, Martinelli et al. 2018.

The maxillary toothrow is lost in FFP PG 14, with only the last two teeth preserved. *Coronelsuchus civali* has the last maxillary teeth as pointed apices and stout molariforms, with a non-isosceles triangular morphology when in lingual view (mesial carinae more distally recurved [Figure 6c]), and D-shaped when are observed from occlusal view (Figures 6c, 7 and 8). They progressively become smaller towards the end of the maxillary toothrow, and at least the last two are inserted in an alveolar groove (Figures 7b and 8).

Both molariforms are rotated in a linguallabial direction and obliquely disposed to the sagittal plane of the skull as occurs to the others advanced notosuchians (*e.g.*, *Notosuchus*, *Adamantinasuchus navae* Nobre & Carvalho 2006, and Yacarerani) mainly sphagesaurids (*i.e.*, *Sphagesaurus*, *Armadillosuchus*, *Caryonosuchus pricei* Kellner et al. 2011 and *Caipirasuchus*), with *Coronelsuchus civali* forming a 30° and 27° angles respectively (Figure 7b). The labial surfaces of the crowns are well convex and much wider than lingual. The lingual surfaces of upper molariforms are depressed and have some few tubercles arising from base to crown



Figure 8. Last molariform teeth from *Coronelsuchus civali gen. et sp. nov*. FFP PG 14. **a** and **b**- lingual-oclusal view of last two maxillary teeth, photo and schematic drawing. **c** and **d**- oclusal view of last two dentary teeth, photo and schematic drawing. **c** and **d**- oclusal view of last two dentary teeth, photo and schematic drawing.

mid-length, with a well-developed and striate tubercle centrally positioned and sided by other minors on each side. (Figures 6c, 7 and 8). The wide elliptical and convex labial surface appear without cingulum, crests, flutes, tubercles or ondulations, except by the submillimeter pebble-pattern texture for enamel coat, which also occurs in the lingual depression (Figure 7). Both mesial and distal carinae of the last two maxillar teeth are serrated by a series composed of few anisomorphic and globularshaped true denticles one after the other, which are labiolingually broad, apically inclined and have extremely reduced midline cutting edge or keel (Figures, 6c, 7 and 8).

Three mandibular teeth from the caudal toothrow are preserved, being the crowns of the first two the best preserved. They are molariform in design but morphologically distinct from their upper counterparts. The crowns are labiolingually more compressed, with the labial surface more convex than the lingual face, in a narrow D-shape profile when in occlusal view to these elements (Figure 8 c and d). Due impregnated matrix at the lingual surface of mandibular teeth, details are cannot be seen. The labial surface of both two dentary teeth are smooth and exhibits a labial depression that radially extends through this entire surface from it mid portion to the apex. A few large tubercles incipiently occur in the step between the outer high and the depressed labial surface in these lower teeth (Figure 8 c and d). Both mesial and distal carinae are serrated by anisomorphic denticles, which are labiolingually broad and globular in shape, similar to those found in upper teeth. As the maxillary molariforms, the crowns of lower teeth are obliquely oriented to the anteroposterior axis of the skul but in a greater angulation and about twice those exhibited by the upper ones.

A distinct and mesiodistally oriented apical wear facet is observed to the rostralmost preserved dentary tooth of FFP PG 14. indicating a precise tooth-to-tooth occlusion (Figure 8 c and d). Striae and microwear facets were not observed yet, which could indicate additional jaw movements as propalinals and laterals (Pol 2003, Andrade & Bertini 2008a, Lecuona & Pol 2008, Ösi 2013).

Stocked in the upper jaw behind the last maxillar tooth, the last mandibular and molariform tooth was displaced from the mandible. Due to its taphonomic condition, much of this tooth cannot be seen, but there is a discreet cervix (neck) between root and crown, being its root longer and slightly wider in comparison with the crown (Figures 5 c2 and c3; 6c, and 8a and b).

