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## A NEW SPECIMEN OF THE TEMNOSPONDYL *AUSTRALERPETON COSGRIFFI* FROM THE LATE PERMIAN OF BRAZIL (RIO DO RASTO FORMATION, PARANÁ BASIN): COMPARATIVE ANATOMY AND PHYLOGENETIC RELATIONSHIPS

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**ABSTRACT**—A new temnospondyl specimen from the Rio do Rasto Formation (late Permian, Paraná Basin) of south Brazil is composed of a left mandible, right pelvis, femur, tibia, and fibula. Preserved lower jaws are rare for *Australerpeton cosgriffi*, and the weak ossification of the temnospondyl postcranium renders their preservation generally uncommon. A detailed comparative description of the material allowed its assignment to *Australerpeton cosgriffi*, and yielded new information about the morphology of mandible, pelvis, and hind limb of that taxon. This long-snouted temnospondyl has uncertain affinities and has been assigned either to stereospondyl Rhinesuchidae or to archegosaurid Platyoposaurinae. Reassessment of the phylogenetic placement of *Australerpeton cosgriffi*, with information drawn from the new specimen, confirms a basal stereospondyl position, between *Peltobatrachus pustulatus* and Rhinesuchidae. The synapomorphies shared with other stereospondyls include tabular and exoccipital contacting in the paroccipital process; parasphenoid articulates with corpus of the pterygoid forming a broad contact along the lateral margins of the parasphenoid plate; internal carotid passes through the dorsal surface of the parasphenoid plate; and parasphenoid denticles field enlarged to a transverse ‘belt’ extending between the pterygoid-parasphenoid articulations. Accordingly, *Australerpeton cosgriffi* represents one of the first stereospondyls, and the oldest long-snouted member of the group. The Paraná Basin can be included within the stereospondyl ancestral range, and dispersion and diversification of this clade appears to have happened before the Permo–Triassic boundary.

**SUPPLEMENTAL DATA**—Supplemental materials are available for this article for free at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP)

### INTRODUCTION

Temnospondyls are the most diverse group of early tetrapods, including about 198 genera (Schoch, 2013) and spanning from the Early Carboniferous (Viséan) to the late Early Cretaceous (Albian) (Milner, 1990). If Lissamphibia belongs into the group (Bolt, 1969, 1977, 1991; Milner, 1988, 1990, 1993, 1994, 2000; Trueb and Cloutier, 1991; Gardner, 2001; Ruta et al., 2003; Ruta and Coates, 2007; Sigurdson and Bolt, 2010; Sigurdson and Green, 2011; Maddin and Anderson, 2012; Maddin et al., 2012), the temnospondyl time range reaches modern days. The interrelationships of major temnospondyl groups remain not well understood, despite recent progress (Schoch and Milner, 2000; Yates and Warren, 2000; Ruta et al., 2007; Schoch, 2013). Following the general pattern proposed by Milner (1990), Holmes (2000) provided a phylogenetic scheme dividing temnospondyls into five major groups: Edopoidea, Trimerorhachoidea, Eryopoidea, Dissorophoidea, and Archegosauroida (which includes the very diverse and advanced Stereospondyli). The archegosauroids represent the Archegosauriformes sensu Schoch and Milner (2000) or Stereospondylomorpha sensu Yates and Warren (2000). The taxon here studied, *Australerpeton cosgriffi*, is phylogenetically included in these clade.

*Australerpeton cosgriffi* is a long-snouted temnospondyl known from the late Permian Rio do Rasto Formation, south Brazil. Originally it was described from a rostrum (UFRGS-PV-0228-P). Formerly referred to *Platyoposaurus* by Barberena and Daemon (1974), this species is known from several, more complete specimens collected during the 1970–1980s (Barberena et al., 1980).

