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RESEARCH PAPER

Interrelationships, palaeobiogeography and early evolution of Stereospondylomorpha (Tetrapoda: Temnospondyli)

Estevan Eltink[1] · **Rainer R. Schoch**[2] · **Max C. Langer**[3]

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Abstract

The stereospondylomorph temnospondyls form a diverse group of early tetrapods that survived the Permian–Triassic extinction event and radiated during the Triassic. They encompass Carboniferous and Permian taxa from central and eastern Europe, such as 'archegosauroids', and early-divergent Gondwanan forms, such as rhinesuchids. By the Early Triassic, the group reached a worldwide distribution, with stereospondyls experiencing an impressive diversification and becoming major aquatic predators in fresh water, brackish, and even marine ecosystems. The origin of Stereospondyli dates back into the Permian, but the phylogenetic relationships of stereospondylomorphs, including 'archegosauroids' and the first stereospondyls remain unclear, representing the focus of the present study. Incorporating new records of the group to a broad revision of the different phylogenic hypotheses, a 37-taxon sample was scored for 221 morphological characters revised from previous works. The parsimony analysis resulted three most parsimonious trees (MPTs) of 737 steps. Their strict consensus tree depicts Sclerocephalidae and Intasuchidae as early-diverging stereospondylomorphs, 'Archegosauroidea' as paraphyletic array of taxa and Konzhukoviidae as the sister-group of a monophyletic Stereospondyli. An early-diverging and monophyletic Rhinesuchidae is divided into Australerpetinae and Rhinesuchinae, as the sister-group of the clade containing the Permian *Peltobatrachus pustulatus*, *Arachana nigra*, and a newly named clade (Superstes = 'survivors') of Triassic stereospondyls, formed by Lydekkerinidae and Neostereospondyli (Capitosauria and Trematosauria). Likelihood ancestral area reconstructions and time-ranging distributions along phylogeny provided a comprehensive description of early Stereospondylomorpha palaeobiogeography history. The initial evolution of the group took place in Laurasian areas (central and eastern Europe) during the Cisuralian and Guadalupian (early-mid Permian), with a broader Pangaean distribution for Platyoposauridae and Konzhukoviidae. Stereospondyls have Africa as their ancestral area, followed by dispersions to other Gondwanan regions during the Guadalupian and Lopingian (mid-late Permian), revealing a remarkable diversity previous to the P-Tr extinction. In the Triassic, Superstes greatly expanded across the Pangaea, highlighting another significant event in the evolution of Stereospondylomorpha.

Keywords Temnospondyli · Stereospondylomorpha · Permian · Systematics · Biogeography

Resumen

Los temnospóndilos estereospondilomorfos forman un grupo diverso de primeros tetrápodos que sobrevivieron al evento de la extinción Pérmico-Triásica y radiaron durante el Triásico. Ellos abarcan taxones del Carbonífero y el Pérmico de Centro y Este de Europa, tales como los "archegosauroides", y las primeras formas Gondwánicas divergentes, como los rhinesúquidos. Durante el Triásico Inicial, el grupo alcanzó una distribución mundial, con estereospóndilos experimentando una diversificación impresionante y convirtiéndose en grandes depredadores acuáticos en ecosistemas de agua dulce, salobre e incluso marinos. El origen de Stereospondyli data del Pérmico, pero las relaciones filogenéticas de los esterespondilomorfos,

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✉ Estevan Eltink
estevan.eltink@univasf.edu.br

Extended author information available on the last page of the article

incluyendo “archegosauroides” y los primeros estereospóndilos permanece poco clara, representando el foco del presente estudio. Incorporando nuevos registros del grupo a una amplia revisión de las diferentes hipótesis filogenéticas, una muestra de 37 taxones fue codificada para 221 caracteres morfológicos revisados de trabajos previos. El análisis de parsimonia resultó en tres arboles más parsimoniosos (MPTs en sus siglas en inglés) de 737 pasos. El árbol de consenso estricto representa Sclerocephalidae y Intasuchidae como los primeros estereospondilomorfos divergentes, “Archegosauroidea” como un grupo parafilético de taxones y Konzhukoviidea como el grupo hermano del monofilético grupo Stereospondyli. Rhinesuchidae es monofilético, divergió tempranamente y se divide en Australerpetinae y Rhinesuchinae, como el grupo hermano del clado que contiene el taxón Pérmico Peltobatrachus pustulatus, Arachana nigra, y el nuevo clado aquí nombrado (Superestes=`supervivientes’) de estereospóndilos Triásicos, formado por Lydekkerinidae y Neostereospondyli (Capitosauria y Trematosauria). La reconstrucción del área ancestral potencial y distribución de rangos temporales a lo largo de la filogenia proporcionan una descripción exhaustiva de la historia paleobiogeográfica de Stereospondylomorpha. La evolución inicial del grupo tuvo lugar en áreas de Laurasia (Europa Central y del Este) durante el Cisuraliense y Guadalupiense (Pérmico inicial-medio), con una amplia distribución en Pangea de Platyoposauridae y Konzhukoviidae. Los esterespóndilos tuvieron África como su área ancestral, seguido de dispersiones en otras regiones Gondwánicas durante el Guadalupiense y Lopingiense (Pérmico medio-tardío), revelando una remarcable diversidad previa a la extinción Pérmico-Triásica. En el Triásico, Superstes se expandió enormemente a través de Pangea, destacando otro evento significativo en la evolución de Stereospondylomorpha.

Palabras clave Temnospondyli · Stereospondylomorpha · Pérmico · Sistemática · Biogeografía

1 Introduction

Temnospondyls comprise the most diverse group of early tetrapods, including about 200 genera and spanning from the Early Carboniferous to the late Early Cretaceous (Milner 1990; Schoch 2013). Following the general pattern of Milner (1990), temnospondyls are divided into five major groups: Edopoidea, Trimerorhachoidea, Eryopoidea, Dissorophoidea, and Archegosauroidea, the latter including the highly diverse Stereospondyli (Schoch 2013). The interrelationships of major temnospondyl groups remain poorly understood, despite recent progress in some parts of the tree (Schoch and Milner 2000; Yates and Warren 2000; Ruta et al. 2007; Schoch 2013). ‘Archegosauroids’ correspond to the Stereospondylomorpha sensu Yates and Warren (2000), which has been shown to be monophyletic, although different authors have divergent concepts about the clade, especially regarding the possible inclusion of brachyopids, *Peltobatrachus*, and plagiosaurids (e.g. Yates and Warren 2000; Schoch and Milner 2014).

Among early-divergent stereospondylomorphs, recent revisions of Carboniferous–Permian forms of central Europe have added data to the understanding of *Sclerocephalus* (Boy 1988; Schoch and Witzmann 2009a), *Glanochthon* (Schoch and Witzmann 2009b), *Archegosaurus* (Witzmann 2005), and *Cheliderpeton* (Werneburg and Steyer 2002). New species have been proposed for well-known stereospondylomorph genera such as *Intasuchus*, *Platyoposaurus*, *Konzhukovia*, and *Triphusuchus* (Gubin 1991, 1997; Shishkin et al. 2000). Often referred to as putative Stereospondyli ‘ancestors’, both *Konzhukovia* and *Triphosuchus* have been considered phylogenetically close, and the understanding of their relationships helped shedding light on the origin of Stereospondyli (Schoch and Milner 2000; Yates and Warren 2000). In addition, the close relationship of Laurasian forms with Gondwanan early-diverging stereospondyls such as *Prionosuchus plummeri* (Price 1948; Cox and Hutchinson 1991) and *Konzhukovia sangabrielensis* (Pacheco et al. 2017), suggest a trans-Pangaean distribution for the group during the mid-Permian (Schoch 2000).

The first stereospondyls appeared in the mid-late Permian (Warren et al. 2000), mostly represented by Rhinesuchidae (Damiani and Rubidge 2003; Eltink et al. 2016; Marsicano et al. 2017), but also including *insertae sedis* forms such as *Peltobatrachus pustulatus* (Panchen 1959). Outside of Africa, the diversity of early Stereospondyli is represented by *Arachana nigra* (Piñeiro et al. 2012), *Parapytanga catarinensis* (Strapasson et al. 2015), and the long-snouted rhinesuchid *Australerpeton cosgriffi* (Barberena 1998; Dias and Schultz 2003; Eltink et al. 2016), all from South America. The Permian diversity is still represented by fragmentary fossils from India (Wernerburg and Schneider 1996). Surviving the end-Permian mass extinction, stereospondyls reached a widespread distribution and noteworthy abundance during the Early Triassic (Milner 1990; Schoch and Milner 2000). The first Triassic stereospondyls known from the Induan includes the miniaturized Lydekkerinidae, *Lydekkerina huxleyi* and *Eolydekkerina magna* (Shishkin et al. 1996; Jeannot et al. 2006). Other stereospondyls such as Capitosauria, Trematosauria, and Rhytidostoidea show a broad range of ecomorphotypes, and occur throughout the Triassic (Schoch 2000; Schoch and Milner 2000; Damiani 2001; Schoch 2013).

Although receiving recent attention due to new or redescribed taxa (e.g. Schoch and Witzmann 2009a), the Permian diversity of Stereospondylomorpha still lack a comprehensive phylogenetic study including taxa from all major groups, such as Sclerocephalidae, Intasuchudae, Platyoposauridae, Melosauridae, Konzhukovidae, and Rhinesuchidae. Also, the diversity recovered from different areas, such as central and eastern Europe, South America and Africa, offers a unique opportunity to explore biogeographic patterns in the Permian. Hence, this work aims to explore the phylogenetic relationships of Stereospondylomorpha and early-diverging Stereospondyli, providing phylogenetic definitions, mapping synapomorphies along the topology, and proposing paleobiogeographc scenarios, via ancestral area reconstructions, for the early history of Stereospondylomorpha and the origins of Stereospondyli.

