UNIVERSIDADE FEDERAL DO PAMPA

Campus São Gabriel

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

DESCRIÇÃO DE UMA NOVA ESPÉCIE DE ANFÍBIO (TETRAPODA:

TEMNOSPONDYLI) PARA A FORMAÇÃO RIO DO RASTO

(PERMIANO DA BACIA DO PARANÁ) E REVISÃO DO STATUS

FILOGENÉTICO DE ARCHEGOSAUROIDEA

DISSERTAÇÃO DE MESTRADO

CRISTIAN PEREIRA PACHECO

2015

UNIVERSIDADE FEDERAL DO PAMPA

DESCRIÇÃO DE UMA NOVA ESPÉCIE DE ANFÍBIO (TETRAPODA: TEMNOSPONDYLI) PARA A FORMAÇÃO RIO DO RASTO (PERMIANO DA BACIA DO PARANÁ) E REVISÃO DO STATUS FILOGENÉTICO DE ARCHEGOSAUROIDEA

CRISTIAN PEREIRA PACHECO

Dissertação apresentada ao Curso de Mestrado do Programa de Pós-Graduação em Ciências Biológicas, Área de Concentração em Ecologia e Sistemática da Universidade Federal do Pampa (UNIPAMPA - *Campus* São Gabriel), como requisito parcial para obtenção de Grau de

Mestre em Ciências Biológicas.

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Resumo

Temnospondyli é um grupo bastante diversificado de tetrápodes basais que surgiu no início do carbonífero passando por grandes fases de radiação e extinção, com picos de diversidade no Permiano e no Triássico. Dentro desse grande grupo inclui-se Archegosauroidea, grupo abundante no Leste Europeu, com registro ainda escasso na América do Sul (até o momento, restritos ao Brasil). Esse grupo é dividido em duas famílias, Archegosauridae e Melosauridae. Até então, os registros indiscutíveis de arquegossauróides formalmente descritos para o Gondwana pertenciam à família Archegosauridae, a saber: *Prionosuchus plummeri* um platiopossauríneo encontrado no estado do Maranhão (Formação Pedra de Fogo) e *Bageherpeton longignathus* encontrado no Rio Grande do Sul na divisa entre Bagé e Aceguá (Formação Rio do Rasto). Neste trabalho apresenta-se a descrição e análise filogenética do primeiro registro indiscutível de um melossaurídeo trifossuquíneo fora do Leste Europeu. Esse novo material (UNIPAMPA PV 00137) consiste em um crânio parcialmente completo coletado em 2008 na Localidade Posto Queimado em São Gabriel-RS, também pertencente à Formação Rio do Rasto. A análise filogenética realizada mostrou 'Archegosauroidea' como um grupo parafilético e agrupou UNIPAMPA PV 00137 juntamente ao clado monofilético Tryphosuchinae, sendo que o espécime brasileiro posicionou-se como táxon basal em relação aos trifossuquíneos russos. *Tryphosuchus paucidens,* espécie tipo do gênero que dá nome a esta subfamília posicionou-se entre formas basais e derivadas do gênero *Konzhukovia*. O holótipo de *T. paucidens* configura-se em material fragmentário e de diagnose pouco clara. Isso, aliado ao resultado desta análise filogenética, justifica a invalidação do táxon como *nomen dubium* e

a elevação de Tryphosuchinae ao status de nova família baseada no gênero *Konzhukovia*. Essa nova família compreende formas em sua grande maioria aquáticas abundantes na Era Mesozoica e com alguns registros esparsos no Paleozoico do Gondwana. A presença de uma espécie basal do gênero *Konzhukovia* (anteriormente exclusiva da Rússia) para o Permiano do Gondwana permite fazer novas considerações acerca de sua origem e irradiação, que tanto pode ter se dado na Laurasia com *Konzhukovia* sendo parte da primeira irradiação de arquegossauróides para o Gondwana ou mesmo *Konzhukovia* ter se originado no Gondwana e migrado para a Laurásia onde as espécies mais derivadas evoluíram. Além disso, o fato de *Konzhukovia* fazer parte de uma família basal a Stereospondyli reforça a hipótese de que estes se originaram e diversificaram no Oeste do Gondwana antes do fim do Permiano ao contrário do que sugere a hipótese de que os Stereospondyli teriam ficado em um refúgio no Leste do Gondwana e teriam se diversificado após a grande extinção no final do Paleozóico.

Palavras chave: Stereospondylomorpha; *Konzhukovia*; Permiano; Formação Rio do Rasto.

Abstract

Temnospondyli is a very diverse group of basal tetrapods that appeared in the Early Carboniferous, going through major phases of radiation and extinction, with peaks of diversity during Permian and Triassic. It includes the Archegosauroidea, an abundant group in Eastern Europe with a few records from South America (so far restricted to Brazil). Achegosauroidea is divided into two families, Archegosauridae e Melosauridae. Until this contribution, unquestionable records of formally described archegosauroids from Gondwana belong to the Archegosauridae, as follows: The platyoposaurinae *Prionosuchus plummeri* from the Maranhão state (Pedra de Fogo Formation) and *Bageherpeton longignathus* from the Rio Grande do Sul state (Rio do Rasto Formation). This work presents the description and phylogenetic analysis of the first indubitable tryphosuchine outside Eastern Europe. The new material (UNIPAMPA PV 00137) consists in a partially complete skull collected in 2008 in the Posto Queimado locality (that also belongs to the Rio do Rasto Formation) from São Gabriel municipality, Rio Grande do Sul state. In the phylogenetic analysis presented 'Achegosauroidea' is a paraphyletic group and UNIPAMPA PV 00137 nesting within the monophyletic clade Tryphosuchinae. The Brazilian new species is basal to Russian tryphosuchines. The type species of Tryphosuchinae, *Tryphosuchus paucidens*, appears among basal and derived forms of the genus *Konzhukovia*. The holotype of *T. paucidens* is fragmentary and lacks a comprehensive diagnosis. This, associate with the phylogenetic results, justify its invalidation as *nomen dubium* and elevates the Tryphosuchinae to the status of a new family based on the genus *Konzhukovia*. This new family comprises mostly aquatic forms

that were abundant during Mesozoic but with scattered Paleozoic records in Gondwana. The presence of a basal species of the genus *Konzhukovia* (previously exclusive from Russia) in the Permian of Gondwana provide new insights about its radiation and dispersion, which may have happend on Laurasia with *Konzhukovia* being part of the first irradiation of archegosauroid to Gondwana or with *konzhukovia* originated on Gondwana and migrated to Laurasia, where the derivated species evolved. Besides, the fact that *Konzhukovia* belongs to a basal family to Stereospondyli reinforces the hypothesis that these ones are originated and diversificated in the West of Gondwana before the end of Permian. However, it is unlikely the hypothesis that the Stereospondyli may have stayed in a refuge in the East of Gondwana and may have diversificated after the great extinction in the end of Paleozoic period.

SUMÁRIO

1. APRESENTAÇÃO

Esta dissertação segue as normas do Programa de Pós-Graduação em Ciências Biológicas da Universidade Federal do Pampa e compõe-se de uma introdução sumária, apresentação do estudo (objetivos e justificativa), artigo submetido a periódico especializado indexado (Qualis Capes B1 e com fator de impacto JCR), conclusão breve e referências bibliográficas.

2.INTRODUÇÃO

Os anfíbios temnospôndilos do Permiano no sul do Brasil estão vinculados à Formação Rio do Rasto (com três espécies formalmente descritas, *Autralerpeton cosgriffi* Barberena, 1998, que foi coletado no nordeste do Estado do Paraná, na Serra do Cadeado, *Bageherpeton longignathus* Dias & Barberena, 2001, encontrado no Rio Grande do Sul na divisa entre Bagé e Aceguá e, mais recentemente, *Parapytanga catarinenses* Strapasson *et al*. 2014, coletado na Serra do Espigão, Estado de Santa Catarina.

No ano de 2008, um material craniano parcialmente completo de um anfíbio temnospôndilo foi encontrado na localidade Posto Queimado no município de São Gabriel, região central do RS. O referido espécime encontra-se tombado no Laboratório de Paleobiologia da Universidade Federal do Pampa sob o número UNIPAMPA PV 00137.

Devido à semelhança com o melossaurídeo russo *Konzhukovia vetusta*, Dias-da-Silva (2012) figurou o novo material como provável Melosauridae. Esse novo registro assinala que provavelmente os arquegossauróides sejam mais diversos fora do Leste Europeu do que sugere o registro atual.

Os arquegossauróides na maioria das análises filogenéticas computacionais aparecem formando um grupo monofilético dentro de Stereospondylomorpha *sensu* Yates & Warren (2000) ou Archegosauriformes *sensu* Schoch & Milner (2000) em relação de grupo irmão de Stereospondyli (Yates & Warren 2000; Ruta *et al.* 2003; Schoch 2013; Eltink & Langer 2014). Porém, existem algumas exceções, por exemplo, em Ruta & Bolt (2006) os arquegossauróides aparecem aninhados com Eryopidae. Em McHugh (2012) eles aparecem dentro de Euskelia e grupo irmão de Eryopoidea em ambos os casos formando um grupo monofilético.

No entanto, esse monofiletismo dos arquegossauróides se deve provavelmente ao fato de que as análises filogenéticas abrangentes de Temnospondyli (ex. Yates & Warren 2000; McHugh 2012; Schoch 2013) utilizam apenas as espécies com registros fósseis mais completos deixando de fora a maioria das espécies, compostas por materiais fragmentários, alegando que a pouca quantidade de dados informativos codificáveis e de dados faltantes (missing data) nesses espécimes acaba resultando em politomias na topologia das árvores de consenso obtidas. Dessa forma, as relações filogenéticas dentro de Archegosauroidea permanecem pouco conhecidas. Assim, análises abrangentes incluindo mais táxons de arquegossauróides são de suma importância para refinar status filogenético deste grupo.

