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

Cristian Pereira Pacheco, Estevan Eltink, Rodrigo Temp Müller & Sérgio Dias-da-Silva

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 Archegosauroidea, Journal of Systematic Palaeontology

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

View supplementary material

Published online: 11 Apr 2016.

Submit your article to this journal

View related articles

View Crossmark data
A new Permian temnospondyl with Russian affinities from South America, the new family Konzhukoviidae, and the phylogenetic status of Archegosauroidea

Cristian Pereira Pacheco, Estevan Eltink, Rodrigo Temp Müller, and Sérgio Dias-da-Silva

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 archegosaurids and other well-supported groups of temnospondyls in order to access the affinities of the new Brazilian species and test the monophyly of Archegosauroidea. Archegosauroidea was not recovered as a monophyletic group, comprising successive paraphyletic taxa. The only monophyletic group of ‘archegosaurids’ 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.

Introduction

Temnospondyls 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 Platyposaurus (Dias & Barberena 2001); Autralerpeton 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...
(Malabarba et al. 2003); a skull from the 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).

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 PROCUBY NAZARIENSIS, and also rhinesuchid remains. Triassic strata in southern Brazil yielded several stereospondyls collected from the Sanga do Cabral Supersequence: San-gaia lavinai (Dias-da-Silva et al. 2006; Dias-da-Silva & Marsicano 2006); a partial skull fragment assigned to a mastodonsaurid (sensu Damiani 2001) (Feltrin et al. 2008; Da-Rosa et al. 2009); a plagiosternine plagosauroid (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 Stereospondyl (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 ?Mastodonsauroida (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.](image)
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* (Pânieiro et al. 2012), *Trucheosaurus major* (Marsicano & Warren 1998; Dias-da-Silva & Marsicano 2011). *Gondwanosaurus biforienisi* (Lydekker 1985), the dubious *Bothriceps australis* (Warren & Marsicano 1998, 2000), *Peltobatrachus pastulatus* (Panchen, 1959), and all of the South African Rhinesuchidae (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 (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 one 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 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 crevasses splay deposits and imundites 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 pareasaurid *Provelosaurus americanus*, the dinocephalian *Pampahenius biccai*, mandibular element of a temnospondyl, the new species described here, the basal anomodont *Tiarajudens excentricus* and an undescribed ptychacephalian 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 Barberena 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 Platyposaurusnae distribution. The Serra do Cadeado area corresponds to Posto Queimado (Capitanian), but may be also younger (Wuchiapinghian, 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. (2013) 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; UNIPAMPA: 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 archegosaurians or stereospondyls: tip of snout expanded so that the snout margins are parallel, or are concave before the tip (shared with archegosaurians); terminal crest lying lateral and parallel to the buttress of the paroccipital process (= external tabular crest; shared with archegosaurians); 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


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 paracoanal 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
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...
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 *Autralerpeton cosgriffi* and *Laccosaurus 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 archegosaurians (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 archegosaurians do not bear...
vomerine denticles (e.g. *Melosaurus* and *Platyopusaurus*). Based on their bases of insertion, the vomerine tusks are as large as the palatine tusks (9.1 mm), as in all Russian konzhukoviids. In other archegosauroids, such as *Platyopusaurus* (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 dunnii* (Polley & Reisz, 2011), Dendrerpetontidae such as *Dendrerpeton acadanum* (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 *Konzhukovia sangabrielensis*. Gubin (1991) noted that the absence of this bone is a common feature in all ‘archegosaurids’, but at least *Platyposaurus 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 postorbital 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 midlength 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 *Archegosaurus 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 quadrojugal 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 konzhukoviids and many other temnospondyls, although in long-snouted archegosauroids such as Platyposaurus (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 capitosaurids, whereas in several brachypterygids and rhynchocephalids 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 shagen 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 palateine 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 sangabrielenensis plus seven archegosauroids are added, in order to access the affinities of K. sangabrielenensis and to test the monophyly of Archegosauroidea sensu Yates & Warren (2000). The seven added archegosauroids are Platyposaurus watsoni, Priosuchus plummeri, Melosaurus uralensis, M. kamaensis, M. platyrhinus, Tryphosuchus paucident and Kozhukovia tarda. Other archegosauroid such as Baghepeton longignathus, Bashkirosaurus cherdynevii, Colidosuchus tchudnovi, Uralosuchus verdochovae and Koina 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, Trimerorhachioidea, 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.
(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 5. Strict consensus of the six most parsimonious trees including the problematic *Tryphosuchus paucidens*, highlighted in bold.

