



Zoological Journal of the Linnean Society, 2015. With figures

# The cranial morphology of the temnospondyl Australerpeton cosgriffi (Tetrapoda: Stereospondyli) from the Middle–Late Permian of Paraná Basin and the phylogenetic relationships of Rhinesuchidae

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Received 20 April 2015; revised 29 July 2015; accepted for publication 4 August 2015

Stereospondyls are a diverse and morphologically distinctive clade of basal tetrapods that rapidly reached a global distribution and high abundance during the Early Triassic. Yet, the first stereospondyls appeared in the Middle-Late Permian of Gondwana, mostly represented by Rhinesuchidae. Australerpeton cosgriffi is a long-snouted representative of the group and one of the most complete temnospondyls known from the Permian of South America. The elements attributed to Au. cosgriffi were recovered from the Middle-Late Permian deposits of the Rio do Rasto Formation (Paraná Basin), in the Serra do Cadeado area of Brazil. Here, we review the cranial anatomy of the species, providing a comparative redescription, new anatomical data and previously unrecognized characters. Australerpeton cosgriffi is nested within Rhinesuchidae based on the anatomy of the tympanic cavity, but its longsnouted condition is unique amongst rhinesuchids. Based on the recovered information and new morphological data, the systematic position of Au. cosgriffi was assessed using a new matrix of 221 characters; of which 196 were selected from previous studies and the remaining are newly proposed. The results show Rhinesuchidae divided into Rhinesuchinae and Australerpetinae. A unique tympanic cavity formed by a well posteroventrally projected tabular horn, stapedial groove, well-developed oblique crest on the pterygoid, and a dorsal pterygoid crest (new term) characterizes the ear region of Rhinesuchidae. Australerpeton cosgriffi is the only undisputed Rhinesuchidae record outside southern Africa and the first long-snouted Stereospondyli, and thus is useful in helping to understand the diversification of the stereospondyls during the Middle/Late Permian of Gondwana.

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ADDITIONAL KEYWORDS: Gondwana – long-snouted rhinesuchid – Palaeozoic – phylogenetics – Rio do Rasto Formation – systematics – Temnospondyli – tympanic cavity.

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# INTRODUCTION

Stereospondyls are a diverse and morphologically distinctive clade of basal tetrapods that rapidly reached a global distribution and high abundance during the Early Triassic (Milner, 1990). Yet, the first stereospondyls appeared in the Middle-Late Permian (Warren, Damiani & Yates, 2000; Dias-da-Silva, 2012), mostly represented by Rhinesuchidae (Damiani & Rubidge, 2003). Fossils of the Permian temnospondyl Australerpeton cosgriffi (Barberena, 1998) were first found in north Paraná State, south Brazil, mainly in the Serra do Cadeado area (Fig. 1). Mendes (1967) first mentioned the important geological exposures of the Rio do Rasto Formation in the Serra do Cadeado area, but studies with vertebrate fossils from the area started with the geological exploration during the building of the Estrada de Ferro Central do Paraná (EFCP) railroad between 1973 and 1974. During this time, the geologists N. R. Correia and J. Aumond collected a tetrapod skull later identified as belonging to the dicynodont Endothiodon (Barberena & Araújo, 1975; Boos et al., 2013). At the same time, the Petróleo Brasileiro S.A. (PETROBRÁS) geologist R.A. Medeiros discovered remains of a long-snouted temnospondyl, identified by Barberena & Daemon (1974) as Platyops, actually Platyoposaurus (Schoch & Milner, 2000), an archegosaurid previously known from the Late Permian

of the Russian Platform (Gubin, 1991). Additional material was collected by M. C. Barberena, in 1975 and 1982. This material included two different temnospondyls: a short-snouted Rhinesuchidae (Barberena & Dias, 1998) and the long-snouted *Au. cosgriffi* (Barberena, 1998). The last expeditions to this area were carried out by the Laboratório de Paleontologia of the Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto (FFCLRP), Universidade de São Paulo (USP), from 2006 to 2008. As a result, new material (LPRP/USP-0011) was collected and assigned to *Au. cosgriffi* (Eltink & Langer, 2014a).

Australerpeton cosgriffi was formally described by Barberena (1998) based on four well-preserved partial skulls (UFRGS-PV-0227-P, UFRGS-PV-0228-P, UFRGS-PV-0229-P, and UFRGS-PV-0230-P). The author included the taxon in a new family Australerpetonidae, within Rhinesuchoidea, confirming an already suggested affinity to rhinesuchids (Barberena, Correia & Aumond, 1980; Barberena, Araújo & Lavina, 1985). Previously, part of the material ascribed to the *Au. cosgriffi* type series had been assigned to Platyoposaurinae, based on the rostrum UFRGS-PV-0228-P (Barberena & Daemon, 1974). The affinity with platyoposaurines was lately endorsed by Wernerburg & Schneider (1996) and Schoch & Milner (2000), close to the *Prionosuchus* and *Platyoposaurus*. Scales and other postcranial remains



**Figure 1.** Geographical position of Serra do Cadeado (white circle) in the context of the Paraná Basin (grey area); the black area corresponds to Permian outcrops.

of Au. cosgriffi (UFRGS-PV-0319-P and UFRGS-PV-0320-P) were described by Dias & Richter (2002) and Dias & Schultz (2003), respectively, in which the latter supported the Rhinesuchidae affinity for Au. cosgriffi. Other works placed Au. cosgriffi in an intermediate position between Archegosauridae and Rhinesuchidae (Witzmann & Schoch, 2006; Schoch et al., 2007; Schoch, 2013), but nested outside Stereospondyli. Recently, Eltink & Langer (2014a) placed Au. cosgriffi within Stereospondyli, as a member of the Rhinesuchidae (Eltink & Langer, 2014b). In this context, the present contribution provides a redescription of the cranial morphology of Au. cosgriffi and its phylogenetic relationships within Rhinesuchidae.

# GEOLOGICAL SETTING

The Palaeozoic and Mesozoic strata exposed in the Serra do Cadeado area correspond to the Teresina, Rio do Rasto, Piramboia, Botucatu and Serra Geral formations (Riccomini, Filho & Almeida, 1984). Structurally, the area is located in the middle portion of the 'Arco de Ponta Grossa' (Ponta Grossa Arch), where sedimentary rocks are sectioned by numerous south-eastnorth-west orientated Cretaceous diabasic dikes, usually associated with subvertical geological faults (Barberena et al., 1980). Lithologically, these units encompass sedimentary sequences that represent the transition from a shallow water environment into a continental landscape dominated by a semi-arid climate (Barberena et al., 1980). The rock layers start with pelites and limestones from the Teresina Formation, overlain by siltstones interbedded with fine-grained sandstones from the base of the Rio do Rasto Formation (Serrinha Member), followed by fine-grained sandstones from the top of the Rio do Rasto Formation (Morro Pelado Member). Finally, both the Piramboia and Botucatu formations include fine- to coarse-grained sandstones (Barberena et al., 1980). The lower contact of the Rio do Rasto Formation with the Teresina Formation is gradational, whereas its upper contact with the Piramboia Formation is usually discordant across the Paraná Basin (Almeida, 1980). Rarely, it is gradational in Serra do Cadeado and other regions of the Paraná Basin (Riccomini et al., 1984; Ragonha, 1989; Lavina, 1991; Lavina, Faccini & Ribeiro, 1993; Rohn, 1994; Lavina & Scherer, 2003; Ferreira-Oliveira & Rohn, 2010).

The fossiliferous localities of Serra do Cadeado are associated with the Rio do Rasto Formation, and include fish, amphibian, synapsid, invertebrate, and plant remains (e.g. Barberena *et al.*, 1985; Rohn, 1994). The Serrinha Member is composed of grey and purple siltstones and mudstones, with calcareous layers and fine sandstones (Rohn, 1994). The sandstones and siltstones bear wavy, cross-bedded lamination, whereas the silt-mudstones beds show a parallel lamination (Schneider *et al.*, 1974; Schobbenhaus *et al.*, 1984). The Morro Pelado Member is mainly characterized by an increase in the proportion of sand compared to the lower Serrinha Member. Internally, it is characterized by some climbing-ripple cross laminations and cross-bedded planing (Barberena *et al.*, 1980; Rohn, 1994). Other significant features include large mud cracks (Lavina, 1991) and geological faults and deformations (Strugale *et al.*, 2003). The contact between the Serrinha and Morro Pelado members is gradational and concordant (Gordon, 1947; Schneider *et al.*, 1974; Soares, 1975; Gama, Bandeira & França, 1982).

According to Schneider et al. (1974), the deposits of the Serrinha Member were formed on a tidal flat progradational succession, comprising a transition between the shallow water deposits of the Teresina Formation and the continental deposits of the Morro Pelado Member. The latter was formed in lakes and alluvial plains, and the upper layers of the member are formed by sand dunes. Rohn (1988, 1994), Ragonha (1989), and Lavina (1991) interpreted the environment of the Rio do Rasto Formation as mainly lacustrine, with large. storm-dominated lakes and fluvial channels formed during torrential rains, and the presence of wind dunes, seen in the upper levels of Morro Pelado Member, as increasing of arid condition. The interpretation of a continental environment for the lower part of the Serrinha Member is based on records of 'conchostracans' (Rohn, 1994; Ferreira-Oliveira, 2007).

