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**To cite this article:** Cristian Pereira Pacheco, Estevan Eltink, Rodrigo Temp Müller & Sérgio Dias-da-Silva (2016): A new Permian temnospondyl with Russian affinities from South America, the new family Konzhukoviidae, and the phylogenetic status of Archegosauroida, Journal of Systematic Palaeontology

**To link to this article:** <http://dx.doi.org/10.1080/14772019.2016.1164763>

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 Published online: 11 Apr 2016.

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# A new Permian temnospondyl with Russian affinities from South America, the new family Konzhukoviidae, and the phylogenetic status of Archegosauroida

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(Received 19 March 2015; accepted 10 February 2016)

A new Permian temnospondyl from South America is described and considered to represent a new species – *Konzhukovia sangabrielensis* sp. nov. – of the genus *Konzhukovia* previously recorded exclusively from Russia. It consists of the anterior half and partial right side of the 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 test the monophyly of Archegosauroida. Archegosauroida was not recovered as a monophyletic group, comprising successive paraphyletic taxa. The only monophyletic group of ‘archegosauroids’ is the ‘Tryphosuchinae’ (in a sister-group relationship with Stereospondyli), composed of *Tryphosuchus paucidens*, *Konzhukovia vetusta*, *K. tarda* and *K. sangabrielensis*. As the diagnosis of *T. paucidens* is unclear and based on incomplete material, nested among three species of *Konzhukovia*, we consider this taxon to be a *nomen dubium* and purge it from the strict consensus tree. An alternative solution would be to erect a new taxonomic combination for *T. paucidens*. In order to solve these taxonomic problems, it is necessary to discover 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 – Konzhukoviidae – to replace ‘Tryphosuchinae’ and accommodate *Konzhukovia vetusta*, *K. tarda* and *K. sangabrielensis*, the new Brazilian species basal to the Russian forms. An early diverging konzhukoviid in Gondwana leads to interesting insights regarding the evolution of the new family, stereospondyl origins, their early diversification and their palaeobiogeographical patterns of distribution.

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**Keywords:** Stereospondylomorpha; *Konzhukovia*; Western Gondwana; Permian; Passa Dois Group; southern Brazil

## Introduction

Temnospondyli is the largest clade of basal tetrapods, comprising approximately 198 genera and 292 species, with more than 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, 2011, 2012; Dias-da-Silva 2012; Dias-da-Silva & Marsicano 2011; Dias-da-Silva & Dias 2013). From the Rio do Rasto Formation, three species have been formally described so far: *Bageherpeton longignathus* Dias & Barberena, 2001, which comprises an incomplete lower jaw, collected in the Rio Grande do Sul, showing affinities with Russian Platyposaurinae (Dias & Barberena 2001); *Australerpeton*

*cosgriffi* Barberena, 1998, from Serra do Cadeado–Paraná, a well-represented temnospondyl comprising a set of skulls (Barberena 1998), with post-crania (Dias & Richter 2002; Dias & Schultz 2003), first described as an australerpetonid rhinesuchoid (Barberena 1998) or as an ‘intermediate’ between Archegosauridae and Rhinesuchidae (Witzmann & Schoch 2006; Schoch *et al.* 2007) but more recently regarded as possessing clear stereospondyl affinities (Eltink & Langer 2014); and *Parapytanga catarinensis* Strapasson *et al.*, 2014 (see Strapasson *et al.* 2015), from Serra do Espigão–Santa Catarina, a fragmentary Stereospondylomorpha which shares similarities with African rhinesuchids (Strapasson *et al.* 2015). Also, some taxa still await formal description: a ‘rhinesuchid-like’ temnospondyl collected in the Serra do Cadeado (Barberena & Dias 1998) and assigned to *Konzhukovia* by Schoch & Milner (2000); an incomplete large lower jaw from Posto Queimado

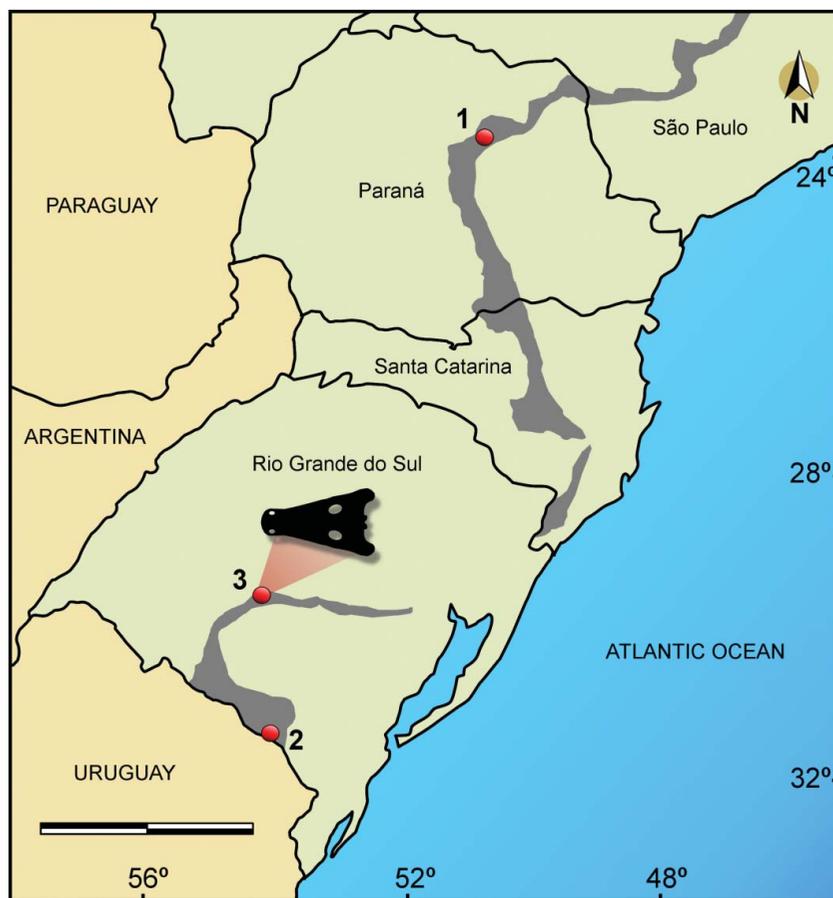
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(Malabarba *et al.* 2003); a skull from the Santa Catarina state—Serra do Espigão, preliminarily regarded as a melosauroid (Signorelli 2005); and material comprising a short-snouted skull, mandible, axial and appendicular skeleton from São Jerônimo da Serra—Paraná (Souza & Vega 2011).