Phylogenetic Results

We obtained 2.760 MLTs with L= 1.590 (steps), IC= 0,295 and IR= 0,692, in a 2.355.699.751 of total rearrangements. In a more inclusive perspective, were recovered Mesoeucrocodylia including Neosuchia and Ziphosuchia as sister clades, with Ziphosuchia (Figure 9) subdivided into two less inclusive clades: Notosuchia and Sebecia (the same recovered by Pinheiro et al. 2018). Aiming to follow the scope of our work, we focused our analyses and discussions on Notosuchia. The base of Notosuchia resulted in a politomy. We did not recover Uruguaysuchidae (e.g., Pol et al. 2014, Leardi et al. 2015). We recovered two main groups of notosuchians. The first is Baurusuchidae (vide Montefeltro et al. 2011) and is formed by hypercarnivorous morphotypes, with Campinasuchus dinizae Carvalho et al. 2011. being the first diverging lineage. The other group is formed by the South Americans and omnivorous sphagesauromorphs. Here, Comahuesuchus is a sister taxon of a diversified clade Sphagesauria nom. nov. Within this clade, Sphagesauridae was



Figure 9. Phylogenetic analyses results. a- Srictu consensus with 88 active taxa and 392 char. – from 2.760 MLTs, 1.590 steps, IC= 0.295, IR= 0.692, with taxa chronologically distributed and associated with Crocodyliform Assemblage Zones (CAZ1-4) proposed by Pinheiro et al. (2018) for Bauru Group. b- alternative positions of *Coronelsuchus civali gen. et sp. nov.* within Sphagesauria *n. nov.*: 1- *C. civali* as siser taxon of Sphagesauridae; 2- *C. civali* within Sphagesauridae and as sister taxon of (*Adamantinasuchus* + *Yararerani*); 3- *C. civali* in a more derived position within Sphagesauridae and as sister taxon of Sphagesaurinae *subfam. nov.* and Caipirasuchinae *subfam. nov.*; and 4- *C. civali* in a more basal position within Sphagesauria and sharing a hipothetical common ancestor with *Notosuchus*. Asterisc (*) refers to the Sphagesauridae family, not recovered as a clade in the consensus tree; white stars means crocodyliforms from Bauru Group deposits.

not supported as monophyletic in the consensus tree, but its politomy regards the variation in the composition of their most basal members (Figure 9) that includes (*Adamantinasuchus* + *Yacarerani*), Shagesaurinae. *subfam. nov* and Caipirasuchinae *subfam. nov*. The new clades are defined and discussed below.

The strict consensus placed *Coronelsuchus civali* in a polytomy (generated from four divergent topologies recovered in the MLTs, Figure 9b) as a member of the first diverging clade with high diversity composed by forms with derived traits among non-baurusuchids Sphagesauria in a potential close evolutionary relationship with *Notosuchus*, or with basal sphagesaurids (*i.e.*, *Adamantinasuchus* and *Yacarerani*).

NEW PHYLOGENETIC DEFINITIONS

Sphagesauria nom. nov.

Diagnosis. Small to large-bodied sphagesauromorph notosuchians, with no tooth size variation in maxillary row (char. 72: 1->0); orientation of distal carina on upper posterior teeth and mesial carina on lower posterior teeth obliquely oriented, at an angle of approximately 45 degrees with the longitudinal axis of the skull (char. 126: 0->1); lateral surface of dentaries below alveolar margin, at mid to posterior region of tooth row, presenting the posterior region of alveolar facing dorsally, forming a broad alveolar shelf that is strongly inset medially from the lateral surface of the dentaries (char. 181: 1->2); large nutrient foramen on the palatal surface of premaxilla-maxilla contact: small or absent (char. 264: 1->0); anterior region of dentary symphysis in ventral view having a distinct anterior process with parallel lateral margins (char. 341: 0->1); presence of tooth-tooth occlusion wear facets in posterior teeth (char. 368: 0->1).

Etymology. Name based on *Sphagesaurus huenei* Price 1950; the first described member of the family Sphagesauridae Kuhn 1968.