The Rio do Rasto Formation provides one of the most important records of the continental Permian of South America (Langer et al., 2008; Dias-da-Silva, 2012). Regarding the age of its deposits in the Serra do Cadeado area, earlier studies suggested a Late Permian age (Wuchiapingian), based on palaeobotanical data (Rohn, 1994) and the occurrence of vertebrates (Barberena & Daemon, 1974; Barberena et al., 1980; Langer, 2000; Malabarba et al., 2003; Cisneros, Abdala & Malabarba, 2005). Langer et al. (2008) interpreted the temporal distribution of the Serra do Cadeado fauna, placing its upper limit at the end of the Middle Permian (Capitanian). Recently, Dias-da-Silva (2012) and Boos et al. (2013) suggested an earlier age for the Serra do Cadeado fauna, ranging from Middle to Late Permian (Rodian to Wuchiapingian), and this was corroborated by the temporal calibration of South African cenozones (Rubidge et al., 2013).

# MATERIAL AND METHODS

## INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York, USA; BP, Bernard Price Institute of Palaeontological Research, Johannesburg, South Africa; CAMZM, University Museum of Zoology, Cambridge, UK; DGM, Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; GPIT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany; LPRP/ USP, Laboratório de Paleontologia de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, Brazil; MB, Museum für Naturkunde, Humboldt Universitat, Berlin, Germany; NHMUK, Natural History Museum, London, UK; PIN, Paleontological Institute, Academy of Science, Moscow, Russia; SAM, Iziko South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TM, Ditsong National Museum of Natural History (Transvaal Museum), Pretoria, South Africa; UFRGS, Laboratório de Paleontologia de Vertebrados, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

#### Specimens examined

Information on the specimens of *Au. cosgriffi* examined in this study is listed below. The best-preserved and most informative specimens are shown in Figure 2. All known material referred to *Au. cosgriffi* was collected in the Rio do Rasto Formation, Serra do Cadeado area (see comments below for additional material collected from other localities).

UFRGS-PV-0227-P (Fig. 2A). A partial skull lacking most of the right side and the prenarial portion of the rostrum (Fig. 3). The specimen was designated by Barberena (1998) as the holotype of Au. cosgriffi and figured in Dias & Schultz (2003: fig 6).

UFRGS-PV-0224-P (Fig. 2B). A dorsoventrally compressed, nearly complete skull, lacking the anterior half of the preorbital region (nasal and premaxilla). Partial left and right mandibles attached to skull (Fig. 4). The specimen was first referred to *Au. cosgriffi* by Eltink & Langer (2014a).

UFRGS-PV-0225-P (Fig. 2C). An almost complete, small skull with right and left mandibles attached, lacking the anterior extremity of the rostrum. The specimen was not cited in the original description of Barberena (1998), but we suggest its referral as a juvenile Au. cosgriffi.

UFRGS-PV-0228-P (Fig. 2D). A near-complete rostrum, from the orbits to the anterior extremity of the premaxilla. The fragment is the only known complete rostrum of *Au. cosgriffi*, but it is deformed and fragmented in different parts. The specimen was included in the type series of *Au. cosgriffi* (Barberena, 1998) and comprises the first record of temnospondyl for the Paraná Basin (Barberena & Daemon, 1974).

UFRGS-PV-0229-P (Fig. 2F). A nearly complete skull, lacking the anterior portion of the frontal. The mandibles are preserved, with the left element almost complete. Although deformed, the symphysis and articular region are relatively well preserved. The right mandible is fragmented. The specimen is part of the type series of Au. cosgriffi (Barberena, 1998) and was figured in Dias & Schultz (2003: fig 6).

UFRGSPV-0230-P (Fig. 2E). Posterior left skull fragment, very well preserved. It is part of the type series of *Au. cosgriffi* and was figured in Dias & Schultz (2003: fig 6).

UFRGS-PV-0240-P. Right mandible fragment (symphysis region).

UFRGS-PV-0243-P. Attached fragments of right and left mandibles.

UFRGS-PV-0319-P. Small fragment of skull roof, fragmentary mandible, almost complete vertebral column, pelvic girdle, hind and forelimb, ribs, and some articulated scales. The specimen was described and figured by Dias & Schultz (2003).

UFRGS-PV-0320-P. Posterior skull fragment, vertebrae, ribs, fragments of a left pelvic girdle and a complete left forelimb, and some isolated scales. The specimen was described and figured by Dias & Schultz (2003).

UFRGS-PV-0348-P. Middle portion of a right mandible.

LPRP/USP-0011. Left mandible, fragmented ribs, complete pelvic girdle, and right femur, tibia, and fibula. The specimen was described and figured by Eltink & Langer (2014a).

#### Comments

Several fragments and isolated bones were described from the Morro Pelado Member (Rio do Rasto Formation), along the highway PR-090, near São Jerônimo da Serra, Paraná, Brazil (Ramos & Vega, 2011). The material consists of mandibular fragments, vertebrae, rib fragments, and a partial scapular girdle. Ramos & Vega (2011) tentatively assigned the material to *Au. cosgriffi* based on its long-snouted morphology, but highlighted the need for additional findings to confirm this taxonomic identification. Silva, Sedor & Fernandes (2012) also reported the finding of further *Au. cosgriffi* specimens formerly referred to simply as 'fossil amphibians' by Sedor & Costa (2001) and Leonardi, Sedor & Costa (2002). Another reference that mention *Au. cosgriffi* is found in Strapasson, Pinheiro & Soares (2014).

## SYSTEMATIC PALAEONTOLOGY

Tetrapoda Goodrich, 1930 Temnospondyli Zittel, 1887–90 Stereospondylomorpha Yates & Warren, 2000 Stereospondyli Fraas, 1889 Rhinesuchidae Watson, 1919 Australerpetinae (this work, see below) Australerpeton cosgriffi Barberena, 1998

*Holotype* UFRGS-PV-0227-P.



**Figure 2.** *Australerpeton cosgriffi* Barberena, 1998. Photographs (above) and interpretative drawings (below) of cranial material in dorsal view. A, UFRGS-PV-0227-P (holotype; partial skull without rostrum and lacking the right side). B, UFRGS-PV-0224-P (partial skull without rostrum). C, UFRGS-PV-0225-P (partial skull without the anterior extremity, possibly a juvenile). D, UFRGS-PV-0228-P (rostrum). E, UFRGS-PV-0230-P (fragment of the left posterior part of skull). F, UFRGS-PV-0229-P (partial skull without rostrum). Scale bars = 5 cm.

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**Figure 3.** *Australerpeton cosgriffi* Barberena, 1998. UFRGS-PV-0227-P (holotype). Photographs (above) and interpretative drawing (below) in dorsal (A), posterior (B), and ventral (C) views. Dark grey areas represent openings or sedimentinfilled fenestrae. Light grey areas represent recessed areas of bone (tympanic cavity), areas of articulation (mandibular and occipital), and denticles on palate. Areas filled with parallel lines are broken surfaces. Abbreviations: cm, crista muscularis; co, choana; cp, cultriform process; ec, ectopterygoid; en, external naris; ex, exoccipital; fcr, falciform crest; fr, frontal; iv, interpterygoid vacuity; jug, jugal; la, lacrimal; memb., ridge corresponding to the basal attachment of the medial membrane of the tympanic cavity (*sensu* Watson, 1962); mx, maxilla; na, nasal; obc, oblique crest; occ, occipital condyle; orb, orbit; pa, parietal; pf, postfrontal; pfe, post-temporal fenestra; pl, palatine; po, postorbital; ppa, postparietal; prf, prefrontal; ps, parasphenoid; pt, pterygoid; qd, quadrate; qj, quadratojugal; sf, subtemporal fenestra; sq, squamosal; st, supratemporal; tab, tabular; tabh, tabular horn; tcr, tympanic crest; tyc, tympanic cavity; vo, vomer; vpj, ventral process of the jugal. Scale bars = 5 cm.



**Figure 4.** *Australerpeton cosgriffi* Barberena, 1998. UFRGS-PV-0224-P, photographs (above) and interpretative drawing (below) in dorsal (A), posterior (B), and ventral (C) views. Dark grey areas represent openings or sediment-infilled fenestrae. Light grey areas represent recessed areas of bone (tympanic cavity), articulation (mandibular and occipital), or denticles on palate. Areas filled with parallel lines are broken surfaces. Abbreviations: afm, articular facet of mandible; an, angular; ar, articular; arg, arcadian groove; arp, arcadian process; bo, basioccipital; cm, crista muscularis; co, choana; cp, cultriform process; ctf, chorda tympanica foramen; de, dentary; ec, ectopterygoid; ex, exoccipital; fcr, falciform crest; fm, foramen magnum; fopq, foramen paraquadratum accessorium; foq, foramen quadratum; fr, frontal; iv, interpterygoid vacuity; jug, jugal; jvp, ventral process of the jugal; la, lacrimal; memb., ridge corresponding to the basal attachment of the medial membrane of the tympanic cavity (*sensu* Watson, 1962); ms, mandibular sulcus; mx, maxilla; na, nasal; occ, occipital condyle; orb, orbit; pa, parietal; par, prearticular; pf, postfrontal; pf, post-temporal fenestra; pgp, postglenoid process; pl, palatine; pmf, posterior Meckelian fenestra; po, postorbital; pra, postparietal; prf, prefrontal; ps, parasphenoid; psp, postsplenial; pt, pterygoid; qd, quadrate; qj, quadratojugal; rap, retroarticular process; san, surangular; sf, subtemporal fenestra; sp, splenial; sq, squamosal; st, supratemporal; tab, tabular; tabh, tabular horn; tcr, tympanic crest; vo, vomer. Scale bars = 5 cm.

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## Paratypes

UFRGS-PV-0228-P; UFRGS-PV-0229-P; UFRGSPV-0230-P.

## Associated and referred material

UFRGS-PV-0224-P; UFRGS-PV-0225-P; UFRGS-PV-0240-P; UFRGS-PV-0243-P; UFRGS-PV-0319-P; UFRGS-PV-0320-P; UFRGS-PV-0348-P; LPRP/USP-0011.