In addition to the Permian records from the Rio do Rasto Formation in southern Brazil, the Parnaíba Basin of northeastern Brazil (Pedra do Fogo Formation, Cisuralian) has yielded several other older taxa: Price (1948) described the large temnospondyl *Prionosuchus plummeri* and Cisneros *et al.* (2015) reported a new tetrapod assemblage that includes a trimerorhachid dvinosaur, an early-diverging dvinosaur, and a captorhinid reptile. The new Permian temnospondyls described by Cisneros *et al.* (2015) comprise two new species, *Timonya anneae* and *Procuhy nazariensis*, and also rhinesuchid remains. Triassic strata in southern Brazil yielded several stereospondyls collected from the Sanga do Cabral Supersequence: *Sangaia lavinai* (Dias-da-Silva *et al.* 2006; Dias-da-Silva & Marsicano 2006); a partial skull fragment assigned to a

mastodonsauroid (*sensu* Damiani 2001) (Feltrin *et al.* 2008; Da-Rosa *et al.* 2009); a plagiosternine plagiosauroid (Dias-da-Silva & Ilha 2009; Dias-da-Silva & Milner 2010); and undetermined taxa (Dias-da-Silva *et al.* 2005; Dias-da-Silva & Schultz 2008; Dias-da-Silva & Da-Rosa 2011; Dias-da-Silva & Dias 2013). Other stereospondyls from the Santa Maria I Sequence (Candelária Sequence *sensu* Horn *et al.* 2014) include an indeterminate Stereospondyli (Dias-da-Silva *et al.* 2011) and *Compsocerops* (Dias-da-Silva *et al.* 2011, 2012). Finally, the Santa Maria II Sequence has yielded an isolated interclavicle ascribed to ?Mastodonsauroidea (Dias-da-Silva *et al.* 2009) (for an updated 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, which shares affinities with Russian stereospondylomorphs. It 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. It was initially reported as a Melosaurinae by Dias-da-Silva (2012),



**Figure 1.** Location map of southern Brazil. The grey area shows the geographical distribution of the Passa Dois Group, which includes the Rio do Rasto Formation (modified from Barberena *et al.* 1985 and Dias-da-Silva 2012). Numbers indicate tetrapod-bearing localities: 1, Serra do Cadeado area; 2, Aceguá; 3, Posto Queimado, with the temnospondyl outline marking the locality of UNIPAMPA PV 00137. Scale bar = 300 km.

but a new phylogenetic analysis shows that it is nested within Tryphosuchinae, basal to Russian forms. Among these, we consider *Tryphosuchus paucidens* as a *nomen dubium* and elevate the taxonomic status of Tryphosuchinae to new family level.

'Tryphosuchinae' formerly consisted of three genera: *Konzhukovia*, *Tryphosuchus* and *Uralosuchus*, all recorded in the upper Permian of the Russian Platform, eastern Europe (Konzhukova 1955; Gubin 1993; Golubev 1995). The new Gondwanian taxon described here provides additional evidence that stem stereospondyls were widely distributed and diverse in both Gondwana and Laurasia during the Permian (Schoch 2000). Recovered as a monophyletic sister-clade of Stereospondyli, 'Tryphosuchinae' is present in the middle–late Permian of Gondwana along with several basal stereospondyls, such as *Australerpeton cosgriffi* (Barberena 1998; Eltink & Langer 2014), *Arachana nigra* (Piñeiro *et al.* 2012), *Trucheosaurus major* (Marsicano & Warren 1998; Dias-da-Silva & Marsicano 2011), *Gondwanosaurus bijoriensis* (Lydekker 1985), the dubious *Bothriceps australis* (Warren & Marsicano 1998, 2000), *Peltobatrachus pustulatus* (Panchen, 1959), and all of the South African Rhinesuchiidae (Schoch & Milner 2000; Damiani & Rubidge 2003; Damiani 2004). South American temnospondyls may therefore help to understand better stereospondyl origins, providing new insights regarding their early diversification and palaeobiogeographical patterns of distribution.

## Geological setting

The Rio do Rasto Formation belongs to the Passa Dois Group, ranging from Guadalupian to Lopingian in age in the Paraná Basin (Barbarena *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 one to preserve continental fossil faunas (Barberena & Daemon 1974; Barberena & Araújo 1975; Barbarena *et al.* 1985; Langer *et al.* 2008; Cisneros *et al.* 2012).

This unit is subdivided into the lower Serrinha Member (150–250 m thick) and upper Morro Pelado Member (250–300 m thick) (Holz *et al.* 2010). The depositional system of the Serrinha Member is mostly interpreted as deposition in lakes or alluvial incursions (Rohn 1994), being characterized by mudstones, siltstones and sandstones whose grain size decreases from bottom to top (Rohn 1994; Holz *et al.* 2010). The depositional environment of the Morro Pelado Member has been interpreted as meandering fluvial to lacustrine, deltaic and aeolian (Rohn 1994), Holz *et al.* (2010a) suggesting alluvial conditions with coalescing flood plains, including crevasse splay deposits and inundites of occasional shallow river channels. Lithologically, it consists of fine to medium

sandstone, stratified and interspersed with red pelites, containing fossil remains of conchostracans, bivalves, hybodont sharks, scales and coprolites of fish, dental plates of dipnoans, plant remains, tetrapod ichnofossils and tetrapod remains (Barberena *et al.* 1980; Lavina 1991; Rohn *et al.* 1997; Malabarba *et al.* 2003; Cisneros *et al.* 2005, 2011, 2012; Dentzien-Dias *et al.* 2008, 2012, 2013; Holz *et al.* 2010; Dias-da-Silva 2012; Silva *et al.* 2012). The rocks outcropping at the Posto Queimado locality belong to the Morro Pelado Member, and are characterized by a sequence of pelites, interspersed with clay lenses, sand and intraformational conglomerates. The latest tetrapod record from Posto Queimado includes the pareasauid *Provelosaurus americanus*, the dinocephalian *Pampahoneus biccai*, mandibular element of a temnospondyl, the new species described here, 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 biostratigraphical correlation of the Rio do Rasto Formation, different tetrapod-based propositions have been suggested (see Barbarena *et al.* 1985; Langer, 2000; Cisneros *et al.* 2005; Dias-da-Silva 2012; Boos *et al.* 2013). The formation at Posto Queimado is of late Wordian–Capitanian (early Guadalupian) age based on the temporal distribution of Russian temnospondyls. The Aceguá fauna is older, being of Roadian–early Wordian age based on the Russian Platyoposaurinae distribution. The Serra do Cadeado area corresponds to Posto Queimado (Capitanian), but may be also younger (Wuchiapingian, early Lopingian) based on the biostratigraphy of southern African rhinesuchids and the synapsid *Endothiodon* (Dias-da-Silva 2012, fig. 5; Boos *et al.* 2013, 2015). However, a detailed evaluation of tetrapod distribution is necessary in order to solve the different hypotheses regarding the ages of the tetrapod-bearing localities of the Rio do Rasto Formation. Recently, Boos *et al.* (2015) stated that it is preferable to discontinue the use of 'local faunas' *sensu* Simpson (1961) for the Serra do Cadeado, Aceguá and Posto Queimado localities due to the lack of a precise stratigraphical context for most fossils from these localities. Moreover, the three localities that correspond to the 'Posto Queimado Local Fauna' might not be contemporary (Boos *et al.* 2015).

