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CENTRO DE CIÊNCIAS NATURAIS E EXATAS  
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EM BIODIVERSIDADE ANIMAL**

**Eduardo Silva Neves**

**UM NOVO ESPÉCIME DE *Procolophon* OWEN, 1876 (PARAREPTILIA,  
PROCOLOPHONIDAE) PARA O TRIÁSSICO INFERIOR  
SULBRASILEIRO**

Santa Maria, RS  
2018

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**UM NOVO ESPÉCIME DE *Procolophon* OWEN, 1876 (PARAREPTILIA,  
PROCOLOPHONIDAE) PARA O TRIÁSSICO INFERIOR SULBRASILEIRO**

Dissertação apresentada ao Curso de Mestrado do Programa de Pós-Graduação em Biodiversidade Animal, Área de Concentração em Sistemática e Biologia Evolutiva, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para obtenção do grau de **Mestre em Ciências Biológicas - Área Biodiversidade Animal**

Orientador: Prof. Dr. Sérgio Dias da Silva

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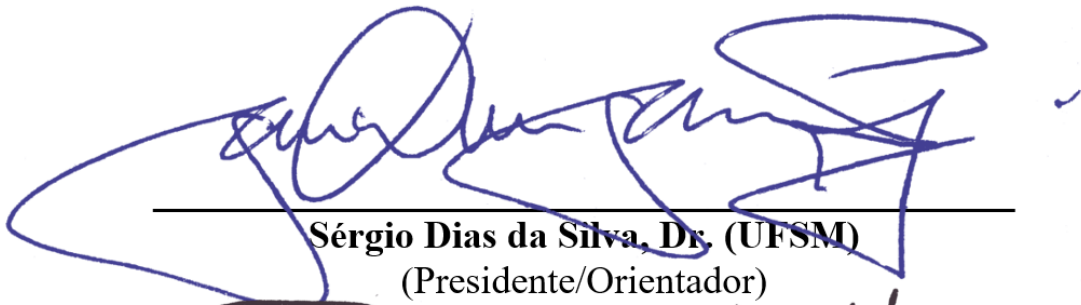
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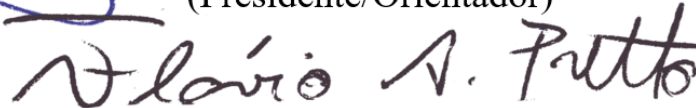
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Aprovado em 27 de fevereiro de 2018:



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**Sérgio Dias da Silva, Dr. (UFSM)**  
(Presidente/Orientador)



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**Flávio Augusto Pretto, Dr. (UFSM)**



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**Felipe Lima Pinheiro, Dr. (UNIPAMPA)**

Santa Maria, RS  
2018

## DEDICATÓRIA

*À minha família, minha namorada, e sua família e aos meus amigos. Dedico também aos meus avôs Luiz Hermeto e Luiz Carlos e meu tio Cássio que infelizmente não estão mais entre nós para presenciar esse momento.*

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## EPÍGRAFE

*"Para se ser feliz até um certo ponto é preciso ter-se sofrido até esse mesmo ponto."*

*(Edgar Allan Poe)*

## RESUMO

Dissertação de Mestrado  
Curso de Pós-Graduação em  
Biodiversidade Animal

Universidade Federal de Santa Maria

### **UM NOVO ESPÉCIME DE *Procolophon* OWEN, 1876 (PARAREPTILIA, PROCOLOPHONIDAE) PARA O TRIÁSSICO INFERIOR SULBRASILEIRO**

AUTOR: Eduardo Silva Neves  
ORIENTADOR: Sérgio Dias da Silva  
Data e local da defesa: Santa Maria/RS, 2018

Essa dissertação apresenta informações sobre um novo crânio (CAPP/UFMS 0189), com mandíbula em oclusão, atribuído a *Procolophon trigoniceps*, coletado no município de São Francisco de Assis, Rio Grande do Sul, (Sítio Bica São Tomé). A atribuição taxonômica preliminar do espécime ao gênero *Procolophon* baseou-se nos dentes molariformes, que apresentam uma expansão labiolingual; o contato entre o pré-frontal, o frontal e o parietal; e a presença da borda posterior da fenestra orbitotemporal no nível da borda posterior do forame pineal. A atribuição a *P. trigoniceps* foi feita com base na presença de oito dentes maxilares bicúspides e uma ampla margem subtemporal arredondada. O objetivo geral foi a descrição da anatomia craniana do espécime e identificação taxonômica no menor nível inclusivo possível, bem como seu posicionamento filogenético. Embora *P. trigoniceps* seja uma espécie bem conhecida, com um grande número de espécimes em coleções de diferentes países, a descrição deste crânio, o primeiro praticamente completo coletado no Brasil, corrobora a presença deste táxon nesta região do Gondwana, uma vez que os estudos previamente realizados em nosso território foram feitos com base em exemplares demasiadamente incompletos em comparação com CAPP/UFMS 0189.

**Palavras-chave:** Procolophonia. Supersequência Sanga do Cabral. Gondwana.



## ABSTRACT

Dissertação de Mestrado  
Curso de Pós-Graduação  
em Biodiversidade Animal

Universidade Federal de Santa Maria

### **UM NOVO ESPÉCIME DE *Procolophon* OWEN, 1876 (PARAREPTILIA, PROCOLOPHONIDAE) PARA O TRIÁSSICO INFERIOR SULBRASILEIRO**

(A NEW SPECIMEN OF *Procolophon* OWEN, 1876 (PARAREPTILIA,  
PROCOLOPHONIDAE) FOR THE LOWER SULBRASILIAN TRIASSIC)

AUTOR: Eduardo Silva Neves

ADVISOR: Sérgio Dias Da Silva

Data e local da defesa: Santa Maria/RS, 2018

This dissertation presents information regarding a new skull (CAPP / UFSM 0189), with mandible in occlusion, ascribed to *Procolophon trigoniceps*. CAPP/UFSM 0189 was collected in the municipality of São Francisco de Assis, Rio Grande do Sul, (Sítio Bica São Tomé). The preliminar taxonomic attribution of the specimen to the genus *Procolophon* was based on the molariform teeth, which presents a labiolingual expansion; the contact between the prefrontal, the frontal and the parietal; and the presence of the posterior border of the orbitotemporal fenestra with of the posterior border of the pineal foramen. The assignment to *P. trigoniceps* was based on the presence of eight maxillary bicuspid teeth and a wide rounded subtemporal margin. The aim of this project was the description of the cranial anatomy of the specimen and its taxonomic identification at the less possible level. Although *P. trigoniceps* is a well known species with a large number of specimens in collections from different countries, description of this material, the first nearly complete collected in Brazil, corroborates de presence of this taxon in this region of Gondwana, as previous studies carried out in this territory were based on incomplete specimens in comparison with CAPP/UFSM 0189.

**Keywords:** Procolophonia. Sanga do Cabral Supersequence. Gondwana.

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## 1. APRESENTAÇÃO

A presente Dissertação está estruturada de acordo com as normas da Universidade Federal de Santa Maria (MDT), sendo composta por um texto integrador, um artigo e conclusões.

O texto integrador apresenta uma breve contextualização dos Parareptilia e dos Procolophonoidaea, partindo-se então diretamente para os Procolophonidae (especificamente, Procolophoninae) objeto de estudo da presente dissertação.

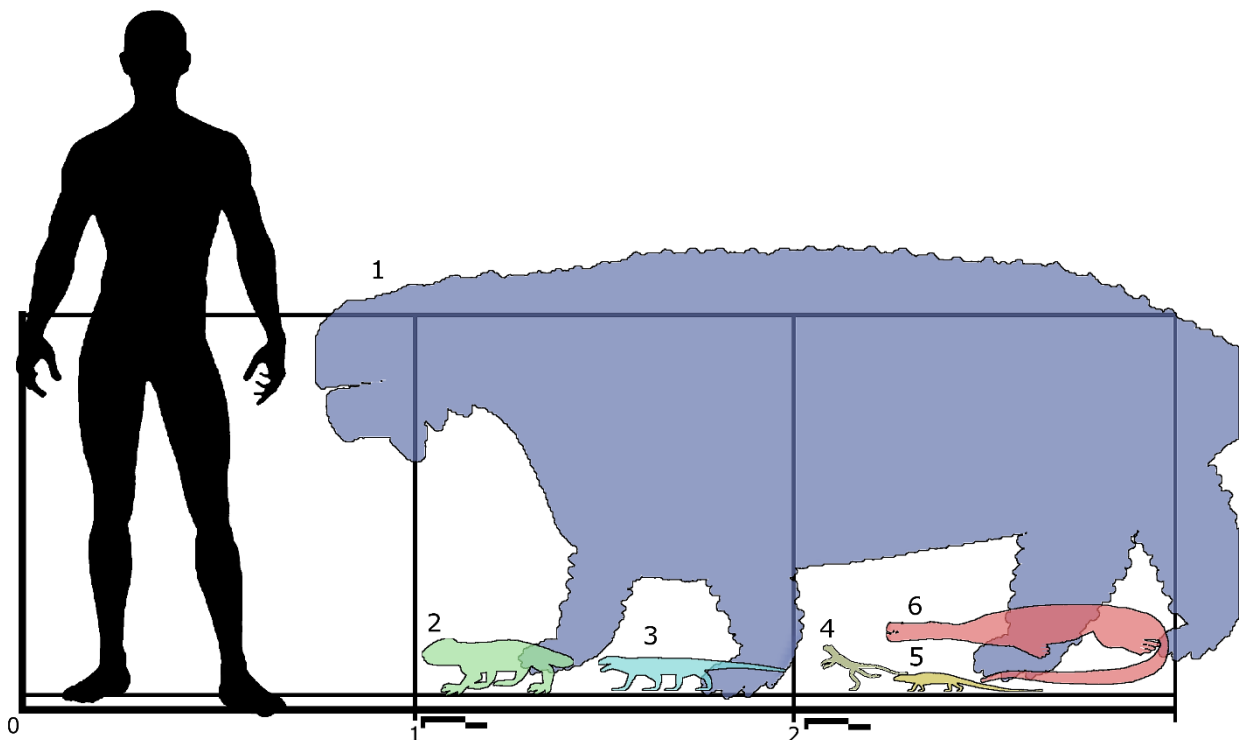
O Artigo 1 trata da descrição, comparação e análise filogenética do material de crânio de *Procolophon trigoniceps*. O artigo será submetido à Historical Biology e está formatado de acordo com as normas de publicação do periódico.

