

## A NEW SPECIMEN OF *AUSTRALERPETON COSGRIFFI* BARBERENA, 1998 (STEREOSPONDYLI: RHINESUCHIDAE) FROM THE MIDDLE/UPPER PERMIAN RIO DO RASTO FORMATION, PARANÁ BASIN, BRAZIL

KARINE LOHMANN AZEVEDO

Programa de Pós-Graduação em Geociências, Universidade Federal do Rio Grande do Sul. Av. Bento Gonçalves, 9500,  
91501-970, Porto Alegre, RS, Brazil. [karine.lohmann@gmail.com](mailto:karine.lohmann@gmail.com)

CRISTINA SILVEIRA VEGA

Departamento de Geologia, Universidade Federal do Paraná, Curitiba, PR, Brazil. [cvega@ufpr.br](mailto:cvega@ufpr.br)

MARINA BENTO SOARES

Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul. Av.  
Bento Gonçalves, 9500, 91.540-000, Porto Alegre, RS, Brazil. [marina.soares@ufrgs.br](mailto:marina.soares@ufrgs.br)

**ABSTRACT** – Here we present a skull and a lower jaw of a temnospondyl specimen collected from the São Jerônimo da Serra Site, an exposure of the Morro Pelado Member of the Rio do Rasto Formation (Middle/Upper Permian, Paraná Basin), Paraná State of southern Brazil. The sedimentary environment in which the fossil was preserved is characterized by a massive reddish mudstone derived from the slow deposition of fine sediments from suspended load in a terminal splay or ephemeral lake setting. The comparative anatomical description of the new specimen allows its assignment to the rhinesuchid *Australerpeton cosgriffi* Barberena. The new specimen represents the most complete skull and lower jaw of this species found up to date. Its high degree of ossification associated with its large skull size (58 cm long) indicates that it was a mature adult. This work, besides confirming several anatomical characteristics of *A. cosgriffi*, reveals previously unknown information about this species: a long cultriform process whose anterior edge surpasses the level of the posterior border of the choanas, being interposed between them; and a pair of longitudinal ridges lacking denticles that run parallel along the premaxillary surface without making contact with the choanae. These features were not reported before in the smaller known skulls of *A. cosgriffi* because they likely develop late in the ontogeny of this species. This new find provides evidence that this unique long-snouted rhinesuchid was a common and successful faunal component of the Middle–Late Permian fluvio/lacustrine ecosystems of southern Brazil, and reaffirms the Rio do Rasto Formation of Brazil as a rich source of information concerning the initial diversification of the Stereospondyli.

**Key words:** *Australerpeton cosgriffi*, Temnospondyli, Rhinesuchidae, Permian, Rio do Rasto Formation.

**RESUMO** – O trabalho apresenta um novo espécime de temnospondílo que consiste em um crânio e uma hemimandíbula esquerda. O fóssil foi coletado no afloramento São Jerônimo da Serra, vinculado ao Membro Morro Pelado da Formação Rio do Rasto (Permiano Médio/Superior, Bacia do Paraná), do Estado do Paraná, Brasil. O ambiente sedimentar no qual o fóssil foi preservado é caracterizado por pelitos maciços avermelhados gerados pela deposição de finos em suspensão, representando espriamentos terminais e lagos efêmeros. A comparação detalhada do material permitiu a sua atribuição ao rinessuquídeo *Australerpeton cosgriffi* Barberena. O novo espécime representa os mais completos crânio e mandíbula já encontrados para esta espécie. O seu alto grau de ossificação associado ao grande tamanho craniano (58 cm de comprimento) indica tratar-se de um adulto pleno. Este trabalho, além de confirmar várias características anatômicas de *A. cosgriffi*, fornece informações inéditas para esta espécie, quais sejam: um longo processo cultriforme cuja extremidade anterior ultrapassa o nível da borda posterior das coanas, ficando interposto entre elas; um par de cristas longitudinais sem denticulos que correm paralelamente na superfície da pré-maxila, sem fazer contato com as coanas. Provavelmente estas características nunca haviam sido antes reportadas nos crânios de indivíduos menores de *A. cosgriffi* porque devem se desenvolver tardiamente na ontogenia desta espécie. O novo achado evidencia que este único rinessuquídeo longirostre era um componente faunístico comum e bem sucedido nos ecossistemas flúvio-lacustres do Permiano Médio/Superior do sul do Brasil, e reafirma a Formação Rio do Rasto como uma rica fonte de informação relativa à diversificação inicial dos Stereospondyli.

**Palavras-chave:** *Australerpeton cosgriffi*, Temnospondyli, Rhinesuchidae, Permiano, Formação Rio do Rasto.

## INTRODUCTION

The Rio do Rasto Formation (Gordon Jr., 1947) is part of the Middle/Upper Permian sequence from the Paraná Basin that crops out in southern Brazil across Paraná, Santa Catarina and Rio Grande do Sul states. This unit is subdivided into the 150–250-meter-thick Serrinha Member, that is formed dominantly by mudstones and fine-grained sandstones at the base, and the 250–300-meter-thick Morro Pelado Member, composed mainly of fine to medium-grained sandstones (Holz *et al.*, 2010).

According to Langer *et al.* (2008), the fossiliferous outcrops of the Morro Pelado Member of the Rio do Rasto Formation are among the most important paleontological records of the continental Middle/Late Permian period in South America. Vertebrates, invertebrates, plants and ichnofossils have already been recorded from these strata (Barberena & Daemon, 1974; Langer, 1998; Barberena & Dias, 1998; Lee, 1997; Barberena, 1998; Richter & Langer, 1998; Dias & Barberena, 2001; Dias & Kroeff, 2002; Leonardi *et al.*, 2002; Malabarba *et al.*, 2003; Cisneros *et al.*, 2005; Dias & Schultz, 2003; Eltink & Langer, 2008, 2010, 2011; Cisneros *et al.*, 2011; Ramos & Vega, 2011; Souza & Vega, 2011; Pauliv *et al.*, 2012; Silva *et al.* 2012; Cisneros *et al.*, 2012; Dentzien-Dias *et al.*, 2012; Boos *et al.*, 2013; Eltink & Langer, 2014; Strapasson *et al.*, 2015; Pauliv *et al.*, 2014; Eltink *et al.*, 2015; Boos *et al.*, 2015; Boos, *et al.*, 2016; Pacheco *et al.*, 2017).

The study of temnospondyl amphibians from the Rio do Rasto Formation started in the 1970s with the publication of *Platyops* sp., a long-snouted Temnospondyli from Paraná State described by Barberena & Daemon (1974). This specimen was later reassigned to *Australerpeton cosgriffi* Barberena, 1998, and further studies have added information about the postcranial skeleton of this taxon (Dias & Richter, 2002; Dias & Schultz, 2003; Ramos & Vega, 2011; Eltink & Langer, 2010, 2011, 2014). *A. cosgriffi* has previously been considered a member of Rhinesuchoidea (Barberena, 1998), Stereospondylomorpha Platyoposaurinae (Werneburg & Schneider, 1996; Schoch & Milner, 2000) and Rhinesuchidae (Dias & Schultz, 2003). In the recent phylogenetic analysis performed by Eltink *et al.* (2015) *A. cosgriffi* nested within Rhinesuchidae, based mainly on the anatomy of the tympanic cavity.