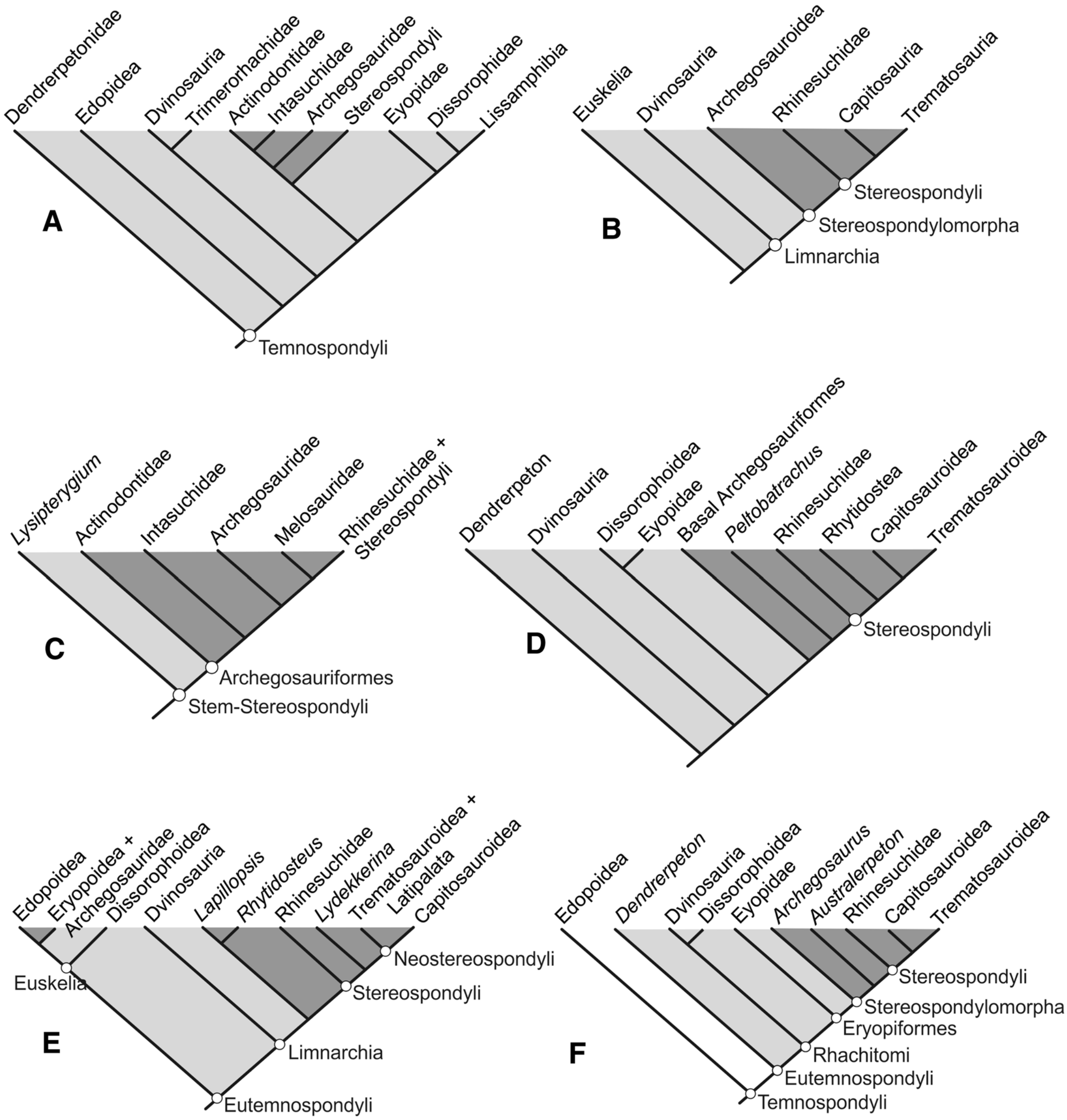


Fig. 1 Phylogenetic hypotheses of Temnospondyli demonstrating the relationships of Stereospondyli and Stereospondylomorpha. **a** Milner (1990). **b** Yates and Warren (2000). **c** Schoch and Milner (2000). **d** Ruta et al. (2007). **e** McHugh (2012). **f** Schoch (2013). The dark gray areas demonstrate the taxonomic coverage proposed for Stereospondylomopha. Light gray areas demonstrate the taxonomic coverage of the present phylogenetic analysis

2 Materials and methods

The selection of Operational Taxonomic Units (UTOs) for the phylogenetic study focused on understanding Stereospondylomorpha relationships (Fig. 1). *Sclerocephalus haueseri*, *Cheliderpeton vranyi*, *Intasuchus silvicola*, and '*Glanocthon latirostre* (Schoch and Witzmann, 2009b) were included in the ingroup following Yates and Warren (2000). Selected 'archegosaurs' (= Archegosauroidea; Yates and Warren 2000; = Archegosauriformes, Schoch and Milner 2000) included *Archegosaurus decheni*, the South-American *Prionosuchus plummeri*, and russian platyoposaurines as *Platyoposaurus stuckenbergi*, *P. watsoni*, and *Collidosuchus tchudinovi*. Melosauridae, a proposed sister-group of stereospondyls (Schoch and Milner 2000), is represented by *Melosaurus uralensis*, *M. platyrhinus*, and *M. kamaensis*, whereas Konzhukoviidae ('Triphosuchinae') includes *Konzhukovia vetusta*, *K. tarda*, *K. sangabrielensis*, and *Tryphosuchus paucidens*. *Parapytanga catarinesis*, a *insetae sedis* stereospondylomorph (Strapasson et al. 2015), has also include as an OTU. Rhinesuchids are represented by *Uranocentrodon senekalensis*, *Broomistega putterili*, *Laccosaurus watsoni*, *Rhinesuchoides capensis*, *Rhinesuchus whaitsi*, *Rhinesuchoides tenuiceps*, *Rhineceps nyasaensis* and *Australerpeton cosgriffi*. Until recently, this group was poorly represented in phylogenetic analyses of Stereospondyli (Yates and Warren 2000; Damiani 2001; Schoch 2013, but Eltink et al. (2016) and Marsicano et al. (2017) recently published a long-awaited taxonomic revision for the group. The latter revision was incorporated in the present work, resulting in updates relative to the study of Eltink et al. (2016), such as '*Rhinesuchus broomianus'* being considered as junior synonym of *Rhinesuchus waitsi* and '*Rhinesuchus*' *capensis* being assigned to *Rhinesuchoides*. Yet, contrary to Marsicano et al. (2017), we do not assign the specimen BP-1-4473 to *Laccosaurus watsoni*. Other stereospondyls of the analysis include *Peltobatrachus pustulatus*, *Arachana nigra*, and *Lapillopsis nana*, in addition to well-known Triassic representatives of major groups such as the lydekkerinids *Eolydekkerina magna* and *Lydekkerina huxleyi*, as well as *Benthosuchus sushkini*, *Mastodonsaurus giganteus*, and *Trematolestes hagdorni*. See the taxon list in the supplementary information.

The outgroup is composed by *Dendrerpeton arcadianum*, *Eryops megacephalus* (Eryopidae), and *Trimerorhachis insignis* (Trimerorhachidae). These taxa are almost always nested outside to the ingroup clade (Milner 1990; Yates and Warren 2000; Schoch 2013), but McHugh (2012) found archegosauroids more closely related to Eryopoidea than to Stereospondyli. Indeed, the choice of outgroup taxa also intended to allow testing the relations among Archegosauridae, Eryopidae, and Stereospondylomorpha. The topologies were rooted in *Dendrerpeton arcadianum*, a generalized temnospondyl that is relatively complete and considered an early-divergent representative of group (Schoch and Milner 2014).

The morphological characters for the analysis were selected based on the matrix of Eltink et al. (2016; see the character list in supplementary material). The taxon-character matrix (37/221) was constructed using the software Mesquite version 2.75 (Maddison and Maddison 2011), and the parsimony searches were performed using TNT version 1.1 (Goloboff et al. 2008) under 'traditional search' with 10000 replicates, randomly adding of taxa (random seed = 0), *hold* = 20, and TBR (tree bisection and reconnection) algorithm. Characters that represent transformation series were ordered (26, 27, 29, 30, 43, 52, 54, 61, 62, 64, 76, 99, 130, 138, 146, 153, 163, 172, 177, 185). Bootstrap (Holmes 2003) and Bremer supports (Bremer 1994) were calculated using the TNT (10000 replicates).

The ancestral areas were reconstructed by defining geographical areas for each OTU (generic categorical character/taxa) and plotting them on the strict consensus tree using Mesquite version 2.75 (Maddison and Maddison 2011). Geographic areas were coded as follows: 0: North America; 1: Central Europe; 2: Eastern Europe; 3: South America; 4: Africa; 5: Australia. Two different methods were used for the ancestral area reconstruction: parsimony and likelihood ancestral states. Due to the high endemism observed in the Stereospondylomorpha, both methods resulted the same optimized distribution. However, the maximum likelihood reconstruction shows proportional likelihoods for each node, which allow better discussion of ancestral areas. The parameters for marginal probability recognition were based on Mk1 model and threshold value was set at 2.

3 Results

The analysis recovered three most parsimonious trees (MPTs) of 737 steps (consistency index = 0.351; retention index = 0.566). The strict consensus of which, including Bremer support and values of bootstrap, is shown in Fig. 2. The MPTs show that the only floating taxon is *Collidosuchus*, resulting in a politomic clade "6" (Fig. 2). Below we provide the inclusivity, supporting synapomorphies, and statistics for each recovered clade, plus phylogenetic definitions of key names when necessary. All synapomorphies of the recovered clades are listed in the electronic supplementary information.