Na seção Conclusões é apresentada uma breve recapitulação dos resultados obtidos em relação aos objetivos propostos para esta dissertação.

## 2.TEXTO INTEGRADOR

O clado Parareptilia surgiu no final do Carbonífero, neste momento representado pelo bolosaurídeo *Erpetonyx arsenaultorum* (Modesto et al., 2015), extinguindo-se no final do Triássico, com o leptopleuroninae *Hypsognathus fenneri* (Colbert, 1946). Apresentando distintas morfologias, os pararrépteis incluem formas totalmente aquáticas, os mesossauros (Mesosauria Seeley, 1892), basais, constituindo-se em grupo irmão de todos os demais pararrépteis (Tsuji et al., 2012), além de formas terrestres de pequeno, médio e grande porte. De forma geral, as dimensões corporais de Parareptilia (Mileretidae Watson, 1954; Nicteroleteridae Efremov, 1938; Bolosauridae Cope, 1878, *Procolophonoidea* Romer, 1956 e Lanthanosuchidae Efremov, 1946) são semelhantes a pequenos lagartos, excetuando os pareiassauros (Pareiasauria Seeley, 1888), único grupo que apresenta espécies de grandes proporções, por exemplo, *Bradysaurus baini* Seeley, 1892, o qual podia alcançar cerca de três metros de comprimento. (Figura 1)

Figura 1 Perspectiva entre humano e diferentes morfotipos de Parareptilia. 1: Pareiasauridae Lydekker, 1889; 2: Procolophonidae Lydekker, 1889; 3: Nyctiphruetidae Efremov, 1938; 4: Bolosauridae Cope, 1878; 5: Millerosauria Watson, 1957; 6: Mesosauridae Baur, 1889.



Os procolofonóides representam a radiação evolutiva de maior sucesso em Parareptilia, uma vez que foram os únicos pararrépteis que sobreviveram ao evento de extinção em massa

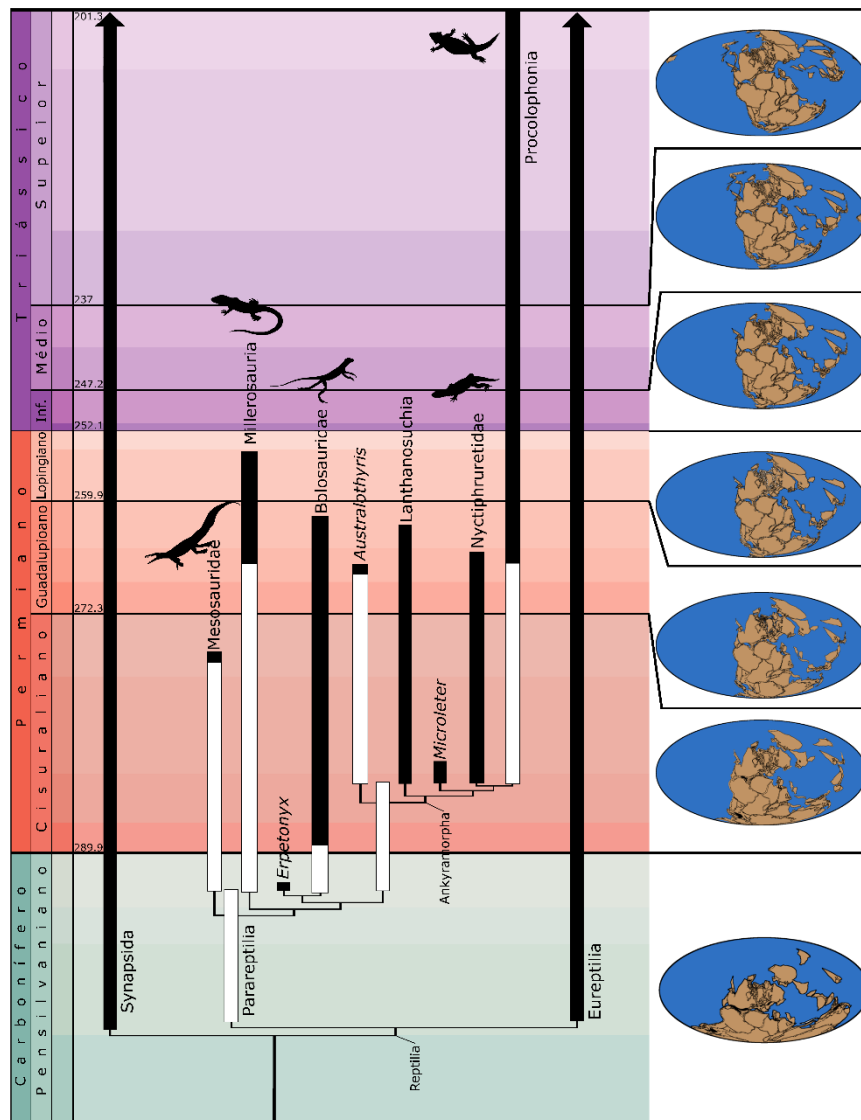
no final do Permiano até o limite Triássico/Jurássico (Tsuji & Muller, 2009). Os procolofonídeos têm sido encontrados em todos os continentes (ver Cisneros 2008b, Tabela 1), inclusive na Antártida (Colbert & Kitching, 1975). Na América do Sul são registrados no Sul do Brasil e norte do Uruguai (Brea et al., 2005; Cisneros et al., 2004; Cisneros & Schultz, 2002; Lavina, 1983, Da-Rosa et al. 2009; Piñeiro et al., 2004, Dias-da-Silva et al., 2017).

Procolophonoidea subdivide-se em dois clados principais: Owenettidae (Broom, 1939) e Procolophonidae. (Lydekker. 1889). O primeiro compreende representantes mais antigos e basais com registro do Permiano Superior ao início do Triássico Superior (Reisz & Laurin, 1991; Reisz & Scott, 2002; Modesto et al., 2003; Ketchum & Barrett, 2004), enquanto que Procolophonidae, mais derivado, inclui formas exclusivamente Triássicas, cosmopolitas e mais diversas que Owenettidae (Modesto et al, 2015).

Os owenetídeos do Permiano diferem notavelmente dos representantes do Triássico. No Permiano são conhecidos dois táxons: *Owenetta rubidgei* Broom. 1939, da África do Sul e *Barasaurus besairiei* Piveteau, 1955, de Madagascar. Para o Triássico, além de *Barasaurus*, há outras três espécies descritas: *Owenetta kitchingorum* Reisz and Scott, 2002, e *Saurodekteles rogersorum* Modesto et al., 2003, ambos da África do Sul; e *Candelaria barbouri* Price, 1947, do Brasil.

Após a extinção permo-triássica, procolofonídeos diversificaram-se e dispersaram-se rapidamente por todos os continentes. Com algumas exceções, em geral apresentam maior tamanho corporal que owenetídeos.

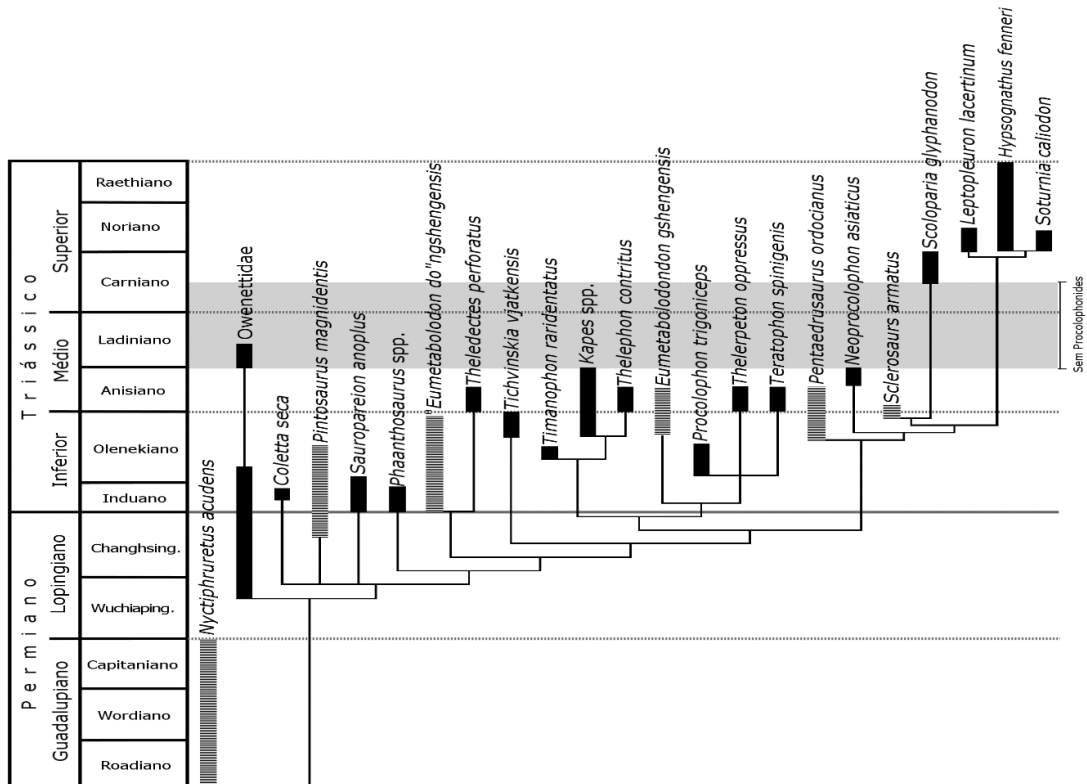
Figura 2. Calibração temporal de Parareptilia, modificado de Modesto et.al 2015. Escala temporal de Comissão Internacional de Estratigrafia (v2017/2). Barras em branco demonstram os *ghost taxa* dos referidos grupos.



Procolophonidae divide-se em dois grupos menos inclusivos, Procolophoninae e Leptopleuroninae, além de um grupo menor, Theledectinae (*sensu* Cisneros, 2008b). O primeiro grupo restringe sua abrangência temporal do início até a metade do Triássico, enquanto o segundo distribui-se por todo o Triássico, sendo o mais longo, extinto no final desse período (figura 3).