Barberena & Dias (1998) have also described a short-snouted Temnospondyli from Paraná State that was identified as a “*Rhinesuchus*-like” form. From Rio Grande do Sul State, an incomplete lower jaw of the Platyoposaurinae *Bageherpeton longignathus* Dias & Barberena, 2001 has been reported. An indeterminate Temnospondyli lower jaw (Malabarba *et al.*, 2003) and a Melosaurinae incomplete skull (Dias-da-Silva, 2012) were also found in Rio Grande do Sul. Also from this region comes *Konzhukovia sangabrielensis* Pacheco *et al.*, 2017, a member of the Konzhukovidae family, with close relationships to Russian forms, and the first temnospondyl from Santa Catarina State, the Stereospondylomorpha *Parapytanga catarinensis* Strapasson *et al.*, 2015, was recently described. Most of these temnospondyl records from

the Rio do Rasto Formation, as well as global ones, consist of cranial and mandibular remains.

Regarding *Australerpeton cosgriffi*, the first recovered remains were collected in the 1970s from sites that crop out along the EFCP (“Estrada de Ferro Central do Paraná”) railroad (Barberena & Daemon, 1974; Barberena, 1998; Dias & Schultz, 2003) in a geographic region known as Serra do Cadeado, located in the northeast of Paraná State. In the 2010s, new outcrops from the Serra do Cadeado were explored revealing more material of *A. cosgriffi* (Ramos & Vega, 2011; Eltink & Langer, 2014). São Jerônimo da Serra Site is where the new fossil material presented here was collected.

The present work describes a new skull and lower jaw of the Temnospondyli *Australerpeton cosgriffi* and presents a revised diagnosis with two new characters for the taxon.

**Institutional abbreviations.** UFPR PV, Universidade Federal do Paraná, Vertebrate Paleontology Collection, Curitiba, Paraná State, Brazil; UFRGS-PV-P, Universidade Federal do Rio Grande do Sul, Vertebrate Paleontology, Permian Collection, Porto Alegre, Rio Grande do Sul State, Brazil.

## GEOGRAPHICAL, GEOLOGICAL AND PALEONTOLOGICAL SETTINGS

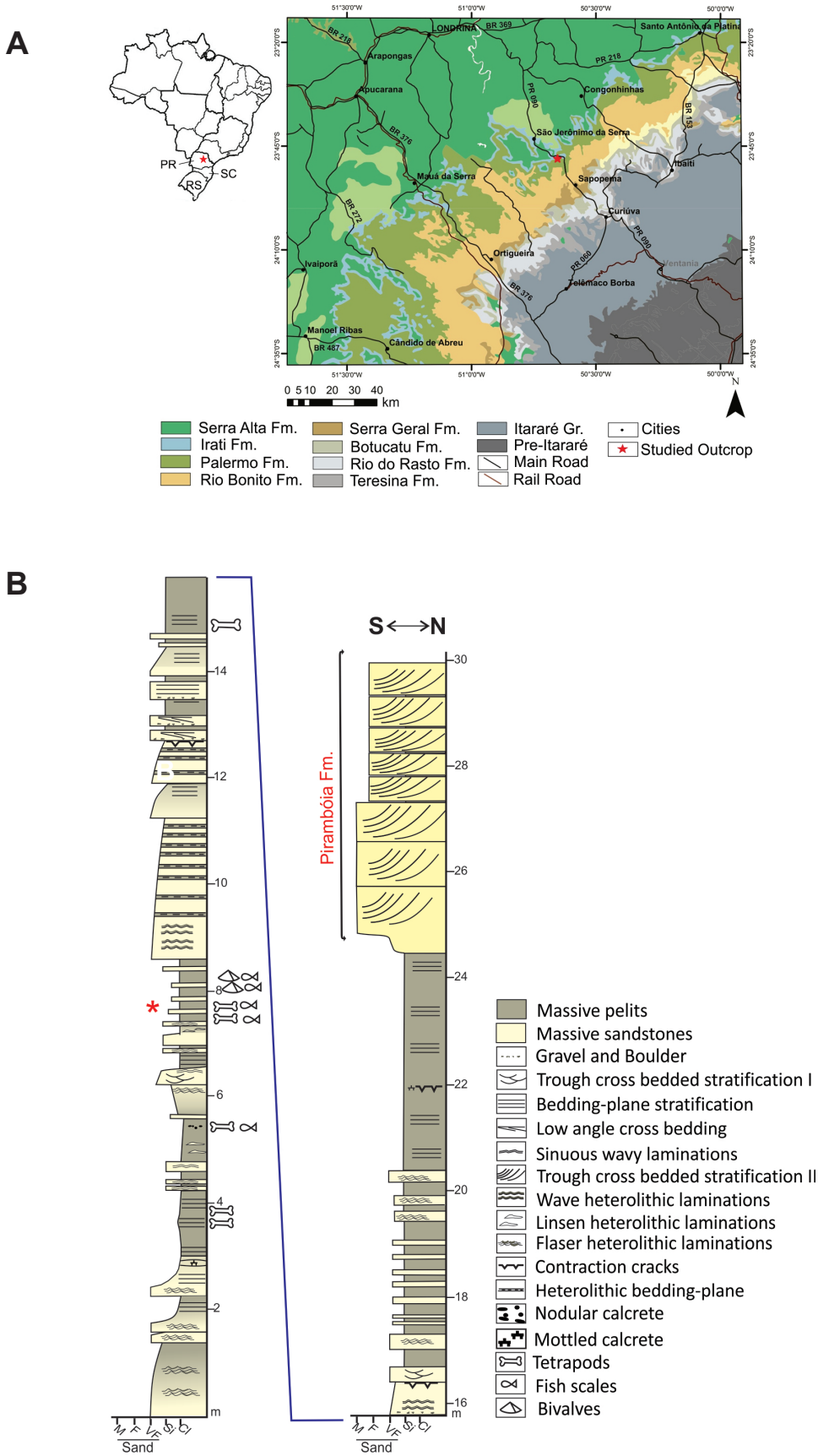
The materials reported here, a skull (UFPR 0199 PV) and a lower jaw (UFPR 0198 PV), were recovered in an outcrop named “São Jerônimo da Serra Site” located in the northeast of Paraná State at 277 km on the PR-090 road, between Sapopema and São Jerônimo da Serra municipalities (UTM 22K 0538201/7368276), in a geographic area known as Serra do Cadeado (Figure 1). This 180-meter-long outcrop is situated at an altitude of 1056 m and reveals a vertical exposure of approximately 25 m.

The São Jerônimo da Serra Site exposes a sedimentary sequence identified as the Morro Pelado Member (Gordon, 1947), and displays a predominantly siltstone succession intercalated with layers of thin to medium sandstones. At its top, it is possible to observe a contact with the overlying eolian sandstones of the Piramboia Formation (Soares, 1975) (Figure 1).

Regarding its fossil content, plants, conchostracans, bivalves, paleonisciform fish scales, ostracods, bone elements (mainly from temnospondyls) and vertebrate ichnofossils have been recovered from this locality (Ramos & Vega, 2011; Souza, 2011; Silva *et al.*, 2012). Mandibular fragments (UFPR 0097 PV, UFPR 0100 PV and UFPR 0099 PV) collected at this site were tentatively identified as *Australerpeton cosgriffi* by Ramos & Vega (2011). Although they are not well preserved, the typical dermal ornamentation of temnospondyl skull bones can be seen.