## Institutional abbreviations

**MV**: Department of Vertebrate Palaeontology, Museum of Victoria, Melbourne, Australia; **PIN**: Paleontological Institute, Academy of Science, Moscow, Russia; **UNI-PAMPA**: Laboratório de Paleobiologia, Universidade Federal do Pampa, São Gabriel, Brazil.

## Systematic palaeontology

**Temnospondyli** von Zittel, 1888  
**Stereospondylomorpha** *sensu* Yates &  
 Warren 2000  
 Family **Konzhukoviidae** fam. nov.

**Diagnosis.** Vomerian medial edges raised, with a narrow strip of the cultriform process exposed between them. Also present in mastodonsauroid stereospondyls, it is unique among non-stereospondyls, so we consider this a synapomorphy for this family, together with the following combination of character states shared with either archegosauroids or stereospondyls: tip of snout expanded so that the snout margins are 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 tusks (shared with stereospondyls); anteroposteriorly compressed maxillary teeth (shared with stereospondyls).

Genus **Konzhukovia** Gubin, 1991

**Type species.** *Konzhukovia vetusta* Gubin, 1991, Capitanian.

**Diagnosis.** As for the family.

**Other species.** *Konzhukovia tarda* Gubin, 1991 (Roadian); *Konzhukovia sangabrielensis* sp. nov. (late Wordian–Capitanian).

***Konzhukovia sangabrielensis*** sp. nov.  
 (Figs. 2–4)

**Etymology.** The specific name *sangabrielensis* is derived from the municipality where the holotype 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, Boqueirão Farm (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.** A konzhukoviid distinguished from all other konzhukoviids by the following combination of characters: the posterolateral process of the vomer extends to the same level as the palatine tusks (and not anteriorly as in the other konzhukoviids); the parachoanal tooth row bears eight teeth (instead of two in *K. vetusta*; this condition is

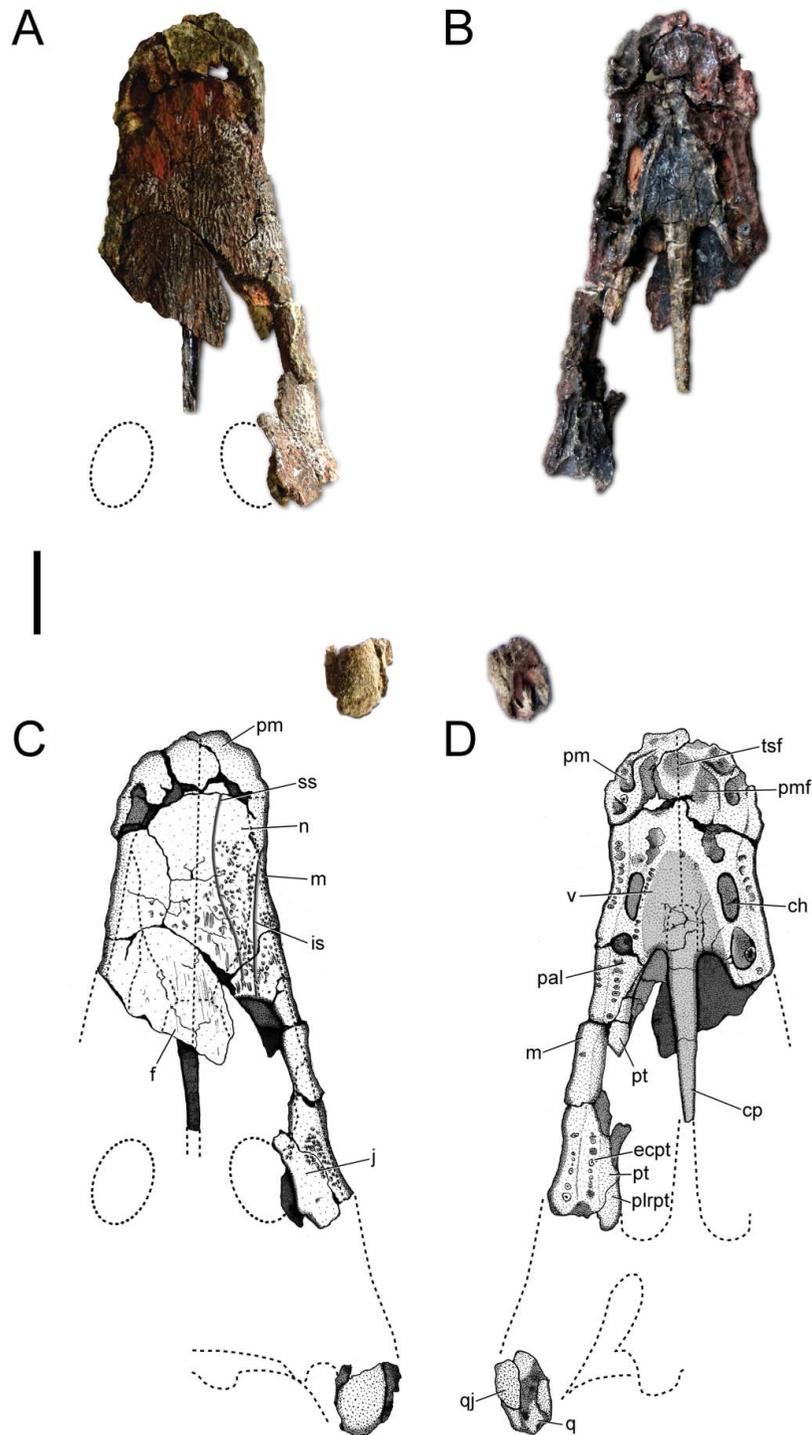
unknown in *K. tarda* and *Tryphosuchus paucidens*); the palatine ramus of the pterygoid extends very posteriorly to the level of the palatine tusks (not slightly posteriorly as *K. vetusta*, and not anteriorly as in *K. tarda*); the width of the cultriform process is 15% of its length (it is less than 10% in *K. vetusta*); and the orbits are placed very posteriorly to the mid length of the skull (not slightly posteriorly as in *K. vetusta* and *K. tarda*).

## Description and comparisons

### Skull

UNIPAMPA PV 00137 comprises the anterior half and part of the right side of the skull roof (maximum 2–2.5 mm thickness) and palate. The orbital and posterior regions are lacking, as the material was eroded when discovered and suffered accidental damage during collection. Overall, the specimen is poorly preserved. Consequently, visualization of cranial sutures is quite difficult, except for some observable medial sutures in the medial series (Fig. 2A). In addition, sutures are barely visible because of the advanced ontogenetic state of the individual, probably a full-grown adult. Hence, they are inferred from anatomical regions and patterns of ossification centres (in fully grown individuals, elongated concentric ridges depart from the ossification centres, a feature far less conspicuous in juvenile individuals). Besides the faintly visible sutures, other characters corroborate that the specimen is an adult, such as the elongated outline of the skull roof (Steyer 2000) and orbits positioned after the midline of the skull (Gubin 1997; Steyer 2000). Accordingly, several bone elements are illustrated with the outline of the fossil in grey to make it possible to visualize the preserved parts in the reconstruction of the new species (Fig. 3A, B).