The taxon was formally described by Barberena (1998), based on four well-preserved partial skulls, and its scales and postcranial anatomy were later described by Dias and Richter (2002) and Dias and Schultz (2003), respectively. After the initial assignment to Platyoposaurinae (Barberena and Daemon, 1974), *A. cosgriffi* was allied to the Rhinesuchidae (Barberena et al., 1980, 1985), whereas Barberena (1998) proposed a new family Australerpetonidae within Rhinesuchoidea. This was challenged by Werneburg and Scheneider (1996) and Schoch and Milner (2000), who endorsed the Archegosauridae affinity of the taxon. Dias and Schultz (2003) supported the Rhinesuchidae hypothesis. Other works place *A. cosgriffi* in an intermediate position between Archegosauridae and Rhinesuchidae (Witzmann and Schoch, 2006; Schoch et al., 2007), but outside of Stereospondyli. In this context, the present study scrutinized the phylogenetic position of *A. cosgriffi*. The analysis was performed based on the anatomical data yielded from the new specimen (LPRP/USP-0011) and the reassessment of previous accounts on *A. cosgriffi* (Barberena, 1998; Dias and Schultz, 2003). Morphological data sources are summarized in Appendix 1.

### Geologic Setting and Biostratigraphic Remarks

Located in north-central Paraná, southern Brazil, the Serra do Cadeado area exposes important outcrops of the Teresina, Rio do Rasto, Pirambóia, Botucatu, and Serra Geral formations (Fig. 1), ranging from Permian to Cretaceous in age (Riccomini et al., 1984). The Rio do Rasto Formation is divided into two members: the lower Serrinha and upper Morro Pelado members (Gordon, 1947). The lower contact of the Rio do Rasto Formation that occurs with the Teresina Formation is gradational. Its upper contact with the Piramboia Formation is usually

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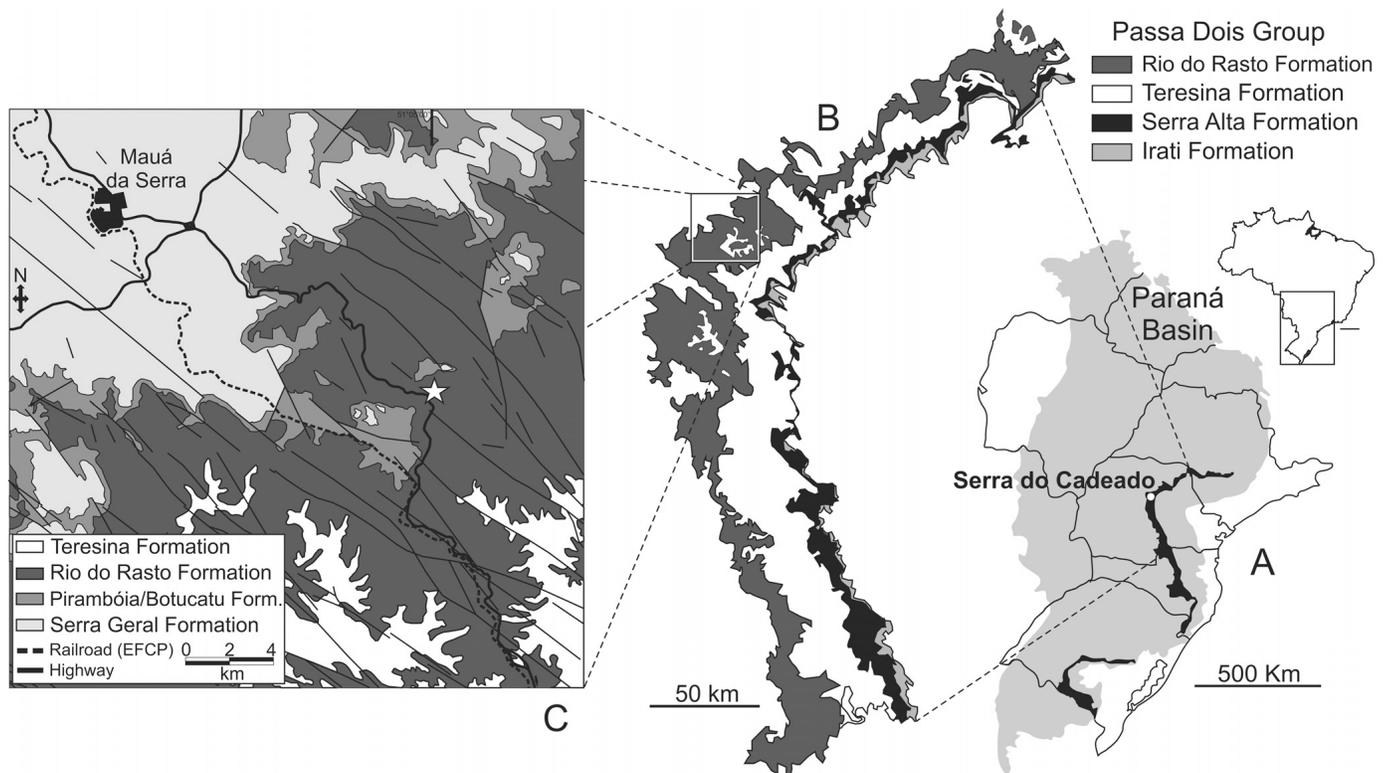