Node-based phylogenetic definition. Within Notosuchia, the most recent common ancestor of, *Coronelsuchus civali, Mariliasuchus, Notosuchus* and all sphagesaurids.

Discussion. Sphagesauria is equivalent to the non-formal term "advanced notosuchian" proposed by Pol et al. (2014), for the natural group formed by omnivorous notosuchians restrict to the Late Cretaceous of South America.

Sphagesaurinae subfam. nov.

Diagnosis. Large-bodied sphagesaurids (*vide* Cunha et al. 2020) presenting two premaxillary teeth (char. 96: 1->3); dorsal border of external nares formed by nasals and premaxillae (char. 113: 0->1); postorbital process of jugal anteriorly placed (char. 132: 1->0); within Sphagesauria *n. nov.* maxillary dental implantation in isolated alveoli (char. 153: 1->0); the well-developed medial crest of quadrate meets the basioccipital on the occipital surface of the skull, excluding the otoccipial from the ventral margin of the occipital surface (char. 335: 1->2).

Etymology. Name based on *Sphagesaurus huenei*; the first described member of the new clade and the family Sphagesauridae.

Node-based phylogenetic definition. The clade within Sphagesauridae comprised the last common ancestor of *Sphagesaurus*, *Armadillosuchus*, *Caryonosuchus* and all of its descendants.

Discussion. At least three groups compose Sphagesauridae and reflect different adaptive zones explored by its members. Sphagesaurinae is defined here to encompass its morphological unity, as recovered in this and previous works that employ similar database (*sup. cit.*).

Caipirasuchinae subfam. nov.

Diagnosis. Medium-bodied sphagesaurids (*vide* Cunha et al. 2020) with the presence of small antorbital fenestra less than half the diameter of the orbit (char. 60: 2->1); dorsal edge of dentary straight with an abrupt dorsal expansion, being straight posteriorly (char. 148: 0->1); jugal anteroventral process between maxilla and ectopterygoid extending anteriorly as a short triangular process that wedges between the ectopterygoid and maxilla on the lateroventral surface of the skull at the level of the orbits ("sickle-like medial process present on the ventral surface of the anterior jugal ramus" *sensu* Andrade & Bertini 2008b [char. 329: 0->1]).

Etymology. Name based on *Caipirasuchus paulistanus* Iori & Carvalho 2011; which is the type species to the genus, as well as the most representative and diverse from this derived new clade.



Figure 10. Right supratemporal fossa and fenestra comparisons between some notosuchian species. **a**- *Coronelsuchus civali gen. et sp. nov.* FFP PG 14; **b**- *Morrinhosuchus luziae* MPMPA 12-0050/07 (from Iori et al 2018); **c**- *Caipirasuchus mineirus* CPPLIP 1463 (from Martinelli et al 2018); **d**- *Notosuchus terrestris* MUCPv 147; **e**- *Mariliasuchus amarali* UFRJ DG 106-R; **f**- *Libycosuchus brevirostris* (holotype unknown number); **g**- *Yacarerani boliviensis* MNK-PAL5063 (from Novas et al 2009); **h**- *Armadillosuchus arrudai* UFRJ DG 303-R; **i**- *Araripesuchus wegeneri* MNN GAD19; **j**- *Simosuchus clarki* UR 8679 (from Kley et al 2010); **k**- *Anatosuchus minor* MNN GAD17; **l**- *Stratiotosuchus maxhechti* Campos et al 2001 DGM 1477-R. Dash lines meaning longitudinal skull axis. Asterisk (*) indicates mirrored left structure. Not in scale. Legends in the text.

Stem-based phylogenetic definition. All species closely related to Caipirasuchus paulistanus, than Sphagesaurus, Armadillosuchus, Caryonosuchus, Mariliasuchus, Adamantinasuchus, Notosuchus, Yacarerani and Coronelsuchus civali.