The vertebrate fossils usually occur in levels that are rich in iron oxide (hematite) and, in fact, are diagenetically altered and covered by a thick layer of this oxide, displaying a black color.

The fossil specimens here described were found at nearly 8 meters up from the base of the exposure, in a layer interpreted



**Figure 1. A**, location map of the São Jerônimo da Serra Site (indicated by the star), Rio do Rasto Formation, in Paraná State (modified from Brasil, 2004). **B**, lithological profile of the São Jerônimo da Serra site showing the fossiliferous levels (modified from Schemiko, 2013). The star indicates the stratum where UFPR 0198 PV and UFPR 199 PV were found. **Abbreviations:** RS, Rio Grande do Sul State; SC, Santa Catarina State; PR, Paraná State.

by Schemiko (2013) as a massive reddish mudstone derived from the slow deposition of fine sediments from suspension.

## MATERIAL AND METHODS

The described materials, UFPR 0199 PV (skull) and UFPR 0198 PV (lower jaw), were found very close to each other at the same point and stratigraphic level, so it is safe to assign them to the same individual. They are housed in the fossil collection of the Laboratório de Paleontologia (LabPaleo) of the Setor de Ciências da Terra of the Universidade Federal do Paraná (UFPR), in Curitiba, State of Paraná, Brazil.

As with all other fossil bones previously collected from the Jerônimo da Serra Site, UFPR 0199 PV and UFPR 0198 PV are adhered to the rock and coated by a dense layer of iron oxide. This coating is hard to remove and also makes difficult the observation of sutures and some important anatomical characteristics. Therefore, mechanical preparation with a pneumatic hammer and Paraloid B-72 resin was needed. Some attempts of chemical preparation with hydrogen peroxide were made, but this methodology was not efficient due to the large size of the specimen. Also, a CT Scan of the jaw was done but the results were not clear enough. In order to prepare both sides of the jaw UFPR 0198 PV, Carbowax resin was used. Due to the fragility of the skull UFPR 0199 PV, only its ventral view was prepared.

The description and comparisons were carried out based on literature and on specimens from the collections of the Laboratório de Paleontologia de Vertebrados of Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil (UFRGS-PV-0224-P, UFRGS-PV-0225-P, UFRGS-PV-0227-P, UFRGS-PV-0228-P, UFRGS-PV-0229-P, UFRGS-PV-0230-P, UFRGS-PV-0317-P) and the Universidade Federal do Paraná (UFPR 0097 PV, UFPR 0099 PV, UFPR100 PV).

The material here studied is attributed to *Australerpeton cosgriffi*, described by Barberena *et al.* (1998) and recently revised by Eltink *et al.* (2015) with more details added. *A. cosgriffi* is a Rhinesuchidae already recorded in the Rio do Rasto Formation from Paraná State; however, a few, but informative features found on the specimens studied here are listed below.

## SYSTEMATIC PALEONTOLOGY

TETRAPODA Goodrich, 1930

TEMNOSPONDYLI Zittel, 1887–90

STEREOSPONDYLOMORPHA Yates & Warren, 2000

STEREOSPONDYLI Fraas, 1889

RHINESUCHIDAE Watson, 1919

AUSTRALERPETINAE Eltink *et al.*, 2015

*Australerpeton cosgriffi* Barberena, 1998  
(Figures 2–4)

**Holotype.** UFRGS-PV-0227-P.

**Paratypes.** UFRGS-PV-0228-P; UFRGS-PV-0229-P; UFRGS-PV-0230-P.

**Referred specimens.** UFRGS-PV-0224-P; UFRGS-PV-0225-P; UFRGS-PV-0240-P; UFRGS-PV-0243-P; UFRGS-PV-0319-P; UFRGS-PV-0320-P; LPRP/USP-0011; UFRGS-PV-0228-P; UFPR 0097 PV; UFPR 0100 PV; UFPR 0099 PV.

**New referred specimens.** UFPR 0199 PV, skull and UFPR 0198 PV, lower jaw.

**Geological and geographical precedence.** Morro Pelado Member, Rio do Rasto Formation, São Jerônimo da Serra Municipality, at the outcrop named “São Jerônimo da Serra Site” (UTM 22K 0538201 / 7368276), Paraná State, Brazil.

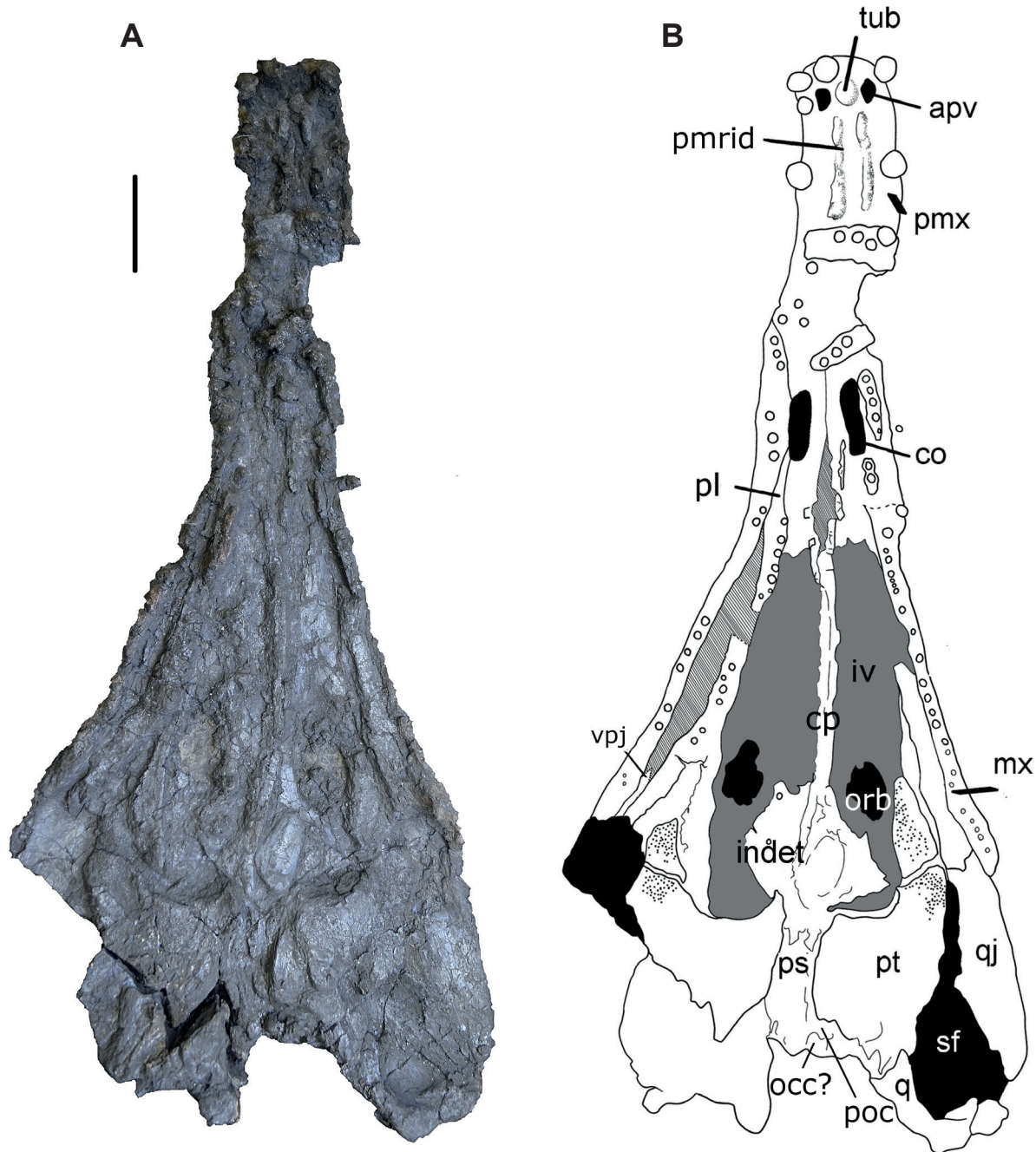
**Age.** Middle/Late Permian.