FIGURE 1. Serra do Cadeado region. **A**, geographic position of Serra do Cadeado in the context of the Paraná Basin (the black area corresponds to the of Passa Dois Group); **B**, surface distribution of the stratigraphic units of the Passa Dois Group in Paraná; **C**, detail of the surface geology of the Serra do Cadeado region (star indicates the site where LPRP/USP-0011 was collected).

discordant across the Paraná Basin (Almeida, 1980), but exceptionally in the Serra do Cadeado area the contact is gradational (Riccomini et al., 1984). The interpreted deposition environment for the Rio do Rasto Formation is mainly lacustrine, with large storm-dominated lake deposits, and fluvial channels formed during torrential rains, with the development of wind dunes in increasingly arid conditions to the top of the formation (Rohn, 1988, 1994; Lavina, 1991).

The fossil record of the Rio do Rasto Formation in Serra do Cadeado includes microfossils, plants remains, 'invertebrates,' and vertebrates (Rohn, 1994), but the tetrapod record is restricted to the upper levels of the stratigraphic unit (Barberena et al., 1980). Fossils referred to *A. cosgriffi* occur only in the upper Morro Pelado Member, whereas remains assigned to the dicynodont *Endothiodon* come from the transition with the Serrinha Member (Barberena and Araújo, 1975). The occurrence of *Endothiodon* offers the soundest criterion for correlating the Rio do Rasto beds at Serra do Cadeado. The genus has been recorded in the upper parts of the *Pristerognathus* Assemblage Zone, in the *Tropidostoma* Assemblage Zone, and in the lower part of the *Cistecephalus* Assemblage Zone of the Karoo Supergroup, South Africa (Rubidge et al., 1995; Rubidge, 2005), and in deposits from India, Malawi, Mozambique, Tanzania, Zambia, and Zimbabwe, which range from Capitanian to Changhsingan (Boos et al., 2013). Based on the possible platyoposaurine affinity of *A. cosgriffi*, Dias-da-Silva (2011) extended to the earlier Wordian age the time range of the Rio do Rasto Formation at Serra do Cadeado (up to Wuchiapingian age). This time range agrees with the geochronology and stratigraphy of Holz et al. (2010) for the Rio do Rasto Formation.

**Institutional Abbreviations**—CAMZM, University Museum of Zoology, Cambridge, U.K.; DGM, Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; GPIT, Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Tübingen, Germany; LPRP/USP, Laboratório de Paleontologia de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, Brazil; MB, Museum für Naturkunde, Humboldt Universität, Berlin, Germany; NHMUK, Natural History Museum, London, U.K.; PIN, Paleontological Institute, Academy of Science, Moscow, Russia; SMNS, Staatliches Museum für Naturkunde in Stuttgart, Baden Württemberg, Germany; UFRGS, Laboratório de Paleontologia de Vertebrados, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

#### SYSTEMATIC PALEONTOLOGY

TETRAPODA Goodrich, 1930

TEMNOSPONDYLI Zittel, 1887–1890

STEREOSPONDYLOMORPHA Yates and Warren, 2000

STEREOSPONDYLI Fraas, 1889

*AUSTRALERPETON COSGRIFFI* Barberena, 1998

(Figs. 2–8)

**Holotype**—UFRGS-PV-0227-P, partial skull lacking most of the right side and the anterior portion of the rostrum.

**Paratypes**—UFRGS-PV-0228-P, complete rostrum; UFRGS-PV-0229-P, posterior part of the skull and complete mandibles; UFRGS-PV-0230-P, fragment of the left posterior part of the skull.