Figura 3. Árvore de consenso estrito e registro geológico de procolofonóides. As barras pretas representam distribuição estratigráfica, as barras tracejadas representam intervalos estratigráficos incertos. O hiato global de registros procolofonóides em rochas Ladiano - Carniano Inferior está apresentando em cinza. Modificado de Cisneros, 2008b)



Dois táxons são descritos para o Brasil: *Procolophon trigoniceps* Owen, 1876 e *Soturnia caliodon* Cisneros & Schultz, 2003. O primeiro espécime foi descoberto no século XIX na região do Karoo, África do Sul, e descrito por Sir Richard Owen. Na década de 1970, o gênero foi encontrado em estratos Eotriássicos da Antártida e, mais tarde, na década de 1980, também foi encontrado no Rio Grande do Sul (Lavina, 1983), possuindo assim ampla distribuição Gondwanica. Embora várias espécies tenham sido descritas, (*P. griersoni* Seeley, 1878; *P. cuneiceps* SEELEY, 1878; *P. laticeps* Seeley, 1878; *P. platyrhinus* Seeley, 1905; *P. sphenorhinus* Seeley, 1905; *P. pricei* Lavina, 1983; *P. brasiliensis* Cisneros & Schultz, 2002), todas elas são hoje tratadas como uma única espécie: *Procolophon trigoniceps* Owen, 1876 (Cisneros, 2008a). As espécies brasileiras *P. pricei* Lavina, 1983 e *P. brasiliensis* Cisneros & Schultz 2002 foram sinonimizadas como *P. trigoniceps* por Cisneros (2008a).

*Procolophon* é também caracterizado por possuir dentes incisivos bastante proeminentes, seguidos de pequenos dentes cônicos e de uma bateria de dentes molares alargados (Carrol & Lindsay, 1985). Esses molares são bem característicos e diferentes dos

outros procolofonídeos, deste modo sendo de fácil identificação a partir de dentes isolados. Pela sua dentição, pode se inferir que *Procolophon* era um herbívoro fibroso, (Cisneros, 2008).

A sinonimização para *Procolophon trigoniceps*, foi feita baseada na distinção dos dentes palatais, variação na presença de fenestra pós-orbital, presente em alguns espécimes da África do Sul, onde alguns exemplares apresentam a fenestra somente em um dos lados do crânio. Além disso, Cisneros (2008a) argumenta que essas características variáveis são de indivíduos em estágios ontogenéticos distintos, além de alguns caracteres erroneamente descritos e codificados.

### **3. OBJETIVOS**

O projeto de Dissertação de Mestrado objetivou tornar conhecida a anatomia craniana de um novo espécime coletado na localidade Bica São Tomé (município de São Francisco de Assis, Rio Grande do Sul) depositado na coleção do Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia, sob número CAPP/UFMS 0189, o qual se constitui em um crânio quase completo, e também realizar sua identificação taxonômica no menor nível inclusivo possível.

#### **3.1 OBJETIVOS ESPECÍFICOS**

- (i) Descrever, através da metodologia usual em paleontologia de vertebrados, detalhes da anatomia de CAPP/UFMS 0189;
- (ii) Através de análise filogenética, testar a identificação taxonômica preliminar do material e sua relação com outros procolofonídeos;
- (iii) Por meio de imagens tomografadas do espécime, obter dados sobre a caixa craniana (*braincase*) de CAPP/UFMS 0189, uma vez que esse tipo de informação ainda é desconhecido para a maioria dos procolofonídeos.

### **4. METODOLOGIA**

O objeto de estudo da presente dissertação, CAPP/UFMS 0189 está depositado no acervo do Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia e foi coletado no sítio Bica São Tomé, no município de São Francisco de Assis, Rio Grande Do Sul.

O material passou por preparação mecânica para a retirada de sedimento e uma melhor visualização de caracteres. Além disso, o material foi tomografado a fim de obter informações sobre a porção interna da caixa craniana. As características anatômicas do espécime foram inseridas em uma matriz de dados para análise filogenética com uso do software *Tree analysis using New Technology* (TNT) (Goloboff and Catalan, 2016).

As imagens tomográficas do material foram feitas no Laboratório de Sedimentologia e Petrologia, na Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS) utilizando Microtomógrafo Skyscan 1173, X-ray. Os *scans* foram feitos com 130 kV, 610 µA, 1100 ms, voxel com tamanho de 32.09 µm, gerando 1800 images no total. *Slices* foram reconstruídos com software NRecon versão 1.6.9.18.

Tabela 1 Lista de táxon e caracteres codificados a partir da matriz modificada de MacDougall et al. (2013), com caracteres adicionados de Cisneros (2008b) (ver seção material e métodos do artigo gerado a partir desta dissertação).

<i>Nyctiphruretus</i>	00000000000?00?00000?000000000000?00000000?0000000000000000
<i>Owenettidae</i>	000000000010?10?0(01)(01)00?0000000000010?000000000?010000010010010000
<i>Coletta</i>	001001000000?10?0???0???0?10100020?011???0?0???????????????????
<i>Pintosaurus</i>	20?????????????????0???0?20100020?01101?10???????????????????
<i>Sauropareion</i>	???01010020?20?100000?110010000020?011010100?1???00?011011111?1
<i>Phaanthosaurus</i>	10101100??(12)0?????????1?????020110020?01001?010???????????????????
<i>“E”_dongshengensis</i>	?????11???0?????????1????????000030?01?01?00???????????????????
<i>Theledectes</i>	?????121030?20??11?????0?21010030?????0000?????????00???????
<i>Tichvinskia</i>	101001021030?20?1110100000021110131001001?01111?0?0???1101?01101
<i>Timanophon</i>	?????1020120?21110101?010?02?11013?0010010011???????????????????
<i>Kapes</i>	1111?1120130?20?11111???00211(12)013100100100(02)10?????????????????1
<i>Thelephon</i>	?0???1(12)101(34)1001?010????????????? ??????120120?20??111?????????????
<i>Eumetabolodon</i>	211111021020?2111??21??10002111013100100100111?1???????????????????
<i>Procolophon</i>	211111011020?2111112100100021(12)00(12)31001(01)0100111101010111101101101
<i>Thelerpeton</i>	2?111?011020?21111121??1?00211101(34)1001001001??????011???11?????
<i>Teratophon</i>	211111(01)110(23)0?21111121?010002111013100100100????1???1011110?????01
<i>Pentaedrusaurus</i>	(12)11111021230?21111111????1121110131?011010011(01)11?0?11111010?110?
<i>Neoprocolophon</i>	??1111?21(02)?0?211?21(12)1?????1??(12)??1(34)1?011??0???????????????????
<i>Sclerosaurus</i>	??????310??311?2??????????3?(12)1?(12)31?????????????11010?11?101111?
<i>Scoloparia</i>	?????0031?311311???1?????1?311002(34)10?????0111?????????????????1?
<i>Leptopleuron</i>	?110002210310311?212111?1113?111(12)41?0111001?10??0?1?????????????0?
<i>Soturnia</i>	10??0?0?????????????1?????113111124111?????120?01?1?????0???????
<i>Hypsognathus</i>	?01(01)0023103113110(12)121111113111114111?11011?????1?1?????0?????0?
<i>Phonodus</i>	1?11111?????0?00?0???1?????????10?(34)0?011101?????????????????????1
<i>Kitchingnathus</i>	(12)0??010?00(02)0?20?110?????00(12)01001200?????????11???????????????????
CAPPA/UFSM 0189	???111?1102???1?0112100?0021100?3100100101111???????????????????

## 5. ARTIGO

### **A new, nearly complete skull of *Procolophon trigoniceps* Owen, 1876 from the Sanga do Cabral Supersequence, Lower Triassic of Southern Brazil, with phylogenetic remarks**

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#### **Financial disclosure statement**

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## **A new, nearly complete skull of *Procolophon trigoniceps* Owen, 1876 from the Sanga do Cabral Supersequence, Lower Triassic of Southern Brazil, with phylogenetic remarks**

The Sanga do Cabral Supersequence comprises the Sanga do Cabral and the Buena Vista formations from Brazil and Uruguay respectively. The Brazilian unit yields an abundant record of the procolophonid *Procolophon trigoniceps*, a biostratigraphic marker for the Lower Triassic, which allows correlation with the Katberg Formation, South Africa. *P. trigoniceps*, has a wide territorial extension, so this is one of the most successful groups after the greatest extinction event, the Permo-Triassic Extinction. We describe a new skull ascribed to *Procolophon trigoniceps*, which so far represents the most complete and best preserved specimen collected at the Lower Triassic Sanga do Cabral Supersequence, Southern Brazil, and assess its phylogenetic relationships. We also use CT scan techniques to assess hidden structures covered by a hard layer of rock matrix as a non-invasive method, which allowed the visualization of the palatal dentition of this new specimen. The actual diversity of procolophonians at the Sanga do Cabral Supersequence is still unknown because most specimens are fragmentary and poorly preserved, so this new, nearly complete skull fills an important gap in the knowledge of South American *P. trigoniceps*, given that previously described specimens of this taxon from this region of Gondwana are quite incomplete in comparison.

Key words: Procolophoninae, Leptopleurinae, Sanga do Cabral, *Procolophon*, Procolophonidae

### INTRODUCTION

Parareptilia Olson, 1947 comprises a diverse set of basal amniotes that range from the Late Carboniferous to the Late Triassic (Modesto et al., 2015). It presents a great variety of body shapes, sizes, and habits, such as the aquatic mesosaurs, the small bipedal bolosaurs, and the medium- to large-size robust and squat pareiasaurs, including some taxa covered by a dermal armor (see Oelofsen and Araújo, 1983; Lee, 1997b; Berman et al., 2000). Other parareptiles

include the millerettids, the nycteroleterids, and the lanthanosuchids (Modesto et al., 2015). Other parareptilian group, Procolophonoidea Romer, 1956, includes small terrestrial lizard-like forms), that include de specimen described in the present study.

Procolophonoidea represents the most diverse and successful evolutionary radiation among Parareptilia, and the only clade surviving the end-Permian extinction (Ruta et al., 2011). Procolophonoids had worldwide distribution (Bartholomai, 1979; Cisneros, 2008b). In South America, they are known from Southern Brazil (*Procolophon trigoniceps*, *Candelaria barbouri*, and *Soturnia caliodon*) and Northern Uruguay (*Pintosaurus magnidentis*) (see Lavina, 1983; Cisneros and Schultz, 2002; Cisneros et al., 2004; Piñeiro et al., 2004; Brea et al., 2005; Dias-da-Silva et al., 2006; Da-Rosa et al., 2009; Dias-da-Silva et al., 2017).