## Type locality and horizon

Serra do Cadeado area, Paraná, Brazil, collected in outcrops along the EFCP railroad and BR-376 highway. The locus typicus coordinates are 24°00′171″S and 51°06′491″W. Upper levels of the Serrinha Member, and lower to middle levels of the Morro Pelado Member, Rio do Rasto Formation (Middle-Late Permian according to Dias-da-Silva, 2012; Boos *et al.*, 2013), Paraná Basin (Barberena *et al.*, 1985).

## Diagnosis

Australerpeton cosgriffi is nested within Rhinesuchidae based on the well posteroventrally projected tabular horn; the presence of a stapedial groove; a welldeveloped oblique crest on the pterygoid; a dorsal pterygoid crest (new term) formed in the contact between pterygoid and squamosal; a well-marked groove along the posterior border of the interpterygoid vacuity; denticles distributed on the ventral surface of parasphenoid with arched posterior margin; and slitlike post-temporal fenestra. Its long-snouted condition, unique amongst Rhinesuchidae, can be recognized by the premaxilla being longer than wide and more than twice the length of external naris, and the skull being narrower at the nasal/frontal contact than half the width at the level of the pineal foramen. In addition, tooth elements from the marginal dentition of Au. cosgriffi are rounded in cross-section (differing from Uranocentrodon senekalesis, Rhinesuchus capensis, Rhineceps nyasaensis, Rhinesuchus whaitsi, Rhinesuchus broomianus) and the posterior premaxillary teeth are larger than the anterior ones (differing from all other known rhinesuchids). Both the ectopterygoid and the ventral process of jugal (= insula jugalis) enter the anterior border of the subtemporal fenestra, an autapomorphy of Au. cosgriffi.

## Australerpetinae (node-based definition)

Australerpeton cosgriffi, Laccosaurus watsoni, and all descendants of their most recent common ancestor.

### Redescription

The first description of *Au. cosgriffi* by Barberena (1998) was mostly based on UFRGS-PV-0227-P and UFRGS-PV-0228-P, with UFRGS-PV-0229-P and UFRGS-PV-0230-P used to describe the occipital surface. The present redescription also takes other specimens into account,

namely UFRGS-PV-0224-P and UFRGS-PV-0225-P (Fig. 2B, C). This detailed redescription agrees in part with that of Barberena (1998) but also differs significantly (see below).

The skull outline is triangular and elongated, with a slender snout that bears a slightly laterally expanded premaxilla in its anterior portion (Fig. 5). This skull morphology is also observed in the stereospondylomorph *Platyoposaurus* (Gubin, 1991) and in some advanced stereospondyls, such as *Aphaneramma* (Woodward, 1904), and is usually related to a piscivorous habit (e.g. Gubin, 1991, 1997; Dias & Schultz, 2003; Eltink & Langer, 2014a). It is also found in Crocodyliformes such as dyrosaurids, pholidosaurs, and thalattosuchians (Brochu, 2001).

The orbits are elliptical in outline and equally distant from both the sagittal axis and the lateral margins. The orbital margins are flush with the plane of the skull roof, as is typical of Rhinesuchidae. By contrast, archegosaurids and lydekkerinids bear slightly elevated orbital margins. In posterior view, the dorsal margin of the skull roof is straight and the interorbital depression, present in the non-Stereospondyli stereospondylomorphs *Melosaurus kamaensis* (PIN 683/ 1) and *Konzhukovia vetusta* (PIN 520/1; Gubin, 1991: fig. 15b), is absent in *Au. cosgriffi* as in other stereospondyls, e.g. *Mastodonsaurus giganteus* (Schoch, 1999).

The surface ornamentation of the skull is typical of temnospondyls, with pits and fine grooves radiating from the ossification centre of the bone. The ridges of the preorbital region are predominantly longitudinally oriented, differing from those radially arranged of the posterior skull roof. Conversely, some basal stereospondyls, such as Rhineceps nyasaensis (CAMZM T.259), U. senekalensis (TM 185), and Lydekkerina huxleyi (NHMUK R. 507), bear a uniform pattern of evenly distributed pits on the skull roof (i.e. neither radial nor longitudinal). Both circumorbital and infraorbital sulci can be identified in the skull surface of Au. cosgriffi. The infraorbital sulcus is gently curved, running across the maxilla and lacrimal. This condition differs from the markedly curved infraorbital sulcus observable in Ly. huxleyi (NHMUK R. 507; Jeannot, Damiani & Rubidge, 2006), which forms the lacrimal flexure, and the strongly curved sulcus in more advanced taxa such as Ma. giganteus (SMNS 54675; Schoch, 1999: fig 1) and Benthosuchus sushkini (PIN 2252; Bystrow & Efremov, 1940), which results in a Z-shaped flexure. There is no signal of a septomaxilla (Barberena, 1998).

The dentition of  $Au. \ cosgriffi$  has the typical unfolding internal labyrinthodont pattern. The external surface of the teeth is marked by longitudinal grooves, and the teeth are rounded in cross-section. According to Schoch (2013), transversely broadened (oval) teeth is



**Figure 5.** Australerpeton cosgriffi Barberena, 1998. Reconstruction of the skull in dorsal view. Dark grey areas represent openings or fenestrae. Light grey areas represent recessed areas of bone (tympanic cavity). Abbreviations: en, external naris; fr, frontal; jug, jugal; la, lacrimal; mx, maxilla; na, nasal; orb, orbit; pa, parietal; pf, postfrontal; po, postorbital; ppa, postparietal; prf, prefrontal; pmx, premaxilla; qd, quadrate; qj, quadratojugal; sq, squamosal; st, supratemporal; tab, tabular. Scale bar = 5 cm.

an apomorphy of Stereospondyli. However, 'higher' non-Stereospondyli stereospondylomorphs, such as K. vetusta (PIN 520/1; Gubin, 1991: fig. 15a) and Tryphosuchus paucidens (PIN 157), possess the same oval broadened teeth, whereas basal stereospondyls such as the rhinesuchids Lac. watsoni (SAM-PK-4010; BP-1-213; Haughton, 1925) and Broomistega putterelli (BP-1-5058; Shishkin & Rubidge, 2000) share rounded teeth. In general, Au. cosgriffi teeth decrease in size posteriorly, but the premaxillary teeth become larger posteriorly (Fig. 6). The posterior enlargement of premaxillary teeth is typical of archegosaurids; however, Au. cosgriffi lacks the maxillary tusks observed in Platyoposaurus stuckenbergi (PIN 49/31; Gubin, 1991: fig. 3b) and Sclerocephalus haueseri (SMNS 81791; Schoch & Witzmann, 2009: fig 4b).

Premaxilla: The premaxilla is elongated. Its anterior margin is rounded and relatively expanded to form a spoon-like outline in dorsal view (Figs 5, 6: 'pmx'). Other long-snouted temnospondyls, such as Prionosuchus plummeri (DGM 320 R, NHMUK 120005; Price, 1948), possess a more marked bulging in the rostral tip (Barberena, 1998). The nasal contact forms a transverse suture, lacking the posterior alary process that is remarkable in nonstereospondyl stereospondylomorphs (e.g. Archegosauridae). The external narial opening is anteroposteriorly orientated, and situated mostly in the dorsal surface of the anterior half of the snout. This is also observable in some long-snouted temnospondyls, such as Archegosaurus decheni (Witzmann, 2005) and trematosaurs (Stever, 2002), but Pr. plummeri bears a conspicuously laterally placed external naris (Price, 1948). On the ventral surface, the lateral margins of the premaxilla are raised relative to those on the medial surface. There are eight teeth and a tubercle that is slightly developed in the centre of the premaxillary, as in Rhineceps nyasaensis (CAMZM T.259; Watson, 1962: fig 7a). Posteriorly, two rounded fossae, the anterior palatal vacuities (Fig. 6: 'apv'), are located close to this tubercle. These are clearly separated from each another, as occurs in most basal temnospondyls, e.g. Eryops megacephalus (AMNH 4673). Conversely, these fossae appear to be joined and to form a bilobed vacuity in Pl. stuckenbergi (Gubin, 1991) and Ly. huxleyi (Jeannot et al., 2006). This structure is single in Eolydekkerina magna (Shishkin, Rubidge & Kitching, 1996) and Lapillopsis nana (Yates, 1999).

*Maxilla*: This bone is narrow and very elongated, forming most of the lateral margin of the skull. In dorsal view, the maxilla extends from the anterior border of the external naris to the level of the posterior border of the orbits (Figs 3–6: 'mx'). Its lateral margin is almost straight and slightly concave in the preorbital region, lacking the lateral expansion that provides a rather subquadratic shape to the dorsal skull outline in short-snouted forms such as *S. haueseri* (Schoch & Witzmann,



**Figure 6.** Australerpeton cosgriffi Barberena, 1998. Reconstruction of skull in ventral view. Dark grey areas represent openings or fenestrae. Light grey areas represent recessed areas of bone, areas of articulation (mandibular and occipital), and denticles on palate. Abbreviations: apv, anterior palatal vacuity; bo, basioccipital; cm, crista muscularis; co, choana; cp, cultriform process; ec, ectopterygoid; iv, interpterygoid vacuity; mx, maxilla; occ, occipital condyle; pl, palatine; pmx, premaxilla; ps, parasphenoid; pt, pterygoid; qd, quadrate; qj, quadratojugal; sf, subtemporal fenestra; tub, medial tubercle of the premaxilla; vo, vomer; vpj, ventral process of the jugal. Scale bar = 5 cm.

2009) and *Er. megacephalus* (Sawin, 1941). It also differs from the maxilla of the Russian Melosaurinae, *Melosaurus kamaensis* (PIN 683/1) and *Me. uralensis* (MB. Am 334 a-c), which have a more prominent concavity in the preorbital margin. There are no tusks in the maxilla of *Au. cosgriffi*. This condition differs from other long-snouted temnospondyls such as platyoposaurines (e.g. *Platyoposaurus* and *Prionosuchus*) and the cochleosaur *Nigerpeton* (Steyer *et al.*, 2006), which bear maxillary tusks and a marked bulging on the lateral margin of the maxilla to accommodate these tusks. Posteriorly, the maxilla has a small point of contact with the quadratojugal.