Neste trabalho são realizadas descrição detalhada e análise filogenética do novo táxon baseado no espécime UNIPAMPA PV 00137 utilizando matriz de dados morfológicos recentemente publicada por Eltink & Langer (2014). Além dos táxons presentes na matriz original, foram adicionados o espécime UNIPAMPA PV 00137 e representantes de todas as subfamílias de arquegossauróides a fim de testar o posicionamento do novo espécime brasileiro, as relações filogenéticas dentro de Archegosauroidea e o posicionamento dos arquegossauróides em relação aos outros grupos de temnospôndilos.

3. SOBRE O ESTUDO

Após esta breve introdução sobre os temnospôndilos e as relações filogenéticas do arquegossauróides, estão estabelecidas bases para atingir os objetivos deste trabalho de mestrado que segue o modelo de dissertação do PPGCB/UNIPAMPA.

3.1 OBJETIVOS

Principal:

Descrevero novo espécime encontrado na Localidade Posto Queimado e verificar o posicionamento filogenético do referido espécime.

Objetivos específicos:

a) Descrição anatômica do novo material de acordo com a metodologia usual de estudo de vertebrados fósseis;

b) Identificação taxonômica do novo espécime no nível menos inclusivo possível;

c) Realização de uma análise filogenética com a inclusão de táxons de arquegossauróides incluindo representantes de todas as subfamílias do grupo, a fim de testar a monofilia de Archegosauroidea e seus diversos subgrupos, além de verificar o posicionamento filogenético da nova espécie brasileira.

3.2 JUSTIFICATIVA

A presença de um novo táxon no Permiano brasileiro atribuível a Archegosauroidea e com clara afinidade morfológica com formas do leste Europeu pode ajudar a elucidar questões ligadas ao entendimento da origem e diversificação das formas que vieram a dominar ecossistemas aquáticos durante a Era Mesozoica (Dias-da-Silva & Marsicano 2011; Gubin 1997; Yates & Warren 2000).

Os fosseis de arquegossauróides são em sua grande maioria bastante incompletos. Em consequência disso, análises filogenéticas abrangentes de Temnospondyli realizadas até o presente momento incluem apenas espécies com registros mais completos (ex. Schoch 2013; Yates & Warren 2000) deixando de fora a maior parte das formas cujos registros são fragmentários para evitar que a grande quantidade de dados faltantes resulte em falta de resolução nas topologias das árvores de consenso geradas.

Desta forma, além da descrição do espécime UNIPAMPA PV 00137, neste trabalho objetivou-se realizar uma análise filogenética incluindo um número diverso de arquegossauróides, mesmo as espécies baseadas em material fragmentário, a fim de testar a

monofilia dos diversos clados propostos para o grupo e a relação deste com os demais temnospôndilos.

4. COMPROVANTE DE SUBMISSÃO DO ARTIGO

p.taylor@nhm.ac.uk
Para eu

Mar 19 em 5:26 PM

19-Mar-2015

Dear Mr Pacheco:

Your manuscript entitled "A new Permian Temnospondyl with Russian affinities in South America, the new family Konzhukoviidae, and the phylogenetic status of Archegosauroidea" has been successfully submitted online and is presently being given full consideration for publication in Journal of Systematic Palaeontology.

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5. **A new Permian Temnospondyl with Russian affinities in South America, the new family Konzhukoviidae, and the phylogenetic status of Archegosauroidea**

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Abstract

A new Permian temnospondyl from South America is described and considered to represent a new species for the genus *Konzhukovia*, previously recorded exclusively in Russia. It consists of the anterior half and nearly the entire right side of skull roof and palate. A comprehensive phylogenetic analysis was performed with several archegosauroids and other well supported groups of temnospondyls in order to access the affinities of the new Brazilian species and also test the monophyly of Archegosauroidea. As a result, Archegosauroidea was not recovered as a monophyletic group, comprising successive paraphyletic taxa. The only monophyletic group of 'archegosauroids' is Tryphosuchinae (in a sister group relationship with Stereospondyli), composed of *Tryphosuchus paucidens, Konzhukovia vetusta, K. tarda,* the new Brazilian species *Konzhukovia gabrielensis.* As *T. paucidens* diagnosis is somehow unclear and based on quite incomplete material and also is

nested among three species of Konzhukovia, we herein consider this taxon a nomen dubium and purge it from the strict consensus tree. An alternative solution would be erecting a new taxonomic combination for *T. paucidens.* In order to solve its taxonomic problems, it is necessary the discovery of more complete material with a clear set of diagnostic characters to either revalidate this taxon or provide a new combination for it. The phylogenetic results support the erection of a new family to replace Tryphosuchinae and accommodate *Konzhukovia vetusta*, *K. tarda* and the new species of the *Konzhukovia*, being the new Brazilian species basal to the Russian forms. A basal form in Gondwana brings interesting insights regarding the evolution of the new family, stereospondyl origins, their early diversification, and palaeobiogeographic patterns of distribution.

Keywords: Stereospondylomorpha; *Konzhukovia*, Western Gondwana; Permian; Rio do Rasto Formation; Southern Brazil

Introduction

Temnospondyli is the largest clade of basal tetrapods, comprising approximately 198 genera and 292 species, with more than a half inhabiting early Mesozoic ecosystems (Schoch 2013). Their occurrence in Southern Brazil is restricted to the Permian, (Rio do Rasto Formation) and Triassic (Sanga do Cabral and Santa Maria supersequences) (Barberena 1998; Dias & Barberena 2001; Dias-da-Silva *et al,* 2005, 2006, 2008, 2009, 2012; Dias-da-Silva 2012; Dias-da-Silva & Marsicano 2011; Dias-da-Silva & Dias 2013).

From the Rio do Rasto Formation, there are three species formally described so far:

Bageherpeton longignathus, which comprises an incomplete lower jaw, collected in the Rio

Grande do Sul state, Southern Brazil, showing affinities with Russian Platyoposaurinae

(Dias & Barberena 2001); *Autralerpeton cosgriffi*, from Serra do Cadeado - Paraná, a well

represented temnospondyl, consisting of skull (Barberena 1998; Eltink & Langer 2014),

postcranium (Dias & Schultz 2003) and scales (Dias & Richter 2002), firstly described as

an australerpetonid rhinesuchoid (Barberena 1998) and then considered in an intermediary

position between Archegosauridae and Rhinesuchidae (Witzmann & Schoch 2006; Schoch

et al. 2007) and more recently regarded as possessing clear stereospondyl affinities (Eltink

& Langer 2014); and *Parapytanga catarinensis*, from Serra do Espigão - Santa Catarina, a

fragmentary Stereospondylomorpha which shares similarities with African rhinesuchids

(Strapason *et al*. 2014). Also, some taxa are still awaiting formal description: a

"Rhinesuchid-like" temnospondyl collected in the Serra do Cadeado (Barberena & Dias

1998), posteriorly assigned to *Konzhukovia* by Schoch & Milner (2000); an incomplete

large lower jaw from the locality of Posto Queimado (Malabarba *et al*. 2003); a skull from

Santa Catarina state - Serra do Espigão – preliminarily regarded as a melosaurid (Signorelli

2005); and material comprising a short-snouted skull, mandible, axial and appendicular

skeleton from São Jerônimo da Serra - Paraná (Souza & Vega 2011).

The Triassic strata from Southern Brazil yielded several records of stereospondyls

collected from the Sanga do Cabral supersequence: *Sangaia lavinai* (Dias-da-Silva *et al*.

2006; Dias-da-Silva & Marsicano 2006); a partially skull assigned to mastodonsauroid

(sensu Damiani 2001) (Feltrin *et al*. 2008; Da-rosa *et al*. 2009); a plagiostenine

plagiosauroid (Dias-da-Silva & Ilha 2009; Dias-da-Silva & Milner 2010); and indetermined

stereospondyls (Dias-da-Silva *et al.* 2005; Dias-da-Silva & Schultz, 2008; Dias-da-Silva & Da-Rosa 2011; Dias-da-Silva & Dias 2013). Other stereospondyls originated from the Santa Maria I Sequence or Candelária Sequence *sensu* Horn *et al.* (2014) include: a Stereospondyli indet. and *Compsocerops* (Dias-da-Silva *et al.* 2011, 2012). Finally, from the Santa Maria II Sequence, an isolated interclavicle ascribed to (?)Mastodonsauroidea (Dias-da-Silva *et al*. 2009) (for an up to date list of published Triassic stereospondyls from Southern Brazil, see Dias-da-Silva & Dias (2013, table 1).

The present contribution is a detailed description and phylogenetic analysis of a new taxon with clear affinities with Russian stereospondylomorphs. The new taxon was recovered from the locality of Posto Queimado (Early Guadalupian, Rio do Rasto Formation), near São Gabriel town, State of Rio Grande do Sul (Fig. 1), Southern Brazil and preliminarily figured as Melosaurinae by Dias-da-Silva (2012), and after a phylogenetic evaluation herein performed, it was recovered nested within Tryphosuchinae, basal to Russian forms. Among them, in this contribution we consider *Tryphosuchus paucidens nomen dubium* and elevate the taxonomic status of Tryphosuchinae to a new family due to both diagnostic and phylogenetic results (see sections Systematic Palaeontology and discussion).