Discussion. As in Sphagesaurinae, Caipirasuchinae is defined here to encompass its morphological unity, as recovered in this and previously works which employ similar database (*sup. cit.*).

DISCUSSION

Anatomy

Coronelsuchus civali presents a mosaic of morphological features, some of that shared with other basal notosuchians, mainly Notosuchus and Mariliasuchus, while others resemble derived sphagesaurids. The supratemporal fenestra and fossa are wide and well rounded (except by an anteromedial constriction of the fronto-postorbital) in the skull table. It is distinct from most notosuchians (e.g., uruguaysuchids, Simosuchus, Notosuchus, Malawisuchus, Morrinhosuchus, sphagesaurids as Caipirasuchus and Armadillosuchus, and baurusuchids, see [Figure 10]), in which it is anteroposteriorly elongated (Price 1959, Gasparini 1971, Gomani 1997, Ortega et al. 2000, Nobre & Carvalho 2002, Kley et al. 2010, O'Connor et al. 2010, Montefeltro et al.2011, Pol et al. 2014, Barrios et al. 2017, Iori et al. 2018, Martinelli et al. 2018). Among notosuchian taxa, the plesiomorphic circular supratemporal fossa and fenestra shape resembles that found in Libycosuchus, Anatosuchus, Mariliasuchus and Yacarerani (Stromer 1914, Zaher et al. 2006, Novas et al. 2009, Sereno & Larsson 2009). The supratemporal fossa in Mariliasuchus is relative bigger than Coronelsuchus civali. The fossa in Coronelsuchus civali is also less quadrangular

in dorsal outline than in Mariliasuchus. The wide and circular supratemporal fossa suggests robust mandibular external adductor muscles (MAME pars profundus, Holliday & Witmer 2007, Bona & Desojo 2011). Such muscle development suggests a fast and weaker bite rather than a slow and stronger one (Iordansky 1964, 2000). It could imply an insectivorous habit within an omnivorous condition (Ösi 2013). The anteromedial frontal-postorbital that evaginates into supratemporal fossa is well-developed in Coronelsuchus civali, despite being found in a minor degree or even incipient in some other notosuchians, as in Araripesuchus (except A. buitreraensis Pol & Apesteguia 2005, and A. tsangatsangana Turner 2006), Notosuchus, Morrinhosuchus, Libicosuchus, Simosuchus, Anatosuchus, sphagesaurids, and baurusuchids (Figures 4 a to c and 7). Such feature can be even verified in other mesoeucrocodylia groups such as crocodilians (e.g., Crocodylus, Alligator Cuvier 1807, Caiman Spix 1825, but not for Gavialis Oppel 1811 and Tomistoma Müller 1846) and sebecians (some peirosaurids as Stolokrosuchus, Lomasuchus palpebrosus Gasparini, Chiappe & Fernandez 1991, and Montealtosuchus arrudacamposi Carvalho, Vasconcellos & Tavares 2007). It still not clear if this structure is related to the fossa varies intraspecifically, but the frontopostorbital emargination process can be a result of the anterolateral enlargement of the endocast (Witmer & Ridgely 2008). In addition, as occur in some basal uruguaysuchids (e.g., Araripesuchus patagonicus, A. wegeneri) the frontal is relative well exposed in the supratemporal fossa (Figure 4 a and b).