In palatal view, the maxilla contacts the vomer anteromedially, bordering most of the anterolateral border of the choana. In the other rhinesuchids, the lateral margin of the choana is entirely formed by the maxilla (without any contribution of the palatine). The contact of the maxilla with the palatine and ectopterygoid is straight. The maxillary teeth decrease in size posteriorly with the last tooth anteriorly placed with respect to the subtemporal fossa. The maxilla forms the anterolateral margin of the subtemporal fossa and this arrangement isolates the jugal from its lateral border (contra Barberena, 1998: fig. 4).

Nasal: Anteriorly, this bone is firmly attached to the premaxilla and extends from the medioposterior border of the external naris, contacting both the maxilla and lacrimal laterally (Figs 3–5: 'na'). The internarial fenestra, present in the basal temnospondyl *Dendrerpeton acadianum* (Holmes, Carroll & Reisz, 1998) and the rhinesuchids *Rhineceps nyasaensis* (Watson, 1962) and BP-1–4473, is absent in *Au. cosgriffi*. Posteriorly, the nasal wedges between the prefrontal and frontal, forming a narrow tip. Its lateral expansion is weak, differing from the character observed in basal Stereospondylomorpha such as *S. haueseri* (Schoch & Witzmann, 2009).

*Lacrimal:* This bone is slender and posteriorly enclosed by the prefrontal and jugal (Figs 3–5: 'la'). It is shorter than the nasal and does not reach the posterior margin of the external naris. This results in the contact between the maxilla and nasal, differing from basal temnospondyls, such as *Trimerorhachis insignis*, and some specimens of *Ly. huxleyi* (Jeannot *et al.*, 2006).

Frontal: This bone is very elongated compared with the others of the skull roof. It tapers anteriorly, extending up to one third of the length of the preorbital (Figs 3–5: 'fr'). Its anterior extremity bears a remarkable pointed process that enters the posterior rim of the nasal. The frontal does not border the orbit, distinguishing Au. cosgriffi from the Russian non-Stereospondyli stereospondylomorphs Melosaurus platyrhinus (PIN 161/1; Golubev, 1995: fig 2), Me. uralensis (MB. Am 334 a-c), Konzhukovia vetusta (PIN 520/1; Gubin, 1991: fig. 6a), and *K. tarda* (PIN 1758/254), in which the frontals briefly contact the medial margin of the orbits. Considered phylogenetically significant in capitosauroids (Mastodonsauroidea *sensu* Damiani, 2001), presence of a broad contribution of the frontal to the orbits, amongst the above-mentioned Russian forms, demonstrates a more wide distribution of this character.

Prefrontal: With a subtriangular shape and anterior tapering (between frontal/nasal and lacrimal), the prefrontal forms part of the anteromedial orbital border (Figs 3-5: 'prf'). UFRGS-PV-0228-P and UFRGS-PV-0225-P show a medial contact with the lacrimal and do not reach the nasal, whereas the prefrontal of UFRGS-PV-0227-P and UFRGS-PV-0229-P extends medially to the nasal, as figured by Barberena (1998: fig. 3). The anterior extension of the prefrontal is the same as that of the frontal, as seen in Arachana nigra (Piñeiro, Ramos & Marsicano, 2012), Lap. nana (Yates, 1999), and Rhinesuchoides tenuiceps (SAM-PK-11489). By contrast, in Peltobatrachus pustulatus (CAMZM T.267) and other rhinesuchids, such as Rhineceps nyasaensis (CAMZM T.259), U. senekalensis (TM 185), Lac. watsoni (BP-1-123), and Br. putterelli (BP-1-5058), the prefrontal extends more anteriorly than the frontal.

Jugal: Most of the lateral surface of the skull is formed by the jugal, including the lateral margin of the orbit (Fig. 5: 'jug'). Its contact with the maxilla is straight and, once the maxilla contacts the quadratojugal, it does not reach the suborbital fenestra (contra Barberena, 1998). Anteromedially, the jugal contacts the prefrontal and lacrimal, resulting in the separation of the lacrimal from the orbit. In basal temnospondyls, such as D. acadianum (Holmes et al., 1998) and Tri. insignis (Milner & Schoch, 2013), the lacrimal enters the orbit. Australerpeton cosgriffi has a moderate preorbital expansion of the jugal, observed in most rhinesuchids except for U. senekalensis (Damiani & Rubidge, 2003: fig. 2F), in which the extension of the jugal is longer than half of the snout length. In ventral view, the jugal is visible at the anterior margin of the subtemporal fenestra (Fig. 6: 'jvp'). The ventral process (insula jugalis sensu Boy, 1988; or ventral alary process sensu Yates & Warren, 2000) is triangular and was not described by Barberena (1998). It is separated from the pterygoid by the ectopterygoid. When present, it is usually posterior to the ectopterygoid and borders exclusively the anterior portion of the subtemporal fenestra (an ambiguous synapomorphy of the Dvinosauroidea and Stereospondylomorpha according to Yates & Warren, 2000). However, here, both this ventral jugal process and the ectopterygoid border the anterior portion of the subtemporal fossa. This unique character is here considered an autapomorphy of Au. cosgriffi.

Postfrontal: The postfrontal contacts the prefrontal anteriorly, forming part of the medioposterior margin of the orbit (Figs 3–5: 'fr'). Posteriorly, the bone is very pointed and wedges between the parietal and postorbital, contacting the supratemporal. In a different way, in *Tri. insignis* (Milner & Schoch, 2013) the contact between the postfrontal and the supratemporal is absent owing to the presence of the intertemporal bone (which is absent in *Au. cosgriffi*).

*Postorbital:* The postorbital medioposteriorly wedges between the prefrontal and supratemporal (Figs 3–5: 'po'). It meets the squamosal and jugal laterally in a weakly developed margin that does not extends along the lateral edge of the orbit. With *Ly. huxleyi* and advanced Capitosauroidea, the postorbital forms a 'hook' that contacts the prefrontal anteriorly and excludes the jugal from the orbital margins (Damiani, 2001; Schoch, 2008).

*Parietal:* Each parietal is elongated, subrectangular, and slightly constricted anteriorly, with the pineal foramen in the middle of the medial suture (Figs 3– 5: 'pa'). The bone is the longest of the skull table. In UFRGS-PV-0224-P, UFRGS-PV-0225-P, and UFRGS-PV-0227-P (Fig. 2A–C), the anterior end of the parietal is placed anteriorly relative to the posterior level of the orbital margin, but in UFRGS-PV-0229-P (Fig. 2F) this margin is posterior to the orbits. The anterior margin of the parietal is blunt in adults of *Au. cosgriffi*, but markedly tapering in the subadult UFRGS-PV-0225-P, as in *Br. putterelli* (Shishkin & Rubidge, 2000), indicating a ontogenetically variable feature.

Postparietal: The postparietal pair forms an irregular hexagon that is anteriorly narrowed (Figs 3-5, 7: 'ppa'). Although broader posteriorly, the postparietal of Au. cosgriffi does not show the condition of Bashkirosaurus cherdyncevi (PIN 164/70; Gubin, 1981) and Platyoposaurus ssp. (Gubin, 1991), in which the postparietal pair is three times wider than long. In posterior view (Fig. 7), the postparietal has a descending lamina that contacts the exoccipital ventrally and separates the foramen magnum from the post-temporal fenestra. The postparietals form the curved dorsal margin of the foramen magnum, as in Rhinesuchoides tenuiceps (SAM-PK-11489), Rhinesuchus capensis (SAM-PK-7419), U. senekalensis (TM 185), and BP-1-4473. This is not the case for other rhinesuchids, which bear a straight dorsal margin, such as Rhineceps nyasaensis (CAMZM T.259) and Lac. watsoni (SAM-PK-4010; BP-1-213).

*Squamosal:* This bone forms most of the posterolateral region of the cheek, being limited by the supratemporal, the postorbital, the jugal, and the quadratojugal (Figs 3–5, 7, 8: 'sq'). Posteriorly, it borders the lateral margin of the otic notch, and shows dorsally a falciform crest (Fig. 8B: 'fcr'). According to Damiani (2001), this falciform crest is present in Rhinesuchidae and well



**Figure 7.** Australerpeton cosgriffi Barberena, 1998. Reconstruction of the skull in posterior view. Dark grey areas represent openings or fenestrae. Light grey areas represent recessed areas of bone (tympanic cavity) and areas of articulation (mandibular and occipital). Abbreviations: bo, basioccipital; ex, exoccipital; fm, foramen magnum; memb, ridge corresponding to the basal attachment of the medial membrane of the tympanic cavity (*sensu* Watson, 1962); occ, occipital condyle; pfe, post-temporal fenestra; ppa, postparietal; ps, parasphenoid; pt, pterygoid; qd, quadrate; qj, quadratojugal; sq, squamosal; tab, tabular; tyc, tympanic cavity. Scale bar = 5 cm.