Figure 6. Strict consensus tree pruned of *Tryphosuchus paucidens* as it is considered a nomen dubium. The grey area encompasses Konzhukovidae 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 Archegosauroidia plus Stereospondyli. Overall, the topology of Stereospondyli in the strict consensus tree does not show significant differences to that proposed by Eltink & Langer (2014). Archegosauroi-consensus tree does not show significant differences to dyli. Overall, the topology of Stereospondyli in the strict sensu Stereospondyli nosauria (Trimerorhachidae), Stereospondylomorpha and archaeosauroids. Limnarchia is the large group that includes Dvinosauria (Trimerorhachidae), Stereospondylomorpha and Stereospondyli *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 ‘melosaurs’. 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 Platyoposaurus will receive better support. As with K. sangabrielensis, P. plummeri comes from Gondwana, and both are important in understanding the radiation of higher ‘archegosaurs’ and the early evolution of Stereospondyli. In a biostatigraphical 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’.

**Discussion**

**Remarks on the phylogenetic status of Archegosauridae**

The phylogenetic status of Archegosauridae 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 Archegosauridae (e.g. whether it forms a clade or a grade) is an unsolved question in phylogenetic studies of Stereospondylomorpha. Other authors have also considered Archegosauridae 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 Archegosauridae to be monophyletic (e.g. Yates & Warren 2000; McHugh 2012; Schoch 2013) encompass a small taxon sample of ‘archegosaurid’ taxa. In this contribution, we included a much larger number of archegosaurids, mainly ‘higher’ archegosaurids (e.g. Russian forms), in order to test their monophyly, to seek a better resolution of archegosaurid relationships and to determine the phylogenetic position of Konzhukovia sangabrielensis. Our results indicate that ‘Archegosauridae’ comprises successive paraphyletic taxa, and only Konzhokoviidae 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 ‘melosaurs’. 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 Platyoposaurus will receive better support. As with K. sangabrielensis, P. plummeri comes from Gondwana, and both are important in understanding the radiation of higher ‘archegosaurs’ and the early evolution of Stereospondyli. In a biostatigraphical 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 Konzhokoviidae 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’**


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 basiocipital 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 Tryphosuchidae in order to accommodate Konzhukovia vetusta, *K. tarda* and *K. sangabrieliensis*, 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-Pangaeans distribution during the middle Permian: varanopid synapsids, nycteropterid 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 ‘platyposaurine archegosauroids’ — *Prionosuchus plummeri* and *Bagheherpeton 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 annae* and *Prochury 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 Pangaean tropical biome was already established, at least during the early Permian (Cisuralian) (Cisneros et al. 2015). Moreover, the platyposaurines *P. plummeri* and *B. longignathus*, and now the konzhukoviid *Konzhukovia sangabrieliensis*, 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 Pangaean 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 suture 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 Gondwana konzhukoviids later returned to Laurasia, where
more derived genera evolved. Further evidence possibly supporting this hypothesis is the presence of dinosaurs and basal capitosaurs in South America, specifically in Permo-Triassic strata from Uruguay (see Piñeiro et al. 2007; Dias-da-Silva et al. 2009). Both capitosaurs and dinosaurs 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 sangabrielenensis may have been part of the initial migration of ‘archegosaurids’ from Laurasia to Gondwana, probably during the middle Permian. According to Dias & Barberena (2001), ‘archegosaurids’ 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 late Permian. The basal position of both P. plummeri and K. sangabrielenensis in comparison to Russian forms favours the first hypothesis, but the older stratigraphical distribution of Russian archegosaurids (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 Konzhukoviiidae 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: Peltopterus scutatus from southern Africa; the rhinesuchid Gondwana saurus bijoiensis and the dubious Lysipterigium rissense (Schoch & Milner 2000) from India (Werneburg & Schneider 1996); the rhytidosteid Trachoesuchus 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 archegosauid’ closely related to Platyposaurus 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 ‘Archegosaurideoidea’ 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 et al. 2014). The recently described Parapytanga catarinensis, a Permian temnospondyl from Gondwana (Strapasson et al. 2015), is nested within Stereospondylophoromorpha 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). Arachaneta 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 huyleyi (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 sangabrielenensis in South America, as well as similarities between Konzhukoviiidae 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 Boris-Siak 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 Melissa Perucchini 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

References


Barberena, M. C. 1998. Australepeton cogriffi n. g., n. sp., a Late Permian rhinosuchoid amphibian from Brazil. Anais da Academia Brasileira de Ciências, 70, 125–137.


Dias E. V. & Schultz C. L. 2003. The first Paleozoic temnospondyl postcranial skeleton from South America. Revista Brasileira de Paleontologia, 6, 29–42.


Dias-da-Silva, S. 2012. Middle–Late Permian tetrapods from the Rio do Rasto Formation, Southern Brazil: a biostatigraphic reassessment. Lethaia, 45, 109–120.


Dias-da-Silva, S., Sengupta, D. P., Cabreira, S. F. & Da Silva, L. R. 2012. The presence of Compsocerops (Brachyoopoidea: Chigutisauridae) (Late Triassic) in southern Brazil with comments on chigutisaurid palaeobiogeography. Palaeontology, 55, 163–172.


Lydekker, R. 1885. Indian Pre-tertiary Vertebrata. The labyrinthsodont from the Bijoji group. Palaeontology, 4, 1–16.