The anteriormost margin of the snout is broken, but rounded in shape. A slight constriction of the skull margin is visible just posterior of the nostrils, so the snout is slightly expanded. Posteriorly, the lateral margins of the snout extend almost parallel and then diverge from each other assuming a rough triangular skull shape. This triangular shape with lateral margins expanded from each other after the constriction posterior to the nostrils is characteristic of archegosaurians (Schoch & Milner 2000; Yates & Warren 2000) but is also found in some eryopids, such as *Erypos megacephalus* (Sawin, 1947). Compared with *Konzhukovia vetusta* (PIN 520/1) and *K. tarda* (PIN 1758/253, 1758/254), *K. sangabrielensis* is more than twice their size and very robust in appearance (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 infra- 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

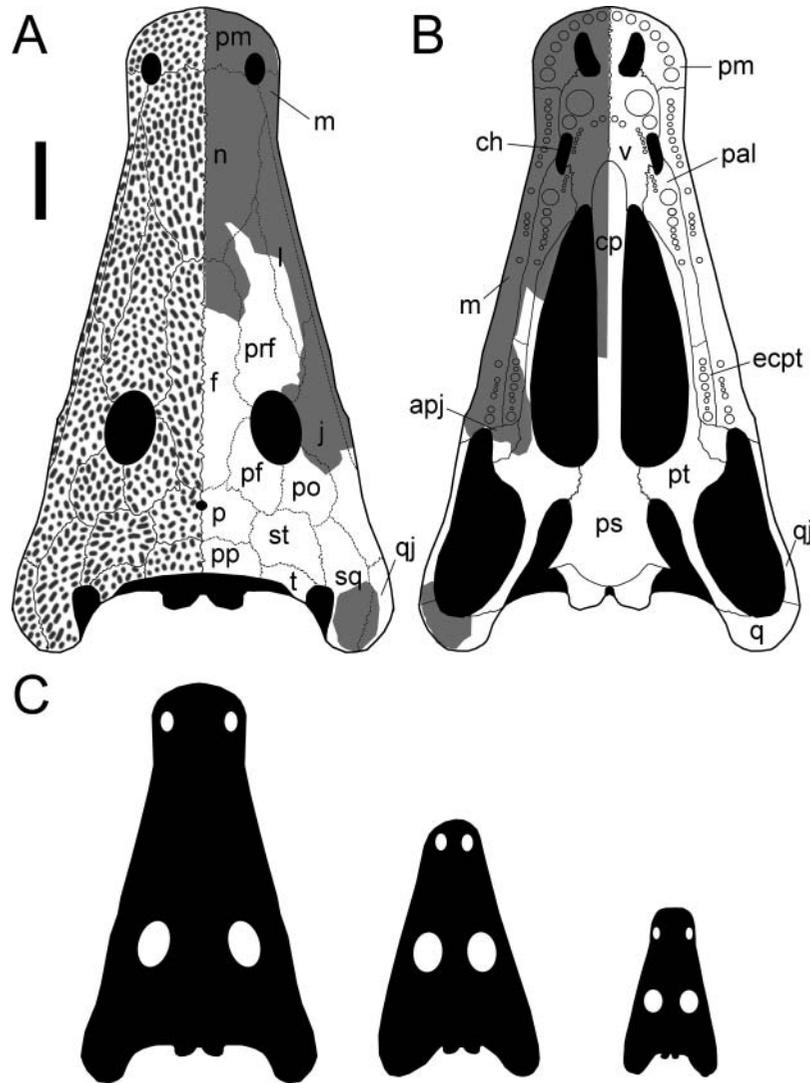


**Figure 2.** *Konzhukovia sangabrielensis* sp. nov., holotype, UNIPAMPA PV00137. Photographs of the partial skull in **A**, dorsal, and **B**, ventral views. Interpretative drawings in **C**, dorsal and **D**, ventral views. Abbreviations: ch, choana; cp, cultriform process; is, infraorbital sensorial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

the lacrimal. The supraorbital sulcus extends posteriorly to the medial limit of the naris, running along to the nasal and the preserved part of the frontal. Due to the poor preservation of the skull, it is not possible to observe exactly 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 (or other sulci) in the right posterorbital region of the cheek.

This specimen is dorsoventrally flattened due to diagenesis, which is intense in most fossils from Posto



**Figure 3.** *Konzhukovia sangabrielensis* sp. nov., reconstruction of the skull (grey areas are preserved parts in the fossil) in **A**, dorsal and **B**, ventral views. **C**, skull outlines of *K. sangabrielensis* (left), *K. tarda* (middle) and *K. vetusta* (right). Abbreviations: cp, cultriform process; ecpt, ectopterygoid; f, frontal; j, jugal; n, nasal; l, lacrimal; p, parietal; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; prf, prefrontal; ps, parasphenoid; pt, pterygoid; sq, squamosal; st, supratemporal; t, tabular.

Queimado, such as *Pampaphoneus biccai* and *Tiarajudens eccentricus* (Cisneros *et al.* 2011, 2012).

### Marginal dentition and tusks

Both marginal dentition and tusks are inferred based on their broken insertion bases along the ventral margin of the skull, so it was only possible to measure the diameter. As is usual in temnospondyls, the dentition is pleurodont and both premaxilla and maxilla preserve signs of 34 teeth, probably more *in vivo*. The teeth are anteroposteriorly compressed, as in *Konzhukovia vetusta* (PIN 520/1) and most stereospondyls (Schoch 2013). In contrast, some Rhinesuchidae (such as *Australerpeton cosgriffi* and *Lacrosaurus watsoni*; see Eltink 2014) show oval-rounded

teeth. The posterior premaxillary teeth are larger than the anterior premaxillary and maxillary teeth (Fig. 2B). This feature is present in basal eryopiforms and all Russian archegosauroids (Schoch & Milner 2000; Schoch 2013; Eltink 2014). In Rhinesuchidae this condition is variable, and in more derived Stereospondyli, such as *Bentosuchus sushkini* (PIN 2-19/2252), the size of the posterior premaxillary teeth is equal to that of the anterior premaxillary and maxillary teeth (Schoch & Milner 2000; Yates & Warren 2000).