**Figure 8.** Australerpeton cosgriffi Barberena, 1998, left otic notch of UFRGS-PV-0230-P. Photograph (A) and interpretative drawing (B), showing the crests of the tympanic cavity. Dark grey areas represent the area of the stapedial groove. Light grey areas represent the lateral wall of the tympanic cavity. Areas filled with parallel lines are broken or restored surfaces. Abbreviations: dpc, dorsal pterygoid crest; fcr, falciform crest; memb., ridge corresponding to the basal attachment of the medial membrane of the tympanic cavity (*sensu* Watson, 1962); obc; oblique crest; pt, pterygoid (ascending lamina); qd, quadrate; qj, quadratojugal; sq, squamosal; st, supratemporal; stg, stapedial groove; tab, tabular; tcr, tympanic crest. Scale bar = 5 cm.

pronounced in Capitosauroidea, but absent in archegosaurs and most of the Mesozoic temnospondyls. Indeed, in archegosaurids such as Arc. decheni (GPIT/Am/00685; SMNS 9706), the posterior margin of the squamosal is smooth. However, the Platyoposaurinae Pl. stuckenbergi (PIN 3968/1) and Platyoposaurus watsoni (PIN 161/39) have a weakly developed falciform crest, and 'advanced' non-Stereospondyli stereospondylomorphs, such as K. vetusta (PIN 521/1) and K. tarda (PIN 1758/253), also possess a well-developed falciform crest, as seen in Au. cosgriffi and other Rhinesuchidae.

In Au. cosgriffi, other Rhinesuchidae, and in Archegosauridae, the squamosal/tabular contact is absent and the supratemporal forms the anterior margin of the otic notch (Dias & Schultz, 2003; contra Barberena, 1998). This is not the case in other Stereospondyli such as Ly. huxleyi (Jeannot et al., 2006). In posterior view (Fig. 7), the dorsal margin of the squamosal is convex and ventrolaterally orientated. According to Shishkin & Rubidge (2000), this pattern is shared with the other Rhinesuchidae, whereas the dorsal margin of the squamosal of lyddekerinids is straight. Supratemporal: The supratemporal forms the posterolateral region of the skull table (Figs 3–5, 8: 'st'). The bone is subquadratic in shape and is shorter than the parietal. It contacts the postparietal and parietal medially, the postfrontal and postorbital anteriorly, and is gently curved in the contact with the squamosal. Its posterolateral edge forms the anteromedial corner of the otic notch.

Tabular: Trapezoid in shape, this bone contacts the postparietal medially, the supratemporal anteriorly, and forms most of the medial border of the otic notch (Figs 5, 7: 'tab'). Posterolaterally, the well-developed tabular horn extends ventrally and has a straight, prominent posterior projection (but not forming a spine; Figs 3B, 4, 7, 8). This is a unique Rhinesuchidae condition. The archegosaurids, such as Arc. decheni (Witzmann, 2005), also bear moderately developed tabular horns but they are medially curved in a slight 'hook'. The basal stereospondyls, such as Ly. huxleyi (Jeannot et al., 2006) and Be. sushkini (Bystrow & Efremov, 1940; Novikov, 2012), bear posterolaterally projected tabular horns, but without the ventral inflection observed in rhinesuchids.

In posterior view, the tabular forms the lateral margin of the slit-like post-temporal fenestra (Figs 3B, 4B, 7). This type of aperture is shared with Rhinesuchidae and non-Stereospondyli stereospondylomorphs, being distinct from other stereospondyls that have triangular and broad fenestrae, e.g. Ly. huxleyi (Jeannot et al., 2006), Ara. nigra (Piñeiro et al., 2012), and Pe. pustulatus (Panchen, 1959). The tabular contacts the exoccipital and forms the paraoccipital bar on the ventral border of the post-temporal fenestra (Fig. 7). The paraoccipital bar is laminar and ventrolaterally expanded, a character shared with Lac. watsoni (SAM-PK-4010; BP-1-213). The suture of the tabular with the exoccipital is oblique; laterodorsally orientated and results in the isolation of the opisthotic from the paraoccipital bar. This differentiates Au. cosgriffi (and other stereospondyls) from archegosaurids, e.g. S. haueseri (Schoch & Witzmann, 2009).

Quadrate: In the posterolateral portion of the skull, at the lowermost ventral level relative to the skull roof, the quadrate (Figs 4-8: 'qd') medially contacts the posterior ramus of the pterygoid, anterodorsally the squamosal, and laterally the quadratojugal. Its ventral surface forms the entire mandibular articulation area, which has a rugose surface texture, and borders the subtemporal fenestra posteriorly. The mandibular articulation is positioned posteriorly relative to the occipital condyles, as in archegosaurids and rhinesuchids (Barberena, 1998). This condition is intermediary between the basal temnospondyls, e.g. Er. megacephalus (Sawin, 1941), and advanced Triassic forms, e.g. Ma. giganteus (Schoch, 1999).

*Quadratojugal:* In posterior view, the quadratojugal Figs (3–8: 'qj') medially contacts the quadrate, lying dorsolateral to the mandibular articulation. Dorsally, it contacts the squamosal, bearing an extension of the falciform crest. Below the crest, both the paraquadratum and paraquadratum accessorium foramina are laterally placed. In lateral view, the quadratojugal briefly contacts the maxilla. Ventrally, it is part of the posterolateral margin of the subtemporal fenestra. Its contact with the maxilla, contra Barberena (1998: fig 4), isolates the jugal from the lateral margin of the fenestra.

Vomer: Forming most of the rostral part of the palate, the vomer is an elongated bone (Figs 3C, 4C, 6: 'vo'), wedging anteriorly on the posterior margin of the premaxilla. Laterally, it contacts the maxilla. The vomer forms the entire medial margin of the choana, bearing a row of seven to eight small teeth. This small tooth row is slightly convex, anteroposteriorly orientated, and placed medially relative to the choana margin. Anteriorly to the choana, there are two large vomerine tusks, as large as the palatine ones. This differs from the plesiomorphic condition, in which the vomerine tusks are smaller than the palatine ones, as in the archegosaurid Me. kamaensis (PIN 683/1). Posteromedially, the cultriform process of the parasphenoid wedges between the vomers. Contrary to Barberena (1998), the posterolateral projection of the vomer reaches the anterior border of the interpterygoid vacuity, as observed in UFRGS-PV-0229-P and UFRGS-PV-0224-P (Figs 3C, 4C, 6), and also present in both Stereospondvli and higher non-Stereospondyli stereospondylomorphs, e.g. K. vetusta (Gubin, 1991). The ventral surface of the vomer is covered by numerous denticles. These denticles are uniform in size and equally distributed, as in U. senekalensis (TM 185). Other rhinesuchids have the vomerine denticles mounting up in some regions, forming agglomerations with a lumpy aspect, e.g. Rhinesuchus broomianus (GPIT/Am/722), Rhineceps nyasaensis (CAMZM T.259), and Br. putterelli (BP-1-1058).

Palatine: This is a very elongated bone (Fig. 6: 'pl'). Its medial margin forms the anterolateral border of the interpterygoid vacuity, where the anterior outline becomes narrow in comparison with the posterior margin. At this point, the palatine prevents contact between the vomer and the pterygoid, differing from the condition found in basal temnospondyls such as Er. megacephalus (Sawin, 1941), in which the vomer contacts the pterygoid. Anteriorly, the palatine forms the posterolateral corner of the choana and bears large two tusks. It presents a tooth row that varies from 12 to 14 teeth. According to Yates & Warren (2000: character 78), there is a trend of increasing palatine teeth across temnospondyl evolution, as basal forms



**Figure 9.** Australerpeton cosgriffi Barberena, 1998. Posterior region of the palate of UFRGS-PV-0229-P. Photograph (A) and interpretative drawing (B). Dark grey areas represent openings or fenestrae. Light grey areas represent recessed areas of bone (tympanic cavity), areas of articulation (occipital) or insertion (pockets for insertion of vertebro-occipital musculature), and denticles on the palate. The black areas represent areas of the dorsal surface. Abbreviations: asd, denticles on the parasphenoid with arch-shaped distribution; bo, basioccipital; cm, crista muscularis; gm, groove possibly for the insertion of a mucous membrane or dentigerous ossicles on the interpretygoid vacuity; iv, interpretygoid vacuity; occ, occipital condyle; poc, 'pockets' for the insertion of the occipital musculature; ps, parasphenoid; pt, pterygoid. Scale bar = 5 cm.

such as *D. acadianum* (Holmes *et al.*, 1998) and *Er. megacephalus* (Sawin, 1941) lack them, *S. haueseri* (Schoch & Witzmann, 2009) bears only two teeth, and other Stereospondylomorpha, such as *Arc. decheni* (Witzmann, 2005), possess more teeth. Yet, the scenario described by Yates & Warren (2000) is possibly more complex, as there is a reversion in *Me. kamaensis* (PIN 683/1) and stereospondyls such as *Ara. nigra* (Piñeiro *et al.*, 2012), *Lap. nana* (Yates, 1999), and Lydekkerinidae (Jeannot *et al.*, 2006), which have fewer palatine teeth.

*Ectopterygoid:* In ventral view, the narrow and long ectopterygoid rises from the posterolateral edge of the palatine, being lateromedially compressed against the maxilla and the pterygoid (Figs 3C, 6: 'ec'). The pterygoid/palatine contact excludes the ectopterygoid from the margins of the interpterygoid vacuity. There is no tusk on the ectopterygoid and its tooth row varies from ten to 14 teeth, being continuous to the palatine tooth row. The ectopterygoid forms part of the anterior margin of the subtemporal fenestra. In a different way, the condition commonly observed in stereospondyls, such as *Lap. nana* (Yates, 1999) and *Be. sushkini* (Bystrow & Efremov, 1940), is the ectopterygoid being excluded from the subtemporal fenestra border.