**Previously Referred Specimens**—UFRGS-PV-0224-P, almost complete skull, lacking its anterior part (nasal and premaxilla), and mandible; UFRGS-PV-0225-P, small skull and mandible, lacking their anterior extremities; UFRGS-PV-0240-P, anterior tip of a right half mandible; UFRGS-PV-0243-P, small slender mandible; UFRGS-PV-0319-P, small fragment of skull table, fragment of mandibular ramus, an almost complete vertebral column, shoulder girdle and forelimb, hind limb and foot, ribs, and some articulated scales; UFRGS-PV-0320-P, posterior part of the skull, vertebrae, presacral ribs, left shoulder girdle, almost complete forelimb, and isolated scales.

**Newly Referred Specimen**—LPRP/USP-0011, partial skeleton composed of a left half mandible, some fragmentary ribs, and right pelvic girdle, femur, tibia, and fibula (Figs. 2–8). The specimen was collected from the lower levels of the Morro Pelado Member in the site known as ‘Monjolo’ (23°58′712″S, 51°05′493″W), km 313 of BR-376 highway, which also yielded the rostrum UFRGS-PV-0228-P.

**Revised Diagnosis**—In addition to the diagnostic traits mentioned by Barberena (1998) and Dias and Schultz (2003), *A. cosgriffi* has (\* = autapomorphies) the following: the lingual splenial/postsplenial suture with a ‘zigzag’ pattern\*; an anterior Meckelian fenestra positioned dorsal to the splenial and ventral to the prearticular\*; a deep pubic notch, anteriorly merged by the pubic crest (shared with *Peltobatrachus pustulatus*); a pelvic depression (shared with *Peltobatrachus pustulatus*, *Uranocentron senekalensis*, and *Melosaurus* sp.); a posterodorsal projection between the ilium and ischium accompanied by a furrow along the border of the pelvis\*; a laminar intertrochanteric fossa\*; a tuberosity on the posterior face of the cnemial crest of the tibia\*; and another tuberosity on the anterior rim of the tibial shaft\*.

## DESCRIPTION

### Mandible

**General Features**—The preserved mandible constitutes a left half (Figs. 2A, 3A). The articular is lacking, whereas the preartic-

ular and surangular are only partially preserved. The mandible curves outward (lateral) anteriorly, but somewhat inward (medial) posteriorly, suggesting a weak constriction in the snout. This weak sigmoid configuration fits the ‘straight-sided margins’ of the skull that Damiani et al. (2000) noted in long-snouted *Trematosuchus* and *Trematosaurus*. The anterior tip is lateromedially expanded and forms a spoon-shaped tip. The mandible height increases posteriorly. The dorsal margin is mainly straight, but the symphyseal area curves upward. The ventral margin is also mainly straight, with both the symphyseal and glenoid portions curved upward. As revealed by natural breakage, the cross-section of the mandible of LPRP/USP-0011 is subcircular anteriorly, and lateromedially flattened posteriorly. As typical of temnospondyls, the mandible has an ornamented external surface. Anteriorly, the dentary and splenial are striated, whereas ridges, pits, and depressions are more evident posteriorly, especially on the angular that has a radial pattern starting at the posteroventral corner of the bone. In addition, on the lingual side of the angular, muscle scars (probably related to the M. adductor mandibulae) appear with various foramina. The scars have a fan-like shape that expands dorsally from an origin on the most ventroposterior point of the bone (detail in Fig. 2A).