The posterior margin of the supratemporal fossa of *Coronelsuchus civali* is continuous, with a smooth longitudinally oblique and marked vascular temporoccipital groove. This structure could be associated with the obliteration (or compression) of posttemporal fenestra, stuck between the skull table and occiput. Regarding the vascular temporoccipital groove, it is also present in Morrinhosuchus and Caipirasuchus mineirus (Figure 10). This unusual set of temporoccipital features were previously documented only for Notosuchus, but putatively can be more widespread among derived notosuchids and even baurusuchids (e.g., Pissarrachampsa sera Montefeltro, Larsson & Langer, 2011). According to Porter et al. (2016), the skull vascular system of Alligator mississippiensis (Daudin 1802) Cuvier 1807 shows a consistent pattern, with most of the veins of the posterior/caudal portion of the head travel with the artery of the same name. However, it could not be the case for this region to some nothosuchians. The tempororbital vessels probably split at the posterior region of the supratemporal fossa, forming a dorsal vessel (or more than one) that passes through the temporoccipital groove. In this scenario, the strongly strangle posttemporal fenestra could be abandoned and lost the function of blood vessel passage in such taxa. Some eusuchian taxa as the large duck-faced longirrostrines Mourasuchus Price 1964, and Aegisuchus witmeri Holliday & Gardner 2012 (Holliday & Gardner 2012, Bona et al. 2013) were related to possessing dorsal vasculature in skull table, but the large and unique vascular temporoccipital groove seeing in Coronelsuchus civali is quite distinct from that. An interesting anatomical matter to future investigations and works inside Notosuchia as a whole.

Based on the few teeth preserved in the specimen FFP PG 14, we observe a specialized dentition of *Coronelsuchus civali* Although it shares a simple morphology of the incisiviforms teeth, as in some notosuchian taxa (*e.g., Mariliasuchus, Adamantinasuchus* and *Notosuchus*), the morphology of the last maxillary teeth is distinguished from any

other notosuchian described so far. The caudal molariform teeth show pointed apices and do not exhibit the tribodont condition (buttonshape tooth with blunt apex [Buffetaut & Ford 1979]), differing from basal notosuchian forms as Uruguaysuchus Rusconi 1933, and Araripesuchus, with the last having bulbous crown with smooth carinae (exception to A. wegeneri). Labial and lingual crown surfaces of upper molariforms from Coronelsuchus civali FFP PG 14 are no symmetric, with the lingual depressed and less wide than the labial, being the last elliptical and well convex, conferring a D-shape general morphology for these teeth when in occlusal view. Among Sphagesauria, such morphology for caudal teeth seeing in Coronelsuchus civali differs in the section from that elliptical of Mariliasuchus and Morrinhosuchus (Zaher et al. 2006, Iori et al. 2018) and those teardropshaped (see Lecuona & Pol 2008), usually found to Notosuchus and sphagesaurids (Pol et al. 2014, Barrios et al. 2017, Martinelli et al. 2018). Either mesial or the distal carinae from upper and lower molariform teeth are serrated by true and globular denticles, close to each other, in construction that despite not the case, resembles more a ziphomorph condition, pointed by Andrade & Bertini (2008a) for Mariliasuchus. Notosuchus and Sphagesaurus, than those sharp cutting edge, numerous and isomorphic denticles present in ziphodont crocodyliforms. as baurusuchids and sebecids (see Prasad & Broin 2002, Andrade & Bertini 2008a).

The worn apical surface of rostralmost dentary molariform preserved is resulted from abrasion of lower tooth apex against hard food components, but also probably by the direct contact with the tubercles from the labial surface of its opposite upper molariform.

Phylogeny

Sphagesauridae was collapsed in our consensus tree as a politomy inside Shagesauria (Figure 9A) due to the instability caused by Coronelsuchus civali which jumps inside and outside this clade as a wild card taxon, placed as the sister of Notosuchus in some trees and therefore it is depicted as a non-sphagesaurid in that. However, we consider the clade as valid, once is recovered in all MLTs, being both synapomorphies and relationships variable with basal sphagesaurians. The internal content observed in MLTs are consistent with previous results that use a similar dataset as a base (e.g., Martinelli et al. 2018, Pinheiro et al. 2018, Cunha et al. 2020). Sphagesauridae can be structured as ((Adamantinasuchus + Yacarerani) + ((Sphagesaurinae) + (Caipirasuchinae))). The clade (Adamantinasuchus + Yacarerani) was not phylogenetically defined and named herein, although its relationship was supported by posterior teeth presenting accessory apicobasally oriented keels bearing cusps or tuberous denticles located lingually and buccally from the major central keel (char. 365: 0->1) in all MLTs. Further works should regard such relationship and new specimens to improve such clade. They also should regard an improvement at the ontogenetic changes of Adamantinasuchus navae (UFRJ-DG 107-R in Nobre & Carvalho 2006), which can be a juvenile specimen and could modify its character statement.