Procolophonoids were small animals, usually measuring from about 150 mm to 400 mm in length (DeBraga, 2011), although recently a large cranial specimen of over 80 mm in length was described (Dias-da-Silva et al., 2017). In most taxa, the procolophonoid skull is free of ornamentation and presents a striking feature: posteriorly expanded orbits, also known as orbitotemporals, alluding to their inferred functionality, which would serve not only as a space for eye accommodation, but also as a recess for jaw muscle attachment (Colbert, 1946; Cisneros et al., 2004). Throughout their evolutionary history, procolophonoids demonstrate a trend towards the acquisition of a robust skeleton with a simultaneous reduction in the number of teeth in more derived taxa.

Procolophonoidea comprises two less inclusive groups, Owenettidae Broom, 1939 and Procolophonidae Lydekker, 1889. The first one, more basal, includes older forms ranging from the Lopingian to possibly the beginning of the Late Triassic (Reisz and Laurin, 1991; Reisz and Scott, 2002; Modesto et al., 2003; Ketchum and Barrett, 2004; see also Marsicano et al., 2016 for an up-to-date geochronology of coeval strata from Argentina). The second

one, Procolophonidae, more derived, is exclusively Triassic (Modesto et al, 2015). The type genus *Procolophon* Owen, 1876 comes from Lower Triassic strata, firstly collected in the 19th century in the Karoo Supergroup, South Africa. Kitching et al. (1972) reported this genus in Antarctica, which was recovered later also in the Rio Grande do Sul state, Southern Brazil (see Brea et al., 2005; Cisneros et al., 2004; Cisneros and Schultz; 2002; Lavina, 1983; Dias-da-Silva et al. 2006, 2017; Da-Rosa et al. 2009, among others). The less inclusive Procolophoninae and Leptopleuroninae comprise the "horned procolophonids", which are named after the presence of protuberant structures in the cranium, and also characterised by a more robust postcranium, a wide rib cage and a considerably larger size in comparison to earlier procolophonids and owenettids (Cisneros, 2008b).

In the present contribution, we describe a new skull ascribed to *Procolophon trigoniceps*, which so far represents the more complete and best preserved specimen collected in the Lower Triassic Sanga do Cabral Supersequence (Rosário do Sul Group, Paraná Basin, Rio Grande do Sul State, Southern Brazil).

### ***Institutional abbreviations***

**CAPPA/UFSM**, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia-Universidade Federal de Santa Maria, Brazil; **UFRGS-PV-T**, Vertebrate Paleontology Collection (PV), Triassic (T), Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil; **PUCRS**, Pontifícia Universidade Católica do Rio Grande do Sul, Brazil; **MCN**, Museu de Ciências Naturais, Porto Alegre, Brazil.

### **GEOLOGICAL SETTING**

The Sanga do Cabral Supersequence comprises the Brazilian Sanga do Cabral and the Uruguayan Buena Vista formations (Zerfass *et al.*, 2003). The Sanga do Cabral Formation

comprises, based on its tetrapod content, Lower Triassic strata correlated with the Lower Triassic Katberg Formation of the Karoo Supergroup from South Africa. Alongside other Lower Triassic units, this supersequence helps to document the biotic recovery following the end-Permian extinction, considered the most severe of the ‘Big Five’ extinction events (Dias-da-Silva et al., 2017).

Andreis et al. (1980) formally proposed the Sanga do Cabral Formation (SCF) for rocks cropping out around the city of Rio Pardo, located centrally in the Rio Grande do Sul State. These outcrops are characterized by orange-coloured, fine-grained sandstones that lie over pinkish to white fine sandstones of the Rio do Rastro Formation. Regarding its fossiliferous content, procolophonids are the most commonly amniotes found in outcrops from SCF, including some incomplete skulls, all ascribed to the genus *Procolophon* (Lavina, 1983; Langer and Lavina, 2000; Cisneros and Schultz, 2002; Dias-da-Silva et al., 2006a, 2017). The abundance of this taxon in SCF permitted a direct correlation with the Lower Triassic *Lystrosaurus* Assemblage Zone of South Africa (Katberg Formation), where *Procolophon* is also quite abundant and restricted to the *Lystrosaurus* AZ (see Barberena et al., 1981; Lavina, 1983; Modesto and Botha-Brink, 2010; Dias-da-Silva et al., 2006a, 2017). Two species of this genus were erected based upon specimens from SCF: “*Procolophon pricei*” (UFRGS-PV231T; Lavina, 1983) and “*P. brasiliensis*” (MCN-PV-1905; Cisneros and Schultz, 2002), which were subsequently referred to *P. trigoniceps* because they fit within the range of individual and ontogenetic variation known for the large sample of *P. trigoniceps* from South Africa (Cisneros, 2008a). Although the best preserved and readily diagnostic specimens (i.e. skull and lower jaws) are unequivocally referred to *P. trigoniceps*, the real diversity of procolophonians in the Sanga do Cabral Supersequence is so far unknown because many specimens are fragmentary and poorly preserved (Langer and Lavina, 2000). For more information, see the comprehensive review by Dias-da-Silva et al. (2017).



## MATERIAL AND METHODS

### ***Material.***

The specimen is housed at the Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia under the abbreviation CAPP/UFMS 0189. It comprises a nearly complete skull with a slight dorsolateral deformation, caused by sedimentary compression during diagenesis (fig. 1 and 2).

### ***Locality and Horizon.***

Ravine at the Bica São Tomé site in the Municipality of São Francisco de Assis, Rio Grande do Sul State, Southern Brazil (29°36'56"S, 55°03'10"W). *Procolophon* Assemblage Zone (*sensu* Zerfass et al., 2003), Lower Triassic, Sanga do Cabral Supersequence, Sanga do Cabral Formation.

### ***Parsimony analysis.***

The matrix was analysed with the free-use program Tree Analysis Using New Technology (TNT) Version 1.5 for Windows (Goloboff and Catalan, 2016) and processed with all characters receiving the same weight using Implicit Enumeration (Hendy and Penny, 1982), and branch-and-bound algorithm. Collapsing rule was employed during the analysis, collapsing the supported branches in an ambiguous way, producing only conservative phylogenetic hypotheses with precise support at all nodes. Here, we employed a modified version of the data matrix by MacDougall et al. (2013) and added characters from the matrix of Cisneros (2008b). Certain multistate characters were reduced into two states (following Sereno, 2007). This led to the modification of characters 11, 13, 34, 36, and 40, so these five characters had become ten characters in the present analysis, as follows: 11, 14, 36, 39 and 44, the modified characters are 12, 15, 37, 40, and 45. As a result, the ordered characters changed to 0, 7, 19, 27, 32, and 33. The in-group comprises *Hypsognathus*, *Scoloparia*, *Leptopleuron*, *Sclerosaurus*, *Neoporolophon*, *Eumetabolodon*, *Pentaesrussaurs*, *Phaanthosaurus*,

*Tichvinskia*, *Kapes*, *Procolophon*, *Coletta*, *Sauropareion*, *Soturnia*, *Pintosaurus*, *Phonodus*, and *Kitchingnathus*. Owenettidae was included in this analysis to serve as outgroup (acting as polarization tool of the obtained trees). Owenettidae characters mainly come from *Barasaurus besairiei* and *Owenetta rubidgei*, because both occupy basal positions within Owenettidae (Cisneros et al., 2008b).

### ***Tomographic analysis.***

CT scanning of the material was performed at the Laboratório de Sedimentologia e Petrologia (Pontifícia Universidade Católica do Rio Grande do Sul, PUCRS) using a Skyscan 1173, X-ray Microtomograph. Scans were made with 130 kV, 610  $\mu$ A, 1100 ms, voxel size of 32.09  $\mu$ m, and comprised 1800 images in total. Slices were then reconstructed with the NRecon software version 1.6.9.18.

## SYSTEMATIC PALEONTOLOGY

Parareptilia Olson 1947

Procolophonomorpha Romer 1964

Procolophonia Seeley 1888

Procolophonoidea Romer 1956

Procolophonidae Lydekker 1889

*Procolophon* Owen 1876

*Procolophon trigoniceps* Owen 1876

## DESCRIPTION

*Skull.* CAPP/UFMS 0189 is an almost complete skull with occluded lower jaws (Figs. 1, 2).

We ascribe this specimen to *Procolophon trigoniceps* based on the presence of eight bicuspoid maxillary teeth and a broad, rounded subtemporal emargination. The skull is 38 mm long, and triangular in dorsal view. The orbits, as usual in procolophonoids, are anteroposteriorly expanded. The pineal opening, located between the two parietals, is distinctly large, 7 mm

long and 4 mm wide. Both jugals are partially preserved, with extensive areas of sutural contact with the quadratojugal and maxilla laterally and reaching the lacrimal and ectopterygoid anteriorly and medially. The premaxillae are poorly preserved but, it is still possible to observe a few premaxillary teeth (Fig. 2, A, B, C III). Similarly, both jugals and the quadratojugals processes ('horns') are not totally preserved. In dorsal view, the left quadratojugal horn shows a higher degree of fracture than the opposite structure. This process ('horn') comprises a sharp, laterally designed curve that distinguishes it from the smooth surface of the quadratojugal. Vessel insertion pores cover the distal portion of the horn.

INSERT Figure 1 ABOUT HERE

INSERT Figure 2 ABOUT HERE

As abovementioned, the material exhibits a slight dorsolateral deformation, caused by sedimentary compression. Large fissures are also present, some of them preventing the observation of certain sutures and anatomical features. These fissures are located between the posterior margins of the pineal opening, passing through the sutures of the parietal bones towards the posterior margin of the skull. The ventrally large fissure passes through the pterygoid, ectopterygoid, part of the palate, prefrontal and lacrimal in dorsal view, continuing through the maxillary and the dentary, in lateral view.

Dorsally, the snout is composed of wide and curved nasals, prefrontals, and lacrimals. The nasals comprise the largest elements of the dorsal portion of snout. Although the premaxilla is highly damaged, its contact with nasal is observable. Thereby, in dorsal view, the nasals, anteriorly contact the premaxilla. Laterally, the nasals contact the maxillae. Both in lateral view and in dorsal view, the nasals contact the lacrimals and prefrontals, between the maxilla and frontal.