*Pterygoid:* As is usual in temnospondyls, this bone radiates with anterior (palatine), posterior (quadrate), medial (parasphenoid), and dorsal (ascending) rami. In ventral view, the posterolateral margin of the interpterygoid vacuity is formed by the palatine ramus of the pterygoid (Figs 3, 4, 6, 7: 'pt'). It extends beyond half the length of the vacuity, but does not reach the

vomer. The retraction of the ramus, not observed in archegosaurids, is considered typical of advanced Stereospondyli (Milner, 1990; Gubin, 1997). The pterygoid ventral surface (Figs 4, 6, 9) is entirely covered by a field of denticles, but is devoid of ornamentation. Triassic stereospondyls bear an ornamented pterygoid, e.g. *Ly. huxleyi* (NHMUK R.507). Amongst Rhinesuchidae, *Rhinesuchus* ssp. (GPIT/Am/722; SAM-PK7419; SAM-PK-11489; SAM-PK-3009) and *Rhineceps nyasaensis* (CAMZM T.259) also lack ornamentation on this bone, but it is present in *Lac. watsoni* (SAM-PK-4010; BP-1–213), *U. senekalensis* (TM 185), and *Br. putterelli* (TM 184; BP-1–1058), being restricted to the lateral border of the palatine ramus.

The anterior border of the pterygoid bears a wellmarked groove (Fig. 9: 'gm'), possibly for attachment of a mucous membrane covering the interpterygoid vacuity (M. Shishkin, pers. comm.), or for the insertion of dentigerous ossicles as in Trematolestes hagdorni (Schoch, 2006). This groove separates the area aspera (covered by denticles) from the smooth inner flange of the vacuity. This is quite conspicuous in stereospondyls such as Rhinesuchidae and Pe. pustulatus (CAMZM T. 267), but more advanced forms possess a less developed groove in comparison. The medioanterior border of the subtemporal fenestra is formed by the pterygoid. Medially, the pterygoid body contacts widely with the parasphenoid, forming a firm and extensive suture (Figs 3C, 4C, 6, 9), differing from the 'peg-and-socket' joint of most non-stereospondyls (Yates & Warren, 2000).

*Parasphenoid:* The parasphenoid is an elongated bone (Fig. 6: 'ps'). Its narrow cultriform process broadens

slightly and regularly anteriorly (Fig. 6: 'cp'). In UFRGS-PV-0227-P and UFRGS-PV-0229-P, the cultriform process anteriorly extends to the anterior margin of the interpterygoid vacuity, differing from the shorter cultriform process of UFRGS-PV-0224-P. The anterior part of the cultriform process is flattened and its middle portion bears a sharp ridge, forming a 'keel'. Its proximal edge (with respect to the parasphenoid body) is rounded in cross-section. The parasphenoid body is also elongated, bearing a ventral medial depression. The ventral surface of the parasphenoid body is fully covered by denticles distributed in an area with an arched posterior margin (Figs 6, 9). This arrangement differs from that seen in Archegosauridae, which bears a button-like concentration of denticles at the base of the cultriform process, as in Arc. decheni (Witzmann, 2005), Pl. stuckenbergi (Gubin, 1991), and K. vetusta (Gubin, 1991). By contrast, Triassic stereospondyls possess denticles distributed in a transverse 'belt', as in Be. sushkini (Bystrow & Efremov, 1940), or denticles may even be absent from the parasphenoid body, as in Ma. giganteus (Schoch, 1999).

Posterior to the suture with the pterygoid, the parasphenoid has a marked constriction, formed by lateral notches. According to Pawley & Warren (2005), these notches characterize the parasphenoid of rhinesuchids, but this condition is also present in non-Stereospondyli stereospondylomorphs from Russia, e.g. K. vetusta (PIN 520/1), Me. kamaensis (PIN 683/1), and Try. paucidens (PIN 157/108). Amongst rhinesuchids, most taxa present well-marked notches, except for the miniaturized Br. putterelli (TM 184). Some basal stereospondyls also bear these lateral notches, for instance Ly. huxleyi (Pawley & Warren, 2005), Lap. nana (Yates, 1999), and Pe. pustulatus (Panchen, 1959). Posterior to the notches, the parasphenoid has posterolateral projections, forming 'lateral flanges'. These flanges are weakly developed in Rhinesuchidae, but they are well developed in the Russian stereospondylomorphs Me. kamaensis (PIN 683/1) and Try. paucidens (PIN 157/108).

Posteroventrally, the parasphenoid body presents two pits for the insertion of the vertebra-occipitalis musculature (Barberena, 1998). Following Watson (1962), these depressions are 'pockets' for the insertion of the recti capitis muscles. Described as semicircular 'pockets' by Barberena (1998), these structures form shallow and posteriorly orientated concavities, which are anteriorly accompanied by the crista muscularis (Figs 6, 9: 'cm'). Each crest is well developed laterally, not confluent in the midline and visible in posterior view, as observed in Rhinesuchidae and Lydekkerinidae (Shishkin et al., 1996). The opposite condition, a crest confluent in the midline (Damiani, 2001), was first defined by Cosgriff (1974) as a 'transverse ridge', and is more common in Triassic stereospondyls, such as Be. sushkini (PIN 2424/10) and Thoosuchus yakovlevi (PIN 3200/473). The posterior limit of the sutural contact with the pterygoid is anterior to the posterior margin of the parasphenoid body. At this point, the carotid foramen is dorsally positioned in *Au. cosgriffi*. The dorsal position of the carotid foramina was first recognized by Shishkin (1968) and later defined by Yates & Warren (2000) as a synapomorphy of Stereospondyli.

Basioccipital: Almost entirely covered by the posterior part of the parasphenoid, the basioccipital is visible between the occipital condyles in both ventral and occipital views (Figs 3, 6, 7: 'bo'). The posterior expansion on the parasphenoid is a feature of Stereospondyli (see states 1 and 2 of character 184 below). Amongst Rhinesuchidae this is also observed in *Rhineceps nyasaensis* (CAMZM T.259), *Lac. watsoni* (BP-1-213), *Rhinesuchoides tenuiceps* (SAM-PK-11489), and *Br. putterelli* (TM 184).

*Exoccipital:* The exoccipital forms the ventrolateral margin of the foramen magnum and the ventromedial margin of the post-temporal fenestra (Figs 3, 4, 7: 'ex'). The condyles are well separated from each other and formed exclusively by the exoccipitals, a typical condition for the Stereospondyli. The size of the occipital condyles corresponds to half of the exoccipital width. Conversely, bilobed occipital condyles also partly composed by the basioccipital are observed in *Er. megacephalus* (Sawin, 1941), as well as in more 'advanced' non-Stereospondyli stereospondylomorphs, such as *K. vetusta* (Gubin, 1991).

Tympanic cavity: The otic notch is shallow (Figs 7, 8) and its medial wall is formed by the tabular, being posteriorly limited by the tabular horn. The lateral wall is formed by the supratemporal anteriorly, and the squamosal posteriorly. The falciform crest (Figs 3, 8: 'fcr') forms the dorsolateral margin of the notch, rising posteromedially from the dorsal squamosal surface and extending also to the quadratojugal. Where the falciform crest originates, the squamosal bears, on the occipital lamina, a transversally orientated tympanic crest (Figs 3, 4, 8: 'tcr'). This term was coined by Shishkin et al. (1996) for Lydekkerinidae, but the structure seems to also be present in Rhinesuchidae, e.g. Rhinesuchus capensis (SAM-PK-7419), U. senekalensis (TM 185), Lac. watsoni (SAM-PK-4010; BP-1-213), Rhinesuchoides tenuiceps (SAM-PK-11489), and Br. putterelli (TM 184, BP-1–5058). The tympanic crest forms the posteroventral border of the otic notch, close to the squamosal/ quadratojugal contact. The posteroventral floor of the tympanic cavity (Fig. 8B) is ventromedially formed by the quadrate, which contacts the ascending ramus of the pterygoid.

The medial face of the ascending ramus of the pterygoid of *Au. cosgriffi* bears a well-developed groove for the insertion of the medial membrane of the tympanic cavity (Watson, 1962: figs 7B, 9B; Barberena, 1998: fig 5; here Fig. 8B: 'memb'). This groove is present in most Stereospondylomorpha, although not in basal forms, e.g. Arc. decheni (GPIT/Am/00685; SMNS 9706) and S. haueseri (MB. Am 1346; SMNS 81791; SMNS 90055). Dorsally, the medial surface of the ascending ramus of the pterygoid houses the oblique crest (Fig. 8B: 'obc') sensu Bystrow & Efremov (1940) or 'otic flange' sensu Watson (1962). This crest is present in most Stereospondyli, e.g. Be. sushkini (Bystrow & Efremov, 1940), being especially well developed in Rhinesuchidae.

At the anterior margin of the otic notch, the ascending ramus of the pterygoid contacts the supratemporal. Posteriorly, the dorsal border of the ascending lamina of the pterygoid is protruded, forming the dorsal pterygoid crest (new term; Fig. 8B: 'dpc'); an anteroposteriorly orientated ridge that appears in the contact of the pterygoid with the occipital lamina of the squamosal. The dorsal pterygoid crest is dorsally placed relative to the oblique crest, and between the ridges a stapedial groove *sensu* Watson (1962) is present, being well developed in Rhinesuchidae and *Ly. huxleyi* (BP-1–5185; CAMZM T. 110; CAMZM T.238; NHMUK R.507).

Mandible: The anterior tip of the dentary bears three tusks followed by a row of small teeth that become increasingly larger posteriorly. Preserved only in UFRGS-PV-0229-P, the symphysis corresponds to one third of the mandibular length. In medial view, as seen in LPRP/USP-0011, the symphysis of Au. cosgriffi has an elongated groove, which extends anteroposteriorly along its surface (Eltink & Langer, 2014a). Medially, the right ramus of UFRGS-PV-0224-P bears an elongated anterior Meckelian fenestra, whereas the left ramus has three small foramina forming a row at the same region. The splenial/postsplenial contact is marked by a zigzag suture. The middle coronoid reaches the dorsal margin of the mandible and the posterior coronoid forms part of the adductor fossa anterior margin, as observable laterally. The posterior Meckelian fenestra is elongated and formed by the prearticular, the postsplenial, and the articular.