Although the consensus tree lacks resolution to *Coronelsuchus civali* within Notosuchia, our analysis indicates that it is a basal member of Sphagesauria (Figure 9a). The politomy in which *C. civali* was recovered has four alternative combinations (Figure 9b1-4). One of them (Figure 9b1) indicates that *C. civali* is a sister taxon of sphagesaurids. The second combination (Figure 9b2) recovers *C. civali* as a

basal sphagesaurid. The third hypothesis (Figure 9b3) assigns C. civali within Sphagesauridae. The fourth topology (Figure 9b4) suggests C. civali as a basal sphagesaurian taxon outside Sphagesauridae, sharing a basal lineage with Notosuchus. Two combinations from the four of Sphagesauria suggest *C. civali* as a basal taxon (hypotheses 1 and 4), while the other two, points to the new taxon as belonging to Sphagesauridae (hypotheses. 2 and 3). Hypothesis 4 is a plausible scenario, regarding the new character - the presence of a smooth temporoccipital groove in posteromedial supratemporal fossa rim in parietal-squamosal contact, interrupting supratemporal fossa edge (char. 388 new: 1). Such characters care clarification if it is or not biologically dependent of the closure or strangulation and dorsally redirection of the postemporal fenestra - char. 389 new: 1). However, these character statements appear only twice among notosuchians: in the group shared by Notosuchus and Coronelsuchus civali and as homoplastic in Caipirasuchinae, once it is also present at least in Morrinhosuchus and Caipirasuchus mineirus (although not mentioned in its original descriptions - *i.e.*, Iori & Carvalho 2009, and Martinelli et al. 2018). The other three hypothesis (1, 2 and 3 – Figure 9b) requires one extra step for the inferred evolution of such character.

The shape of supratemporal fossa (char. 392 new) suggests affinities between *Coronelsuchus civali* and basal notosuchians or sphagesaurians than the more specialized forms (such as baurusuchids and sphagesaurids). The wide and circular shaped fenestra (related to MAME musculature) occurs among the Ziphosuchia: *Stolokrosuchus* and *Barreirosuchus franciscoi* lori & Garcia 2012 (Sebecia), and to *Libycosuchus*, *Anatosuchus*, *Mariliasuchus*, *Coronelsuchus civali* and *Yacarerani* (Notosuchia; Figure 10). Despite its homoplastic features, the



Figure 11. Vertical profile composite of the Bauru Group (Paraná Basin), with their Crocodyliformes Assemblage Zones (CAZ).

supratemporal fossa shape supports the basal assignment of *C. civali* among Notosuchia (hypothesis four; Figure 9 b4).

Biostratigraphy

Coronelsuchus civali corresponds to the CAZ 1 (Late Turonian–Early Coniacian) of the Araçatuba Formation, together with other small body length sphagesaurian (*Mariliasuchus* spp, *Adamantinasuchus*), a large-bodied sphagesaurid *Caryonosuchus*, as well as itasuchids (*e.g.*, *Pepesuchus deiseae* Campos et al. 2011). The top of the CAZ1 is the Subaerial Unconformity 2 (SU2, Figure 11) and the Santonian volcanic event (see Gibson et al. 1995, 1997). The borders of the Paraná Basin are marked by the erosion and loss of the Upper Coniacian to Lower Santonian intervals due to the uplift, which occurred by the intense magmatism, which also affected the adjacent marginal basins as Mato Grosso grabens, São Francisco Basin and Santos Basin. The CAZ2 (Early Campanian) occurs after the Santonian volcanic event (Gibson et al. 1995, 1997), which is marked by the first record of Baurusuchidae. The CAZ3 (Middle-Late Campanian) is the most diverse taxonomically, with its record marked by Peirosauridae, Itasuchidae and most diverse baurusuchidae sphagesaurian clades. From the above exposed, the Santonian volcanic event is a factor that affect in the irradiation of the Crocodyliformes in the Bauru Group.