1. Eryopiformes. Synapomorphies: 3 (1); 19 (1); 30 (1); 42 (1); 44 (1); 54 (1); 55 (1); 59 (1); 64 (2); 70 (1); 89 (0); 105 (1); 117 (1); 175 (0); 185 (1); 211 (1). Support: Bootstrap = 90%, Bremer support = 10.
2. Stereospondylomorpha. Synapomorphies: 7 (3); 62 (1); 96 (1); 149 (1); 190 (1); 194 (1). Support:

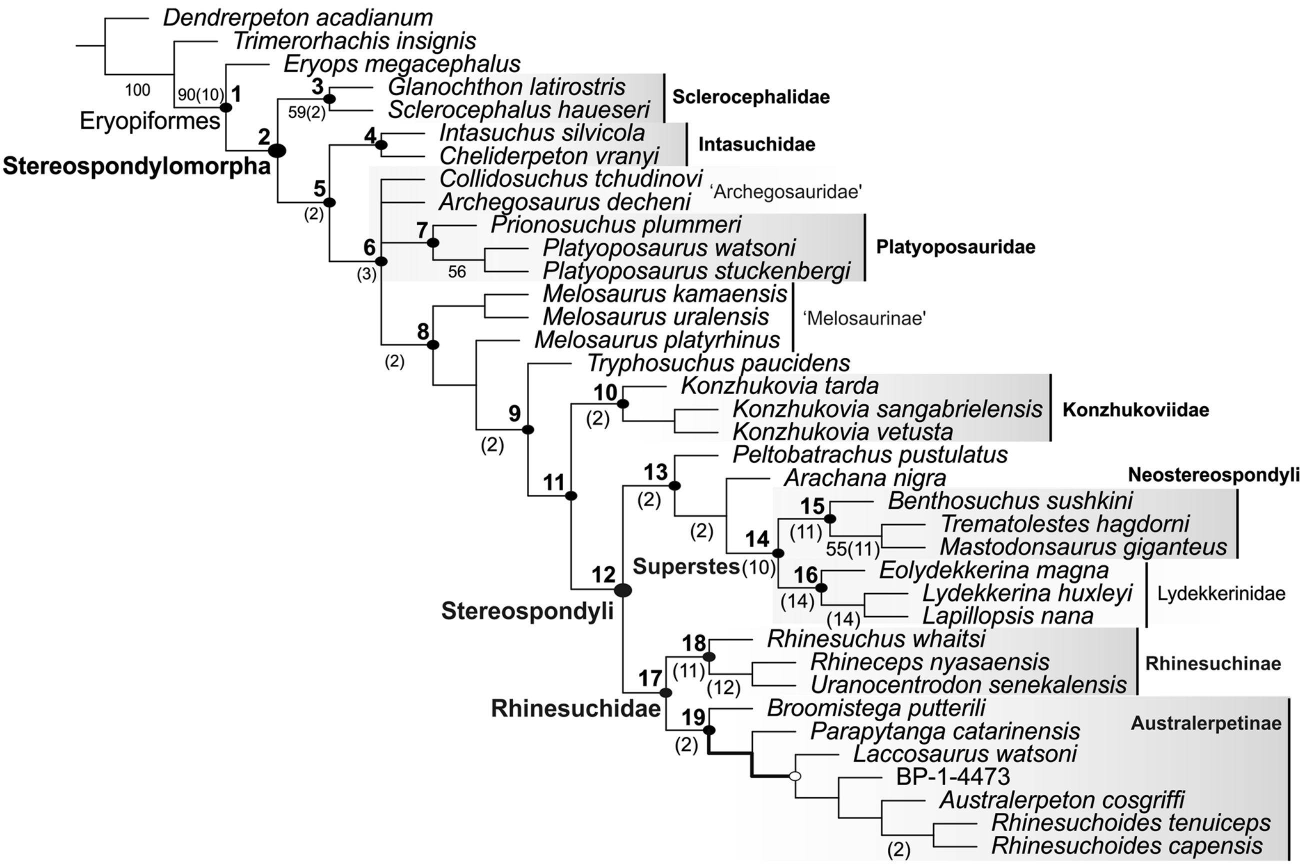


Fig. 2 The strict consensus tree resulted from three most parsimonious trees, with 737 steps, depicting the phylogenetic relationship of Stereospondylomorpha. Decay indices (Bremer support) with values above 1 are given below the nodes. Bootstrap percentages are given after the Bremer support values (ins) for clades with values above 50%. The nodes (black dots) are listed for mapping synapomorphies (see results for detail). Gray areas indicate supra generic taxa. The thick line in the Rhinesuchidae clade indicates a changing of Australerpetinae phylogenetic definition

Bootstrap = 28%, Bremer support = 1. Definition (branch-based). The most inclusive clade containing *Uranocentrodon senekalensis* and *Mastodonsaurus giganteus*, but not *Eryops megacephalus* (Schoch 2013).

3. Sclerocephalidae. Synapomorphies: 33 (1); Char. 35 (1); 37 (1); 63 (0); 94 (1); 137 (1). Support: Bootstrap = 59%, Bremer support = 2. Definition (node-based). The least inclusive clade containing *Glanochthon latirostre* and *Sclerocephalus haueseri*.
4. Intasuchidae. Synapomorphies: 29 (1); 45 (1); 68 (1). Support: Bootstrap = 31%, Bremer support = 1. Definition (node-based). The least inclusive clade containing *Intasuchus silvicola* and *Cheliderpeton vranyi*.
5. Intasuchidae + 'Archegosauridae' + 'Melosauridae' + Konzhukoviidae + Stereospondyli. Synapomorphies: 61 (2); 110 (1); 122 (1); 123 (2). Support: Bootstrap = 32%, Bremer support = 2.
6. 'Archegosauridae' + Platyoposauridae + 'Melosaurinae' + Konzhukoviidae + Stereospondyli. Synapomorphies: 1 (1); 2 (1); 12 (1); 22 (1); 65 (1); 74 (1); 78 (1); 87 (0); 96 (2); 131 (1). Support: Bootstrap = 36%, Bremer support = 3.
7. Platyoposauridae. Synapomorphies: 3 (0); 5 (1); 73 (1); 76 (1); 215 (0). Support: Bootstrap = 22%, Bremer support = 1. Definition (node). The least inclusive clade containing *Platyoposarus stuckenbergi* and *Prionosuchus plummeri*.
8. 'Melosaurinae' + *Tryphosuchus* + Konzhukoviidae + Stereospondyli. Synapomorphies: 7 (2); 22 (0); 37 (1); 69 (1); 100 (1); 102 (1); 119 (1); 126 (1); 148 (0). Support: Bootstrap = 17%, Bremer support = 2.
9. *Tryphosuchus* + Konzhukoviidae + Stereospondyli. Synapomorphies: 82 (1); 85 (1); 92 (0); 112 (1). Support: Bootstrap = 11%, Bremer support = 2.
10. Konzhukoviidae. Synapomorphies: 24 (0); 39 (1); 101 (2); 119 (0). Support: Bootstrap = 19%, Bremer support = 2. Definition (node-based). The least inclusive clade containing *Konzhukovia vetusta*, *Konzhukovia tarda* and *Konzhukovia sangabrielensis*.

11. Konzhukoviidae + Stereospondyli. Synapomorphies: 121 (0); 161 (0). Support: Bootstrap = 2%, Bremer support = 2.
12. Stereospondyli. Synapomorphies: 1 (0); 6 (0); 11 (0); 12 (0); 40 (0); 57 (1); 64: (1); 70 (0); 78 (0); 105 (2); 111 (2); 115 (2); 116 (1); 125 (0); 130 (1). Support: Bootstrap = 31%, Bremer support = 2. Definition (branch-based). The most inclusive clade containing *Mastodonsaurus giganteus* and *Rhinesuchus whaitsi*, but not *Konzhukovia vetusta*.
13. *Arachana* + *Peltobatrachus* + Superstes. Synapomorphies: 32 (1); 153 (1); 178 (1); 182 (1). Support: Bootstrap = 11%, Bremer support = 2.
14. Superstes clade nov. Synapomorphies: 27 (1); 33 (1); 113 (1); 115 (1); 132 (1); 137 (1). Support: Bootstrap = 10%, Bremer support = 10. Definition (node-based). The least inclusive clade containing *Lydekkerina huxleyi* and *Mastodonsaurus giganteus*.
15. Neostereospondyli. Synapomorphies: 7 (3); 103 (2); 110 (0); 117 (0); 120 (0); 191 (1); 195 (1); 196 (1); 219 (1). Support: Bootstrap = 42%, Bremer support = 11. Definition (branch-based). The most inclusive clade containing *Mastodonsaurus giganteus* and *Trematolestes hagdorni*, but not *Lydekkerina huxleyi*.
16. Lydekkerinidae. Synapomorphies: 6 (1); 15 (1); 67 (0); 69 (0); 96 (1). Support: Bootstrap = 2%, Bremer support = 14. Definition (branch-based). The most inclusive clade containing *Lydekkerina huxleyi*, but not *Mastodonsaurus giganteus*.
17. Rhinesuchidae. Synapomorphies: 3 (0); 7 (1); 8 (0); 61 (3); 92 (3); 130 (2); 143 (0); 144 (1); 215 (0); 218 (1). Support: Bootstrap = 6%, Bremer support = 2. Definition (node-based). The most inclusive clade containing *Australerpeton cosgriffi* and *Rhinesuchus whaitsi*.
18. Rhinesuchinae. Synapomorphies: 19 (0); 133 (1); 148 (1); 166 (1). Support: Bootstrap = 0%, Bremer support = 11. Definition (branch-based). The most inclusive clade containing *Rhinesuchus whaitsi*, but not *Australerpeton cosgriffi* or *Laccosaurus watsoni*.
19. Australerpetinae. Synapomorphies: 4 (0); 113 (1); 118 (1); 138 (1); 157 (1). Support: Bootstrap = 0%, Bremer support = 2. Definition (branch-based). The most inclusive clade containing *Australerpeton cosgriffi*, but not *Rhinesuchus whaitsi*.