**Emended diagnosis.** In addition to the diagnostic characters postulated by Barberena (1998), Dias & Schultz (2003), Eltink & Langer (2014) and Eltink *et al.* (2015), we propose the following characters (\* = autapomorphies) to diagnose adult individuals of *Australerpeton cosgriffi*: a long cultriform process whose anterior edge surpasses the level of the posterior border of the choanas, being interposed between them (shared with *Mastodonsaurus giganteus*, *Konzhukovia vetusta* and *K. sangabrielensis*); a pair of longitudinal ridges devoid of denticles that run parallel along the premaxilla surface without making contact with the choanae\*.

## DESCRIPTION AND COMPARISONS

### General skull aspect

As explained above, only the ventral view of the skull UFPR 0199 PV was exposed, not being possible to prepare the opposite side owing to the fragility of the material. The skull exhibits a triangular shape with an elongated snout that ends with a slightly expanded premaxillary tip (Figure 2). It is 58 cm long and, in general, the skull is well preserved, being broken only in the left posterolateral portion. This skull morphology, which is usually related to a piscivorous diet (Dias & Schultz, 2003), is typical of *Australerpeton cosgriffi* and it is also observed in stereospondylomorphs like *Platyoposaurus stuckenbergi* according to Gubin (1991). The shape of the rostrum is compatible with several *A. cosgriffi* specimens (*e.g.* UFRGS-PV-0227-P; UFRGS-PV-0225-P; UFRGS-PV-0228-P), but the size of the skull UFPR 0199 PV surpasses the previously largest-known specimen, UFRGS-PV-0228-P, a rostrum which belonged to an animal with an estimated skull size of *ca.* 50 cm. It is also important to emphasize that while UFRGS-PV-0228-P is an isolated rostrum, UFPR 0199 PV is a complete skull, never before recorded for *A. cosgriffi*. A large number of teeth are preserved; they are rounded in cross-section, having the typical infolding internal labyrinthodont pattern. The external surfaces are marked by longitudinal grooves. In general, the teeth of UFPR 0199 PV decrease in size posteriorly. The pair of elongated choanas can be easily seen, as well as the wide interpterygoid vacuities and the long parasphenoid cultriform process. On the posterior part of the parasphenoid cultriform process there are two unidentified fragments of bones. The posterior portion of the skull (on the left side) is broken, and thus, part of the pterygoid, the subtemporal fenestra, the quadrate and the quadratojugal are missing.

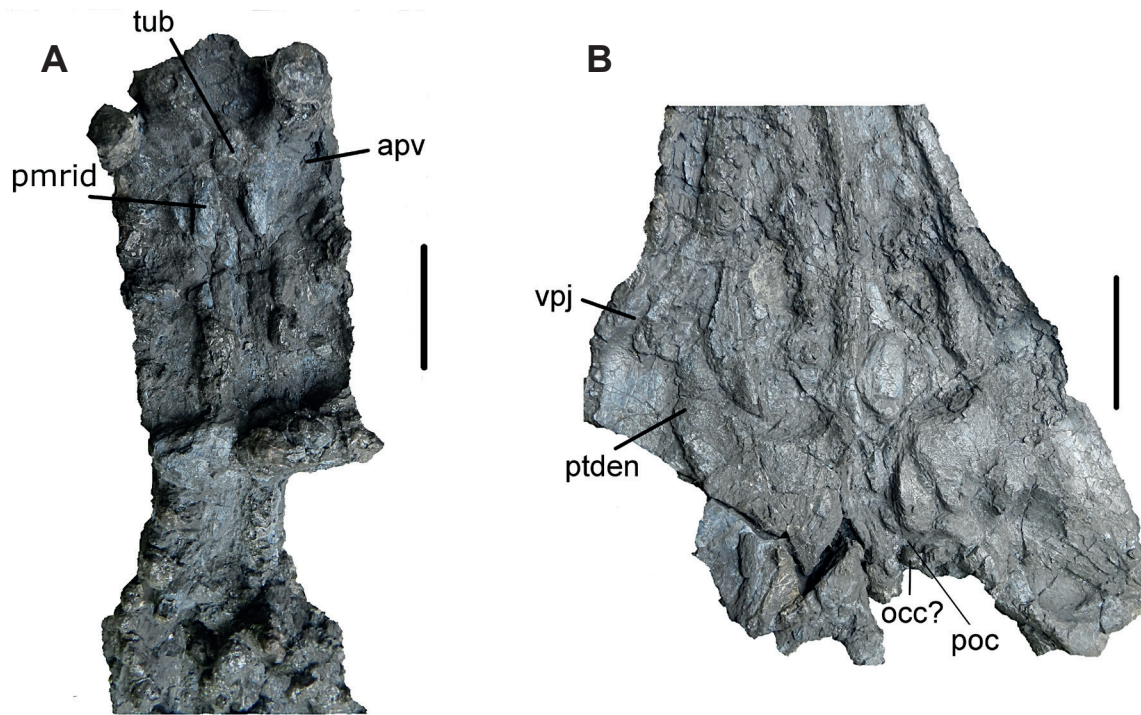


**Figure 2.** **A**, photo of the skull UFPR 0199 PV in ventral view. **B**, reconstruction. Black areas represent orbital openings and subtemporal fenestra. Grey area represents the interpterygoid vacuities. Shaded lined areas represent recessed areas of bone, and dots represent denticles on the palate. **Abbreviations:** *apv*, anterior palatal vacuity; *co*, choana; *cp*, cultriform process; *pmrid*, premaxillary ridges; *iv*, interpterygoid vacuity; *mx*, maxilla; *ec*, ectopterygoid; *pl*, palatine; *pmx*, premaxilla; *ps*, parasphenoid; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *sf*, subtemporal fenestra; *tub*, medial tubercle of the premaxilla; *v*, vomer; *orb*, orbit; *vpj*, ventral process of the jugal; *poc*, 'pockets' for the insertion of the occipital musculature; *occ?*, occipital condyle. Scale bars = 50 mm.