Formerly, "Tryphosuchinae" (here elevated to a new family) consisted of three genera: *Konzhukovia*, *Tryphosuchus* and *Uralosuchus*, all recorded in the Upper Permian of the Russian Plataform, Eastern Europe (Konzhukova 1955; Gubin 1993; Golubev 1995).The new gondwanic taxon presented here provides additional evidence to the hypothesis that stem stereospondyls were widely distributed and diverse in both Gondwana and Laurasia during Permian (Schoch 2000). Recovered as a monophyletic sister clade of

Stereospondyli, the "Tryphosuchinae" is present in the middle Permian of Gondwana among several basal stereospondyls, such as *Australerpeton cosgriffi* (Barberena 1998; Eltink & Langer 2014), *Trucheosaurus major* (Marsicano & Warren 1998; Dias-da-Silva & Marsicano 2011), *Gonduanosaurus bijoriensis* (Werneburg & Scheneider 1996),the dubious *Bothriceps australis* (Warren & Marsicano 1998, 2000); and all the South African Rhinesuchidae (Damiani 2004; Damiani & Rubidge 2003; Schoch & Milner 2000). South American temnospondyls may help to understand stereospondyl origins, providing new insights regarding their early diversification and palaeobiogeographic patterns of distribution.

Geological setting

The Rio do Rasto Formation belongs to the Passa Dois Group, ranging from middle to upper Permian strata from the Paraná Basin (Barberena *et al.* 1985; Dias & Barberena 2001; Holz *et al*. 2010 & Dias-da-Silva 2012). Among the Permian units from southern South America, the Rio do Rasto Formation is the only stratigraphic unit to preserve continental fossil faunas (Barberena & Daemon 1974; Barberena & Araújo 1975; Barberena *et al.* 1985; Langer *et al.* 2008; Cisneros *et al.* 2012).

This unit is subdivided into the lower Serrinha Member (150–250 meters of thickness) and upper Morro Pelado Member (250–300 meters of thickness) (Holz *et al.* 2010). The depositional system of the Serrinha Member is mostly interpreted as originated by deposition of lakes or alluvial incursions (Rohn 1994), being characterized by mudstones, siltstones and sandstones whose grain decreases from bottom to top (Rohn

1997; Holz *et al.* 2010). The deposition of the Morro Pelado Member was interpreted from meandering rivers or lacustrine, deltaic and eolian (Rohn 1994), being recently suggested that occurred in alluvial conditions , with coalescing flood plains, including the deposition of crevasse splay deposits, and inundites of occasional shallow river channels (Holz *et al.* 2010). Lithologically, it consists of fine to medium sandstone, stratified and interspersed with red pelites, containing fossil remains of conchostracans, bivalves, sharks, scales and coprolites of fishes, dental plates of dipnoans, plant remains, and tetrapods (e.g Barberena *et al.* 1980; Dentzien-Dias *et.al.*2008; 2012; 2013; Lavina 1991; Ragonha 1989; Malabarba *et al*. 2003; Cisneros *et al*. 2005, 2011, 2012; Dias-da-Silva 2012; Rohn 1997; Holz *et al.* 2010). The rocks outcropping Posto Queimado locality belongs to the Morro Pelado Member, being characterized by a sequence of pelites, interspersed with clay lenses, sand and intraformational conglomerates. The latest tetrapod records from the Posto Queimado local fauna includes the pareasaurid *Provelosaurus americanus*, the dinocephalian *Pampaphoneus biccai*, mandibular element of a temnospondyl, the new taxon herein presented, the basal anomodont *Tiarajudens excentricus*, and an undescribed pylacephalid dicynodont (Malabarba *et al.* 2003; Cisneros *et al.* 2005, 2011, 2012; Ilha *et al.* 2011; Dias-da-Silva 2012).

Regarding the age and biostratigraphic correlation of the Rio do Rasto Formation, different tetrapod-based propositions were suggested (see Barberena *et al.* 1985; Langer 1998, 2000; Cisneros *et al.* 2005; Langer *et al.* 2009; Dias-da-Silva 2012; Boos *et al.* 2013). Accordingly, the age of Posto Queimado local fauna is late Wordian-Capitanian (early Guadalupian), based on the temporal distribution of Russian temnospondyls. The Aceguá local fauna is older, being correlated to Roadian-early Wordian based on the

Russian Platyoposaurinae distribution. The Serra Serra do Cadeado area corresponds to

Posto Queimado (Capitanian), but also younger Wuchiapinghian (early Lopingian) based

on the bioestratigraphy of southern Africa rhinesuchids and the sinapsid *Endothiodon*

(Dias-da-Silva 2012, fig. 5; Boos *et al*. 2013, fig. 6). However, a detailed vertical

evaluation of tetrapod distribution is mandatory in order to solve the different hypotheses

regarding the temporal range of the tetrapod-bearing localities of the Rio do Rasto

Formation.

Institutional abbreviations

MV: Department of Vertebrate Palaeontology at the Museum of Victoria, Melbourne,

Australia; PIN: Paleontological Institute, Academy of Science, Moscow, Russia;

UNIPAMPA: Laboratório de Paleobiologia, Universidade Federal do Pampa, São Gabriel,

Brazil.

Systematic Paleontology

Temnospondyli von Zittel, 1888

Stereospondylomorpha *sensu* Yates & Warren, 2000

Konzhukoviidae nov.

Diagnosis of Konzhukoviidae nov. Vomerian medial edges raised, with a narrow strip of

cultriform process exposed between them. In spite of being present also in mastodonsauroid

stereospondyls, it is unique among non-stereospondyls, so we consider this an

autapomorphic state character for this family, together with the following combination of

state characters shared with either archegosauroids or stereospondyls: tip of snout expanded

so that the snout margins run parallel, or are concave before the tip (shared with

archegosauroids); terminal crest lying lateral and parallel to the buttress of the paroccipital

process (=external tabular crest) (shared with archegosauroids); triangular process of the

premaxilla absent, posterior margin of the premaxilla forming a simple suture with the

nasal (shared with stereospondyls); vomers with a straight tooth row running transversely

between the vomerine fangs (shared with stereospondyls); vomerine tusks as large as

palatine ones (shared with stereospondyls); anteroposteriorly compressed maxillary teeth

(shared with stereospondyls).

Konzhukovia Gubin (1991)

Type species. *Konzhukovia vetusta*

Diagnosis of *Konzhukovia*. As for the family.

Konzhukovia gabrielensis sp. nov.

(Figs 2, 3)

Etymology. The specific name *gabrielensis* is derived from the municipality where the

hototype was recovered (São Gabriel, Rio Grande do Sul State, southern Brazil).

Holotype. UNIPAMPA PV 00137, a partial skull.

Type locality and horizon. Locality of Posto Queimado, farm Boqueirão (S 30 00′ 08″; W

54 05′ 09″), São Gabriel, Rio Grande do Sul state, Southern Brazil. Passa Dois Group, Rio

do Rasto Formation, Morro Pelado Member, Early Guadalupian.

Diagnosis of *Konzhukovia gabrielensis*. A konzhukoviid distinguished from all other

konzhukoviids by the following combination of characters: The posterolateral process of

the vomer extends in the same level to the palatine tusks, whereas in the other

konzhukoviids, the posterolateral process of the vomer extends anteriorly to the palatine

tusks; The parachoanal tooth row in *K. gabrielensis* presents eight teeth whereas *K. vetusta*

presents two teeth in the parachoanal tooth row (this condition is unknown in *K. tarda* and

Tryphochus paucidens); the palatine ramus of the pterygoid extends well posteriorly to the

level of the palatine tusks (in *K. tarda* the palatine ramus extends anteriorly to the palatine

tusk and in *K. vetusta* the palatine ramus extends slightly after the palatine tusk); width of

cultriform process 15% of its length (in *K. vetusta* the width of cultriform process is less

than 10% of its length); the orbits placed well beyond the middle length of the skull (in *K.*

vetusta and *K. tarda* the orbits are placed slightly after the midline of the skull).

Description and comparison

Skull

UNIPAMPA PV 00137 comprises the anterior half and a portion of the entire right side of

skull roof and palate, so the left posterior region is lacking, as well as part of the right one,

as the material was partially eroded and suffered accidental damage during collecting.

Overall, the specimen is poorly preserved. Consequently, visualization of cranial sutures is

quite difficult, excepting for some observable medial sutures in the medial series (Fig. 2A).

Also, sutures are barely visible because of the advanced ontogenetic state of UNIPAMPA

PV00137, probably a fully grown adult. Hence, they are inferred from anatomical regions

and pattern of ossification centers as well. Accordingly, several bone elements are illustrated with dashed lines and a full inferred reconstruction of the new specimen is also provided (Fig. 3A, B). The anteriormost margin of the snout is broken, but was clearly rounded in shape. It is possible to observe the presence of a slight constriction after the posterior limit of the nostrils, so the snout is expanded. Beyond the constriction, the lateral margins of the snout run parallel and then diverge from each other assuming a rough triangular shape. This triangular shape with lateral margin expanded from each other after the constriction posterior to the nostrils, is recurrent in archegosaurians (Yates & Warren 2000; Schoch & Milner 2000). It is important to consider that, when compared with *Konzhukovia vetusta* (PIN 520/1) and *K. tarda* (PIN 1758/253; PIN 1758/254) (much smaller adult individuals in comparison), UNIPAMPA PV 00137 is more than twice their size, a very robust and large specimen in comparison (Fig. 3C). In most dermal bones of the skull roof the ornamentation displays a pattern of ridges enclosing depressions, which become elongated in areas of skull elongation. Both infraorbital and supraorbital sensory sulci are present, anterior to the right orbital margin. The infraorbital sulcus runs along the maxilla and extends posteriorly to the posterior end of the lacrimal. The supraorbital sulcus extends posteriorly to medial limit of the naris, runs along to the nasal and the preserved part of the frontal. Due to the poor preservation of the skull it is not possible to exactly observe both anterior and posterior ends of the sensory sulci. For the same reason, it is not possible to confirm the presence of the infraorbital sensory sulcus in the right posterorbital region of the cheek.