The vomerine tooth row bears two denticles (3.6 mm) that run transversely between the vomerine tusks (9.1 mm), as in *Konzhukovia vetusta* (PIN 1758/253) and *Tryphosuchus paucidens* (PIN 157/100). Conversely, *K. tarda* (PIN 1758/253) and other archegosauroids do not bear



**Figure 4.** The single tusk of *Konzhlukovia sangabrielensis* sp. nov. found isolated in the interpterygoid vacuity. Scale bar = 30 mm.

vomerine denticles (e.g. *Melosaurus* and *Platyoposaurus*). Based on their bases of insertion, the vomerine tusks are as large as the palatine tusks (9.1 mm), as in all Russian konzhlukoviids. In other archegosauroids, such as *Platyoposaurus* (PIN 49/1) and *Archegosaurus* (MV P198458), the vomerine tusks are smaller than the palatine tusks (Gubin 1997). Only a single tusk of 31 mm in length is preserved, an element found isolated but included in a layer of matrix in the interpterygoid vacuity (Fig. 4). A parachoanal tooth row (3.7 mm) bearing eight denticles is preserved on the left side. In *K. vetusta* and *K. tarda*, the region of the parachoanal tooth row is badly preserved but seems to be present. The preserved part of the ectopterygoid bears enlarged tusks (8.6 mm) at its anterior end and a tooth row containing at least eight teeth (3.8 mm). Ectopterygoid tusks are present in archegosauroids but absent in all stereospondyls except for, for instance, *Rhineceps nyasaensis* (Watson, 1962). The palatine tooth row (3.8 mm) bears at least eight teeth, as in all archegosauroids except for *Melosaurus* (PIN 3968/2), which lacks

a palatine tooth row. In poorly preserved taxa such as *K. tarda*, this character is not visible.

#### Dorsal surface of skull roof

The skull roof is complete between the nostrils, and lacks the internarial fenestra that is present in basal groups, for example the trematopids *Phonerpeton pricei* (Dilkes, 1990) and *Acheloma dunni* (Polley & Reisz, 2011), Dendrerpetontidae such as *Dendrerpeton acadianum* (see Holmes *et al.* 1998), and some rhinesuchid stereospondyls including *Rhineceps nyasaensis* (Watson, 1962). By phylogenetic inference, we postulate that the septomaxilla is probably absent in *Konzhlukovia sangabrielensis*. 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). 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 the medial limit of the nostrils and possibly sutures with the lacrimal, the prefrontal and the 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 the anteriormost part remains. Therefore, we infer that its suture with the nasal is excluded from the narial margins. The presence of the lacrimal is inferred in UNIPAMPA PV00137, because the absence of this bone is conspicuous among trematosaurian stereospondyls only (e.g. Steyer 2002; Schoch 2006). It probably contacts the maxilla, the nasal and the preserved part of the prefrontal. The anterior half of the jugal is preserved and contacts the maxilla slightly extending posterior to the orbit forming its ventrolateral margin (Fig. 2A).

Only the lateral border of the right orbit is preserved, which is composed of the jugal. Although the left posterorbital half of the skull is lacking and part of the posteriormost right side is isolated, it is possible to infer the position of the orbits in the skull through measurements performed on the material *in situ* and using photographs taken during fieldwork because the outline was impressed in the sediment. The orbits are located behind the mid-length of the skull and well between the midline and the lateral border, meaning that they are relatively widely separated from each other, though not as lateral as in brachyopoids and rhytidosteids (Schoch & Milner 2000). In young specimens of *Achegosaurus decheni* (MV P198458), the orbits are close to the mid length of the skull, but with increasing size and strong development of the preorbital zone through ontogeny, they move posteriorly and, in large forms, they are placed on the boundary

between the second and posterior third of the skull (Gubin 1997; Witzmann 2006). In addition, their medial or lateral position, which is very variable in temnospondyls, is linked with the plasticity in width of both the jugal and the frontal (Eltink 2014). The quadrate and partial quadratojugal are preserved and isolated from the skull but they were in their original position attached to the skull before being accidentally damaged during collection.

### Ventral surface of the skull and palatal complex

In ventral view, the contact between the premaxilla and the maxilla occurs shortly posterior to the palatal fossae and well anterior to the choanae (Fig. 2B). It is not possible to observe the *foramen premaxillare*, which is present in *Archegosaurus* (Gubin 1997). The maxilla forms most of the lateral border of choanae. In *Melosaurus*, this character differs from most of the archegosauroids, as lateral processes of the vomer and palatine are visible, reducing the maxillary contribution to the lateral border of the choanae (Golubev 1995). The choanal shape is long and oval (Fig. 2B), as in all konzhuoviids and many other temnospondyls, although in long-snouted archegosauroids such as *Platyoposaurus* (PIN 49/1) it assumes a slit-like form (Yates & Warren 2000). On the ventral surface of the premaxilla, near the edge of the snout, the paired anterior palatal fossae are oval. On the anterior wall of the fossae, there is a round pronounced platform, the *tuberculum subrostrale medium* (Fig. 2B, D). 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, but its approximate full length is inferred based on the preserved anterior border of the palatine ramus of the pterygoid (Fig. 2D). Anteriorly, it is inserted between the 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 the midpoint, its width is 15% of the length, different from all other archegosauroids where the width is less than 10% of the length (Fig. 2B, D). The interpterygoid vacuities are slightly oval and elongated, with a total width of less than 90% of their length, as in other archegosauroids and many capitosauroids, whereas in several brachyopoids and rhytidosteids the width is more than 90% of the length (Yates & Warren 2000; Dias-da-Silva & Marsicano 2011).

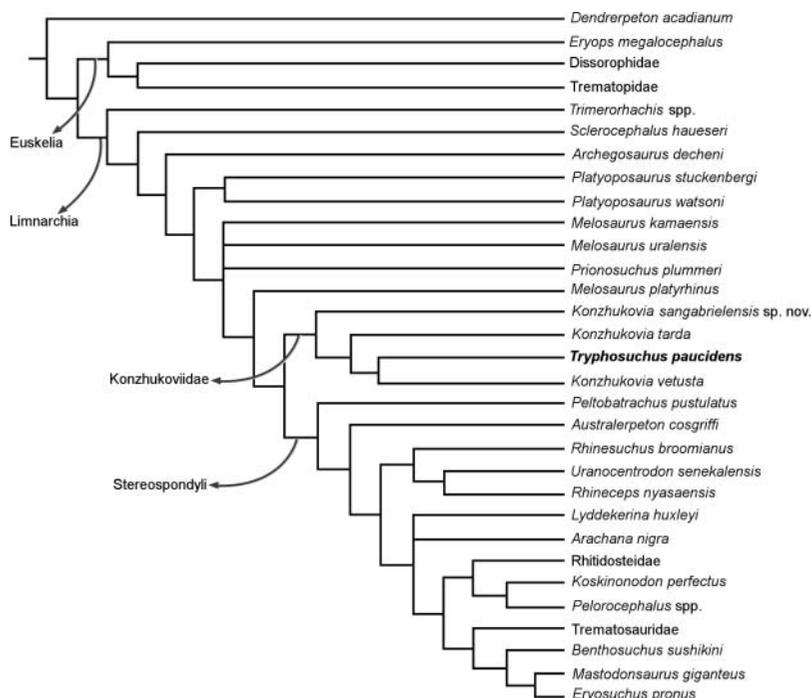
The vomer forms a narrow bar between the posterior margin of the anterior palatal fossa and the anterior end of the cultriform process, which is inserted into the vomer raising their edges and forming a narrow strip. The shagreen covering the ventral vomerian surface is not visible; this feature is present in other archegosauroids – for instance, *Archegosaurus* (Gubin 1997). Also, the vomer laterally sutures with the maxilla, and its posterolateral