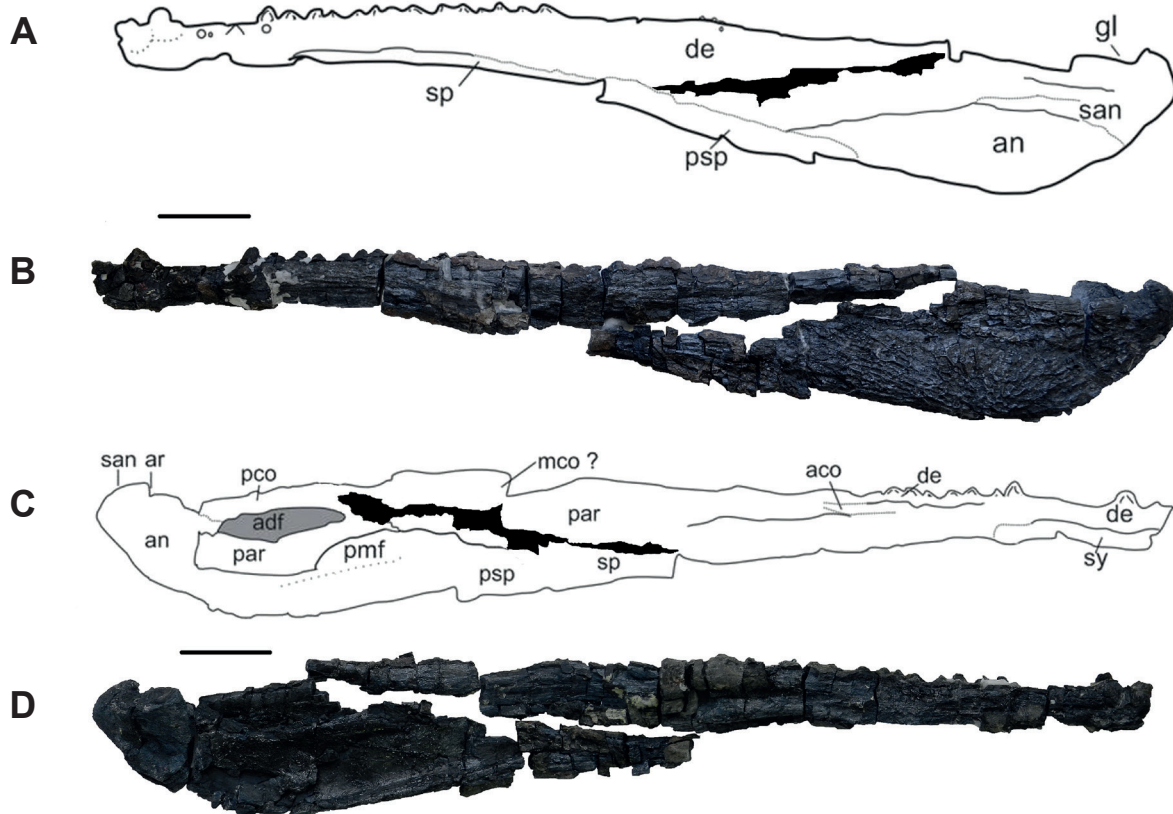
The orbits are placed in the medial part of the skull through the interpterygoid vacuities. Ignoring the thick layer of iron oxide covering the bones, the osseous tissue is usually very thin, being nearly 4 mm thick.

**Premaxilla.** This bone is longer than wide, 13 cm in length, and more than twice the length of the external naris, defining a long-snouted condition like in *Australerpeton cosgriffi*. There are five tusks on the premaxilla, bent slightly backwards. On the anteriormost part of the bone, there is a

small central tubercle similar to the one found in rhinesuchids like *Rhineceps nyasaensis* (Haughton, 1927) according to Watson (1962). Behind the tubercle there is a pair of fossae, the anterior palatal vacuities, which set the jaw teeth (Figure 2). These fossae are clearly separated, opposite to the condition seen in *Platyoposaurus stuckenbergi*, in which they appear as just one bilobed structure (Gubin, 1991) or in *Eolydekkerina magna* and *Lapillopsis nana* (Shishkin *et al.*, 1996; Yates, 1999), in which the palatal vacuity is a single



**Figure 3.** Photo of the skull UFPR 0199 PV in ventral view. **A**, anterior part; **B**, posterior part. **Abbreviations:** **apv**, anterior palatal vacuity; **pmrid**, premaxillary ridges; **ptden**, denticle os pterigoyd; **tub**, medial tubercle of the premaxilla; **vpj**, ventral process of the jugal; **poc**, 'pockets' for the insertion of the occipital musculature; **occ?**, occipital condyle. Scale bars: A = 30 mm; B = 50 mm.



**Figure 4.** UFPR 0198 PV, left mandible. **A**, drawing of labial view; **B**, photo in labial view; **C**, drawing of lingual view; **D**, photo of in lingual view. **Abbreviations:** **an**, angular; **de**, dentary; **pco**, posterior coronoid; **mco?**, middle coronoid; **aco**, anterior coronoid; **psp**, postsplenial; **san**, surangular; **ar**, articular; **sp**, splenial; **pmf**, posterior Meckelian fenestra; **sy**, symphysis; **par**, prearticular; **adf**, adductor fossa; **pga**, post-glenoid area. Black areas represent recessed bones. Scale bars = 50 mm.

structure without divisions. As in UFPR 0199 PV, Eltink *et al.* (2015) described these structures in *A. cosgriffi*, in which the central tubercle is well developed and the anterior palatal vacuities are placed posterior, but close to it. Posterior to the tubercle, and medial to the anterior palatal vacuities, UFPR 0199 PV exhibits a pair of prominent longitudinal ridges devoid of denticles or tusks that run parallel along the premaxilla surface (Figure 2C), resembling what was described in *Archegosaurus decheni* by Witzmann (2006). However, the ridges of *Archegosaurus* are placed in the vomer, instead in the premaxillae. Therefore, Witzmann (2006, p. 145; figs. 17, 18b) reported for *Archegosaurus* “an elevated strip of bone bearing teeth and denticles begins anteromedial to the choana and extends posteriorly parallel to the medial choanal margin at least in large and medium-sized skulls. On its widest part, the elevation bears a large tusk with appropriate, anteromedially located replacement pit. Apart from these teeth, the elevation is covered densely by denticles”. In this taxon, the choanae anterior margins are placed in the vomer but very close to the premaxillae posterior limit, while in the Brazilian form the choanae are placed more posteriorly, in the middle portion of the vomer surface, far from the premaxillae posterior border. Although it is not possible to see how far the ridges extend along the palate in UFPR 0199 PV, they do not run parallel to the whole medial choanal borders as in *Archegosaurus*. Our considerations are reinforced by the holotype of *Australerpeton* (UFRGS-PV-0227-P), in which the vomer was preserved and no sign of any ridges is observable on its surface (Barberena 1998; Eltink *et al.*, 2015). Such premaxillary ridges had never been described for *A. cosgriffi*, probably because UFPR 0199 PV is the most complete specimen found to date and the only one with good preservation of the whole rostrum. In addition to UFPR 0199 PV, only a single preserved rostrum (UFRGS-PV-0228-P) with preserved premaxillae is known, but although in this specimen it is possible to see the tubercle, it is not possible to observe if the ridges are also present because the anterior end of the rostrum is laterally compressed, and in consequence the palate is obliterated by the two teeth rows. We consider these premaxillary ridges as an autapomorphy of *A. cosgriffi*, since they are different from that of *Archegosaurus decheni* in their position, respectively premaxillae and vomer, and due to the absence of denticles or tusks in the former and their presence in the latter. Three tusks are placed anteriorly to the palatal vacuities and central tubercle, right at the tip of the snout, while another two large teeth are symmetrically positioned on each side, posterior to the anterior palatal vacuities and lateral to the premaxillary ridges. Besides these, there is no sign of any small premaxillary teeth. This organization differs from the reconstruction of *A. cosgriffi* presented by Barberena (1998), based on UFRGS-PV-0228-P, a rostrum, in which two or three premaxillary tusks are positioned on each side anterior to the palatal vacuities, two small teeth are placed lateral to the palatal vacuities and three more posterior larger teeth complete the series. This is the same condition described by Eltink *et al.* (2015) in *A. cosgriffi*. The posterior enlargement of the premaxillary teeth, a character included in

the diagnosis of *A. cosgriffi* by Eltink *et al.* (2015) and which makes it different from all other known rhinesuchids, is not well observed probably because the small premaxillary teeth are not preserved. This premaxillary tooth enlargement is also observed in some archegosaurids like *Archegosaurus decheni* (Witzmann, 2006; Eltink *et al.*, 2015). There is a displaced fragment of the maxilla just over the contact area between the premaxilla, maxilla and vomer, precluding the visualization of the sutural relationships.