This specimen is dorsoventrally flattened due to taphonomic compression, a frequent and intense process observed in most fossils from the Posto Queimado local fauna,

as for example in *Pampaphoneus biccai* and *Tiarajudens eccentricus* (Cisneros *et al.* 2011; 2012).

In ventral view, the premaxilla, maxilla, vomer, palatine, ectopterygoid, part of the pterygoid and quadrate are preserved. The dorsal view preserves the premaxilla, maxilla, nasal, lacrimal, prefrontal, frontal, quadrate, jugal (comprising the lateral margin of the right orbit), and quadratojugal. Quadrate, quadrate ramus of the pterygoid, and quadratojugal are sutured but isolated from the remaining material.

Dorsal surface of skull roof

It is not possible to be certain about the presence of the septomaxilla due to the low thickness of the skull roof (as after death of the animal, this could cause the loss of this small and thin element before burial), which is about 2-2.5mm thick at most. However, Gubin (1991) noted that the absence of this bone is a common feature in all 'archegosauroids', but at least *Platyoposaurus watsoni* (PIN 161/123, 161/124) possesses a well-developed septomaxilla (Gubin 1997). By phylogenetic inference, we postulate that this element is probably absent in *K. gabrielensis*.

The skull roof is complete between the nostrils, without the internarial fenestra that is present in basal groups (e.g Trematopidae and Dendrerpetontidae). This fenestra is also present in the rhinesuchid stereospondyl *Rhineceps nyasaensis* (Watson 1962). The nostrils are oval, with wide lateral openings placed well beyond the anterior edge of the snout, as in *K. vetusta* (PIN 520/I) and *K. tarda* (PIN 1758/253). The nostril margins comprise the premaxilla, maxilla, and nasal. The nasal is a large bone which extends posteriorly to

medial limit of the nostrils and possibly sutures with lacrimal, prefrontal, and frontal as in all other archegosauroids (Schoch & Milner 2000). It does not possess a ventral flange, as this structure is present only in dissorophoids (Schoch 2012). The prefrontal is fragmented and only composed by its anteriormost limit. Thereby, we infer that it sutures with the nasal, being excluded from narial margins. The presence of the lacrimal is inferred in UNIPAMPA PV00137, because the absence of this bone is conspicuous among trematosaurian stereospondyls (Schoch 2006). It probably contacts maxilla, nasal, and the preserved part of the prefrontal. The anterior half of jugal is preserved and contacts the maxilla slightly extending posterior to the orbit, forming its ventrolateral margin (Fig 2A).

Only the right lateral border of the orbit is preserved, which is composed by the jugal. Although the left posterorbital half of the skull is lacking and part of the posteriormost right limit is isolated, it is possible to infer the position of the orbits in the skull through measuremens performed on the material *in situ* and using photographs taken during field work, once the outline was impress in the sediment. The orbits are located behind the midlength of the skull and between midline and lateral border, meaning that they are widely separated from each other but not as lateral as in brachyopoid and rhytdosteid trematosaurians (Schoch & Milner 2000). In young specimens of *Achegosaurus decheni* (MV P198458), orbits are located close to the middle of the skull length, but with increasing size and rapid development of the preorbital zone, they move posteriorly and, in large forms, they are placed on the boundary between second and posterior thirds of the skull (Gubin 1997). In addition, their medial or lateral position is variable in temnospondyls because of the plasticity in width of both jugal and frontal (Eltink, 2014). Quadrate, quadratojugal and quadrate ramus of the pterygoid are preserved and isolated from the skull

but found near their original positions in the fossil site. The projecting spike on the quadratojugal is not present in *K. gabrielensis.*

Marginal dentition and tusks

Both marginal dentition and tusks are inferred based on their broken insertion basis along ventral margin. As usual in temnospondyls, the dentition is pleurodont and premaxilla plus maxilla preserve signs of 34 teeth, but probably much more were present in the living individual. The teeth are anteroposteriorly compressed as in *Konzhukovia vetusta* (PIN 520/1). This condition is present in most stereospondyls and reverse in Rhinesuchidae (e.g oval dentition in *Australerpeton*) (Eltink 2014). The posterior premaxillary teeth are larger than the anterior premaxillary and maxillary ones (Fig. 2B). This feature is present in basal eryopiforms and all Russian archegosauroids (Schoch & Milner 2000; Schoch 2013; Eltink 2014). In Rhinesuchidae this is a variable condition and in more derived Stereospondyli the size of the posterior premaxillary teeth is equal to that of anterior premaxillary and maxillary ones, for instance in *Benthosuchus sushkini* (PIN 2-I9/2252) (Yates & Warren 2000; Schoch & Milner 2000).

Only a single tusk measuring 31 mm in length is preserved in the specimen. It was found detached and inserted in the interpterygoid vacuity. It was covered with rock matrix, being exposed during preparation. In vomers there is a vomerine tooth row with two vomerine denticles that run transversely between the vomerine tusks as in *Konzhukovia vetusta* (PIN 1758/253) and *"Tryphosuchus paucidens"* (PIN 157/100). Converselly, *K. tarda* (PIN 1758/253) apparently does not bear vomerine denticles similarly to other

archegosauroid genera (e.g *Melosaurus* and *Platyoposaurus*). Based upon their basis of insertion, vomerine tusks are as large as palatine ones, as in all Russian konzhukoviids. In other archegosauroids such as *Platyoposaurus* (PIN 49/1) and *Archegosaurus* (MV P198458 , vomerine tusks are smaller than palatine ones (Gubin 1997). A parachoanal tooth row bearing eight denticles is present in the preserved left side. In *K. vetusta* and *K. tarda* the region of the parachoanal tooth rows is badly preserved, but they seem to be present, although quantification is not possible. Both non-preservation of additional vomerine denticles and numeric difference of parachoanal denticles between right and left skull sides in the UNIPAMPA PV00137 are taphonomic. The preserved part of the ectopterygoid bears enlarged tusks at its anterior end and a tooth row with probably more than eight teeth. Ectopterygoid tusks are present in archgosauroids and absent in the most stereospondyls with some exceptions, for instance in *Rhineceps nyasaensis* (Schoch & Milner 2000)*.* The palatine tooth row also probably bears more than eight teeth. *Melosaurus* (PIN 3968/2) does not present a palatine tooth row, whereas in the remaining archegosauroids the palatine tooth row presents more than eight teeth, similar to UNIPAMPA PV00137. In poorly preserved taxa as *K. tarda*, visualization of this character is difficult.

Ventral surface and Palatal complex

The contact betweem premaxilla and maxilla occurs shortly after the palatal fossae and well before the choanae. It is not possible to observe the presence of the *foramen premaxillare* as present in *Archegosaurus* or the foramina connected by a narrow furrow as occurs in

Melosaurus (PIN 3968/2), *Tryphosuchus* (PIN 157/100)*,* and some Triassic temnospondyls, such as *Parotosuchus* (Watson 1958 fig 15) and *Thoosuchus* (Gubin 1997)*.* The maxilla forms most of the lateral border of choanae. In *Melosaurus* this character differs from most archegosauroids, as lateral processes of vomeri and palatines approaches one another resulting in a reduction of maxillary contribution in the lateral border of choanae (Golubev 1995). The choanal shape is long and oval as in all konzhukoviids, although in long-snouted archegosauroids such as *Platyoposaurus* (PIN 49/1) it assumes a slit-like form (Yates & Warren 2000). In the ventral surface of the premaxilla, near the edge of the snout, there are two oval premaxillary fossae, being the anterior palatal fossa paired and perforated. On the anterior wall of the fossae, there is a round platform, the *tuberculum subrostrale medium*. This structure has been noted in *Eryops* (Sawin 1941), *Dvinosaurus* (Shishkin 1973) and all archegosauroids (Gubin 1991). The cultriform process of the parasphenoid is nearly complete, it inserts between vomers raising their medial margins. Among archegosauroids, this character is only present in *Konzhukovia vetusta* and *K. tarda* (Gubin 1991)*.* The ventral surface of the cultriform process is flat. At its midpoint the width is more than 10% of its length, different from all other archegosauroids where the width is less than 10% of its length (Fig. 2B). The interpterygoid vacuities are slightly oval and elongated, with a total width of less than 90% of their length as in other archegosauroids and rhytidosteids where it is more than 90% of their length (Yates & Warren 2000).