4 Discussion

4.1 Topology, synapomorphies and phylogenetic definitions

Our results recover Eryopiformes as the sister-group of Stereospondylomorpha (Schoch 2013), differing from the Euskelia concept as proposed by Yates and Warren (2000), in which *Trimerorhachis insignis* is closer to Stereospondylomorpha than *Eryops megacephalus*. As for Stereospondylomorpha, its node-based definition proposed by Yates and Warren (2000) uses *Archegosaurus* and *Parotosuchus* as internal specifiers. However, applying this definition in the present hypothesis excludes Sclerocephalidae and Intasuchidae from stereospondylomorphs. Schoch (2013) proposed a new definition for the group, as the most inclusive clade containing *Uranocentrodon senekalensis* and *Mastodonsaurus giganteus*, but not *Eryops megacephalus*, which is followed here. Synapomorphies mapped for the clade include: a terminal crest lying lateral and parallel to the buttress of the paroccipital process (62-1), which was found as an ambiguous synapomophy of Capitosauria by Yates and Warren (2000: character 29); the presence of palatine teeth (96-1), a transformation series (Yates and Warren 2000) leading to more than eight teeth (96-2) in clade “8” (except for reversions such as in Lydekkerinidae); the contribution of the splenial to the mandible symphysis (149); and pronounced anteroposterior elongation in the clavicle (190 and 194) compared with Eryopidae (Witzmann and Voigt 2015). The relative increase in length of the interclavicle was considered a synapomorphy for the clade in the analysis of Witzmann and Schoch (2006). The dorsal contact of the nasal and maxilla (71) was found as synapomorphies of the clade by Yates and Warren (2000) and Schoch (2013). This is confirmed here, but the lacrimal separates the nasal and maxilla in the Intasuchidae.

If ‘Archegosauroidea’ (or Archegosauriformes) forms a clade is a recurrent question in studies of stereospondylomorphs (Schoch 2013). For Milner (1990), Gubin (1997), Pawley and Warren (2005), Schoch and Witzmann (2009b), and Witzmann and Schoch (2006), the group is paraphyletic, with ‘Archegosauridae’ closer to Stereospondyli than Sclerocephalidae. For Yates and Warren (2000), Ruta et al. (2003), and McHugh (2012), ‘Archegosauroidea’ is considered monophyletic, but in the first two studies, the clade is sister to Stereospondyli, and in the latter it is part of the Eryopoidea/Euskelia group. Here, ‘Archegosauroidea’ is recovered as paraphyletic, composed by successive clades: Sclerocephalidae, Intasuchidae, Platyoposauridae, and Konzhukovidae, towards Stereospondyli (Fig. 2).

The earliest branching Stereospondylomorpha lineage is Sclerocephalidae (node 3, Fig. 2), with *Sclerocephalus haueseri* and *Glanochthon latirostre* as sister-taxa, as also found by Yates and Warren (2000). The phylogenetic definition of Sclerocephalidae (Actinodontidae), by Yates and Warren (2000) includes *Sclerocephalus haueseri* and all archegosauroids sharing a more recent common ancestor with it than with *Archegosaurus*. As for Intasuchidae, the present analysis found it (node 4, Fig. 2) closer to ‘Archegosauridae’ than to Sclerocephalidae, and formed by *Intasuchus* *silvicola* and *Cheliderpeton vranyi*. This differs from the hypotheses of Schoch and Milner (2000), Ruta et al. (2007), and Schoch and Witzmann (2009b), in which *Glanochton latirostre* appears closer to *Intasuchus silvicola* (Schoch 2013). Stayton and Ruta (2006) found a remarkable separation in skull morphospace between *Glanochthon latirostre* and *Intasuchus silvicola*, due to the longer snout of the latter. Yet, synapomorphies found for Sclerocephalidae indicated a slight elongation also in that clade, as defined by the elongation of the nasal (33) and narrowing of the lacrimal (35, 37).

The relationships of “Clade 6” (Fig. 2) show ‘Archegosauridae’ in a polytomy that encompasses *Archeosaurus decheni* and *Collidosuchus tchudinovi*, and *Platyoposaurus watsoni*, *Platyoposaurus stuckenbergi* and *Prionosuchus plummeri*, forming Platyoposaurinae (Schoch and Milner 2000). The paraphyletic ‘Archegosauridae’ is observed in Gubin (1997) and Schoch et al. (2007), differing from the monophyletic ‘Archegosauridae’ of Yates and Warren (2000). The position of *Collidosuchus tchudinov* varies among the obtained MPTs, being either the earliest diverging lineage of ‘Clade 6’, sister-taxon of *Archeosaurus decheni*, or closer to Platyoposaurinae. The synapomorphies supporting ‘Clade 6’ are related to the skull elongation (1, 2, 12), vomerine plate elongation (78), increasing of palatine tooth number (96), and retraction of anterior pterygoid extension (131), which are all well-known stereospondyl traits. These characters support Gubin (1997) and Schoch and Milner (2000) hypotheses, in which the group is characterizes by its anteroposterior skull elongation. The presence of a palatal tubercle in the anterior palatal region (65) is regarded as synapomorphic for the clade, in agreement with Gubin (1997) and Yates and Warren (2000). Based on its supposed monophyly, Yates and Warren (2000) defined Archegosauridae as a stem-based taxon including *Archegosaurus*, and all archegosauroids that share a more recent common ancestor with it than with *Sclerocephalus*, but this cannot be adequately applied in the results obtained here, as it would include Stereospondyli. Within ‘Archegosauridae’, the notorious long-snouted Platyoposaurinae (sensu Schoch and Milner 2000) form a clade (node 7, Fig. 2) composed of the genus *Platyoposaurus* and *Prionosuchus plummeri*. Synapomorphies of group are also related to the skull elongation, as observed in the elongation of the naris (5). The clade differs from other ‘archegosaurids’ by the flat preorbital region (3), the maxillary morphology marked by a stepped margin, correlated with enlarged teeth (73), and the lateral processes of vomer and palatine approaching one another so as to reduce the maxillary contribution to the margin of the choana (76).

Schoch and Milner (2000), divided Melosauridae in two groups, ‘Melosaurinae’ and ‘Tryphosuchinae’, and previous works show the related taxa forming either a paraphyletic group (Gubin 1997), or a clade (Ruta et al. 2007). In the present analysis, ‘Melosauridae’ was recovered as paraphyletic, with *Melosaurus uralensis* and *Melosaurus kamaensis* as sister-taxa, and *Melosaurus platyrhinus* as sister to a clade containing *Tryphosuchus paucidens,* Konzhukoviidae, and Stereospondyli. Pacheco et al. (2017) erected Konzhukoviidae, including *Tryphosuchus paucidens*. In the present analysis, the family is recovered as monophyletic (node 10, Fig. 2), but composed only of *Konzhukovia sangabrielensis* and *Konzhukovia vetusta* forming the sister-clade to *Konzhukovia tarda*. This differs from the proposal of Gubin (1997), in which *Konzhukovia* is closer to *Melosaurus* than to Stereospondyli. The synapomorphies of Konzhukoviidae (Figs. 3, 4) include a narrower interorbital distance (24), the lateral orbital margin without prefrontal contribution (39), anterior tapering interpterygoid vacuities (101), and short articulation between parasphenoid and pterygoid (119). The anterior tapering of the interpterygoid vacuities is also seen in some Australerpetinae, such as *Rhinesuchoides* and *Australerpeton*. The anteroposterior elongation of the skull seen in konzhukoviids is typical of non-Stereospondyli stereospondylomorphs. However, characters of the occiput and the posterior palate distinguish them form other members of that grade (Eltink et al. 2016). The absence of a parasphenoid central depression (121) is synapomorphic for the Konzhukoviidae plus Stereospondyli clade, but the short articulation between parasphenoid and pterygoid (119) is not seen in the latter group (Fig. 5).

The present analysis found Stereospondyli (node 12, Fig. 2) divided in two groups: Rhinesuchidae and the lineage of Triassic stereospondyls plus *Arachana nigra* and *Peltobatrachus pustulatus*. The monophyly of this group was previously recovered in the analyses of Milner (1990), Yates and Warren (2000), Witzmann and Schoch (2006), Schoch et al. (2007), Schoch (2013), Eltink et al. (2016), Marsicano et al. (2017). Compared to non-Stereospondyli stereospondylomorphs, it is possible to see a reversion from the long-snouted condition, as evident in the parabolic shape of the preorbital region (1), the internarial distance narrower than the interorbital distance (11), snout margins continually converging towards their tip (12), and a short vomerine plate, as wide as long (78). Other important synapomorphies are observed in the occipital region, with the tabular and exoccipital contacting the paroccipital process (57), in the parasphenoid/pterygoid morphology, as seen in the ventral pockets of the parasphenoid (105), the internal carotid and intracranial branches passing through the dorsal surface of the parasphenoid plate (111), the parasphenoid denticle field enlarged to a transverse ‘belt’ (115), the anteroventral margin of the pterygoid and parasphenoid corpora bearing a line of insertion for the palatal mucous membrane covering the interperygoid vacuities (116), lack of sulcus behind the pterygoid articulation on the ventral surface the

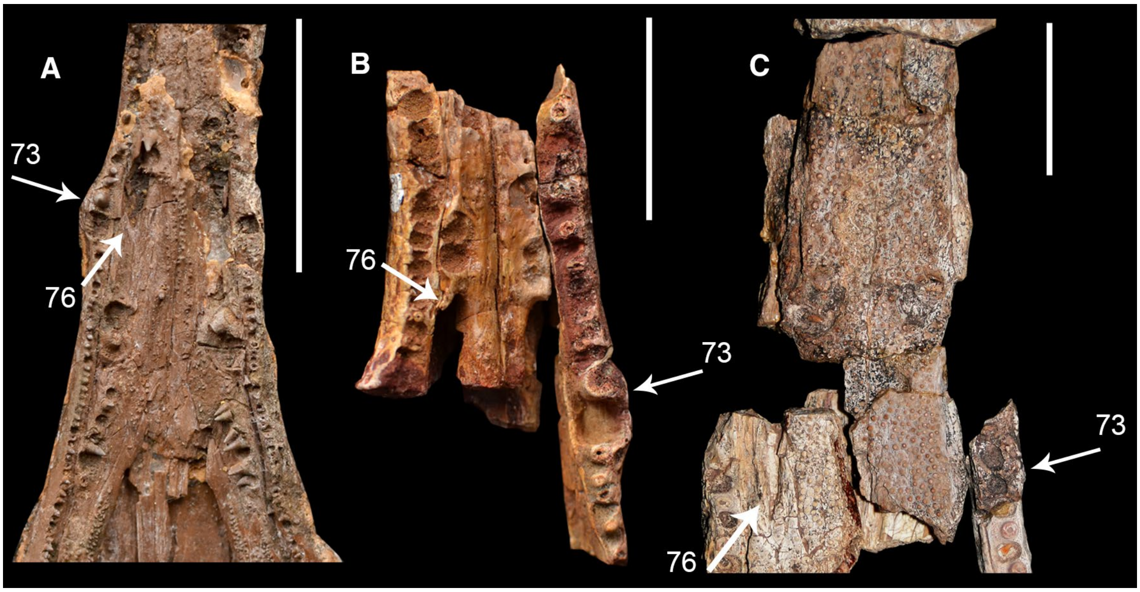


Fig. 3 Palatal view of **a** *Platyoposaurus watsoni* (PIN 161/55); **b** *Platyoposaurus stuckenbergi* (PIN 3968/3); **c** *Prionosuchus plummeri* (DGM 320-R). The white arrows indicate synapomorphies of Platyoposauridae. Character 73—maxilla morphology bears a stepped margin, correlated with enlarged teeth. Character 76—lateral processes of vomer and palatine approach one another so as to reduce the maxillary contribution. Scales: 3 cm