**Maxilla.** The maxilla surrounds the skull laterally, reaching the anterior edge of the subtemporal fenestrae, and bears teeth along its whole extension. At least 24 teeth can be observed on the right side and 16 on the left. This is a very low number in comparison to UFRGS-PV-0228-P, which bears 55 to 57 maxillary teeth (Barberena, 1998). Probably many teeth were detached from their alveoli and the iron oxide cover precludes their observation. Even though, there is possible to observe that the teeth become smaller posteriorly as in *Australerpeton cosgriffi* (Eltink *et al.*, 2015). The maxilla borders most of the anterolateral part of the choana, and then contacts the vomer anteromedially. As already mentioned, is not possible to observe its anterior contact with the premaxilla. The maxilla is delimited by the palatine on its posteromedial side as in *Platyoposaurus stuckenbergi*, *Prionosuchus plummeri*, *Melosaurus* spp. and *A. cosgriffi* (Gubin, 1991; Schoch & Milner, 2000; Eltink *et al.*, 2015). Posterior to the palatine, the medial border of the maxilla meets the ectopterygoid along a long suture. The contact with the quadratojugal is situated on the lateral border of the subtemporal fenestra. The maxilla participates in the anterolateral margin of the subtemporal fenestra as in other *A. cosgriffi* specimens. This character is shared with *A. decheni* (Witzmann, 2006; Eltink *et al.*, 2015). As in *A. cosgriffi* (Barberena, 1998; Eltink *et al.*, 2015), apparently there are no tusks in the maxilla, differing from platyoposaurines (like *Platyoposaurus* and *Prionosuchus*) and the cochleosaur *Nigerpeton* (Steyer *et al.*, 2006). Nevertheless, we must consider that the premaxillary-maxillary region is distorted precisely in the place where the tusks may have been present. In consequence, we cannot confirm this character.

**Vomer.** The vomers take up great part of the rostral region. Each bone contacts anteriorly with the premaxilla along a suture, which cannot be seen. Anteromedially, it contacts the maxilla, and most posterolaterally, the palatine. The vomer borders the choana anteromedially and posteromedially, and makes up the anterior rim of the interpterygoid vacuity that is present in both Stereospondyli and higher non-Stereospondyli stereospondylomorphs (Gubin, 1991). Denticles and tusks are not seen on the surface of the vomer, differing from the holotype of *A. cosgriffi* (UFRGS-PV-227-P) (Barberena, 1998; Eltink *et al.*, 2015). However, because of the superposition over the vomer of part of the cultriform process and what is probably the maxilla, it is not possible to assure with certainty that both the denticles and the vomerian tusks are absent or damaged.

**Palatine.** The palatine is better preserved on the left side of the skull in ventral view. It encompasses the anterolateral border

of the interpterygoid vacuity. Laterally, it contacts the maxilla and forms part of the posterolateral border of the choana as in *Australerpeton cosgriffi* (Barberena, 1998; Eltink *et al.*, 2015). The same condition described by Barberena (1998) and Eltink *et al.* (2015) for the positioning of the palatine in *A. cosgriffi* is here assumed, that is the palatine preventing contact between the vomer and the pterygoid. This state differs from that found in basal temnospondyls, in which the vomer contacts the palatine ramus of the pterygoid. Some Temnospondyli like *Kosukovia vetusta*, *Eryops megacephalus* and *Australerpeton cosgriffi* (Gubin, 1997; Pawley & Warren 2006; Eltink *et al.*, 2015) have palatine tusks. UFPR 199 PV also has a tusk (only one, on the right side of the skull) posterior to the choana, in the same position as the palatine tusk in the *A. cosgriffi* holotype (Barberena, 1998). However, Eltink *et al.* (2015) reported the presence of two tusks on the palatine of *A. cosgriffi*.

**Ectopterygoid.** The ectopterygoid is a narrow bone, located between the pterygoid (medially) and the maxilla (laterally). In UFPR 199 PV the ectopterygoid is overlapping the pterygoid, and although probable, it is not possible to confirm the contribution of the ectopterygoid to the margin of the subtemporal fenestra, as in *Australerpeton cosgriffi* (Eltink *et al.*, 2015). Some denticles are seen on the preserved portion of the ectopterygoid in both sides of the skull.

**Jugal.** The ventral process of the jugal in UFPR 199 PV is visible only in the left side of the skull (Figure 3B) and its sutural relationships are not clear enough, but it can be seen that this process forms the anterior border of the subtemporal fenestra within the ectopterygoid. The same condition was considered by Eltink *et al.* (2015) as an autapomorphy of *Australerpeton cosgriffi*.

**Pterygoid.** Both pterygoids of UFPR 0199 PV are broken in the same area in their medial portion. It is hard to observe the palatine ramus as well as its anteriormost limit. However, we can infer that in UFPR 0199 PV, as in *Australerpeton cosgriffi*, the palatine ramus of pterygoid does not reach the vomer (Eltink *et al.*, 2015). This is the typical condition of the advanced Stereospondyli (Milner, 1990; Gubin, 1997). Medially, the pterygoid body forms an extensive suture with the parasphenoid as seen in some rhinesuchids like *A. cosgriffi* (Eltink *et al.*, 2015) and *Laccosaurus watsoni* (Houghton, 1925) and contacts the subtemporal fenestra. The posterolateral border of the interpterygoid vacuity is defined by the palatine ramus of the pterygoid. The quadrate ramus of the pterygoid reaches the posterior border of the skull and contacts the quadrate. There are denticles covering the ventral part of the pterygoid as seen by Eltink *et al.* (2015) in *A. cosgriffi*, as well as observed in *Platyposaurus stuckenbergi* (Figure 3B). The pterygoid of UFPR 0199 PV lacks ornamentation as in *A. cosgriffi* and *Rhineceps nyasaensis*, differing from some stereospondyls like *Lydekkerina huxleyi*, *Laccosaurus watsoni* and *Uranocentron senekalensis* (Watson, 1962; Yates & Warren, 2000; Schoch & Milner, 2000; Eltink *et al.*, 2015).