The vomer forms a narrow bar between the posterior margin of the anterior palatal fossa and the anterior end of the cultriform process is inserted into it raising their edges and forming a narrow strip. It is not possible to observe a fine shagreen covering its ventral surface, a feature present in other archegosauroids, for instance, in *Archegosaurus* (Gubin

1997). Also, the vomer laterally sutures with the maxilla and its posterolateral process extends to the same level to the palatine tusks. The posterolateral process extends well anteriorly to the palatine tusks in *K. vetusta* and *K. tarda* (Gubin 1991) and posteriorly in *Eryops* (Pawley & Warren 2006) and *Australerpeton* (Eltink & Langer 2014). The palatine composes part of the interpterygoid vacuits. The pterygoids are fragmented and just a small parts of the palatine and quadrate ramus. The palatine ramus extends posteriorly to the level of the palatine tusks and anterior to the anteriormost ectopterygoid tooth. Also, it is not possible to observe if it contacts the vomers as occurs in platyoposaurine archegosauroids. The palatine retraction is common in derived stereospondyls (Yates & Warren 2000; Schoch & Milner 2000), but it is a variable character (Eltink 2014). In *K. tarda* the palatine ramus of the pterygoid extends anterior to palatine tusks, whereas in *K.vetusta* it ends at the same level (Gubin 1991).

Phylogenetic analysis

In a recent contribution,(Eltink & Langer, 2014, Supplementary data) performed a comprehensive cladistic analysis with 133 characters in order to access the affinities of the rhinesuchid temnospondyl *Australerpeton cosgriffi*. The same data matrix was used in the present study, in which *Konzhukovia gabrielensis* plus seven archegosauroids were added, in order to access the affinities of *K. gabrielensis* and test the monophyly of Archegosauroidea *sensu* Yates & Warren (2000). Thus, this comprehensive analysis encompasses archegosauroid taxa which were already in the analysis of Eltink & Langer

(2014), and adds the following ones: *Platyoposaurus watsoni; Prionosuchus plummeri; Melosaurus uralensis; M. kamaensis; M. platyrhinus; Tryphosuchus paucidens; Kozhukovia tarda,* and the new species *Konzhukovia gabrielensis. Bageherpeton*, *Bashkirosaurus, Colidosuchus*, *Uralosuchus* and *Koinia* were not included in the final version of this contribution, as both their fragmentary preservation and uninformative data considerably increase the amount of most parcimonious trees (MPTs) and generate a largely unsolved strict consensus tree. A total of 31 taxa were analyzed (see Supplementary Data). All representatives of the major temnospondyl groups comprising Eutemnospondyli *sensu* Schoch (2013) (Dissorophoidea, Eryopoidea, Trimerorhachoidea, Archegosauroidea, and Stereospondyli) were included in the contribution by Eltink & Langer (2014). *Dendrerpeton acadianum* (Holmes *et al*., 1998) was used as outgroup. This temnospondyl is relatively complete and considered a basal temnospondyl (Holmes *et al.* 1998; Holmes 2000; Schoch 2013; Eltink & Langer 2014).

The phylogenetic analysis was performed with TNT version 1.1 (Goloboff *et al*., 2008) 'traditional search' (random seed = 0, TBR, hold = 10). The parsimonious analysis resulted in six most parsimonious trees (MPTs) with 355 steps each (consistency index = 0.431; retention index = 0.674). The strict consensus tree is depicted in Figure 4. Due to the large amount of missing data and homoplasy, most nodes are poorly supported (e. g. most decay indexes equals 1 and generally low Bootstrap values, see fig. 4B). This is a recurrent problem working with temnospondyl phylogenies, as the postcranial skeleton of most taxa is conservative and there is a large amount non-informative state characters plus of missing data for many taxa (Pawley 2007; Pawley & Warren 2006). However, as already pointed out by Dias-da-Silva & Marsicano (2011) these obstacles should not prevent attempts to

understand the phylogenetic relationships of long stablished fragmentary and/or highly homoplastic fossil taxa.

Results and discussion

Euskelia and Limnarchia (proposed by Yates & Warren, 2000) were recovered, with Euskelia more basal relative to Limnarchia. The Limnarchia comprises the large group that includes Dvinosauria (Trimerorhachidae), Stereospondylomorpha and Stereospondyli. Stereospondylomorpha comprises Archegosauroidea plus Sterospondyli. Overall, the topology of Stereospondyli in the strict consensus tree does not show significant differences from that proposed by Eltink & Langer (2014). Archegosauroidea *sensu* Yates & Warren (2000) (= Archegosauriformes *sensu* Schoch & Milner 2000) was not recovered as a monophyletic group in the present analysis. It comprises successive paraphyletic taxa regarding Konzhukoviidae nov. and Stereospondyli, both monophyletic.

Remarks on the phylogenetic status of Archegosauroidea

The phylogenetic status of Archegosauroidea is subject of great controversy. It was previosously recovered as the monophyletic sister-group of Stereospondyli (Yates & Warren 2000; Ruta *et al.* 2003; McHugh 2012). The group was regarded as a less inclusive clade nested within Eryopidae (Ruta & Bolt 2006), within Euskelia in a sister-group relationship with Eryopoidea or forming successive paraphyletic taxa of Eryopiformes

(Schoch 2013). According to this last author, the phylogenetic status of Archegosauroidea (e. g. if it comprises either a clade or paraphyletic grade) is an unsolved question in phylogenetic studies of Stereospondylomorpha. Other authors also consider Archegosauroidea as comprising successive paraphyletic taxa, closer to Stereospondyli than Actinodontidae: Milner (1990), Gubin (1997), Pawley & Warren (2005), Schoch & Witzmann (2009) and Witzmann & Schoch (2006). However and as already stated, the group is considered monophyletic by Yates & Warren (2000), Ruta *et al.* (2003) and McHugh (2012). It is important to point out that most of above mentioned phylogenetic analyses (e.g Yates & Warren 2000; McHugh 2012; and Schoch 2013) encompasses a small taxa sample of 'archegosauroids'. In this contribution we included a much a larger number of archegosauroids, mainly 'higher' archegosauroids (e.g. Russian forms), in order to retest their monophyly, seeking for a better resolution of archegosauroid relationships, and finally determining the phylogenetic position of *Konzhukovia gabrielensis*. As a result, 'Archegosauroidea' comprises successive paraphyletic taxa and only Konzhokoviidae nov. was recovered as a monophyletic group in a sister group relationship with Stereospondyli. 'Archegosauridae', comprising 'Archegosaurinae' plus 'Platyoposaurinae' and 'Melosaurinae' *sensu* (Schoch & Milner 2000) were recovered as paraphyletic grades. The 'platyoposaurines' *Platyoposaurus watsoni* and *Platyoposaurus stuckenbergi* are sister taxa, whereas *Prionosuchus plummeri* forms a polytomy together with 'melosaurids'. The position of *Prionosuchus plummeri* is problematic, probably due to the small number of the codable characters in the highly fragmentary holotype. Pricei (1948) included *P. plummeri* in the 'Archegosauridae', considering it a basal 'platyoposaurinae', associated with *P. stuckenbergi* and with *P. watsoni*. On the other hand, Cox & Hutchinson (1991); Schoch & Milner (2000) consider *P. plummeri* a derived 'Platyoposaurinae'. It is quite reasonable that

with the collecting of more complete material assigned to *P. plummeri*, the monophyletic status of Platyoposaurinae could receive a better support. As *K. gabrielensis, P. plummeri* comes from Gondwana, and therefore quite important to the understanding of higher 'archegosauroids' radiation and early evolution of Stereospondyli as well.

In a biostratigraphic reassesstment of Rio do Rasto Formation, Dias-da-Silva (2012) figured and assign preliminarily to "Melosaurinae" the material now described as *Konzhukovia gabrielensis*. However, as already mentioned, 'Melosaurinae' is also paraphyletic and forms a polytomy comprising *Melosaurus uralensis, M. kamaensis,* and *P. plummeri*. All these taxa are related to a large clade that includes *M. platyrhinus,* which is basal to Konzhokoviidae nov. plus Stereospondyli. 'Melosaurinae' and Konzhokoviidae are placed in an unsolved tricotomy according to Gubin (1991:112) and recovered as sister groups by Ruta *et. al* (2007). Konzhukoviidae (=Tryphosuchinae see the next section) is monophyletic in all recovered trees with *Konzhukovia gabrielensis* sp. nov. basal to *Konzhukovia vetusta* plus *K. tarda*.

The validity of *Tryphosuchus* and "Tryphosuchinae".

Tryphosuchinae was recovered as a monophyletic sister-group of Stereospondyli. Russian tryphosuchines plus *Konzhukovia gabrielensis* encompass the only monophyletic 'archegosauroids' recovered in the present analysis and *T. paucidens* is a fragmentary taxon nested among three much better preserved species of *Konzhukovia*. Also, the diagnosis of *T. paucidens* is somehow unclear and based on quite incomplete material, we herein consider this taxon a *nomen dubium* and purge it from the strict consensus tree (Fig. 4A, B).

An alternative solution would be erecting a new combination for this taxon, namely

Konzhukovia paucidens, due to its position among *Konzhukovia* (Fig. 4A). In order to do

so, it is necessary the discovery of more complete material with a clear set of diagnostic

characters in order to either revalidate this taxon or provide a new combination for it.

Hence, we erect the new family Konzhokoviidae nov. to replace Tryphosuchinae in order to

accommodate *Konzhukovia vetusta*, *K. tarda*, and *K. gabrielensis*, being the new Brazilian

species the basalmost konzhukoviid (Fig. 4B). As the "Tryphosuchinae" Uralosuchus is

composed by a very incomplete material (only mandible), the small number of codable

characters placed it in the polytomy with the basal "archegosauroids", thereby it was

excluded the matrix.