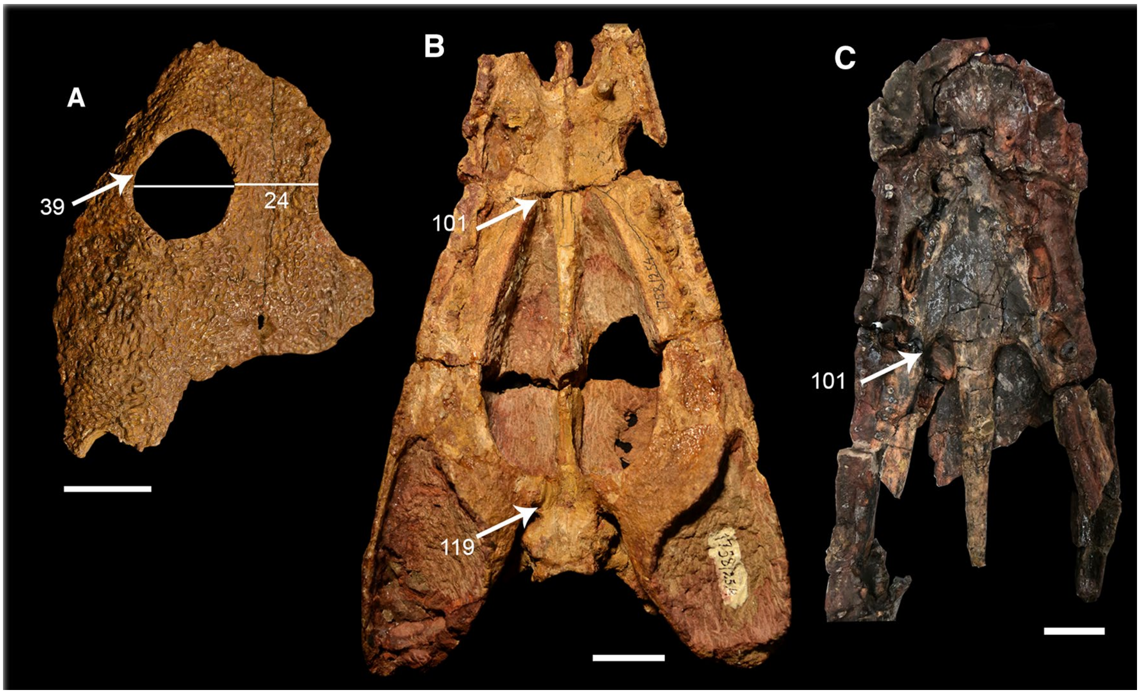


Fig. 4 Dorsal view of skull fragment of **a** *Konzhukovia vetusta* (PIN 520/1); palatal view of **b** *Konzhukovia tarda* (PIN 1758/254); and **c** *Konzhukovia sangabrielensis* (UNIPAMPA PV 00137). The white arrows indicate synapomorphies of Konzhukoviidae. Character 24—narrower interorbital distance. Character 39—the lateral orbital margin without prefrontal contribution. Character 101—anterior tapering of interpterygoid vacuities. Character 119—short articulation between parasphenoid and pterygoid. Scales: 3 cm

parasphenoid plate (125), and the presence of an oblique ridge (130) (Fig. 5).

The Stereospondyli was first recognized by Zittel (1888) based on their typical vertebrae. Subsequently, the term

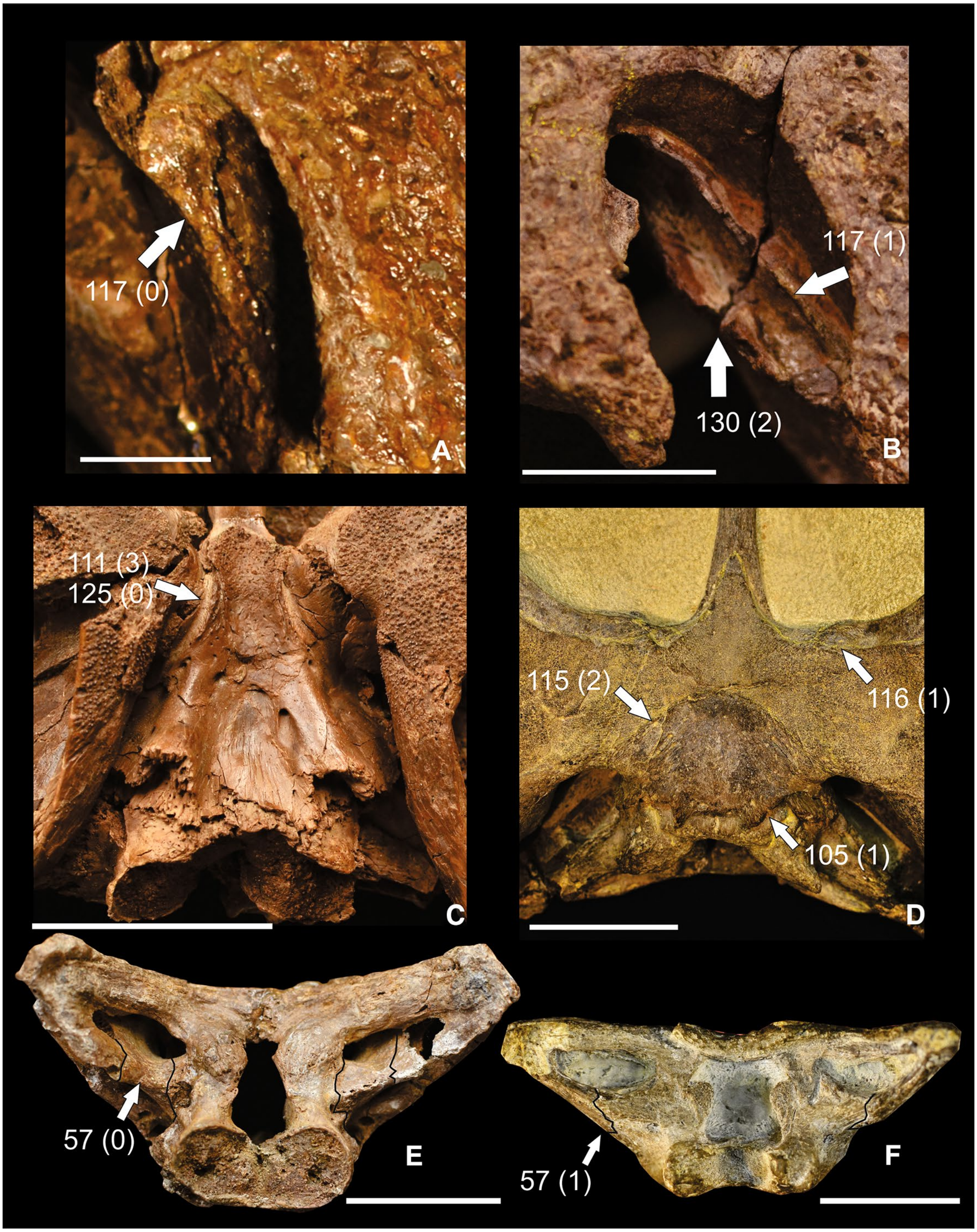


Fig. 5 Important synapomorphies comparing ‘archegosauroids’ and stereospondyls. Otic region (**a**, **b**), posterior palatal region (**c**, **d**); and in occipital region (**e**, **f**). **a** *Konzhukovia vetusta* (PIN 520/1), dorsal view of right otic notch. **b** *Rhineceps nyasaensis* (CAMZM T.259), posterolateral view of right otic notch. **c** *Platyoposaurus watsoni* (PIN 161/20). Ventral view of parasphenoid. **d** *Uranocentrodon senekalensis* (TM 185) Ventral view of parasphenoid. **e** *Platyoposaurus stuckenbergi* (PIN 3968/1). Posterior skull in occipital view. **f** *Lydekkerina huxleyi* (BP-1-5079). Posterior skull in occipital view. Character 57—tabular and exoccipital contacting in the paroccipital process. Character 105—ventral pockets on parasphenoid. Character 111—internal carotid and intracranial branches passing through the dorsal surface of the parasphenoid plate. Character 115—parasphenoid denticle field enlarged to a transverse ‘belt’. Character 116—line of insertion of the palatal mucous membrane that covered the interpterygoid vacuity. Character 117—dorsal pterygoid crest formed in the contact between ascending lamina of pterygoid and descending lamina of squamosal. Character 125—no sulcus behind the pterygoid articulation on the ventral surface the parasphenoid plate. Character 130—the presence of oblique ridge. Scales: 5 cm (**e**, **d**); 3 cm (**a**–**c**, **f**)

'stereospondylous' was used by Fraas (1889) to designate 'labyrinthodonts' with a vertebral structure composed of disc-shaped intercentra and reduced/lost pleurocentra (later considered an ambiguous character to define Stereospondyli). Afterward, Watson (1919; 1962) and Romer (1947) characterized the group based on Permo-Triassic representatives, providing anatomical evidence for the grouping beyond vertebral anatomy. Watson (1919) recognized Stereospondyli as a natural group within Rhachitomi, a term that has fallen into disuse and was recently resurrected by Schoch (2013). Yet, Watson (1919) excludes lineages as Rhinesuchidae and Lydekkerinidae from Stereospondyli. Romer (1947) adapted Watson (1919) proposals to an evolutionary context, erecting Rhinesuchoidea with the genus *Rhinesuchus* typifying early stereospondyls. In the present analysis, synapomorphies of Stereospondyli are clustered in the posterior palate region, which unlike those of non Stereospondyli stereospondylomorphs are modified in terms of skull kinetics (Fortuny et al. 2016), showing a tight articulation between parasphenoid and pterygoid (123). In addition, the occipital region (otic region) bears novelties in the hearing apparatus (Fig. 5), as exemplified by stapedial groove (144) and the oblique ridge (130).