process extends to the same level as the palatine tusks. This posterolateral process extends well anteriorly to the palatine tusks in *K. vetusta* and *K. tarda* (Gubin 1991) but posteriorly to the tusks in *Eryops* (Pawley & Warren 2006) and *Australerpeton* (Eltink & Langer 2014). The palatine forms the anteriormost lateral part of the interpterygoid vacuities. The pterygoids are fragmented and preserve only a small part of the palatine and quadrate rami. The palatine ramus of the pterygoid extends posteriorly to the level of the palatine tusks and anteriorly to the anteriormost ectopterygoid tooth. The contact is not observable between the palatine ramus of the pterygoid and the vomers, as occurs in archegosauroids. The retraction of the palatine ramus of pterygoid is common in derived stereospondyls (Schoch & Milner 2000; Yates & Warren 2000), but this character varies among early diverging stereospondyls, such as Rhinesuchidae (Eltink 2014). In *K. tarda*, the palatine ramus of the pterygoid extends anteriorly to the palatine tusks, whereas in *K. vetusta* it ends at the same level (Gubin 1991).

### Phylogenetic analysis

A recent publication (Eltink & Langer 2014) contains a comprehensive cladistic analysis using 133 characters to access the affinities of the rhinesuchid temnospondyl *Australerpeton cosgriffi*. The same data matrix is used in the current study, in which *Konzhukovia sangabrielensis* plus seven archegosauroids are added, in order to access the affinities of *K. sangabrielensis* and to test the monophyly of Archegosauroidea *sensu* Yates & Warren (2000). The seven added archegosauroids are *Platyoposaurus watsoni*, *Prionosuchus plummeri*, *Melosaurus uralensis*, *M. kamaensis*, *M. platyrhinus*, *Tryphosuchus paucidens* and *Kozhukovia tarda*. Other archegosauroids such as *Bageherpeton longignathus*, *Bashkirosaurus cherdyncevi*, *Colidosuchus tchudnovi*, *Uralosuchus tverdochebovae* and *Koinia silantjevi* were not included due to their fragmentary preservation and uninformative data. A total of 31 taxa were analysed. All representatives of the major temnospondyl groups comprising Eutemnospondyli *sensu* Schoch (2013) (Dissorophoidea, Eryopoidea, Trimerorhachoidea, Archegosauroidea and Stereospondyli) were included by Eltink & Langer (2014). *Dendrerpeton acadianum* (Holmes *et al.*, 1998) was used as outgroup as it is relatively complete and considered basal (Holmes *et al.* 1998; Holmes 2000; Schoch 2013; Eltink & Langer 2014).

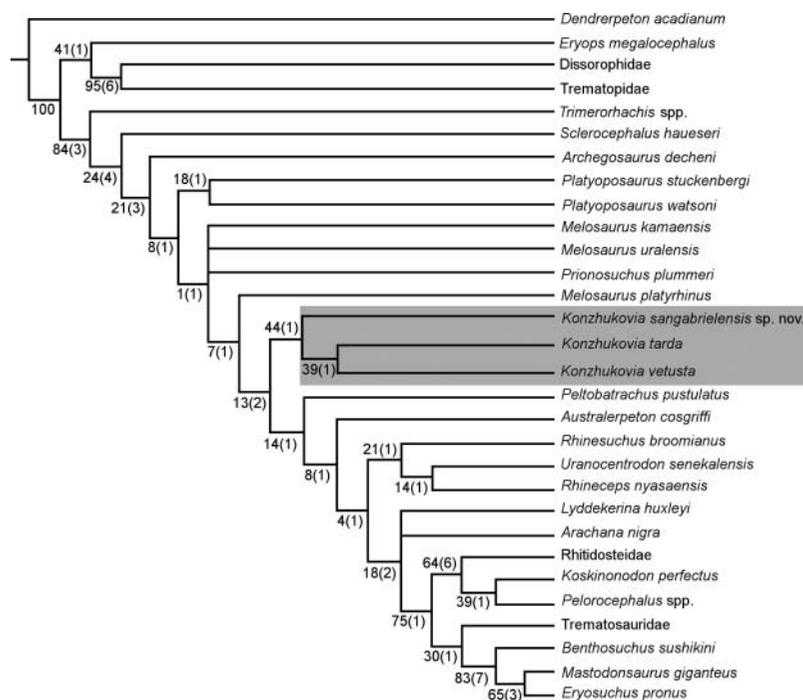
The phylogenetic analysis was performed with TNT version 1.1 (Goloboff *et al.* 2008) using a ‘traditional search’ (random seed = 0, tree bisection and reconnection (TBR), hold = 10). The multistate characters 14, 18, 33, 38, 45, 57, 71, 87 and 94 were treated as additive. The parsimony analysis resulted in six most parsimonious trees



**Figure 5.** Strict consensus of the six most parsimonious trees including the problematic *Tryphosuchus paucidens*, highlighted in bold.

(MPTs) which were found with 355 steps each (consistency index = 0.431; retention index = 0.674). The strict consensus tree is depicted in Figure 5. Due to the large amount of missing data and homoplasy, most nodes are

poorly supported: most decay indices are equal to 1, and bootstrap values are generally low (Fig. 6). This is a recurrent problem working with temnospondyl phylogenies, as the postcranial skeletons of most taxa are conservative



**Figure 6.** Strict consensus tree pruned of *Tryphosuchus paucidens* as it is considered a *nomen dubium*. The grey area encompasses Konzhukoviidae fam. nov. Tree length = 355 steps; consistency index = 0.431; retention index = 0.674. Bootstrap and Bremer support (between parentheses) values are indicated for each node.

and there is a large amount of missing data for many taxa (Pawley & Warren 2006; Pawley 2007).

## Results

Euskelia and Limnarchia *sensu* Yates & Warren (2000) were recovered, with Euskelia more basal than Limnarchia. Limnarchia is the large group that includes Dvinosauria (Trimerorhachidae), Stereospondylomorpha and Stereospondyli *sensu* Yates & Warren (2000). Stereospondylomorpha comprises Archegosauroida plus Stereospondyli. Overall, the topology of Stereospondyli in the strict consensus tree does not show significant differences to that proposed by Eltink & Langer (2014). Archegosauroida *sensu* Yates & Warren (2000) (= Archegosauriformes *sensu* Schoch & Milner 2000) was not recovered as a monophyletic group in the present analysis. Konzhukoviidae (=Tryphosuchinae; see below) was found to be the sister group of Stereospondyli and the only monophyletic clade among archegosauroids. *Konzhukovia sangabrielensis* sp. nov. is basal to the Russian taxa *K. vetusta* and *K. tarda* (Fig. 5).