**On the presence of a basal konzhukoviidae in Gondwana and its phylogenetic and
palaeobiogeographic implications**

According to Schoch (2000) and Cisneros *et al.* (2012), a barrier-free connection between

Laurasia and Gondwana allowed the migration of several groups of Permian tetrapods

across Pangaea. Numerous groups reached a trans-Pangaean distribution during the Middle

Permian: varanopid synapsids, nycteroleterid parareptiles, dinocephalians, biarmosuchians

and basal anomodont therapsids (Rubidge 1991; Reisz & Laurin 2001, 2002; Li 2001;

Lucas 2002; Sidor & Wellman 2003; Anderson & Reisz 2004; Sidor & Smith 2007; Botha-

Brink & Modesto 2009; Cisneros & Tsuji 2009; Modesto *et al.* 2009; Liu & Rubidge 2010;

Fröbisch & Reisz 2011; Cisneros *et al.* 2011; 2012; Dias-da-Silva 2012). Also, a

compelling evidence in the support of a free faunistic transit between these Pangaean

subcontinents is the presence of two fully aquatic 'platyoposaurine archegosaurids' *Prionosuchus plummeri* and *Bageherpeton longignathus* in western Gondwana (Cox & Hutchinson 1991; Schoch & Milner 2000; Golubev 2000; Dias & Barberena 2001; Golubev 2005; Lucas 2005; Dias-da-Silva *et al*. 2009). Moreover, *P. plummeri*, *B. longignathus,* and now *Konzhukovia gabrielensis* support the evidence that Western Gondwanan non-stereospondyls played a significant role regarding temnospondyl radiation during Permian (see also Schoch 2000).

Cisneros *et al.* (2012) used the wide distribution of several continental tetrapods, as well as the close phylogenetic relationship of the Brazilian dinocephalian *Pampaphoneus biccai* with South African and Russian dinocephalians, to argue in favor of a migration route via western Pangaea, instead of across eastern Pangaea via the Cathaysian bridge. The authors postulated a Pangaea B-type continental reconstruction where South America was juxtaposed against the Appalachians (Cisneros *et al.* 2012, fig. 3). The presence of a Brazilian taxon closely related to Russian *K. vetusta and K. tarda* in Western Gondwana fully supports this hypothesis.

Golubev (1995) erected the subfamily 'Tryphosuchinae'. Before, 'Melosauridae' Fritsch 1885 was composed by five genera: *Melosaurus* Meyer 1857; *Konzhukovia* Gubin 1991; *Tryphosuchus* Konzhukova 1955; *Koinia* Gubin 1993 and *Uralosuchus* Gubin 1993. Golubev (1995) combined *Melosaurs* and *Koinia* into the subfamily 'Melosaurinae' Huene, 1931 (type genus *Melosaurus* Meyer 1857). Thereafter, *Konzhukovia*, *Tryphosuchus* and *Uralosuchus* were combined into the subfamily 'Tryphosuchinae' (type genus *Tryphosuchus* Konzhukova 1955). *Konzhukovia* is the best known genus and its sutural pattern of the skull roof, structure of the palate, and occiput closely resembles rhinesuchid

stereospondyls (Schoch & Milner 2000). Regarding *Tryphosuchus*, Yates & Warren (2000), based on the sensory sulci on the lower jaw, ornamented pterygoids, and presence of a single anterior palatal vacuity, suggested the possibility that it may be more closely related to later stereospondyls than to its contemporaneous 'archegosauroids'. Due to the similarities of both *Konzhukovia* and *Tryphosuchus* with Rhinesuchidae, Gubin (1997) suggested that the common ancestry of these taxa might help solving the question of the origin of Stereospondyli.

Regarding the origin of Konzhukoviidae, two different scenarios are herein proposed, taking into account the barrier-free connection between northern and southern Pangaea during Permian. Firstly, 'archegosauroids' came from Laurasia to Gondwana, and them descendants of gondwanan konzhukoviids later returned to Laurasia, where more derived genera evolved. Another compelling, but not strictly related evidence to support this hypothesis, is the presence of dvinosaurids and basal capitosaurids in South America, specifically in Permo-Triassic strata from Uruguay (see Piñeiro *et al.* 2007; Dias-da-Silva *et al.* 2009). Both capitosaurids and dvinosaurids are recorded in much younger laurasian deposits. Secondly, similarly to Schoch's (2000) hypothesis, *Konzhukovia gabrielensis* may have been part of the initial migration of 'archegosauroids' from Laurasia to the Gondwana probably during Middle Permian. According to Dias & Barberena (2001) 'archegosauroids' arrived in South America from Laurasia and initially occupied the north of South America (*P. plummeri* from the Pedra de Fogo Formation) and later reached the southern portion of this landmass during Late Permian. However, the basal position of both *P. plummeri* and *K. gabrielensis*, in comparison to Russian forms favors the first hypothesis. However, at this point, both possibilities should be taken with caution, as the skull of *Konzhukovia vetusta* is

complete, but little information is available regarding its postcranial skeleton. *K. gabrielensis* possesses an even lesser complete skull in comparison and, at this point, no information at all is available regarding its postcranial skeleton. Thus, in spite of being the sister taxon of Stereospondyli, the inner relationships of Konzhukoviidae should be carefully considered. Accordingly, more complete remains of konzhukoviids both in Laurasia and Gondwana, are necessary to improve information to support any given hypotheses about the origin and radiation of this family.

Remarks on the early diversification of Stereospondyli

Most stereospondyls comprise Mesozoic forms, with a few valid Paleozoic taxa, all from Gondwana (Yates & Warren 2000) and represented by basal forms: from Southern Africa, *Peltobatrachus pustulatus*; the rhinesuchid *Gondwanasaurus bijoriensis* and dubious *Lysipterigium risinense* (Schoch & Milner 2000) - both from India (Werneburg and Scheneider 1996); the rhytidosteid *Trucheosaurus major* (Marsicano & Warren 1998; Dias-da-Silva & Marsicano 2011) and the brachyopomorph *Bothriceps australis,* both from the uppermost Permian of Australia (Warren and Marsicano, 1998, 2000); and all rhinesuchids from Southern Africa (Damiani & Rubidge 2003; Damiani 2004). From South America, *Australerpeton cosgriffi* was considered a rhinesuchoid (Barberena, 1998), but Werneburg & Scheneider (1996) and Schoch & Milner (2000) considered a 'platyoposaurine' 'archegosaurid', close related to *Platyoposaurus* and *Prionosuchus*. In a further description of the postcranial skeleton of *A. cosgriffi*, Dias & Schultz (2003) sustained its original assignation as a member of Rhinesuchidae. Other contributions place the Brazilian

rhinesuchid in an intermediary position between the 'Archegosauroidea' and Rhinesuchidae (Witzmann & Schoch 2006; Schoch *et al.* 2007). Eltink & Langer (2014) place *Australerpeton* within Stereospondyli, showing morphological characters supporting its inclusion in the clade, and recently, being corroborated the position of *A. cosgriffi* as an advanced Rhinesuchidae (Eltink 2014; Eltink *et al*. in preparation). A recently described taxon, *Parapytanga catarinensis*, a new Permian temnospondyl from Gondwana (Strapasson *et al*. 2014) is nested within Stereospondylomorpha, but outside Stereospondyli. In spite of its overall incompleteness, it shares some similarities with South African rhinesuchids. Further information from more complete remains of *Parapytanga* might support its inclusion within Stereospondyli (Strapasson *et al.* 2014). A derived rhinesuchid-like form, *Arachana nigra*, was also described by Piñeiro *et al.* (2012) for the Permo-Triassic of Uruguay. It is basal to a large clade that comprises Trematosauria plus Capitosauria, quite similar to *Lydekkerina huxleyi*.

The rhinesuchid *Australerpeton* and also the possibility that *Parapytanga* belongs to Rhinesuchidae, as well as the presence of several other Gondwanan stereospondyls in the Permian, corroborates Ruta *et al.* (2007) hypothesis that basal diversification of the group occurred during the Late Palaeozoic. Also, as stated by (Warren *et al.* 2000; Yates & Warren 2000) Stereospondyli have begun its radiation from a restricted geographical area (a 'safe haven') in the landmass that nowadays comprises Australia. Instead, the overwhelming presence of stem and basal stereospondyls in South America support the origins of Stereospondyli in Western Gondwana (Dias-da-Silva *et al.* 2009; Dias-da-Silva & Marsicano 2011; and this contribution). The presence of *Konzhukovia gabrielensis* in South America as well as similarities of Konzhokoviidae with the Rhinesuchidae (endemic

to Gondwana) (Schoch & Milner 2000; Yates & Warren 2000) strengthen the likelihood of this scenario.

Acknowledgements

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Figure captions

Figure 1: Location map of Southern Brazil. The grey area shows the geographic distribution of the Passa Dois Group, in which the Rio do Rasto Formation is included (modified from Barberena *et al*. 1985 and Dias-da-Silva 2012). Numbers indicate the tetrapod-bearing localities, as follows: 1, Serra do Cadeado Area; 2, Aceguá; 3, Locality of Posto Queimado - the star and temnospondyl outline mark the location from where UNIPAMPA PV 00137 was recovered. Scale bar = 300 km.

Figure 2: *Konzhukovia gabrielensis* sp. nov., holotype UNIPAMPA PV00137. Photographs of the partial skull in **A**, dorsal, and **B**, ventral. Interpretative drawings in **C**, dorsal and **D**, ventral. Abbreviations: ch, choana; cp, cultriform process; is, infraorbital sensorial sulcus; j, jugal; m, maxilla; n, nasal; pal, palatine; pm, premaxilla; premaxillary foramen; pt, pterygoid; q, quadrate; qj, quadrato jugal; ss, supraorbiatl sulcus; tsm, tuberculum subrostrale medium; v, vomer.