In the present analysis, Rhinesuchidae is recovered as the major sister-clade of the Triassic radiation of stereospondyls (node 17, Fig. 2). Its monophyly was previously recovered by Ruta et al. (2007), McHugh (2012), Eltink et al. (2016), and Marsicano et al. (2017). Among the synapomorphies supporting the clade are a flattened preorbital region (3), a anterodorsally open naris (7), and a prenarial region as long or longer than the naris (8). Other characters supporting Rhinesuchidae are clustered in the otic and occipital regions (Eltink et al. 2016). This includes a tabular horn and directed ventrolaterally with a sharp ventral inflection (61), the oblique ridge forming a large sharp edged crest (130), the exposure of posttemporal fenestra in occipital view, with a horizontal paraoccipital bar (143), and the stapedial groove (144). Postcranial synapomorphies include deep femoral intercondylar (213) and fibular fossae (215), which help differentiating rhinesuchids from more aquatic Neostereospondyli. Two branch-based definitions are availabre for Rhinesuchidae: the most inclusive clade containing *Uranocentrodon senekalensis*, but not *Lydekkerina huxleyi*, *Trematosaurus brauni*, and *Mastodonsaurus giganteus* (Schoch 2013), and the clade containing all taxa more closely related to *Rhinesuchus whaitsi*, than to *Lydekkerina huxleyi*, or *Peltobatrachus pustulatus* (Marsicano et al. 2017). Regarding the results of the present phylogenetic analysis, the second definition seems to be appropriate, as it completely excludes *Peltobatrachus pustulatus* from Rhinesuchidae.

Rhinesuchidae is here divided into two clades, Rhinesuchinae (node 18, Fig. 2) and Australerpetinae, as proposed by Eltink et al. (2016). Rhinesuchinae encompasses *Rhinesuchus whaitsi*, *Uranocentrodon senekalensis*, and *Rhineceps nyasaensis*. Synapomorphies of that clade include orbital margins flush with plane of skull roof (19), no posterolateral flange of palatine ramus of the pterygoid (133), posterior Meckelian foramen bounded by the prearticular and postsplenial (148), and chorda tympanic foramen located only in the prearticular (166). Within Rhinesuchinae, the gigantic *Rhineceps nyasaensis* and *Uranocentrodon senekalesis* form sister-taxa, as also found by Marsicano et al. (2017), grouped by synapomorphies such as the nasal elongation compared to lacrimal and frontal (33, 45).

The Australerpetinae (node 19, Fig. 2) includes rhinesuchids with skull elongation, as *Laccosarus watsoni* and *Australerpeton cosgriffi*, as indicated by the posterior elongation of the Meckelian fenestra, reaching 1/4 to 1/3 of mandible length (157). Other synapomorphies include marginal teeth circular or moderately oval (4), retracted palatine ramus of the pterygoid, with the palatines contributing to the margin of the interpterygoid vacuities (113), tympanic crest present in the squamosal (118), and parasphenoid covering the basioccipital, but not the occipital condyles (138). The phylogenetic relationships encompass a pectinated arrangement with *Broomistega puttereli*, *Parapytanga catarinensis*, *Laccosaurus watsoni*, BP-1-4473, and *Australerpeton cosgriffi*, successive closer to the *Rhinesuchoides capensis* plus *R. tenuiceps* clade. The *Rhinesuchoides* clade was also found by Marsicano et al. (2017), but as a more early-diverging clade. Likewise, *Australerpeton cosgriffi* was found here as sister to *Rhinesuchoides*, whereas it was considered by Marsicano et al. (2017) as a long snouted early-divergent form. The synapomorphies of the *Australerpeton* plus *Rhinesuchoides* clade includes prefrontal and frontal with same length (40) and anteriorly tapered interpetrygoid vacuities (101), which are respectively shared with non-Stereospondyli stereospondylomophs and Konzhukoviidae. The specimen BP-1-4473 appears as sister to *Australerpeton cosgriffi* plus *Rhinesuchoides*. Unlike Marsicano et al. (2017) it is not considered here as a *Laccosaurus watsoni* specimen. The following autapomophies are observed in BP-1-4473: internarial fenestra (9), ectopterygoid with denticles (99), cultriform process with central ventral ridge (103), and pterygoids without denticles (134). Morphologically similar to *Australerpeton cosgriffi*, the fragmentary *Parapytanga catarinensis* was recovered here as an Australerpetinae, and not as a non-stereospondyl Stereospondylomopha (Strapasson et al. 2015). Finally, the miniaturized and younger rhinesuchid, *Broomistega puttereli*, appears as the earliest-diverging taxon within Australerpetinae. This differs from the Marsicano et al. (2017) proposal, in which the taxon is close to *Laccosaurus watsoni* and *Rhinesuchus whaitsi.* Applied to the present hypothesis, the phylogenetic definition of Australerpetinae as *Australerpeton cosgriffi*, *Laccosaurus watsoni*, and all descendants of their most recent common ancestor (Eltink et al. 2016) excludes *Broomistega puttereli* and *Parapytanga catarinensis* from the clade. Therefore, a new branch-based definition is proposed here (Fig. 2).

The Triassic stereospondyls plus *Arachana nigra* and *Peltobatrachus pustulatus* (node 13, Fig. 2) have synapomorphies originally proposed as stereospondyl synapomorphies, such as a narrower intercentrum canal (178) and reduced or absent pleurocentra (182). These characters, associated with a triangular posttemporal fenestra (32) and a distinctive process in the postglenoid area (153) differentiates the group from early-branching Rhinesuchidae. The stereospondyl affinity of *Peltobatrachus pustulatus* was already suggested by Yates and Warren (2000). Although *Arachana nigra* was considered a Stereospondyli *insertae sedis* with rhinesuchid features (Piñeiro et al. 2012), it bears synapomorphies of the Triassic stereospondyls, as squamosal-tabular suture on the dorsal skull roof (53), the crista muscularis of parasphenoid not visible in occipital view (106) and leveled with the posterior border of parasphenoid-pterygoid suture (108), the absence of parasphenoid body notches (126), and a parasphenoid covering the basioccipital, but not the occipital condyles (138).

The clade congregating most Triassic stereospondyls is here termed Superstes (node 14, Fig. 2). The group encompasses Lydekkerinidae and Neostereospondyli (Capitosauria and Trematosauria) and represents the stereospondyl Triassic “survivor”. Synapomorphies include an infra-orbital sulcus with a step-like flexure between the orbit and the naris (27), lacrimal shorter than the nasal (33), posterior retraction of the palatine ramus of pterigoid (113, 132), parasphenoid denticle field enlarged into a transverse belt (115), and no ossified basioccipital (137). Schoch (2013) named a comparable clade as ‘post-rhinesuchid Stereospondyls’, with synapomorphies such as the vomer-pterygoid separation by the palatine corresponding to characters 113 and 132.

One of the Superstes branches (node 16, Fig. 2) encompasses classical lydekkerinids plus *Lapillopsis nana*. Classical lydekkerinids are usually regarded as an early Stereospondyli, although their precise relationships have been debated (Milner 1990; Schoch and Milner 2000; Warren 2000; Yates and Warren 2000; Damiani 2001). The Lapillopsidae are either an early-branching stereospondyls, or non-Stereospondyli stereospondylomorph (Yates 1999; Yates and Warren 2000; Schoch 2013). Here, *Lapillopsis nana* appears as the sister-taxon of *Lydekkerina huxleyi*, forming the sister-clade to *Eolydekkerina magna*. This interrelationship is quite unexpected and ‘Lydekkerinidae’ would be considered as paraphyletic if Lapillopsidae was represented by *Lapillopsis nana*. Dias-da-Silva and Hewison (2013) provided a comprehensive phylogeny of lydekkerinids and recovered *Lapillopsis nana* as sister-taxon of the classical lydekkerinids. The main synapomorphies of Lydekkerinidae (including *Lapillopsis nana*) include a naris above the dorsal rostral plane (6) and ornamentation of uniformly small pits enclosed by a network of ridges (67). The characters supporting the *Lapillopsis nana* plus *Lydekkerina huxleyi* clade include the length of the posterior skull table 65–50% of the width (13), orbits located about half way along the skull length (21), the crista muscularis behind the posterior border of the parasphenoid-pterygoid suture (108), and conspicuous notches on the postero-lateral surfaces of the parasphenoid body (126). In addition, the presence of ectopterygoid tusks (94) also supports the clade. This is a typical lydekkerinid character (Shishkin et al. 1996), but bears intraspecific variation in *Lydekkerina huxleyi* (Jeannot et al. 2006). Maybe the miniaturization of *Lapillopsis nana* and *Lydekkerina huxleyi* causes the attraction of these taxa and to achieve more clarity about Lydekkerinidae relationships, a specific analysis including Lydekkerinidae, Lapillopsidae, and Rhytidosteidae would be necessary. The present results support a position for Lydekkerinidae as early-diverging stereospondyls and a close relation between the Australian *Lapillopsis nana* and the South-African/Australian *Lydekkerina huxleyi* (Dias-da-Silva and Hewison 2013).