## Discussion

### Remarks on the phylogenetic status of Archegosauroida

The phylogenetic status of Archegosauroida is controversial: previously recovered as the monophyletic sister group of Stereospondyli (Yates & Warren 2000; Ruta *et al.* 2003; McHugh 2012), it 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 Archegosauroida (e.g. whether it forms a clade or a grade) is an unsolved question in phylogenetic studies of Stereospondylomorpha. Other authors have also considered Archegosauroida as comprising successive paraphyletic taxa, closer to Stereospondyli than Actinodontidae, such as Milner (1990), Gubin (1997), Pawley & Warren (2005), Schoch & Witzmann (2009) and Witzmann & Schoch (2006). However, the analyses considering the Archegosauroida to be monophyletic (e.g. Yates & Warren 2000; McHugh 2012; Schoch 2013) encompass a small taxon sample of 'archegosauroid' taxa. In this contribution, we included a much larger number of archegosauroids, mainly 'higher' archegosauroids (e.g. Russian forms), in order to test their monophyly, to seek a better resolution of archegosauroid relationships and to determine the phylogenetic position of *Konzhukovia sangabrielensis*. Our results indicate that 'Archegosauroida' comprises successive paraphyletic

taxa, and only Konzhukoviidae fam. nov. is recovered as a monophyletic group in a sister-group relationship with Stereospondyli. 'Archegosauridae', comprising 'Archegosaurinae' plus 'Platyoposaurinae' and 'Melosaurinae' *sensu* Schoch & Milner (2000), was recovered as paraphyletic. The 'platyoposaurines' *Platyoposaurus watsoni* and *Platyoposaurus stuckenbergi* are sister taxa, whereas *Prionosuchus plummeri* was placed in a polytomy together with 'melosaurids'. The position of *Prionosuchus plummeri* is problematic, probably due to the large amount of missing data in the highly fragmentary holotype. Price (1948) included *P. plummeri* in the 'Archegosauridae', considering it to be a basal 'platyoposaurinae' associated with *P. stuckenbergi* and with *P. watsoni*. On the other hand, Cox & Hutchinson (1991) and Schoch & Milner (2000) considered *P. plummeri* to be a derived 'platyoposaurinae'. It is quite reasonable to suppose that after the discovery of more complete material of *P. plummeri*, the monophyletic status of Platyoposaurinae will receive better support. As with *K. sangabrielensis*, *P. plummeri* comes from Gondwana, and both are important in understanding the radiation of higher 'archegosauroids' and the early evolution of Stereospondyli. In a biostratigraphical reassessment of the Rio do Rasto Formation, Dias-da-Silva (2012) figured and made a preliminary assignment of the material now described as *Konzhukovia sangabrielensis* sp. nov. to 'Melosaurinae'. However, as already mentioned, 'Melosaurinae' is also paraphyletic and forms a polytomy comprising *Melosaurus uralensis*, *M. kamaensis* and *P. plummeri*. All of these taxa are related to a large clade that includes *M. platyrhinus*, which is basal to Konzhukoviidae fam. nov. plus Stereospondyli. 'Melosaurinae' and Konzhukoviidae are placed in an unsolved trichotomy according to Gubin (1991, p. 112) and recovered as sister groups by Ruta *et al.* (2007).

### *Tryphosuchus* and the 'Tryphosuchinae'

Before Golubev (1995) erected the subfamily 'Tryphosuchinae', 'Melosauridae' Fritsch, 1885 contained five genera: *Melosaurus* Meyer, 1857, *Konzhukovia* Gubin, 1991, *Tryphosuchus* Konzhukova, 1955, *Koinia* Gubin, 1993 and *Uralosuchus* Gubin, 1993. Golubev (1995) combined *Melosaurus* and *Koinia* into the subfamily 'Melosaurinae' Huene, 1931 (the type genus of which is *Melosaurus* Meyer, 1857). Thereafter, *Konzhukovia*, *Tryphosuchus* and *Uralosuchus* were combined into the subfamily 'Tryphosuchinae' (type genus *Tryphosuchus* Konzhukova, 1955).

The present analysis recovered 'Tryphosuchinae', represented by *Tryphosuchus paucidens*, *Konzhukovia vetusta*, *K. tarda* and *K. sangabrielensis*, as the monophyletic sister group of Stereospondyli. The Russian 'tryphosuchines' plus *Konzhukovia sangabrielensis*

encompass the only monophyletic ‘archegosauroids’ recovered, and *T. paucidens* is a fragmentary taxon nested among three much better preserved species of *Konzhukovia*. Also, the diagnosis of *T. paucidens* Konzhukova, 1955 *sensu* Schoch & Milner (2000) is unclear and based on quite incomplete material, as the features used to distinguish *T. paucidens* from *T. kinelensis* – shallow or deep excavatio tympanica, the angle of torsion of the humerus, and the dorsal blade of the ilium barely or distinctly divided – may be taphonomic. The ossified basioccipital forming most of the bilobed occipital condyle used in the diagnosis of *T. paucidens* is present in basal forms such as *Eryops megacephalus* and also Russian konzhukoviids such as *Konzhukovia vetusta* (Eltink 2014). Therefore, we consider this taxon a *nomen dubium* and purge it from the strict consensus tree (Fig. 6). An alternative solution would be erecting a new combination for this taxon, namely *Konzhukovia paucidens*, due to its assignment to *Konzhukovia*. In order to do so, it will be necessary to discover more complete material with a clear set of diagnostic characters that would allow revalidation of this taxon or provide a new combination for it. Likewise, the ‘tryphosuchines’ *Uralosuchus tverdochlebovae* and *Tryphosuchus kinelensis* are represented by very incomplete material: *Uralosuchus* comprises only a mandible, and *T. kinelensis* the right half of a pelvis, a humerus and skull fragments. The position of these specimens in the consensus tree is dubious, probably because of the small number of codeable characters; *Uralosuchus* is placed basally to the ‘archegosauroids’ and *T. kinelensis* is placed with derived stereospondyls. Therefore, we opted to purge these species from the data matrix. Hence, we erect the new family Konzhukoviidae fam. nov. to replace Tryphosuchinae in order to accommodate *Konzhukovia vetusta*, *K. tarda* and *K. sangabrielensis*, the new Brazilian species which is the basalmost konzhukoviid (Fig. 5).