The medial wall of the adductor fossa, formed by the prearticular, is lower than the lateral wall and formed by the surangular. Anteriorly, the prearticular extends forward to the level of the anterior Meckelian fenestra. Posteriorly, the chorda tympanica foramen is present between the prearticular and the articular. Laterally, the surangular occupies most of the dorsoposterior portion of the mandible and ventrally the angular is bordered by the prearticular. The glenoid of skull articulation elevates higher relative to the dentary. The postglenoid region is weakly developed, as observed in the retroarticular process and the arcadian process sensu Warren & Black (1985). Both the mandibular and arcadian grooves are shallow (Fig. 4). Reduced processes and grooves in the postglenoid region are observed in Rhinesuchidae, e.g. Rhineceps nyasaensis

(CAMZM T.259) and Russian stereospondylomorphs, e.g. *Me. kamaensis* (PIN 683/1). By contrast, a welldeveloped postglenoid region is typical of Triassic forms (Jupp & Warren, 1986).

In addition to the above-mentioned information available for UFRGS-PV-0224-P and UFRGS-PV-0229-P, see Eltink & Langer (2014a) for more detailed information on the mandible of *Au. cosgriffi*.

## PHYLOGENETIC ANALYSIS

The phylogenetic investigation presented here is focused on the position of  $Au. \ cosgriffi$  within Rhinesuchidae. In spite of its alleged Archegosauridae affinities (Wernerburg & Schneider, 1996; Schoch & Milner, 2000), or 'intermediate' position between Stereospondyli and Archegosauridae (Witzmann & Schoch, 2006; Schoch *et al.*, 2007; Schoch, 2013), a recently published broader analysis demonstrated the nesting of  $Au. \ cosgriffi$  within Rhinesuchidae (Eltink & Langer, 2014b), corroborating previous proposals (Barberena, 1998; Dias & Schultz, 2003).

The terminal taxa used in the analysis encompass all well-known Rhinesuchidae (see Supporting Information Appendix S1). A taxonomic revision of this family is needed (Damiani & Rubidge, 2003) and is currently in progress by C. A. Marsicano & B. S. Rubidge (unpubl. data). In addition to named rhinesuchids, the analysis also included the specimen BP-1-4473 and the Serra do Cadeado short-snouted rhinesuchid (Barberena & Dias, 1998; E. V. Dias; S. Dias-da-Silva & C. L. Schultz, unpubl. data). Moreover, representatives of other wellknown Triassic stereospondyls groups were also included, i.e. Ly. huxleyi, Be. sushkini, and Ma. giganteus, in addition to the incertae sedis Lap. nana and Pe. pustulatus. The ingroup also included the Russian 'advanced' stereospondylomorphs, K. vetusta and Try. paucidens - both considered stem-taxa of Stereospondyli (Schoch & Milner, 2000; Yates & Warren, 2000) - and well-known basal temnospondyls, such as Er. megacephalus and Tri. insignis. The well-known, relatively complete, and generalized basal temnospondyl D. acadianum (Holmes et al., 1998; Holmes, 2000) was used to root the most parsimonious trees (MPTs).

In order to assess the affinities of *Au. cosgriffi*, 221 characters were scored for the above taxa. Onehundred and ninety-six characters were taken literally or modified/adapted from previous studies that applied explicit numeric cladistics to deal with temnospondyls, i.e. Bolt & Lombard (2001), Carroll (1995), Coates (1996), Damiani (2001), Holmes *et al.* (1998), Laurin & Reisz (1997), Lebedev & Coates (1995), McHugh (2012), Morales & Shishkin (2002), Pawley & Warren (2005), Piñeiro, Marsicano & Lorenzo (2007), Ruta & Coates (2007), Ruta & Bolt (2008), Schoch & Witzmann (2009), Schoch (2008, 2013), Schoch *et al.* (2007), Warren



**Figure 10.** The most parsimonious tree that resulted from the phylogenetic analysis, with 509 steps, depicting the position of *Australerpeton cosgriffi*. 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%.

& Marsicano (2000), Witzmann & Schoch (2006), and Yates & Warren (2000). In addition, 25 new characters were proposed (see Supporting Information Appendix S2).

The taxon-character matrix (21/221) was constructed using the software MESQUITE v. 2.75 (Maddison & Maddison, 2011). The parsimony analysis was performed using TNT v. 1.1 (Goloboff, Farris & Nixon, 2008) under the implicit enumeration ('traditional search') option with 10 000 replicates, random addition of taxa (random seed = 0), *hold* = 10, and the tree bisection and reconnection algorithm for branch swapping. The characters 21, 22, 24, 25, 34, 41, 43, 70, 91, 102, 112, 133, 179, 180, 182, 185, 194, and 212 were ordered, as seen in their original proposition (see Supporting Information Appendix S2). Bootstrap (Holmes, 2003) and Bremer support (Bremer, 1994) values were calculated using 10 000 replicates, and the optimization indexes [consistency (CI) and retention (RI)] using the TNT default.

The analysis recovered a single MPT of 509 steps (CI = 0.497; rescaled consistency index = 0.250;

RI = 0.504). The tree, including Bremer support and bootstrap values, is shown in Figure 10. The results demonstrate that: (1) Au. cosgriffi is an apical member of the Rhinesuchidae, sister taxon of the Serra do Cadeado short-snouted rhinesuchid, and is also close to Br. putterelli; (2) Rhinesuchidae is monophyletic and divided into two less inclusive clades, one comprising the clade (Rhinesuchus broomianus, Rhineceps nyasaensis, and Rhinesuchus whaitsi), and the other encompassing U. senekalensis and another clade of long-snouted rhinesuchids; (3) Stereospondyli is monophyletic, divided here into the Rhinesuchidae and a clade of Triassic temnospondyls (Ly. huxleyi, Ma. giganteus, and Be. sushkini) that also includes the miniaturized Pe. pustulatus and Lap. nana; (4) the Russian stereospondylomorphs Try. paucidens and K. vetusta form the sister-clade of the Stereospondyli. The related synapomorphies are discussed below (for a complete synapomorphies list see Supporting Information Appendix S4).



Figure 11. Part of the most parsimonious tree, including only Stereospondylomorpha. The rectangles represent all supporting synapomorphies mapped onto each node; state 0 in white and states 1, 2 or 3 in black.

## DISCUSSION

## PHYLOGENETIC RELATIONSHIPS OF RHINESUCHIDAE

Our analysis recovered Rhinesuchidae as the sistergroup of a clade formed here by *Pe. pustulatus* and *Lap. nana*, and the Triassic stereospondyls. The synapomorphies of Rhinesuchidae include three character states of the tympanic cavity: a large and sharpedged oblique ridge (character 91-2); a ventrolaterally directed tabular horn with a sharp ventral inflection (character 179-3); and the presence of a stapedial groove (character 210-1). Although some of these characters were previously recognized as typical of Rhinesuchidae (for the tabular horn, see Schoch & Milner, 2000), they were never considered synapomorphic for the clade prior to this contribution (Fig. 11).

As discussed by Damiani & Rubidge (2003) the phylogenetic relationships of Rhinesuchidae are still poorly understood, and previous analyses employed only a few taxa (e.g. *Rhineceps nyasaensis* and/or U. senekalensis) as representatives of the group, e.g. Yates & Warren (2000), Damiani (2001), and Schoch (2013). The present analysis included several rhinesuchids never used before in phylogenetic studies. As a result, we found that Rhinesuchidae is composed of two clades, named the Rhinesuchidae is composed of two clades, named the Rhinesuchiae and the Australerpetinae (Figs 10, 11). These clades are nodebased and defined as *Rhinesuchus whaitsi*, *Rhineceps nyasaensis*, and all descendants of their most recent common ancestor; and *Australerpeton cosgriffi*, *Lac. watsoni*, and all descendants of their most recent common ancestor, respectively.

The clade Rhinesuchinae encompasses Rhinesuchus whaitsi, Rhinesuchus broomianus, and Rhineceps *nyasaensis*. Most synapomorphies supporting the clade are recognized in the palate: smooth ventral surface of the palatine ramus of the pterygoid (character 83-0); absence of flange in the palatine ramus of the pterygoid (character 94-1); tabular horn with a spine in the medial border of the otic notch (character 180-2); and denticles grouped in some areas of the palatal surface (character 192-3). In the recovered topology, not all species referred previously to Rhinesuchus are included in the Rhinesuchinae: 'Rhinesuchus' capensis nests within Australerpetinae. close to *Rhinesuchoides* tenuiceps. The skull elongation of 'Rhinesuchus' capensis, the presence of a tympanic crest sensu Shishkin et al. (1996), the anterior tapering of the interpterygoid vacuities (character 195-2), the posterolaterally facing parasphenoid pockets (character 76-1), and the ectopterygoid tusks (character 68-0) support this phylogenetic affinity. As a result, pending future corroboration of the hypothesis presented here, a different generic affinity will have to be proposed for 'Rhinesuchus' capensis, given that it is not the type species of the genus (*Rhinesuchus whaitsi*, see Broom, 1908).

The sister-group of the Rhinesuchinae is a clade comprising U. senekalensis and the Australerpetinae. Regarding U. senekalensis, Romer (1947) created the family Uranocentrodontidae, but later studies placed this taxon simply within the Rhinesuchidae (Carroll, 1988; Schoch & Milner, 2000; McHugh, 2012). The synapomorphies supporting U. senekalensis as the sistertaxon of Australerpetinae are the presence of a tympanic crest sensu Shishkin et al. (1996) (character 202-1) and a foramen magnum with a curved dorsal margin (character 208-0). However, the compression of the marginal tooth row, the morphology of the snout (wide and blunt prefrontal, anteriorly elongated jugal, and medial depression between elevated orbits) and the palatal region (absence of parasphenoid central depression, presence of contact of the palatine ramus of pterygoid and vomer, basioccipital visible in ventral view) differentiate U. senekalensis from the Australerpetinae.