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Figure 4: Strict consensus of six most parsimonious trees. In **A**, including the problematic *Tryphosuchus paucidens,* highlighted in bold. In **B**, *T. paucidens* is pruned from the strict consensus three as it is considered *nomen nudum* (see results and discussion). The grey area in **B** depicts Konzhukoviidae nov.. Tree length = 355 steps; consistency index = 0.431; retention index = 0.674. Bootstrap values and Bremer Support (between parentheses) are indicated for each node.

Appendix 1

State character codding for K. gabrielensis, K. tarda, Platyoposaurus watsoni, *Melosaurus uralensis, Melosaurus kamaensis, Melosaurus platyrhinus, Tryphosuchus paucidens, Prionosuchus plummeri* in the dataset of Eltink & Langer's (2014). Missing data are marked as '?'. **A** indicates polymorphic states '[01]'.

Konzhukovia gabrielensis sp. nov.
?00??1???0?10???1??01??2?0???000?????0???????110??101??1100?10??01?0021????0?
??1??????????????????????????1??????????????1?0??1???

Konzhukovia tarda
100?1111??01?10?10?01?1200010000100?0000100000100100?103010011?00010012110
010??01?????????????????????????1????????1????100??11??

Melosaurus kamaensis

1000011100?10?0010?010?2?00??00010??00????000011010001?30100110?011010001?0
1??0011??????1??????????????????????0????????1????10A1?01??

Melosaurus platyrhinus

1000011?0001?00110?01012000100?0?0???0????????110?0?01??01???11???1?1?21?????
???1??00110???

Melosaurus uralensis

100?01110001010????01012000??000?????0?????????????????????1?????????????????
??1??????1??????????????????????????????01??????

Platyoposaurus watsoni

1000?111001?010010001012000?0??0100?0000?0000?11010001130100?100?0?0?0201?0
1??00????????????????00?????????????????1????00011?0??

Prionosuchus plummeri

1?0?0????0?1????10?01???????0???????????????1?????????01???0??????10?0????????
1????????????????????????0???????00?1???????1??????

Tryphosuchus paucidens

????????????????????????????????1???0????0???????10????31???11?00????1201?????0?
?110?01010000????????????????1??????????????0??11??

Appendix 2

Konzhukovia vetusta was included in the analysis Eltink & Langer (2014). Based on personal observation of the holotype, code changes were perfomed as follows:

(17) Sensory sulci absent from the skull roof of adults (0), extensive sensory sulci present on the skull of adults (1). In Eltink & Langer (2014) (0); here (1).

(21) Snout margins continually converging towards tip (0), tip of snout expanded so that the snout margins run parallel, or are concave before the tip (1). In Eltink & Langer (2014) (0); here (1).

(48) Pterygoids extend anteriorly to the palatine tusks (0) pterygoids not extending anterior to the level of the palatine tusks (1). In Eltink & Langer (2014) (0); here (1).

(53) Ectopterygoid with enlarged tusks at its anterior end (0) ectopterygoid tusks absent (1). In Eltink & Langer (2014) (1); here (0).

(57) Vomers without a row of teeth between the vomerine fangs (0), a straight tooth row running transversely between the vomerine fangs (1), 'v'-shaped transverse vomerine tooth row (2).In Eltink & Langer (2014) (0); here (1).

(71) Absence of a tooth row behind the palatine tusks (0), 4–6 palatine teeth (1), more than eight palatine teeth (2). In Eltink & Langer (2014) (1); here (2).

7. CONCLUSÃO

A nova espécie descrita no artigo científico que integra essa dissertação aumenta a representatividade dos Temnospondyli para esta região do Pangeia. Além disso, a constatação da existência de um mesmo gênero do leste europeu e de uma nova espécie de anfíbio arquegossauróide corrobora com a hipótese de que esse grupo teve uma ampla distribuição não só na Laurásia como também no Gondwana. Também, o fato da nova espécie estar presente no único clado recuperado dentro de 'Archegosauroidea' em relação de grupo irmão com Stereospondyli agregou informações que corroboram hipóteses recentes sobre a origem e diversificação deste grupo amplamente distribuído na Era Mesozoica (Dias-da-Silva & Marsicano 2011; Gubin 1997; Yates & Warren 2000; dentre outros).

Do mesmo modo, o registro desse novo espécime juntamente com tetrápodes permianos descritos nos últimos anos poderá ajudar no refinamento bioestratigráficos da Formação Rio do Rasto.

Archegosauroidea mostrou-se composto por sucessivos táxons parafiléticos, onde apenas "Tryphosuchinae" foi recuperado como um clado. "Tryphosuchinae" compreende *Konzhukovia vetusta, K. tarda, "Tryphosuchus paucidens"* e a nova espécie brasileira. Pelo fato de ser baseado em materiais muito fragmentários e por sua posição dentro do gênero *Konzhukovia, T. paucidens* foi considerado *nomen dubium*. Assim, foi erigida uma nova família para acomodar a nova espécie brasileira e os demais espécimes russos que

compõem este grupo. Este resultado foi de fundamental importância para entender as relações dos 'arquegossauróides' mais derivados e sua relação com Stereospondyli.

Apesar dos interessantes resultados obtidos na presente dissertação, verificou-se que esforços contínuos de prospecção e coleta de novos materiais preferencialmente mais completos na Formação Rio do Rasto são necessários para um maior entendimento sobre os padrões evolutivos e biogeográficos desse interessante grupo de tetrápodes basais.

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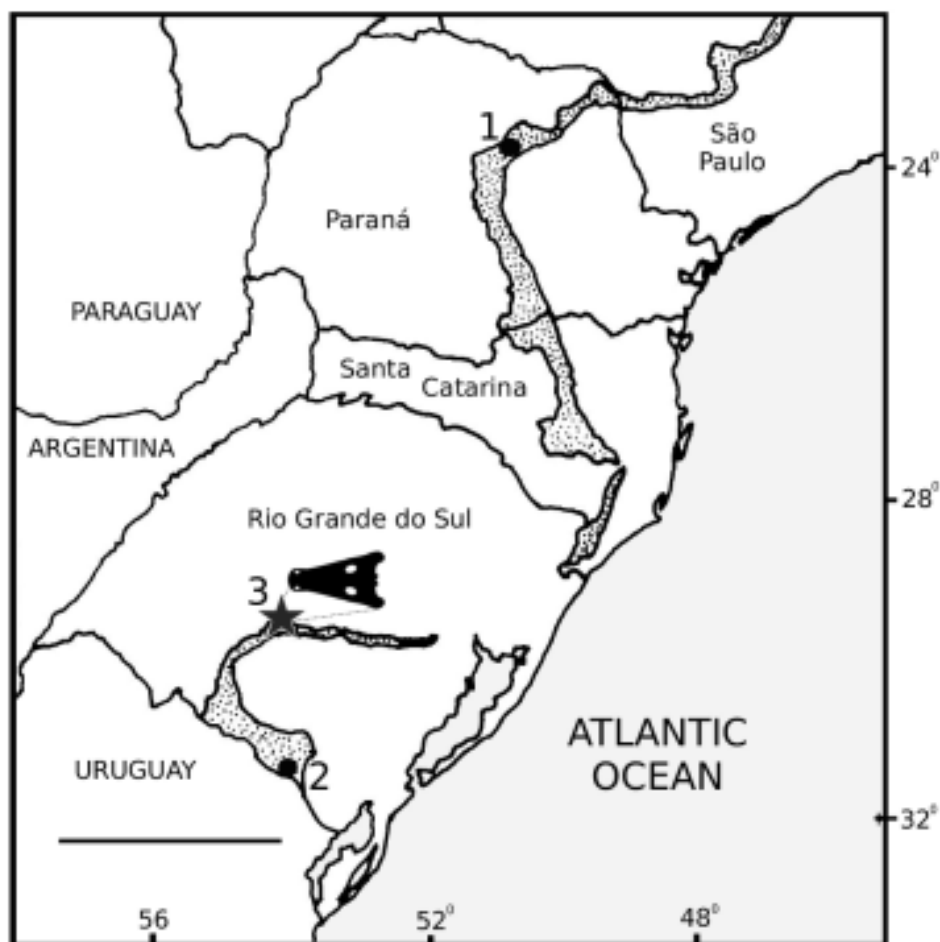
9. FIGURAS