### A konzhukoviid in Gondwana: palaeobiogeographical and phylogenetic implications

According to Schoch (2000), Steyer *et al.* (2006) 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 attained a trans-Pangaean distribution during the middle Permian: varanopid synapsids, nycteroleterid parareptiles, dinocephalians, biarmosuchians and basal anomodont therapsids (Rubidge 1991; Li 2001; Reisz & Laurin 2001, 2002; Lucas 2002; Sidor & Wellman 2003; Anderson & Reisz 2004; Sidor & Smith 2007; Botha-Brink & Modesto 2009; Cisneros & Tsuji 2009; Cisneros *et al.* 2011, 2012; Fröbisch & Reisz 2011; Dias-da-Silva 2012). Additional evidence supporting free faunistic transit between these Pangaean subcontinents comes from the presence of two fully aquatic ‘platyoposaurine

archegosauroids’ – *Prionosuchus plummeri* and *Bageherpeton longignathus* – in western Gondwana (Cox & Hutchinson 1991; Schoch & Milner 2000; Golubev 2000; Dias & Barberena 2001; Lucas 2005; Dias-da-Silva *et al.* 2009). In addition, Cisneros *et al.* (2015) recently reported new records from the Pedra do Fogo Formation (Cisuralian) that shed light on patterns of tetrapod distribution: two new temnospondyls, *Timonya anneae* and *Procuhy nazariensis*, rhinesuchid remains and the reptile *Captorhinus aguti* (Cope, 1882). The similarity of the tetrapod assemblage of the Pedra do Fogo Formation to contemporaneous equatorial communities from North America suggests that the range of these equatorial communities extended into the Gondwanan tropics and provides evidence that an extensive Pangaeian tropical biome was already established, at least during the early Permian (Cisuralian) (Cisneros *et al.* 2015). Moreover, the platyoposaurines *P. plummeri* and *B. longignathus*, and now the konzhukoviid *Konzhukovia sangabrielensis*, support evidence that Western Gondwanan non-stereospondyl Stereospondylomorpha played a significant role in temnospondyl radiation during the 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 favour of a migration route via western Pangaea, instead of across eastern Pangaea via the Cathaysian bridge (Sengör & Atayman 2009). The authors postulated a Pangaea B-type Morel & Irving (1981) 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 the Russian *K. vetusta* and *K. tarda* in Western Gondwana supports this hypothesis.

*Konzhukovia* is the best-known tryphosuchine (Schoch & Milner 2000) and the sutural pattern of its skull roof, structure of the palate, and occiput closely resemble those of rhinesuchid stereospondyls (Schoch & Milner 2000). Yates & Warren (2000) suggested that *Tryphosuchus* may be more closely related to later stereospondyls than to its contemporaneous ‘archegosauroids’, based on the sensory sulci on the lower jaw, ornamented pterygoids and presence of a single anterior palatal vacuity. Due to the similarities of both *Konzhukovia* and *Tryphosuchus* with Rhinesuchidae, Gubin (1997) suggested that the common ancestry of these taxa might help to solve the question of the origin of Stereospondyli.

Regarding the origin of Konzhukoviidae, two different scenarios can be proposed, taking into account the barrier-free connection between northern and southern Pangaea during the Permian. Firstly, ‘archegosauroids’ came from Laurasia to Gondwana, and the descendants of Gondwanan konzhukoviids later returned to Laurasia, where

more derived genera evolved. Further evidence possibly supporting 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. However, the derived genera of konzhukoviids may have evolved from ancestral stocks already in Laurasia. Secondly, similarly to Schoch's (2000) hypothesis, *Konzhukovia sangabrielensis* may have been part of the initial migration of 'archegosauroids' from Laurasia to Gondwana, probably during the 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 do Fogo Formation) and later reached the southern portion of this landmass during the middle–late Permian.

The basal position of both *P. plummeri* and *K. sangabrielensis* in comparison to Russian forms favours the first hypothesis, but the older stratigraphical distribution of Russian archegosauroids (Roadian) corroborates the second hypothesis. In both scenarios, vicariance processes might have occurred during speciation and consequent diversification. Thus, in spite of being the sister taxon of Stereospondyli, the internal 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 Palaeozoic taxa, all from Gondwana (Yates & Warren 2000) and represented by 'basal' forms: *Peltobatrachus pustulatus* from southern Africa; the rhinesuchid *Gondwanasaurus bijoriensis* and the dubious *Lysipterigium risinense* (Schoch & Milner 2000) from India (Werneburg & Schneider 1996); the rhytidosteid *Trucheosaurus major* (Marsicano & Warren 1998; Dias-da-Silva & Marsicano 2011) and the brachyopomorph *Bothriceps australis* from Australia (Warren & 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 & Schneider (1996) and Schoch & Milner (2000) considered it a 'platyoposaurine archegosauroid' closely related to *Platyoposaurus* and *Prionosuchus*. In a further description of the postcranial skeleton of *A. cosgriffi*, Dias & Schultz (2003) maintained its original assignment to Rhinesuchidae. Recent contributions place the Brazilian rhinesuchid in an intermediate position between 'Archegosauroidea' and Rhinesuchidae

(Witzmann & Schoch 2006; Schoch *et al.* 2007). Eltink & Langer (2014) placed *Australerpeton* within Stereospondyli and corroborated the position of *A. cosgriffi* as an advanced Rhinesuchidae (Eltink 2014; Eltink *et al.* 2015). The recently described *Parapytanga catarinensis*, a Permian temnospondyl from Gondwana (Strapasson *et al.* 2015), is nested within Stereospondylomorpha but outside Stereospondyli. In spite of its overall incompleteness, it shares similarities with South African rhinesuchids. Further information from more complete skeletons of *Parapytanga* might support its inclusion within Stereospondyli (Strapasson *et al.* 2015). *Arachana nigra*, a derived rhinesuchid-like form, was also described by Piñeiro *et al.* (2012) from the putative Permo–Triassic of Uruguay. It has a basal position within a large clade that comprises Trematosauria plus Capitosauria, quite similar to *Lydekkerina huxleyi* (Pawley & Warren 2005). Also, the suggested but still unidentified rhinesuchids from the Pedra do Fogo Formation would comprise the oldest known members of this clade (Cisneros *et al.* 2015).

The rhinesuchids from the Pedra do Fogo Formation, *Australerpeton* and also the possibility that *Parapytanga* belongs to the Rhinesuchidae, as well as the presence of several other Gondwanan stereospondyls in the Permian, corroborate the hypothesis of Ruta *et al.* (2007) that the basal diversification of the group occurred during the late Palaeozoic. Also, Warren *et al.* (2000) and Yates & Warren (2000) stated that Stereospondyli may have begun 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; this contribution). The presence of *Konzhukovia sangabrielensis* in South America, as well as similarities between Konzhukoviidae and Rhinesuchidae (endemic to Gondwana) (Schoch & Milner 2000; Yates & Warren 2000), strengthen the likelihood of this scenario.

### Acknowledgements

We are grateful to José Bicca for his kindness in permitting fieldwork on his property. SDS and EE thank Yuri Gubin, Mikhail Shishkin and Igor Novikov for their hospitality during a research visit to Russia and for allowing the examination of the temnospondyl collection of the Borissiak Paleontological Institute (PIN RAS, Moscow, Russia). We would like to thank an anonymous reviewer and J-Sébastien Steyer for their constructive comments, which helped us to improve the manuscript. We also thank Melise Peruchini for her technical support. This work was funded by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq Research Grant, process

number 301801/2012-6 to SDS) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES Scholarship to CPP and RTM).

## Supplemental data

Supplemental material for this article can be accessed at: <http://dx.doi.org/10.1080/14772019.2016.1164763>

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