The other rhinesuchids correspond to the Australerpetinae, a group that clearly shows anteroposterior skull elongation, which occurs to a remarkable extent in Au. cosgriffi and Lac. watsoni. The name Australerpetinae is a modification of Australerpetonidae Barberena, 1998, using a lower coordinate category and a corrected suffix. The main synapomorphies that support the clade are the tapering of the preorbital region (character 1-1), retraction of the palatine ramus of the pterygoid, and the palatine contributing to the interpterygoid vacuity margin (character 197-1). The latter character was formerly regarded as synapomorphic for the Stereospondyli (Schoch & Milner, 2000; Yates & Warren, 2000). The reversion to a circular or moderately oval crosssection of the marginal teeth (character 3-0) also represents an Australerpetinae synapomorphy, as anteroposteriorly compressed teeth (character 3-1) are synapomorphic for the Stereospondyli (Schoch, 2013).

# AUSTRALERPETON COSGRIFFI, A LONG-SNOUTED BASAL STEREOSPONDYLI

The long-snouted morphology of Au. cosgriffi diverges from other basal stereospondyls that are shortsnouted, e.g. Lap. nana (Yates, 1999), Ara. nigra (Piñeiro et al., 2012), Pe. pustulatus (Panchen, 1959), and Ly. huxleyi (Jeannot et al., 2006). Amongst the characters observed in basal stereospondyls, some are related to the short-snouted morphology (with synapomorphies indicated by asterisks): parabolic preorbital region (character 1-0); prenarial portion shorter than naris (character 5-0); lacrimal shorter than nasal (character 28-1\*); premaxilla outline parabolically rounded (character 53-0); vomerine plate short, as wide as long (character 60-0); prefrontal longer than frontal, indicating a retraction in the frontal length (character 173-0\*).

However, Au. cosgriffi shares with other stereospondyls the contact between tabular and exoccipital in the paroccipital process (character 46-1\*) and the oblique ridge on the posterior face of the quadrate ramus of the pterygoid (character 91-1\*), differentiating it from non-Stereospondyli Stereospondylomorpha, such as K. vetusta (Gubin, 1991) and Pl. stuckenbergi (Gubin, 1991). These species have the opisthotic forming part of the paraoccipital bar and the oblique crest absent, or rudimentary as in K. vetusta (PIN 521/1). In the posterior region of the palate (Fig. 12), the parasphenoid denticle field enlarged to a transverse 'belt' (or posterior margin arch-shaped) (character 199-1/2\*) and the ridges on the borders of the interpterygoid vacuity (character 200-1\*) are described as synapomorphies of Stereospondyli. In addition, Au. cosgriffi and stereospondyls share the parasphenoid bearing an extensive suture with the pterygoid (character 84-2); ventral 'pockets' on the flat ventral surface of the



**Figure 12.** Parasphenoids of Eryopiformes in ventral view, including Stereospondyli (see characters 27, 76, 82, 199, 209 in Supporting information Appendix S2). A, *Eryops megacephalus* (AMNH 4673). B, *Platyoposaurus watsoni* (PIN 161/20). C, *Australerpeton cosgriffi* (UFRGS-PV-0224-P). D, *Uranocentrodon senekalensis* (TM 185). E, *Lydekkerina huxleyi* (CAMZM T.238). F, *Benthosuchus sushkini* (PIN 219/2257). Scale bars: A, D = 5 cm, B, C, F = 3 cm, E = 1 cm.

parasphenoid (character 76-2); and the internal carotid artery passing through the dorsal surface of the parasphenoid plate (character 82-2).

Regarding the status of  $Au. \ cosgriffi$  as a longsnouted basal stereospondyl, the elongation of the snout is convergent with that of the Russian non-Stereospondyli stereospondylomorphs. Both taxa were present at the same time (Middle–Late Permian), in Gondwana and Laurasia, respectively, but represent different groups. The long-snouted morphology of



**Figure 13.** Tympanic cavities of Eryopiformes, including Stereospondyli (see characters 91, 201, 210 in Supporting information Appendix S2). A, *Eryops megacephalus* (AMNH 23529), dorsal view of the right otic notch. B, *Platyoposaurus watsoni* (PIN 161/39), posterolateral view of the right otic notch. C, *Konzhukovia vetusta* (PIN 520/1), dorsal view of the right otic notch. D, *Australerpeton cosgriffi* (UFRGS-PV-0230-P), posterolateral view of the left otic notch. E, *Rhineceps nyasaensis* (CAMZM T.259), posterolateral view of the right otic notch. F, *Uranocentrodon senekalensis* (TM 185), posterolateral view of the left otic notch. Scale bars: A–C, E, F = 3 cm; D = 1 cm. The arrows indicate the dorsal pterygoid crest (white), the stapedial groove (black), and the oblique crest (yellow).

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Figure 14. Reconstruction of *Australerpeton cosgriffi* in its environment (Middle–Late Permian, Rio do Rasto Formation, Paraná Basin) by Rodolfo Nogueira.

Platyoposaurinae (e.g. *Pl. stuckenbergi*), Archegosaurinae (e.g. *Collidosuchus tchudinovi*), and Tryphosuchinae (e.g. *K. vetusta*) is convergent when the tapering of the preorbital region (character 1-1) and the narrowing of the vomerine plate (character 60-1) are observed; here considered as plastic characters. *Au. cosgriffi* shows that long-snouted forms seem to have been present early in Stereospondyli evolution (Middle/Late Permian), which later was represented by Triassic Trematosauridae, such as the Lonchorhynchinae *Aphanerama rostratum* and *Cosgriffus campi*.

## MODIFICATIONS OF THE TYMPANIC CAVITY DURING EARLY STEREOSPONDYL EVOLUTION

Amongst basal Eryopiformes sensu Schoch (2013), the tympanic cavity is reduced and the border of the otic notch is slit-like, e.g. Er. megacephalus (Sawin, 1941), Platyoposaurus spp. (Gubin, 1991), Arc. decheni (Witzmann, 2005), Melosaurus spp. (Gubin, 1991), and Konzhukovia spp. (Gubin, 1991). The lateral wall of the tympanic cavity is smooth, except for the presence of a very low and short dorsal pterygoid crest proximally along the contact between the ascending ramus of the pterygoid and the occipital lamina of the squamosal (Fig. 13). This pattern differs from that of stereospondyls, in which that border is larger and more rounded (character 182-1), and the tabular horn is directed more ventrolaterally, with a sharp ventral inflection (character 179-3). Rhinesuchids have two crests on the lateral wall of the tympanic cavity, the dorsally placed 'dorsal pterygoid crest' and the ventrally

placed 'oblique crest' (character 91-2), both being well developed and forming sharp ridges. Between these crests lies the stapedial groove (character 210-1), first described in *Rhineceps nyasaensis* (Watson, 1962).

Some rhinesuchids, e.g. Australerpetinae and U. senekalensis (TM 185), bear the tympanic crest positioned posterolaterally in the tympanic cavity (character 202-1). This crest was first observed in Eo. magna by Shishkin et al. (1996), and was considered as typical of lydekkerinids. Differing from rhinesuchids, Triassic stereospondyls, such as Be. sushkini (Bystrow & Efremov, 1940), have a rounded and less strongly developed 'oblique crest' compared with rhinesuchids. The 'dorsal pterygoid crest' is also not developed along the pterygoid/squamosal contact. In the same area where dorsal pterygoid ridge is present, some advanced stereospondyls, such as Thoosuchus yakovlevi (PIN 3200/473), bear the palatoquadrate fissure.

# CONCLUSIONS

- 1. The redescription of the skull material given here provides a more comprehensive understanding of the morphology of *Au. cosgriffi*.
- 2. Rhinesuchidae is confirmed to be monophyletic, in a sister-group relationship with *Pe. pustulatus* plus Triassic stereospondyls, and comprises two main groups, Rhinesuchinae and Australerpetinae, most synapomorphies of which are located in the tympanic cavity.

- 3. Australerpeton cosgriffi belongs to the Rhinesuchidae, and represents the only well-known Rhinesuchidae outside southern Africa.
- 4. *Australerpeton cosgriffi* is considered to be the oldest long-snouted stereospondyl known to date (Fig. 14), although a few rhinesuchids show moderate skull elongation.

## ACKNOWLEDGEMENTS

The research was supported by Fundação de Amparo à Pesquisa no Estado de São Paulo (FAPESP; 2009/ 54656-9). Rodrigo Rocha Machado (DGM), Cesar Leandro Schultz (UFRGS), Rainer Schoch (SMNS), Philipe Havlik (GPIT), Florian Witzmann (MB), Mathew Lowe (CAMZM), Lorna Steel and Andrew Milner (UKNHM), Yuri Gubin and Mikhail Shishkin (PIN), Bernhard Zipfel and Bruce Rubidge (BPI), Sheena Kaal (IZIKO), Heidi Fourie (TM), and Carl Mehling (AMNH) provided access to specimens. We thank Rainer Schoch and Mikhail Shishkin for many fruitful discussions and first-hand information. Useful comments by an anonymous reviewer and J-Sebastien Stever helped to improve the manuscript. E.E. expresses deepest gratitude to Antonio M. Nogueira and Theresia C. E. Nogueira for their support and encouragement during the research.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

- **Appendix S1.** List of taxa used in the phylogenetic analysis and notes on taxonomic assumptions.
- Appendix S2. List of characters used in the phylogenetic analysis.
- **Appendix S3.** Nexus file for the phylogenetic analysis.

Appendix S4. List of synapomorphies.