The other branch of Superstes corresponds to Neostereospondyli (node 15, Fig. 2), including two Mesozoic stereospondyl groups, Capitosauria and Trematosauria (McHugh 2012). In the recovered tree, *Mastodonsaurus giganteus* plus *Trematolestes hagdorni* form the sister-clade to *Benthosuchus sushkini*. The phylogenetic node-based definition (McHugh 2012) includes *Mastodonsaurus giganteus, Metoposaurus bakeri,* and *Trematosuchus sobeyi*, which applied to the present hypothesis, would exclude *Benthosuchus sushkini* from the group. That taxon does not have a consensual position, but is usually associated with Trematosauroidea (Schoch and Milner 2000). Instead, a branch-based definition is here proposed, including *Lydekkerina huxleyi* as an external specifier, so that *Benthosuchus sushkini* is include under the name. Among synapomorphies Neostereospondyli are: cultriform process with deep ventral crest (103, 120) and straight posterolateral margin of parasphenoid (110). Other synapomorphies are related to the pectoral girdle such as interclavicle and clavicles in contact (191), broad-based clavicles, with anteriorly pronounced sigmoidal curvature (195), and dorsal process of the clavicular flange with thickened central rib along the anterior edge of the dorsal process (196), in addition to unossified carpals (219). As opposed to the more terrestrial adaptations observed in Lydekkerinidae (Canoville and Chinsamy 2015), all these Neostereospondyli characters reveal aquatic adaptations, as displayed by most of its members (Schoch and Milner 2000).

4.2 Ancestral area reconstruction, time ranging and early evolution of Stereospondylomorpha

Stereospondylomorpha area reconstructions (Fig. 6) depicts that the early evolution of the group occurred in Laurasia

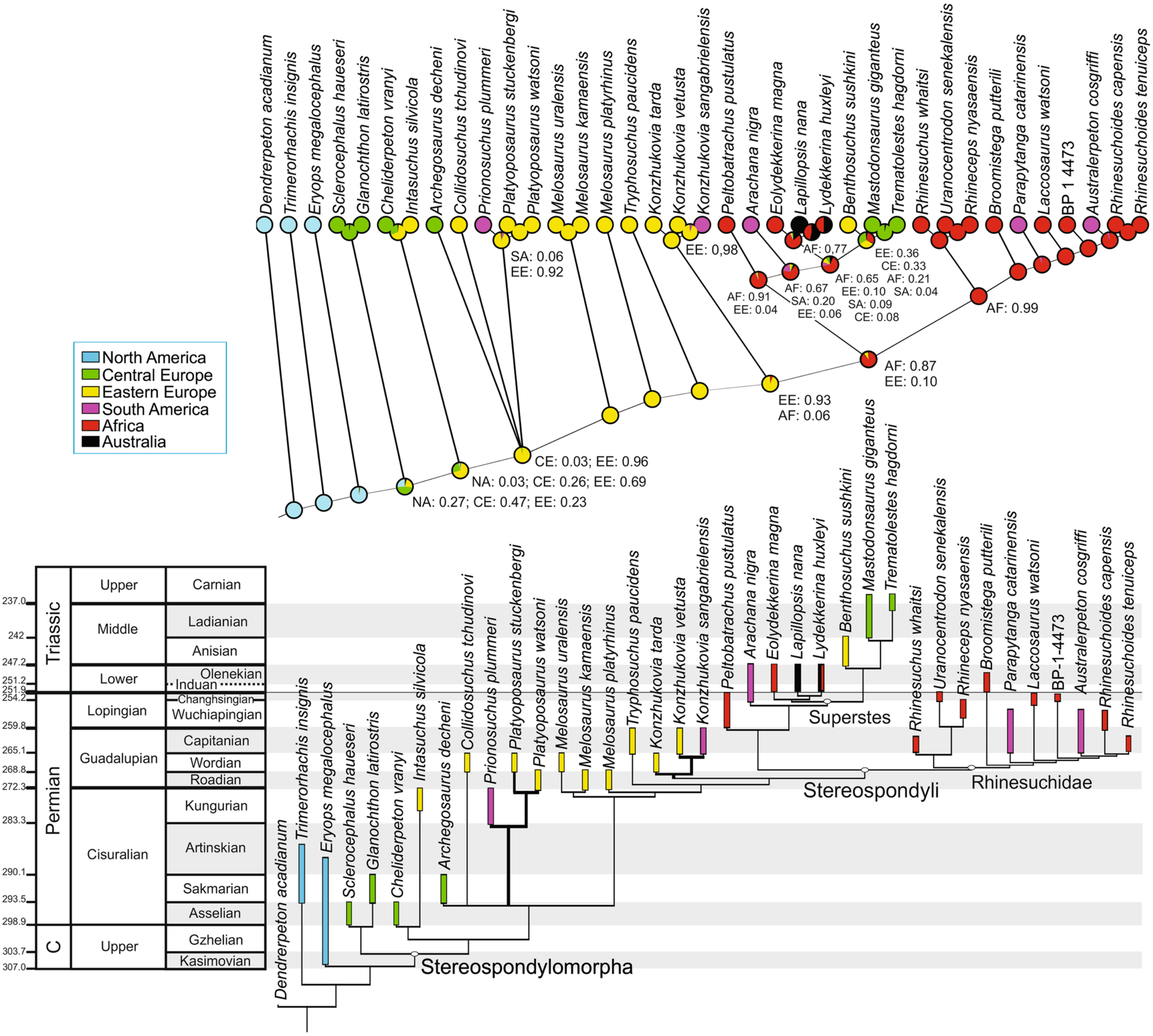


Fig. 6 **a** Temporally calibrated cladogram, showing the interrelationships of Stereospondylomorpha (*below*). Thick lines represent Platyoposauridae and Konzhukoviidae lineages branches. Geological time scale according to GSS–ICS International Chronostratigraphic Chart (2013; updated). **b** Ancestral areas reconstruction optimized in the strict consensus tree (*above*). Likelihood proportions (with more than 0.03) are shown below the nodes. *NA* North America, *CE* Central Europe, *EE* Eastern Europe, *SA* South America, *AF* Africa, *AU* Australia

(likelihood probabilities = 0.47 proportions for central Europe = 0.27, for North America, and = 0.23 for eastern Europe), with cladogenetic events starting in the Gzhelian (Carboniferous), before the first Cisuralian (Permian) record of the group. With the establishment of the Pangaean supercontinent during the Early Permian, an orogenetic rim was formed in the southern border of Laurasia (Ziegler et al. 1997; Şengör and Atayman 2009). This barrier, although preventing a connection with Gondwana, allowed connection among Laurussian areas, as seen by the occurrence of Eryopidae in North America (*Eryops megacephalus*), central Europe (*Onchiodon labyrinthicus*), and eastern Europe (*Clamosaurus nocturnus*) (Schoch and Milner 2014). However, no early stereospondylomorph has been reported from North America, possibly as a result of the distance between basins (Schoch 2000).

Permian basins in central Europe, as the Saar-Nahe Basin, were characterized by lake environments yielding aquatic representative of early Stereospondylomorpha (Boy 1994), such as the Asselian-Sakmarian (Cisuralian) *Sclerocephalus haueseri*, *Glanochthon latirostris* and *Chelidepeton vranyi*, fitting the remarkable Asselian diversity of temnospondyls

(Ruta and Benton 2008). One exception among those early branching forms is *Intasuchus silvicola*, from the Kungurian of the northern Urals (Milner 1993; Schoch and Milner 2000), which makes eastern Europe the most likely ancestral range of both Intasuchidae and the clade it form with other stereospondylomorphs (=0.69). The lack of early stereospondylomorphs in Gondwana seems to result from the prevalence of a subpolar climate in the area between the Namurian–Westphalian and late Asselian, forming glacial deposits that almost completely lack macrofauna (Kemp et al. 1977; Truswell 1980; Jones and Truswell 1992). In the post-glacial mid Asselian, macrofauna gets more diverse, reflecting the climatic amelioration (Stephenson et al. 2007).

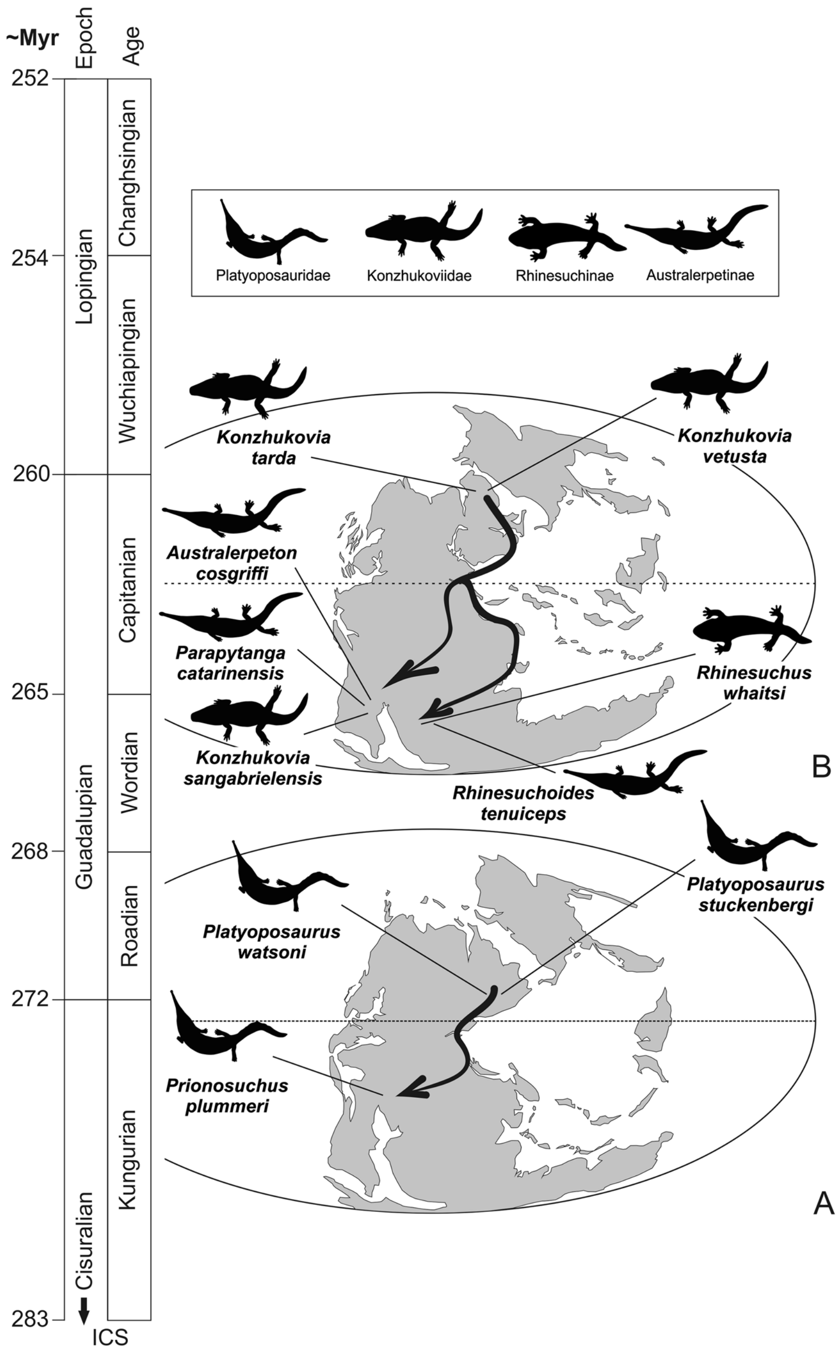
The appearing of long-snouted forms through the Cisuralian marks a change in ancestral area reconstruction from central to eastern Europe (probability of 0.96 for 'Clade 6'), even when considering the occurrence of *Archegosaurus decheni* in the Sakmarian of the former area. The Guadalupian representatives of 'Archegosauridae' in Russia, e.g. the genera *Platyoposaurus*, *Collidosuchus*, *Melosaurus*, and *Konzhukovia*, fills the Middle Permian fossil record hiatus, the 'Olson's Gap' (Benton 2012), characterizing an increasing diversity of stereospondylomorphs and temnospondyls in general (Ruta and Benton 2008). Instead, the time range distribution of stereospondylomorphs shows an apparent hiatus during the Artinskian. This could be related to the early stages of the well-known mid Permian diversity drop among tetrapod faunas, which extends from the late Cisuralian to the middle Guadalupian (Lucas and Heckert 2001; Ruta and Benton 2008).