**Parasphenoid.** In UFPR 0199 PV the parasphenoid body is very developed. It contacts laterally with the pterygoid, and anteriorly it projects a thin and long cultriform process. This process is broken at its anteriormost part and has slid

to the right over the vomer. The cultriform process is very long (approximately 25 cm), surpassing the anterior border of the vacuities and reaching the level of the choanas on the vomer. There are differences between the lengths of this process among known specimens of *A. cosgriffi*. In UFRGS-PV-0227-P and UFRGS-PV-0229-P, the cultriform process extends anteriorly to the anterior margin of the interpterygoid vacuity, differing from the shorter cultriform process of UFRGS-PV-0224-P. Barberena (1998) described *Australerpeton cosgriffi* as having a process reaching 13.7 cm in length (in a skull of nearly 50 cm length) and almost reaching the level of the choanas. UFPR 0199 PV has the longest cultriform process among *A. cosgriffi* specimens. In this specimen the anterior edge of the cultriform process is inserted between the vomers, as in other described *A. cosgriffi* specimens as well as in other rhinesuchids (Schoch & Milner, 2000), but it surpasses the level of the posterior border of the choanas, being interposed between them. This condition is unprecedented for *A. cosgriffi*, and it is also observed in *Mastodonsaurus giganteus*, *Konzhukovia vetusta* and *K. sangabrielensis* (Pacheco *et al.*, 2017). The parasphenoid borders the oval and elongated interpterygoid vacuities medially for its full extension. The interpterygoid vacuities in UFPR 0199 PV are nearly 18 cm in length in around a 58 cm skull, almost the same proportion described by Barberena (1998) for *A. cosgriffi*. This author described interpterygoid vacuities 13.7 cm long in a skull of 50 cm in length (UFRGS-PV-0227-P). The interpterygoid vacuities of UFPR 0199 PV have a total width of 4 cm, which corresponds to less than 90% of their length as in *Konzhukovia gabrielensis* (Pacheco *et al.*, 2017). This pattern of longer than wide interpterygoid vacuities is also found in *A. cosgriffi* (Eltink *et al.*, 2015). Denticles, frequently observed on Stereospondyli parasphenoids, including that of *A. cosgriffi* (Eltink *et al.*, 2015), are not observed in UFPR 0199 PV, particularly the denticles reported by Eltink *et al.* (2015) on the posterior margin of the parasphenoid. Posteriorly, the semicircular ‘pockets’ for the insertion of muscles as in *A. cosgriffi* (Barberena, 1998) are partially present in the parasphenoid of UFPR 0199 PV.

**Quadratojugal.** It is a wide bone that laterally borders the subtemporal fenestra and posteriorly joins the quadrate. It contacts with the maxilla as observed in *Australerpeton cosgriffi* by Eltink *et al.* (2015).

**Quadrate.** The quadrate is a robust bone that borders the posterior area of the subtemporal fenestra. It is limited medially by the pterygoid and laterally by the quadratojugal. As in *A. cosgriffi*, other rhinesuchids and also archegosaurids, the mandibular articulation is positioned posteriorly relative to the occipital condyles (Barberena, 1988; Eltink *et al.*, 2015). The rugose surface texture of the quadrate mentioned by Eltink *et al.* (2015) for *A. cosgriffi* was not observed in UFPR 0199 PV.

**Mandible.** UFPR 0198 PV is a completely preserved mandibular left ramus, although it is fragmented into 11 parts (Figure 4). It is 57 cm long. In the same way as UFPR 0199 PV, it is covered by a thick layer of iron oxide. Due to the presence of fractures and the oxide layer, some sutures



were only able to be inferred and are dotted or not identified on the figures. In general, the anterior edge is lateromedially expanded and forms a spoon-shaped tip as in *Australerpeton cosgriffi* (Eltink & Langer, 2014). The mandibular depth increases posteriorly. In labial view, the rough ornamentation on the posterior region can be easily observed, mainly on the angular where it has a polygonal sculpture as seen in *A. cosgriffi* and several temnospondyls like *Mastodonsaurus giganteus* and *Gerrothorax pustuloglomeratu* (Eltink & Langer, 2014). Anteriorly, the ornament becomes more striped and radial. Lingually the texture is smooth. In labial view, the dentary, the splenial, the postsplenial, the angular, and the surangular can be seen. In lingual view, the surangular, the articular, the angular, the adductor window, the posterior Meckelian fenestra, the prearticular, the postsplenial, the splenial, the coronoid series, and the dentary are preserved, although the sutures between them are not so clear (Figure 4). The adductor window is clearly visible and is formed by the postcoronoid, the angular, the articular, and the prearticular. The posterior Meckelian fenestra is hard to delimit, and the anterior Meckelian fenestra is not well observed because of the fractures but is probably positioned dorsal to the splenial end, ventral to the prearticular. The post-glenoid area (PGA) is very short and it is not possible to see the sutures to classify for certain the type of PGA (Jupp & Warren, 1986). UFPR 198 PV PGA is shorter than Melosaurids like *Mastodonsaurus giganteus*, and similar to Rhinesuchids like *Rhineceps nyasaensis* (Schoch & Milner, 2000). The PGA of UFPR 0198 PV is formed mainly by the surangular and articular. The symphysis of UFPR 0198 PV has also been inferred, and was probably formed by the dentary and the splenial. The rugose texture of the splenial and the sulcate pattern of the dentary noted by Eltink & Langer (2014) in *A. cosgriffi* are not visible. Neither does UFPR 0198 PV display the bar-like structure as described in *Bageherpeton longignathus* by Dias & Barberena (2001) in lingual view as well as the participation of the coronoids on the symphysis (also seen in *Prionosuchus plummeri* Price, 1947 and *Platyoposaurus stuckenbergi* Gubin, 1991). The symphysis of UFPR 0198 PV probably exhibits the same condition as *A. cosgriffi* with a large participation of the dentary (Eltink & Langer, 2014).

The dentary is the longest bone of the jaw and it is well preserved. On both sides, teeth are present. The dentary bears 19 preserved conical teeth, which get smaller posteriorly. They show the typical temnospondyl pattern, with labyrinthodont infolding in transverse section and longitudinal grooves on the surface. Two tusks are preserved, followed by three small displaced teeth and a bigger tooth. The number of tusks varies a lot in temnospondyls. Eltink & Langer (2014) described one specimen of *Australerpeton cosgriffi* with three symphyseal tusks, 76 alveoli, and 48 preserved teeth in the dentary. In labial view, the dentary covers almost the whole jaw, except for the posteriormost part where it contacts the angular and the surangular. The *sulcus oralis* cannot be seen. It is possible to infer that the dentary contacts the splenial, postsplenial, angular and surangular labially; lingually its ventral limit is made up by the three coronoids and by the splenial. Unfortunately, the sutures and limits are not clearly observable in UFPR 0198 PV, as shown on Figure 4.

The angular is a well-developed bone on the posterior part of the mandible. In labial view, its anterior part ends between the dentary and postsplenial. In lingual view it is possible to observe that the angular contacts the prearticular but the rest of the contacts are not clear. The angular probably contacts the posterior Meckelian fenestra and the postsplenial as seen in *Australerpeton cosgriffi* according to Eltink & Langer (2014). It is the most ornamented bone in the jaw.

The splenial contacts are not well preserved, since the inferior part, mainly laterally, is not well preserved. Splenial is a wedge-shaped bone narrowing posteriorly to meet the postsplenial and anterior to the anterior coronoid. This condition is the same as in *Australerpeton cosgriffi*, but the lingual zigzag suture between the splenial and postsplenial identified as an autapomorphy for this species (Eltink & Langer 2014) was not observed in UFPR 0198 PV.

The postsplenial bone appears on the lingual and labial sides, forming the middle portion of the jaw. It probably contacts posteriorly with the posterior Meckelian fenestra, anteriorly with the splenial and medially with the prearticular. It is not possible to discern the contacts with the angular described for *Australerpeton cosgriffi* by Eltink & Langer (2014).