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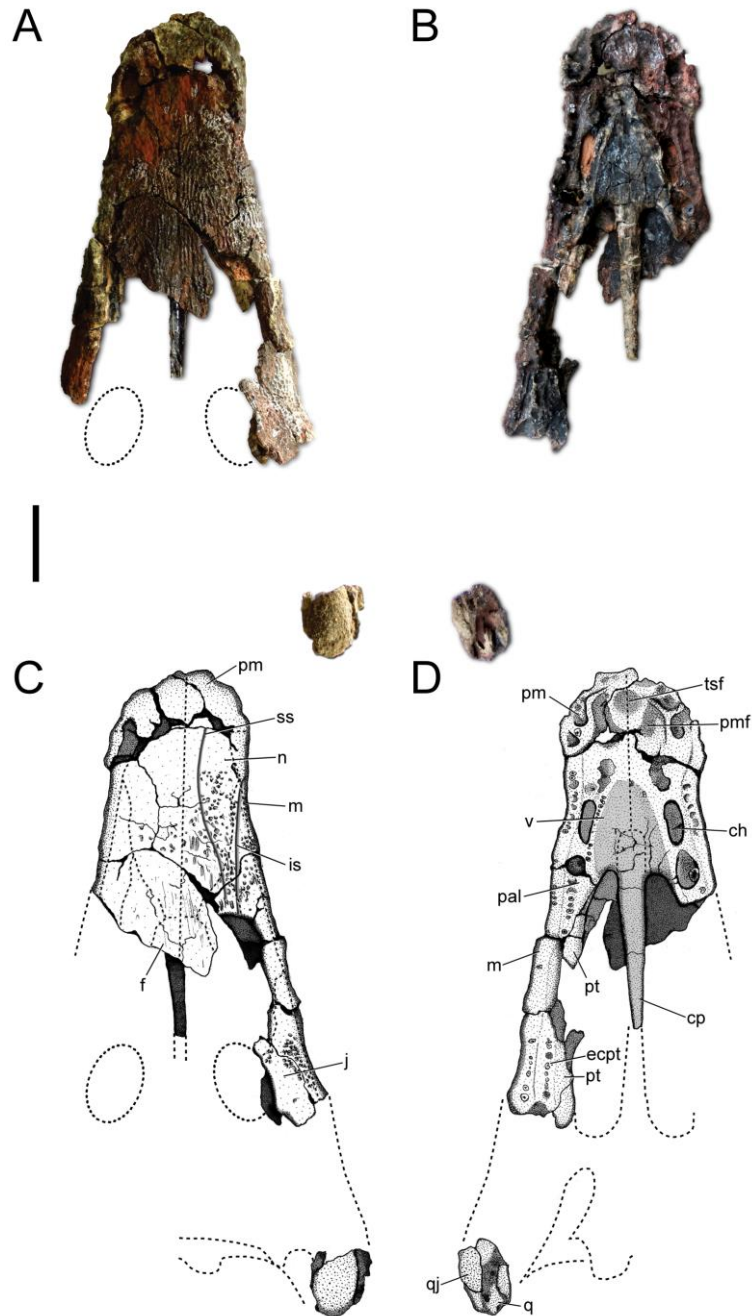
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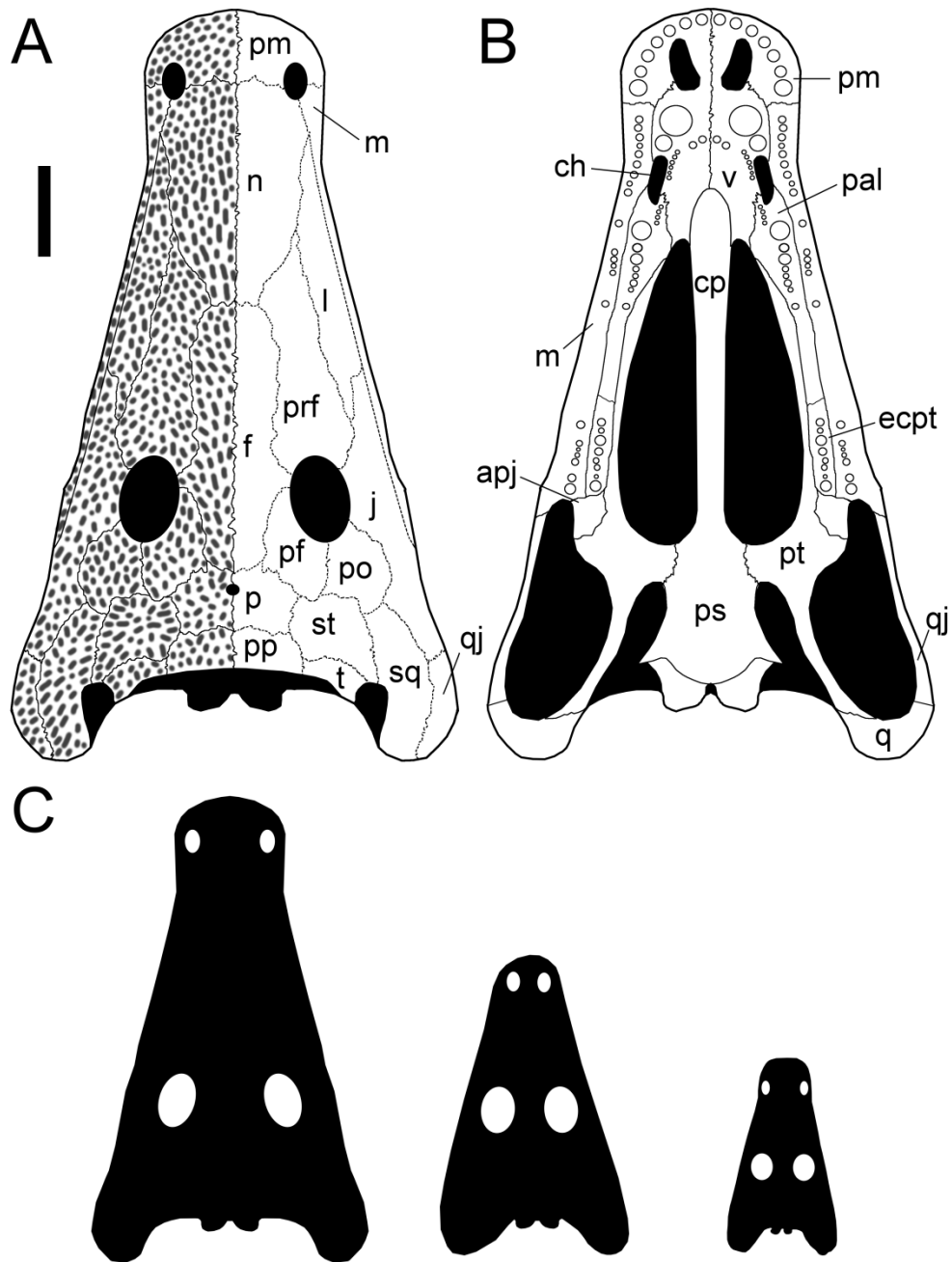
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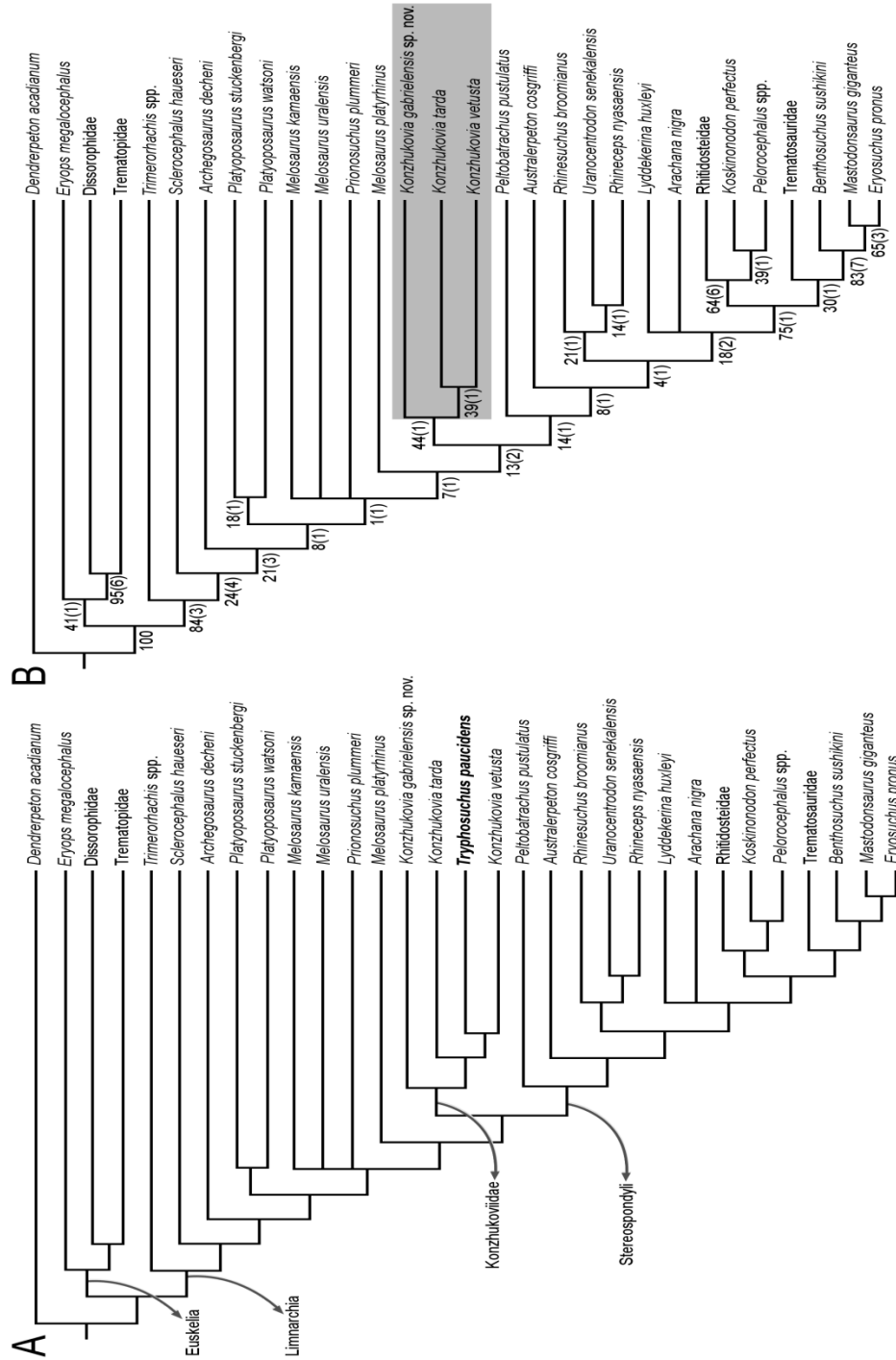
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