The prefrontals are presented as narrow bars that project anteriorly between the frontal and the lacrimal. In left lateral view, they are located posterior to the lacrimal (Fig. 2BI), whereas in right lateral view the lacrimal extends dorsally beyond the anterior limit of the lacrimal (Fig. 2BII). Sutural contacts among prefrontals, lacrimals, and ectopterygoids are marked by a series of foramina. Together with the prefrontal, the lacrimal participate to the anterior limit of the orbitotemporal fenestra, in which, inside, the lacrimal contacts the dorsal portions of the palatine and the ectopterygoid. In dorsal view, the frontal contacts the prefrontal, the nasal, the postfrontal, and the parietal. The paired frontals form a long longitudinal bar between the orbitotemporal fenestrae, forming raised crests on the dorsal margins of each opening.

The premaxillae are highly eroded, with just a small portion exposed and intact. Yet each element preserves a few fragmented teeth, approximately two or three teeth (Fig 2, B III). The septomaxilla, the maxillary depression, and the anterior portion of the nasal, are missing. The maxilla is widely expanded dorsally dorsal to the tooth line, and present nine teeth. Laterally, it large contact with the jugal on its anterior margin, and with the ventral margin of the nasal. Ventrally, between the contact of the jugal and the nasal, it contacts the lacrimal. In the left maxilla, there are two foramina located dorsally to the second and fourth teeth.

The cheek region is one of the most distinctive areas of the procolophonid skull, as it is anteriorly retracted by an expansion of the orbitotemporal margin, ventrally by an emargination posterior to the tooth row, and posteriorly by the occipital notch. The squamosal, squared-shaped in lateral view has a small superficial exposure dorsal to the quadratojugal. It contacts the postorbital, the quadratojugal and the supratemporal. In a posterior view, the squamosal projects ventrally, and contacts the quadrate.

The postfrontal is a narrow, thin bone that contributes to the posterodorsal orbitotemporal margin. As in other specimens of *Procolophon*, it is separated from the postorbital by the parietal. The postorbitals contact the supratemporal, squamosal, parietal, a small portion of the quadratojugal, and a large area of contact with the jugal, in dorsal and lateral views. The parietals and the supratemporals form the dorsal margin of the occipital surface, which is clearly distinguished from the sculpted dorsal surface of the skull by an acute angle. In dorsal view, the parietals contact the posterior portion of frontal, postfrontal and postorbital. Also forming the posterior margin of the orbitotemporal fenestra, the parietals prevent the contact of the postfrontal with the postorbital. Laterally, the parietals form the posteromedial margin of the orbitotemporals between the postfrontals and postorbitals. The supratemporal overlaps the squamosal and extends forward almost until the orbitotemporal margin. Dorsally, the supratemporal presents a depression on its posterior portion, which extends into the parietal, also. CAPPA/UFSM 0189 does not present the acute processes at the lateral borders of the supratemporal, as stated by Carroll and Lindsay, (1985) (Figure 1A). The entire posterior border of the cranial roof is delimited by this depression. Laterally, it forms the dorsal margin in a deep optic notch. Posteriorly, the supratemporal descends as a wide plate behind the paroccipital process. The quadrate is visible only posteriorly, just dorsal the jaw joint. Its lateral surface is mostly covered by the quadratojugal, the posterior surface by the squamosal, and the medial surface by the quadrate ramus of the pterygoid.

The parabasisphenoid comprise, massive, narrow and paired tubers separated by a deep cleft. Anteriorly, between both tuberi, there are two small rounded crests separated by a tiny cultriform process, which is broken halfway to its length and is a quite thin shaft that projects anteriorly in the medial portion. Its ventral surface is convex from side to side and narrows evenly to a sharp point. The vomers (observable through computed tomography) are narrow, parallel bones attached anteriorly to the premaxilla and posteriorly to the palatines

and pterygoids (Fig. 3). Regarding the palatal dentition at the adjacent borders of the mesial portion of the pterygoid vacuity there are three denticles, on both sides, as in UFRGS PV 231 T (see Lavina, 1983). The vomerine denticles are composed of eight large elements arranged in two transverse rows (or “arches”), one anterior with five-denticles, and other posterior with three elements (Fig 3).

Noteworthy, one denticle at the posterior arch portion is not completely formed (Fig 3), so only two teeth are completely formed (Fig. 3). The lower “arc” has one additional tooth position than the number of denticles shown in Figure 3. Besides these large teeth, both vomeri also have two parallel rows of denticles posterior to the transverse rows, the left one composed of two elements and the right one with three denticles.

The anterior and posterior maxillary teeth are small and conical (i. e. not transversally expanded), whereas the remaining ones are transversely expanded, as usual in procolophonids. The maxilla is transversally widened to support the transversally enlarged dental elements, especially on its posteriormost portion. In anterior and posterior view, the occlusal surfaces are smoothly concave. There is a clear interdigitating pattern between the upper and lower teeth (see Gow, 1977).

INSERT Figure 3 ABOUT HERE

*Lower jaw.* The articular surface is a nearly transversely oriented condyle, which is slightly anteromedially inclined. Medially, there is the rounded “saddle”-shaped depression that serves as contact surface with the quadrate. A slight longitudinal ridge separates this area from the lateral portion of the posterodorsal joint surface. The angular and the surangular extends for more than half the length of the maxilla. The angulation of the angular extends into the lower jaw and reaches anteriorly as a narrow process forward the medial portion of

the inframeckelian fossa. The coronoid forms a distinct rounded process, extending over the dorsal surface of the tooth line, and is overlapped by the prearticular and the splenial medially and the dentary laterally. The prearticular is a large bone that deflects medially to underlie the articular bone medial to the condylar joint. It presents a triangular process situated between the splenial and the coronoid, the latter of which extends anteriorly to the base of the posteriormost tooth of the dentary. The splenial is the largest medial bone, extending from the articular condyle to the symphysis. Dorsally, it reaches the base of the tooth row.

## RESULTS AND DISCUSSION

The taxonomic attribution of the specimen to the genus *Procolophon* was based particularly on the molariform teeth that exhibit a labiolingual expansion; the contact between the prefrontal, the frontal, and the parietal; and the presence of the posterior border of the orbitotemporal fenestra at the level of the posterior border of the pineal foramen.

UFRGS PV 0494 T (Dias-da-Silva et al., 2006) represents a skull that is ~50% larger than the specimens described by Carroll and Lindsay (1985, fig 1), approximately 60 mm from the anteriormost part of the snout to the margin of the supratemporal, based on the dimensions of the supratemporal aperture. The palatal bones do not exhibit a large number of denticles, presenting four palatine, one ectopterygoidal, seven pterygoidal, and two vomerine teeth.

UFSM 11049a (Dias-da-Silva et al., 2017) so far represents the largest described specimen of *Procolophon*, in which maxillary tooth row accommodating nine teeth on each rami. UFSM 110409a exhibits a large number of denticles (24) in the vomer, the palatine, and the pterygoid. CAPP/UFMS 0189 comprises 44.7% of the size of UFSM 11049, and only two teeth less in the maxilla.

The quadratojugal process (quadratojugal ‘horn’) is less prominent than that from specimens described in Carrol and Lindsay (1985) and other South African ones (see Cisneros, 2008a). UFSM 11049a does not preserve the quadratojugal ‘horn’. The species synonymized by Cisneros (2008a), '*P. brasiliensis*' Cisneros and Schultz, 2002 and '*P. pricei*' Lavina, 1983, also do not preserve a horn on the quadratojugal. Conversely, the specimen UFRGS PV 0494 T (see Dias-da-Silva et.al. 2006) presents a well-developed quadratojugal process, but it does not preserve details such as vessel insertion pores. Dias-da-Silva et.al. (2006) described the quadratojugal as a large, globular boss, an individual variation in the genus *Procolophon*, so both size and shape of the quadratojugal process may present intraspecific and ontogenetic modifications (Dias-da-Silva et al., 2006).

*Phylogenetic analysis.* Thirty nine of the 64 morphological characters of the data matrix were coded for CAPP/UFMS 0189. The analysis recovered three most parsimonious trees (MPTs) of 130 steps each (consistency index = 0.636 and retention index = 0.785). Two analyses were performed, one including and other excluding *Procolophon trigoniceps*. In the first analysis CAPP/UFMS 0189 was recovered as the sister taxon of *P. trigoniceps* in all three MPTs, forming a clade with either *Thelerpeton oppressus* and *Teratophon spinigenis* (summarized as a trichotomy in the strict consensus tree; Fig 4). When *P. trigoniceps* was excluded from the analysis, CAPP/UFMS 0189 was placed in the same position, as the sister taxon of either with either *Thelerpeton oppressus* or *Teratophon spinigenis* in the MPTs, therefore corroborating our assignment of the material to *P. trigoniceps* based upon the previous examination of its morphology. It is important to point out that CAPP/UFMS 0189 does not possess any autapomorphic feature that would support it as belonging to other taxon than *P. trigoniceps*.

INSERT Figure 4 ABOUT HERE



Our analysis included a larger number of characters and operational taxonomic units (OTUs) and resulted in a slightly higher number of steps (130) than the previous from MacDougall (2012) (with 129 steps). Only *Leptopleuron*, *Hypsognathus*, and *Soturnia* were recovered as a clade when one extra step was added. With two extra steps, Procolophonidae collapsed in a polytomic node. The bootstrap support (under 1000 replicates) is also low (below 50% for most clades). The Bremer support is also low, as well as in MacDougall et al. (2013) and Cisneros (2008b), with values of either one or two for nodes within Procolophonidae. It is important to point out that low support values are a common issue in phylogenetic studies of Procolophonoidea, possibly due to the large amount of missing data, and uninformative character states, and this situation was extensively discussed by Cisneros (2008b), Säilä (2008), Modesto et al. (2010), MacDougall and Modesto (2011) and MacDougall et al. (2013). The present analysis recovered Leptopleuroninae as a monophyletic group. MacDougall et al. (2013) had recovered a non-resolved polyphyletic Leptopleuroninae, with *Sclerosaurus*, *Scoloparia*, *Leptopleuron*, *Soturnia*, and *Hypsognathus* forming a clade, and *Pentaedrusarus*, *Phonodus*, and *Neoprocolophon* lying in a basal polytomy (Fig. 5 C).