On the lingual surface of the jaw, the prearticular forms a long strip. Ventrally, it contacts the splenial and the postsplenial. Posteriorly it borders the adductor fossa and anteriorly it reaches the middle and anterior coronoid. This bone borders the dorsal part of the adductor fossa, and posteriorly extends a little further than described by Eltink & Langer (2014) for *Australerpeton cosgriffi*. This characteristic reduces the participation of the angular on the adductor fossa. In some temnospondyls like *Sclerocephalus haeuseri* the angular does not even form the adductor fossa (Schoch & Witzmann, 2009). Anteriorly it probably reaches the middle coronoid.

The sutures between the coronoid series are not visible. The three coronoids do not bear teeth, as observed in many temnospondyls such as in *Australerpeton cosgriffi* by Eltink & Langer (2014), *Archegosaurus decheni* by Witzmann (2006) and *Sclerocephalus haeuseri* by Schoch & Witzmann (2009). The elongated posterior coronoid, which is only observed in UFPR 0198 PV in lingual view, forms the dorsal margin of the adductor fossa as in *A. cosgriffi* (Eltink & Langer, 2014); in the anterior part it probably reaches the middle coronoid. The anterior coronoid probably contacts the dentary and the splenial.

Articular and surangular. The sutures on the post-glenoid area are not visible. The articular and the surangular form the posterior part of the mandible setting up the post-glenoid area. The surangular is ornamented.

## DICUSSION

A recent phylogenetic analysis performed by Eltink *et al.* (2015) nested *Australerpeton cosgriffi* within Rhinesuchidae based on: the well-posteroventrally projected tabular horn; the presence of a stapedial groove, a well-developed oblique crest on the pterygoid, a dorsal pterygoid crest formed in the contact

between the pterygoid and squamosal, a well-marked groove along the posterior border of the interpterygoid vacuity, denticles distributed on the ventral surface of the parasphenoid with an arched posterior margin, and a slit-like post-temporal fenestra. Unfortunately, most of these characteristics, as well as several of the diagnostic features noted by Barberena (1998) related to the palatal view of the skull of *A. cosgriffi*, are not verifiable in the studied specimen. In UFPR 0199 PV the bad preservation of the sutures, and perhaps the superposition of dorsal and ventral surfaces precludes the identification of most of the traits. This could be the reason for the non-observation of the denticles on the parasphenoid, which are well developed in *A. cosgriffi*.

Eltink *et al.* (2015) ascribed both the ectopterygoid and the ventral process of the jugal (= *insula jugalis*) entering the anterior border of the subtemporal fenestra as an autapomorphy of the skull of *Australerpeton cosgriffi*. In UFPR 0199 PV, in fact, the ectopterygoid forms the subtemporal fenestral margin, and at the left side of the skull is possible to identify this process, but the area is not so clear and the right side is damage.

Eltink *et al.* (2015) maintained that the long-snouted condition of *Australerpeton cosgriffi* is unique amongst Rhinesuchidae, and can be recognized by the premaxilla being longer than wide and more than twice the length of the external naris. Additionally, the skull is narrower at the nasal/frontal contact than half the width at the level of the pineal foramen. The very long-snouted condition, as well as these proportions, is also observed in UFPR 0199 PV.

Tooth elements from the marginal dentition of *Australerpeton cosgriffi* are rounded in cross-section as seen in UFPR 0199 PV, and this trait differs from other rhinesuchids such as *Uranocentron senekalensis*, *Rhinesuchus capensis*, *Rhineceps nyasaensis*, *Rhinesuchus whaitsi* and *Rhinesuchus broomianus* that have more compressed teeth. The descriptions of *Australerpeton cosgriffi* by Barberena (1998) and Eltink *et al.* (2015) show that the posterior premaxillary teeth are larger than the anterior ones (differing from all other known rhinesuchids). In UFPR 0199 PV the teeth, mainly the small premaxillary ones, are not well preserved, precluding comparisons.

Some new unprecedented characteristics described for *Australerpeton cosgriffi* are revealed in UFPR 0199 PV. Firstly, the huge length of the cultriform process of the parasphenoid, reaching the level of the choanas. Secondly, the pair of longitudinal ridges running parallel on the premaxilla surface, medially to the anterior palatal vacuities. These ridges are similar to what is seen in the vomer of the archegosaurid *Archegosaurus decheni* (Witzmann, 2006). But contrasting with the condition of *Archegosaurus*, the ridges of UFPR 0199 PV are placed on the premaxillae surface without touching the choanae anterior borders in the vomer and lack teeth. These structures have probably never been described for *A. cosgriffi* because UFPR 0199 PV is the biggest and most complete specimen found up to date, and the only one with a complete preservation of the rostrum. Besides UFPR 0199 PV, the only other preserved rostrum is UFRGS-PV-0228-P, which is laterally compressed.

The jaw of UFPR 0198 PV is similar in all aspects to the other *Australerpeton cosgriffi* specimens. It includes the bone positions and relationships, the ornamentation pattern on the labial face, the disposition and size of the teeth, and the size of the post-glenoid area. The post-glenoid area of UFPR 0198 PV is the most complete among all *A. cosgriffi* specimens, mainly because it is not attached to the skull; unfortunately, the presence of the iron oxide cover precludes the visualization of any sutures.

## CONCLUSIONS

The individual represented by specimens UFPR 0198 PV and UFPR 0199 PV shares anatomical characteristics of *Australerpeton cosgriffi*, including the presence of the ventral process of the jugal, pointed out as an autapomorphy of the latter by Eltink *et al.* (2015). The comparative description presented in this contribution allows its assignment to this species. The high degree of ossification and its size denote that UFPR 0198 PV and UFPR 0199 PV represent a mature adult individual.

Compared to *Australerpeton cosgriffi*, the few observed differences, like the absence of denticles on the parasphenoid surface and vomer could be due to preservation artifacts. Notwithstanding, the long cultriform process of the parasphenoid and the long parallel ridges on the premaxilla, are up to date only preserved in this specimen. Therefore, we propose these characters to be added to the diagnosis for *A. cosgriffi*. UFPR 0198 PV and UFPR 0199 PV comprise the biggest and the most complete *A. cosgriffi* specimen ever found (although the preserved portion of UFPR 0199 PV shows only the ventral side). Possibly these traits could arise late in the ontogeny of this species, and, due to this, only in this specimen are they well developed.

The discovery of UFPR 0198 PV and UFPR 0199 PV at the São Jerônimo da Serra Site corroborates the presence of *Australerpeton cosgriffi* in this outcrop, which was first reported by Ramos & Vega (2011), but based only on mandibular fragments. Together with the outcrops along the EFCP railroad and the Monjolo Site (Barberena, 1998; Eltink & Langer, 2014; Eltink *et al.*, 2015), São Jerônimo da Serra is confirmed as the third site of the Serra do Cadeado region (Morro Pelado Member of Rio do Rasto Formation) recording *A. cosgriffi*, one of the oldest stereospondyls, that is nested within Rhinesuchidae (Eltink *et al.*, 2015). This provides new evidence that this unique, long-snouted rhinesuchid used to be a common and successful faunal component of the Middle–Late Permian fluvio/lacustrine ecosystems of southern Brazil, reinforcing the idea of a basal stereospondyl diversification outside South Africa.

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