The oldest CAZ1 is also the less taxonomically diverse CAZ so far (Figure 11). However, when compared to the Gondwana crocodyliform record and the latest CAZ3, it indicates that it could be a collector artefact. In addition, the CAZ1 could be older than the actual interval considered here, comprising the Santo Anastácio Formation and consequently the Cenomanian-Turonian transgressive event. The Itasuchidae record is marked by a gap, due to the absence of material found in the CAZ2 so far. A large temporal interval of the record is considered for the itasuchid *Pepesuchus*, which was found in the Tartaruguito site (Campos et al. 2011), at the top of the CAZ1 (base of the Adamantina/Presidente Prudente formations). and in the Catanduva municipality (top of the Adamantina Formation, CAZ3) according to Iori et al. (2011).

Recently, Geroto & Bertini (2018) described a new specimen of *Pepesuchus*, but this new material (MCT 1723-R) has no provenance. Based on the rock matrix associated, the red sandstone was assigned to the Adamantina Formation (Geroto & Bertini 2018), although such lithology is common among the unities of the Bauru Group, such as Presidente Prudente, Santo Anastácio and Marília formations. In addition, *Pepesuchus* is widespread along with the chronostratigraphic interval, ranging from the Turonian-Early Coniacian to the Early Maastrichtian (about 18 million years).

Finally, Martinelli et al. (2018) observed, based on the CAZs proposed by Pinheiro et al. (2018), that the fossiliferous outcrops of Campina Verde (Triângulo Mineiro) have a different age regarding the outcrops from western São Paulo (*i.e.*, General Salgado), but that further combined studies are still needed. Here, we support that there is more than one CAZ with sphagesaurids and baurusuchids of different ages. The sphagesaurid *Caipirasuchus mineirus* is in CAZ2 together with the baurusuchid *Baurusuchus pachecoi* Price 1945 due to their correlation with the lower interval of the Adamantina Formation, a depositional sequence below that cropping out in the General Salgado. The depositional sequence of the upper interval of the Adamantina Formation cropping out in General Salgado (Buriti/São José Farm, Rao X Farm and Usina Generalco site) is correlated to the depositional sequence of this unit in Monte Alto (Figures 2 and 3). Based on the current findings, *Coronelsuchus civali* confirms an older appearing for Sphagesauria.

CONCLUSIONS

Besides the singular heterodont dentition (FFP PG 14) the cranial morphology (FFP PG 13) of Coronelsuchus civali reveals peculiar characteristics, as the configuration and position of postemporal fenestra opening and the temporoccipital groove in posteromedial supratemporal fossa rim - which implies in a distinct configuration of blood vessels in the posterior cranial portion, a feature only previously mentioned for Notosuchus. The new taxon here described is a basal member of Sphagesauria, the most diverse notosuchian group that includes small to large omnivorous morphotypes restricted to Upper Cretaceous of South America, probably evolving in pre-Turonian times. Stratigraphically the new taxon is the first crocodyliform from the top deposits of Aracatuba Formation, which indicates the fossiliferous potential for this formation for the study of Crocodyliformes.

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Author contributions

The conceptualization of this project was developed by AEPP, LGS, PVLGCP and FMS. The collecting, preparation, and curation of studied specimens were made by KLNB, ASB, PVLGCP, LORC and FMS. Geological analysis of fossil sites was carried by FMS and RRCR. Anatomical description and comparisons were performed by AEPP, LGS, KLNB, ASB and PVLGCP. Scorings of the matrix was performed by LGS and AEPP. Phylogenetic analysis was performed by LGS and AEPP. Figures were prepared by AEPP and FMS. All authors have contributed to the discussion of results, the manuscript input, the English revision, and approved the final version.