INSERT Figure 5 ABOUT HERE

Similar to the results found in MacDougall et al. (2013), we recovered Procolophoninae consisting of only four taxa (*Eumetabolodon*, *Teratophon*, *Theleperpeton*, and *Procolophon*) with no evidence that *Timanophon*, *Theleperpeton*, and *Kapes* are procolophonines. In the strict consensus tree, *Eumetabolodon* is the sister and basalmost taxon regarding *Teratophon*, *Theleperpeton*, and *Procolophon*. Cisneros (2008b) anticipated the collapse of this clade was in which analysis Procolophoninae was dismantled with the addition of a single extra step. The author also erected Theledectinae to include *Theledectes perforatus* (Gow, 1977a) and '*Eumetabolodon*' *dongshengensis*. Our analysis also recovered a

monophyletic Theledectinae, which is an interesting result because this clade comprises two small procolophonids from South Africa and China. The most distinctive feature of theledectines is the presence of monocuspitate marginal teeth with circular bases, significantly different from those of Owenettidae, in which dentition is also circular in cross section, but with a slender morphology in comparison.

## CONCLUSION

The specimen CAPP/UFMS 0189 comprises the most complete procolophonine skull so far described from South America. Although its preservation prevents a clear visualization of certain anatomic features, those observable allowed its assignment as a new specimen of *Procolophon trigoniceps*, increasing its representation in South America, fully corroborating its wide territorial distribution, as stated by Cisneros (2008).

It is important to point out that, as stated by Langer and Lavina (2000) and Dias-da-Silva et al. (2017), the Sanga do Cabral Supersequence preserves many other fragmentary and poorly preserved procolophonoid specimens, so the real diversity of procolophonoids in South America may be underestimated, considering the diversity of procolophonoids already present in the coeval Katberg Formation of South Africa. In conclusion, increasing efforts of collecting, as well as the discovery of new SCS's outcrops must be continuous in order to better estimate both abundance and biodiversity of procolophonoids in South America.

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## Appendix 1.

## Supplementary material

## MATRIX

## Nyctiphruetus

00000000000?00?00000?000000000000?000000000?000000000000000000

## Owenettidae

000000000010?10?0[01][01]00?0000000000010?000000000?010000010010010000

## Barasaurus

000000000010?10?01000?0010000000010?????1????01?00001001001100?

## Coletta

001001000000?10?0???0???0?10100020?011???0?0???????????????????

## Pintosaurus

20?????????????????0???0?20100020?01101??10???????????????????

## Sauropareion

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## Phaanthosaurus

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## Eumetabolodon\_dongshengensis

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## Theledectes

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## Tichvinskia

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## Timanophon

?????1020120?21110101?010?02?11013?0010010011???????????????????



Kapes

1111?1120130?20?11111????00211[12]013100100100[02]10??????????????????1

Thelephon

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Eumetabolodon

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Procolophon

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Thelerpeton

2?111?011020?21111121??1?00211101[34]1001001001??????011???11?????

Teratophon

211111[01]110[23]0?21111121?010002111013100100100????1???1011110?????01

Pentaedrusaurus

[12]11111021230?21111111????1121110131?011010011[01]11?0?11111010?110?

Neoprocolophon

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Sclerosaurus

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Scoloparia

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Leptopleuron

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Soturnia

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Hypsognathus

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Phonodus

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Kitchingnathus

[12]0??010?00[02]0?20??110?????00[12]01001200???????111???????????????????

CAPPA/UFSM 0189

???111011020??100112100??0021100?3100100001111??????????????????1

## Character list

\* ordered character

<sup>1</sup> modified character

<sup>2</sup> created character

(0) Maxilla premaxillary subnarial process: present (0); absent (1); premaxilla posterodorsally expanded (2).\*

(1) External naris: posterior or at level of first premaxillary tooth (0); anterior to first premaxillary tooth (1).

(2) External naris: anteroposteriorly elongated (0); subcircular or dorsoventrally expanded (1).

(3) Wide internarial bar: absent (0); present (1).

(4) Snout: long and flat (0); deep and short (1).

(5) Maxillary depression: absent (0); present (1).

(6) Prefrontal: medial border straight (0); medial border with a medial process (1); confined to the orbital rim (2).

(7) Posterior margin of orbitotemporal fenestra: anterior to posterior margin of pineal foramen (0); at level of posterior-most point of the pineal foramen (1); beyond the posterior border of the pineal foramen (2); considerably beyond the posterior border of the pineal foramen (3).\*

(8) Pineal opening insertion: in a shallow fossa (0); flush with dorsal surface (1).

(9) Contour of the pineal opening: rounded (0); 'teardropshaped' (1); straight posterior border (2).

- (10) Postfrontal: contacts frontal, parietal, and postorbital (0); contacts frontal, parietal, postorbital, and supratemporal (1); contacts frontal and parietal only (2); absent and area occupied by parietal or fused to parietal (3).
- (11) Jugal lateral processes: absent (0); present (1).<sup>1</sup>
- (12) If the Jugal lateral process is present: one (0); two (1).<sup>2</sup>
- (13) Temporal ventral margin: roughly straight (0); acutely emarginated (1); broadly excavated (2); convex (3).
- (14) Quadratojugal lateral surface: spineless (0); with spine (1).<sup>1</sup>
- (15) If quadratojugal lateral is spined: one spine (0); two or more (1).<sup>2</sup>
- (16) Squamosal ventral margin terminates: at least as far ventrally as quadratojugal (0); dorsal to quadratojugal in the tympanic notch (1).
- (17) Posterior margin of the skull roof: concave (0); acute posterior process (1); broad posterior emargination (2).
- (18) Postparietals: present (0); absent/fused (1).
- (19) Supratemporal posterolateral margin: rounded (0); acute (1); prominent spine (2).\*
- (20) Vomer width: broader than choana (0); roughly equal or narrower (1).
- (21) Epipterygoid columella: ends freely (0); contacts dorsally prootic and supraoccipital (1).
- (22) Parasphenoid cultriform process: directed anteriorly and tapers to sharp tip (0); projects vertically as robust pillar (1).

- (23) Relation of basioccipital tuber and quadrate condyle: approximately level (0); basioccipital projected far posteriorly (1).
- (24) Occipital condyle: uniform (0); tripartite (1).
- (25) Dentary ventral and dorsal surfaces: nearly parallel (0); oblique (1).
- (26) Relation of articular bone to marginal dentary teeth: roughly in line (0); well below (1).
- (27) Number of premaxillary teeth: five or more (0); four (1); three (2); two (3).\*
- (28) Premaxillary teeth: subequal in size (0); enlarged mesialmost teeth (1).
- (29) Maxillary teeth with labiolingually expanded bases: absent (0); present (1).
- (30) Presence of prominently bulbous teeth in the maxilla: absent (0); present (1).
- (31) Maxillary tooth cervices: not constricted (0); constricted (1).
- (32) Maxillary tooth cusps: one (0); two (1); two and anterior monocuspid teeth absent (2).\*
- (33) Number of maxillary teeth: 40 or more (0); 35 to 15 (1); 12 to 10 (2); eight to six (3); five or less (4).\*
- (34) Maxillary cheek teeth: not inset (0); inset (1).
- (35) Deep occlusal depression in maxillary teeth: absent (0); present (1).
- (36) Anterior vomerine dentition: present (0); entirely absent (1).<sup>1</sup>
- (37) If anterior vomerine dentition is present: several denticles (0); true teeth (1).<sup>2</sup>
- (38) Vomerine denticles or teeth along posterior medial suture: present (0); absent (1).
- (39) Palatine dentition: present (0); absent (1).<sup>1</sup>

- (40) If palatine dentition is present: denticles (0); true teeth (1).<sup>2</sup>
- (41) Pterygoid dentition: present (0); absent (1).
- (42) Dentary incisors: two or more (0); one (1).
- (43) Dentary teeth in basal cross-section: circular (0); labiolingually expanded (1); mesiodistally elongated (2).
- (44) Dentary molariform tooth cusps: one (0); two adjacent cusps (1); two widely separated cusps (2).<sup>1</sup>
- (45) If dentary molariform teeth had two cusps: very close (0); widely separated (1).<sup>2</sup>
- (46) Posterior dorsal zygapophyses: gracile (0); robust (1).
- (47) Presacral pleurocentral ridge: bearing a longitudinal sulcus (0); longitudinal sulcus absent (1).
- (48) Number of caudal vertebrae: 20 or more (0); 17 or less (1).
- (49) Ossified presacral intercentra: present (0); absent (1).
- (50) Rib cage: narrow (0); broad (1).
- (51) Posteromedial margin of lateral processes of the interclavicle: concave (0); straight (1).
- (52) Interclavicle medial ridge: smooth (0); prominent (1).
- (53) Distal ends of interclavicular lateral processes: straight (0); posteriorly recurved (1).
- (54) Ectepicondylar foramen or groove on humerus: present (0); absent (1).
- (56) Entepicondylar process: reduced (0); prominent (1).

(57) Entepicondylar foramen on humerus: present (0); absent (1).

(58) Nonterminal manual phalanges on digits II, III, and IV: long, slender (0); short, robust (1).

(59) Length ratio of unguals/penultimate phalanges on manus: unguals short (0); unguals long (1).

(60) Iliac anterior margin: convex (0); straight (1).

(61) Femur/humerus length ratio: femur longer than humerus (0); femur length equal to humerus (1).

(62) Femur: slender (0); robust (1).

(63) Osteoderms: absent (0); present (1).

(64) Lacrimal-ectopterygoid contact: absent (0); present (1).

### Figure Caption

Fig. 1 CAPP/UFMS 0189. (A, B, C), in dorsal view (I), ventral view (II), occipital view (III). a, angular; art, articular; co, coronoid; cult. p., cultiform process; d, dentary; ect, ectopterygoid; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pal, palatine; pf, postfrontal; pm, premaxilla; po, postorbital; pra, prearticular; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sq, squamosal; st, supratemporal

Fig. 2 CAPP/UFMS 0189. (A, B, C), in lateral views (I, II), anterior view (III). a, angular; art, articular; co, coronoid; d, dentary; ect, ectopterygoid; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pal, palatine; pf, postfrontal; pm, premaxilla; po, postorbital; pra, prearticular; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sq, squamosal; st, supratemporal

Fig. 3 CT image in axial view of CAPP/UFMS 0189 showing the vomerine, palatines and pterygoids teeth. Scale bar 10-mm.