Represented by *Platyoposaurus watsoni* and *P. stuckenbergi* from the Russian Urals and *Prionosuchus plummeri* from northern Brazil, the Platyoposauridae spanned from the Kungurian (Cisuralian) to the Roadian (Guadalupian), with a distributional encompassing both Laurasia and Gondwana. Additionally, there are fragmented fossils associated with this group in India and southern South America (Wernerburg and Schneider 1996; Dias and Barberena 2001). Eastern Europe is reconstructed as the ancestral area of Platyoposauridae (=0.92), with its basal split occurring previous to the Kungurian. With an early-diverging taxon recorded in the southern hemisphere (Parnaíba Basin), platyoposaurids represented the first biogeographically extensive radiation of temnospondyls (Schoch 2000). Other Parnaíba Basin temnospondyls, such as the dvinosaurian *Timonya anneae* and the trimerorhachid *Procuhy nazariensis* are associated to North American faunas (Cisneros et al. 2015). Indeed, it remains unclear how platyoposaurids overcame the Central Pangaean Mountains, which configured a high altitudinal range at the time (Fluteau et al. 2001). When the Tropical Summerwet biome expanded along the Tethys shores (Rees et al. 2002), one possibility is a dispersive route along coastal drainages systems in a moment of mid Permian (Fig. 7). The crossing of North Africa by platyoposaurids is enigmatic, but the Moradi Formation of Niger has yielded 'relictual' early-diverging temnospondyls, such as the cochleosaurid *Nigerpeton ricqlesi* (Sidor et al. 2005; Steyer et al. 2006) and temnospondyl fragments have also been reported from the Late Permian of the Argana Basin, Morocco (Steyer and Jalil 2009). Although these records are temporally placed in the Guadalupian–Lopingian, their location shed some light on the geographical connection between the discussed Pangaea faunas.

During the early Guadalupian, Russian forms compose the bulk of the non-Stereospondyli Stereospondylomopha diversity, in a moment when temnospondyls experienced a low peak of diversity (Ruta and Benton 2008). The record of *Konzhukovia sangabrielensis* in the Paraná Basin (Capitanian), demonstrates that Konzhukoviidae also expanded its geographic range to Gondwana, but the presence of *Konzhukovia tarda* (Wordian) and *Konzhukovia vetusta* (Capitanian) results in a reconstruction of eastern Europe as the ancestral area for the group (=0.98). Unlike the late Cisuralian *Prionosuchus plummeri*, the age of *Konzhukovia sangabrielensis* indicates a Wordian cladogenetic event. The Rio do Rasto vertebrate fauna has strong affinities with the Guadalupian–Lopingian faunas of South Africa (Cisneros et al. 2012; Boos et al. 2015), but the dinocephalian *Pampaphoneus biccai* supports equally close relationships to eastern Europe (Cisneros et al. 2012). The record of *Prionosuchus plummeri* and *Konzhukovia sangabrielensis* reinforce two-fold biogeographic expansion events proposed by Schoch (2000) and Pacheco et al. (2017). At the mid to late Permian boundary the diversity of temnospondyls was relatively stable (Ruta and Benton 2008). In the Wordian-Capitanian boundary, platyoposaurids and melosaurids were already extinct, and the end of the Capitanian witnessed the last 'archegosaurids', represented by Konzhukoviids. Due to their morphologic similarities to Rhinesuchidae, *Triphosuchus paucidens* and the genus *Konzhukovia* shed light on the origin of Stereospondyli (Gubin 1997; Schoch 2000; Yates and Warren, 2000). Their common ancestral area is reconstructed as eastern Europe (=0.93), with the related cladogenetic events happening in the Roadian (early mid-Permian).

The origin of Stereospondyli is usually acknowledged as Gondwanan (Milner 1990; Schoch and Milner 2000; Schoch 2000; Yates and Warren 2000), either in the Karoo Basin or in Australia (Yates and Warren 2000). Here, the ancestral area reconstruction strongly supports an African origin for Stereospondyli (=0.87). The temporal range of Rhinesuchidae indicates that the initial cladogenetic split of Stereospondyli occurred in the Wordian, bringing the origin of the group to the same period. Although possible records were reported for the Satpuna and Parnaíba basins, respectively in India (Wernerburg and Schneider 1996) and Brazil (Cisneros et al. 2015), uncontroversial records of

Fig. 7 Permian maps showing biogeographic distribution of **a** Platyoposauridae during the Kungurian-Roadian, and **b** Konzhukoviidae and Rhinesuchidae during the Wordian-Capitanian. The black arrows indicate possible routes of dispersion. Geological time scale according to GSS–ICS International Chronostratigraphic Chart (Cohen et al. 2013). Maps modified after Scotese (2002)



Rhinesuchidae are restricted to the Paraná and Karoo basins (Eltink et al. 2016; Marsicano et al. 2017). This represents a relatively wide geographic distribution right before the Permian–Triassic mass extinction, connecting distant tetrapod assemblages outside from Africa than those basins considered by Sidor et al. (2013). The ancestral area of Rhinesuchidae was also reconstructed as Africa (=0.99), but the oldest records of that group occur both in that continent, in the *Tapinocephalus* assemblage zone (Capitanian) of the Karoo Basin, and in South America, represented by forms such as *Australerpeton*.

In the Lopingian, the distribution of early-diverging stereospondyls is restricted to Gondwana. The Permo-Triassic extinction affected most of these forms, e.g. *Peltobatrachus pustulatus* and Rhinesuchidae (except *Broomistega puttereli*). Conversely, stereospondyls are uncommon in the Palaeozoic, known only from Gondwana (Yates and Warren 2000). Ruta et al. (2007) noted diversification shifts occurring also right before the end-Permian extinction, against Milner (1990) extinction-driven pattern of diversification, with no major-groups appearing in the Late Permian. However, their 'burst' in the Triassic was preceded by important cladogenetic events during the Guadalupian and Lopingian, as exemplified by rhinesuchids (Fig. 6). As observed by Ruta et al. (2007), important extinction events occurred across Laurasia before the end-Palaeozoic, together with a series of cladogenetic events, leading to the origin of several new groups in the southern hemisphere. A temporal comparison of the Stereospondyli and non-Stereospondyli stereospondylomorphs record demonstrates a substitution during the Capitanian, but this seems to be an exclusive Gondwanan pattern, as Laurussia 'archegosaurids' were extinct before Lopingian and stereospondyls occur in the area only in the Triassic.

Across the Permo-Triassic extinction, Superstes represents the Stereospondyli survivors, of which the early-diverging Lydekkerinidae (including Lapillopsidae) are the Early Triassic representatives. Interestingly, these forms are miniaturized stereospondyls, with an apparent response to the ecological collapse caused by the end-Permian extinction. Most of the smallest temnospondyls known from Karoo Basin lived at the immediate aftermath extinction (Tarailo 2018). The ancestral area reconstruction for the clade indicates an African origin (=0.65), but latter showing the cosmopolitanism also observed in amniotes immediately after Perm-Triassic extinction (Button et al. 2017). A burst in temnospondyl diversity is observed in the Induan (Ruta and Benton 2008) and our analysis corroborates the worldwide expansion of group. An exception is North America, where a fossil record discontinuity that divides the Paleozoic and post-Paleozoic sedimentary record (Peters 2006) can explain the lack of Triassic Superstes. Neostereospondyli includes the most abundant clades of Triassic stereospondyls (Capitosauria and Trematosauria), whose ancestral area reconstruction is ambiguous among central Europe (=0.33), eastern Europe (=0.36) and Africa (=0.21). The group is very diverse in the Triassic, and larger taxa sample of Neostereospondyli would surely contribute to a better understanding of the origin and radiation of this lineage in the future analyses.

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Affiliations

Estevan Eltink[1] · Rainer R. Schoch[2] · Max C. Langer[3]

Rainer R. Schoch
rainer.schoch@smns-bw.de

Max C. Langer
mclanger@ffclrp.usp.br

[1] Universidade Federal do Vale do São Francisco, Colegiado de Ecologia, Av. Tomaz Guimarães, S/N, Bairro Santos Dumont, Senhor do Bonfim, Bahia, Brazil

[2] Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany

[3] Universidade de São Paulo, FFCLRP, Laboratório de Paleontologia, Av Bandeirantes 3900, Ribeirão Preto 14040-901, Brazil