Fig. 4. Strict consensus tree from three most parsimonious trees. Tree Length = 130 steps. Consistency index=0.636, and Retention Index=0.785. Bootstrap/Bremmer values. A= 42/1.

Fig. 5. Strict consensus trees of Cisneros (2008b) (A), MacDougall et al. (2013) (B) and our results (C). Different colors characterize different groups described and Cisneros (2008b). Green = Procolophonidae (Procolophonidae excluding Theledectines, Procolophonines, and Leptopleuronines); Yellow = Theledectinae; Red = Procolophoninae (*sensu* Cisneros 2008); Blue = Leptopleuroninae (*sensu* Cisneros 2008); and Gray = Taxa included in the matrix by MacDougall et al. (2013) (*Kitchingnathus untabeni* and *Phonodus dutoitorum*).



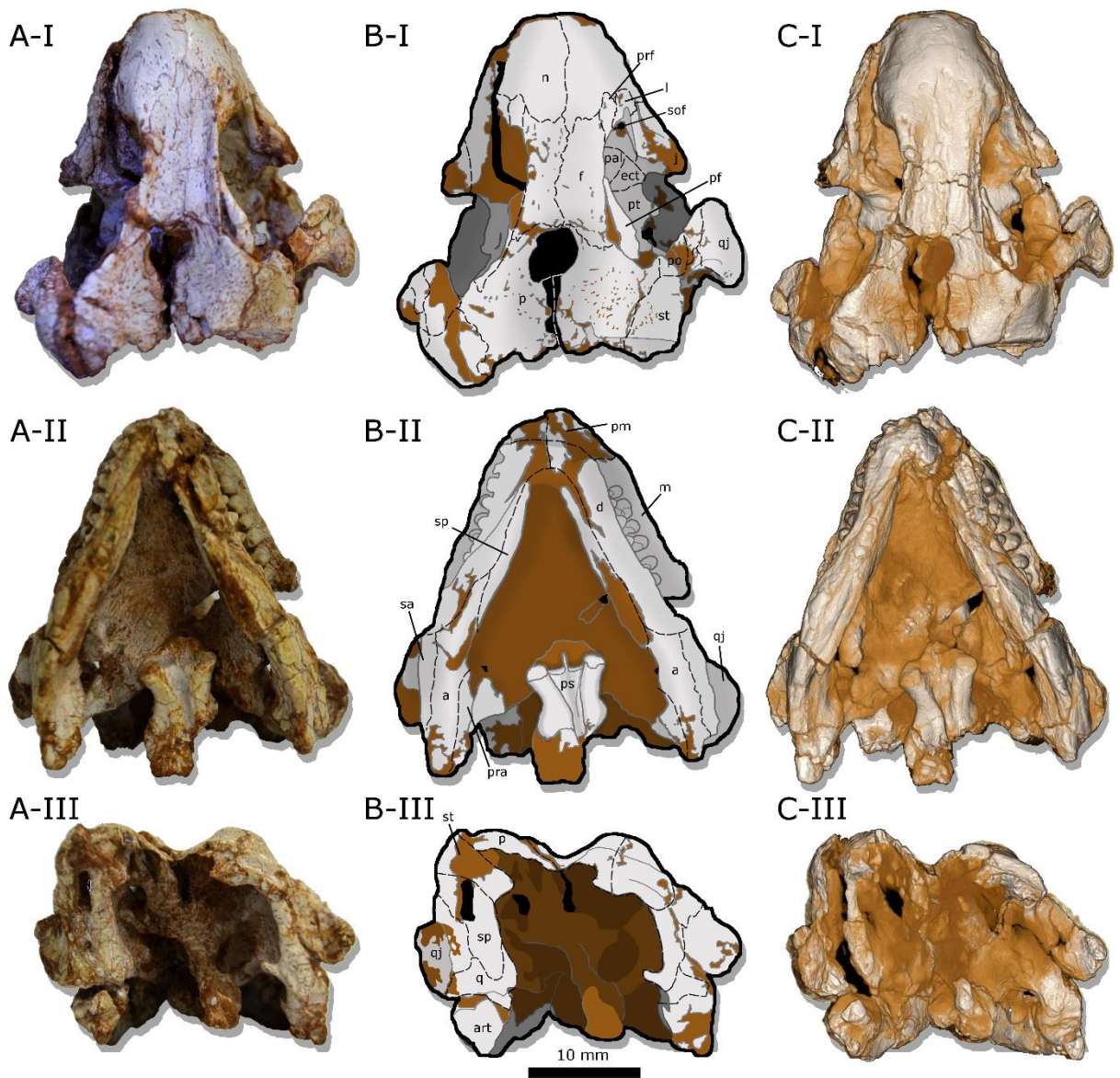


Figure 1

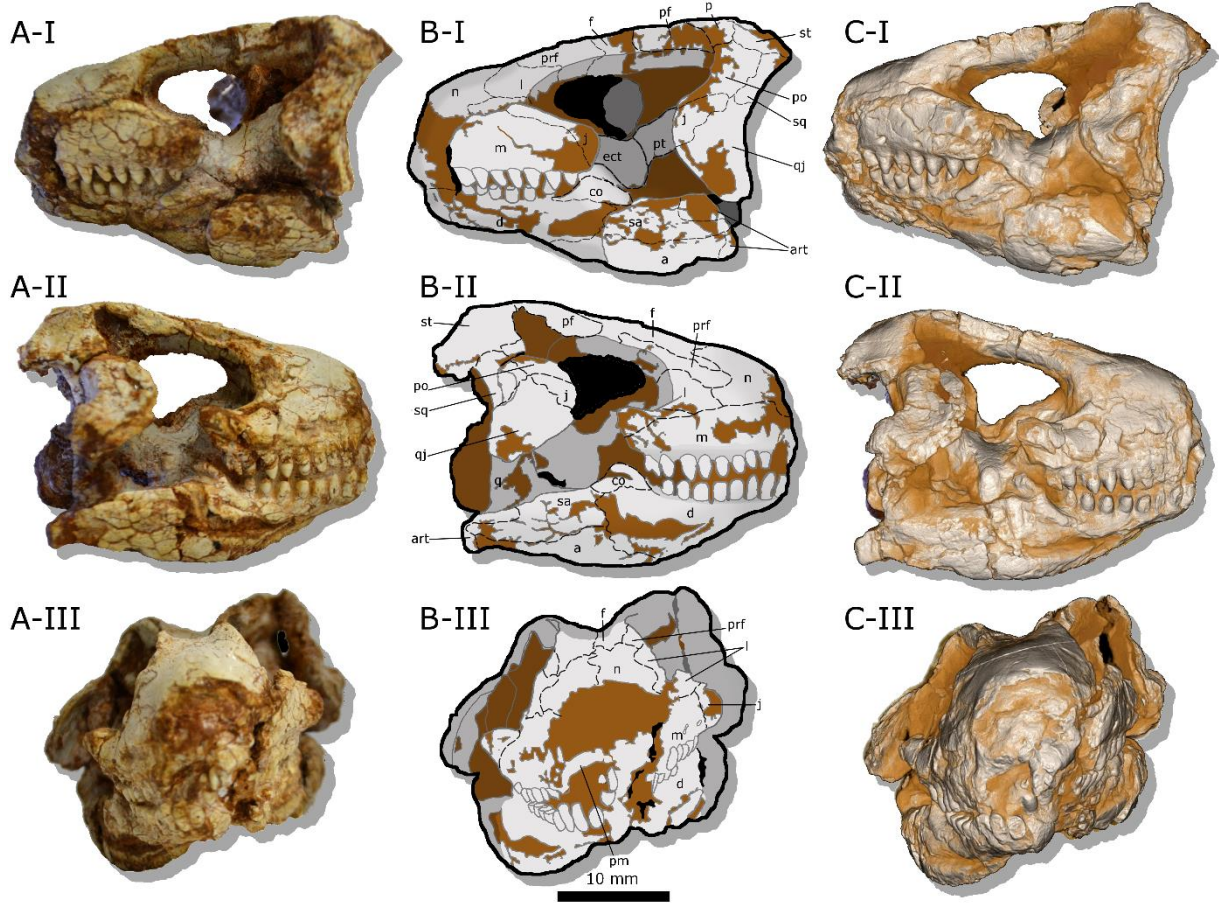


Figure 2

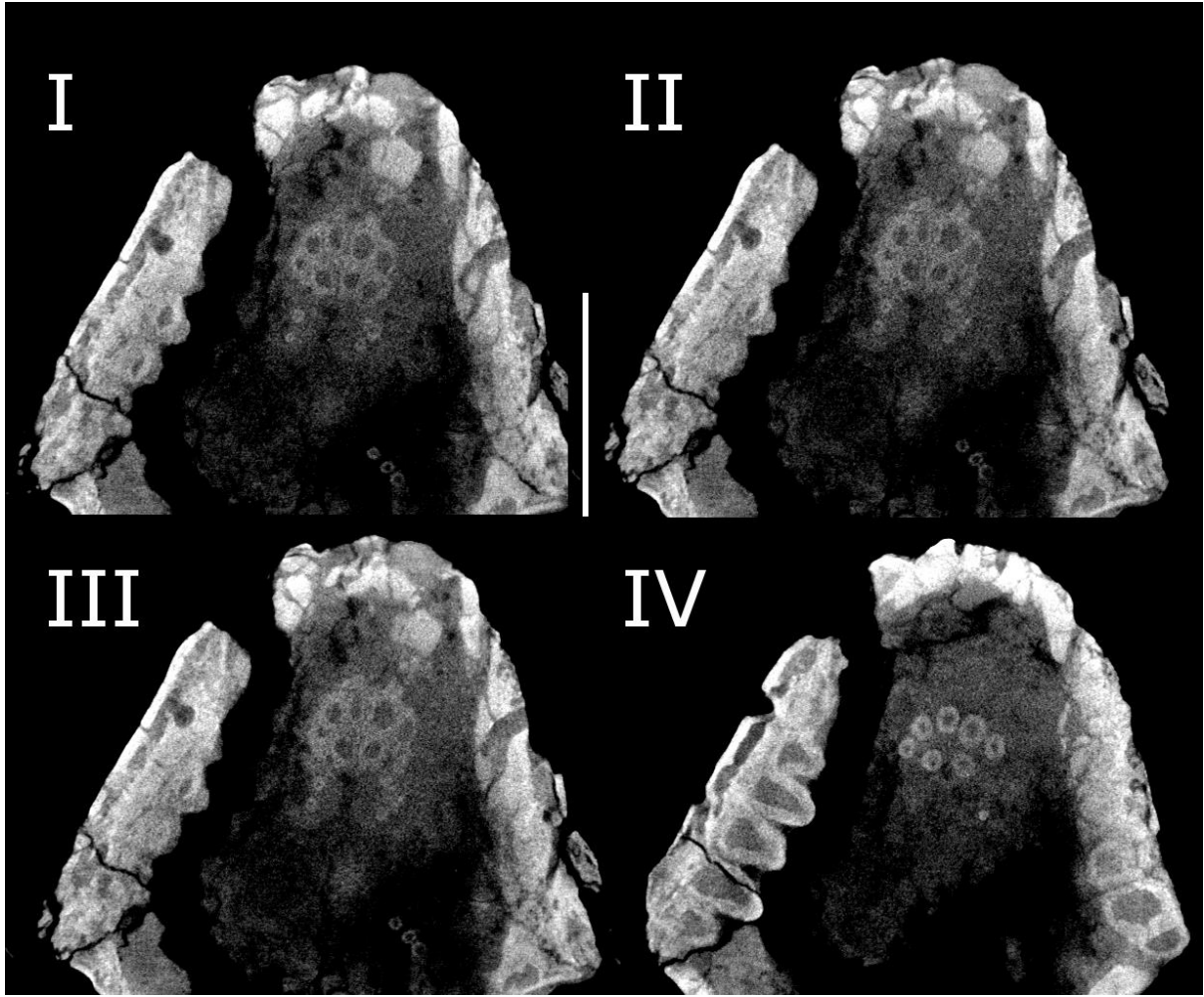


Figure 3

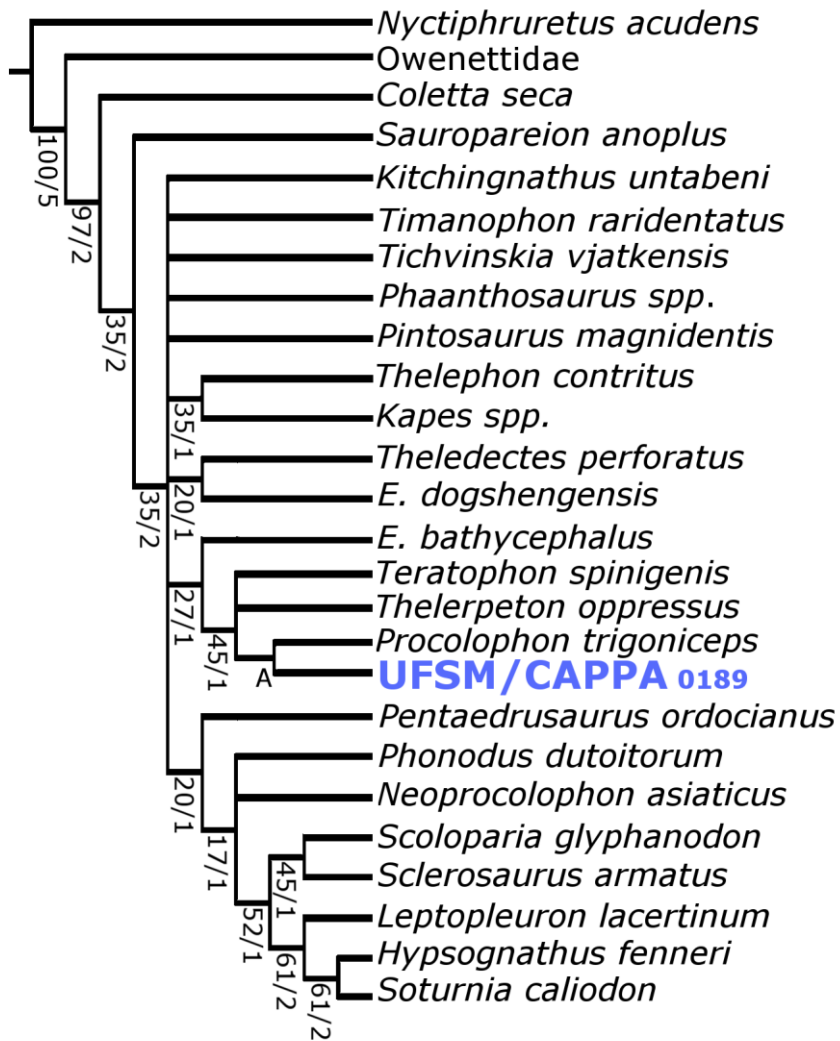


Figure 4

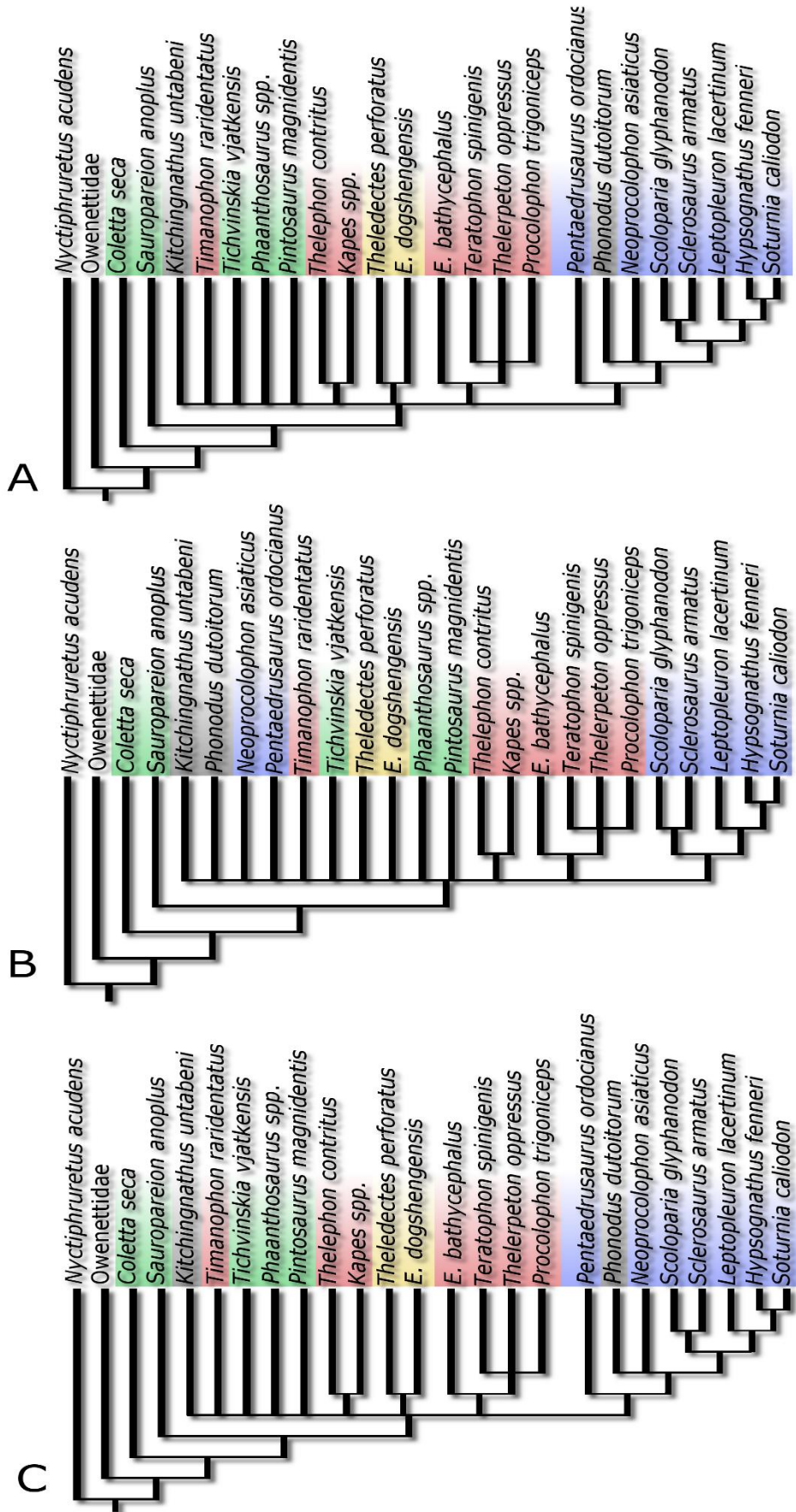


Figure 5

## 6. CONCLUSÃO

O espécime CAPP/UFMS 0189 apresentado neste estudo possui todas as características necessárias para sua atribuição a *P. trigoniceps*, além de exibir características distintas dos demais materiais descritos na literatura, como a quantidade, posição, morfologia e dimensões da dentição palatal, especificamente no vômer, palato e pterigóide.

A designação prévia de CAPP/UFMS 0189 a *P. trigoniceps* foi confirmada pela análise filogenética, uma vez que o espécime foi recuperado em relação de grupo-irmão com *P. trigoniceps*, em todas as árvores geradas neste estudo.

A descrição de estruturas internas do crânio e dados sobre a caixa craniana (*braincase*), não foram possíveis devido às características da rocha matriz. Diferentemente do tipo de sedimento que recobre os elementos palatais, a rocha que poderia ter preservado o molde interno não favoreceu sua preservação. Uma segunda possibilidade que pode explicar a não preservação de tais estruturas, é a presença de uma grande fissura que tange o material antero-posteriormente.

Apesar do alto grau de dureza da rocha que envolvia os elementos palatais, a aquisição de imagens tomográficas produziu bons resultados, permitindo boa visualização e assim possibilitando a descrição da dentição palatal e a verificação de que a distribuição de seus denticulos difere substancialmente daquilo presente em outros espécimes anteriormente descritos.

Embora *P. trigoniceps* seja uma espécie muito bem estudada, com um grande número de espécimes em diferentes coleções de vários países, a descrição deste crânio quase completo corrobora plenamente a presença dessa espécie nesta região do Gondwana, concordando com as propostas de autores prévios, concordando com as propostas de autores prévios.

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