The symphysis extends for about one-fourth of the total length of the mandible. In dorsal view, the articulation surface forms an angle of 10° (*Platyoposaurus stuckenbergi* shows a 15° angle) to the main axis of the mandible (Fig. 3E). The symphysis is formed by the splenial and dentary, the latter occupying the anterior three-quarters of its extension (Fig. 3D). On the medial symphyseal surface, the splenial is rugose and the dentary is sulcate. At midheight of the medial symphyseal surface, an anterior foramen extends posteriorly as a deep furrow (Fig. 3A, D; UFRGS-PV-229-P), which probably had some communication with the Meckelian canal. Only the anterior one-third of the adductor fossa is preserved. Its lingual wall is formed by the prearticular ventrally. The posterior coronoid forms the anterolateral margin, excluding the surangular. Two sensory sulci (sulcus oralis or sulcus dentalis) are seen near the dorsal margin of the mandible.

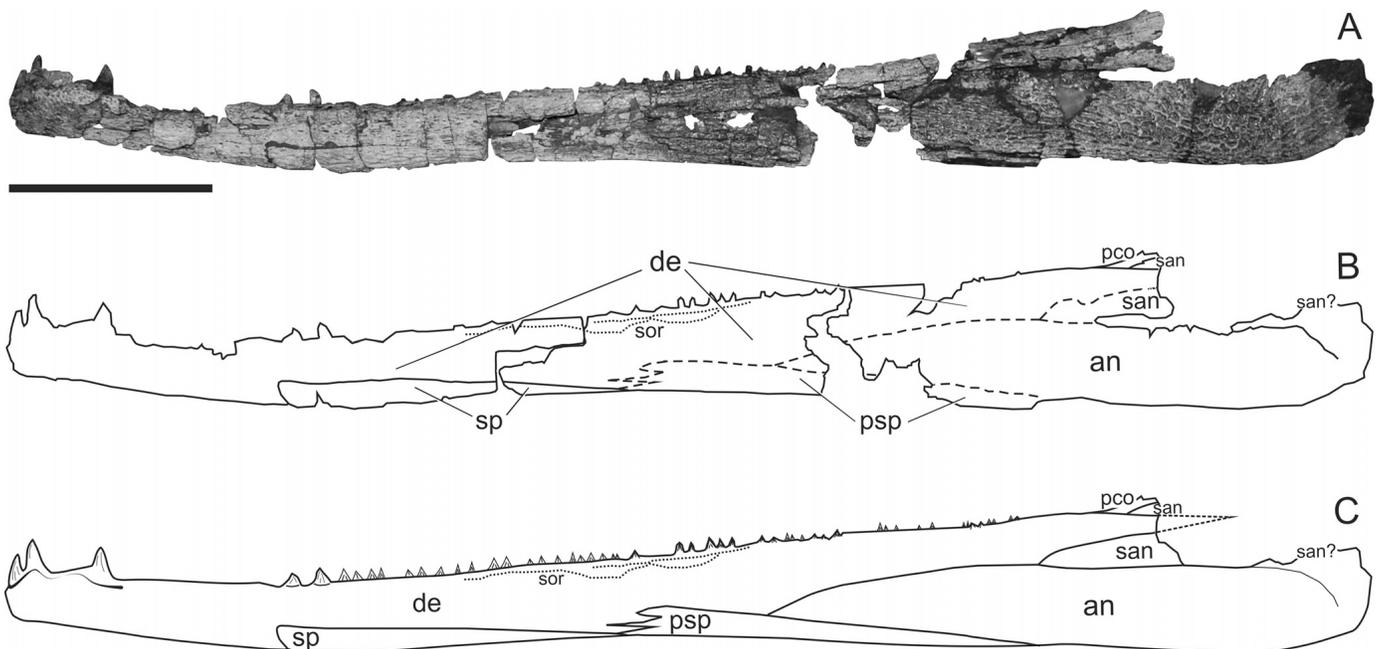


FIGURE 2. *Australerpeton cosgriffi*, LPRP/USP-0011. Left mandible in labial view. **A**, photograph of the preserved parts; **B**, drawing of preserved bones (dashed lines indicate inferred bone boundary); **C**, reconstruction. **Abbreviations:** an, angular; de, dentary; pco, posterior coronoid; psp, post-splenial; san, surangular; sor, sulcus oralis; sp, splenial. Scale bar equals 10 cm.

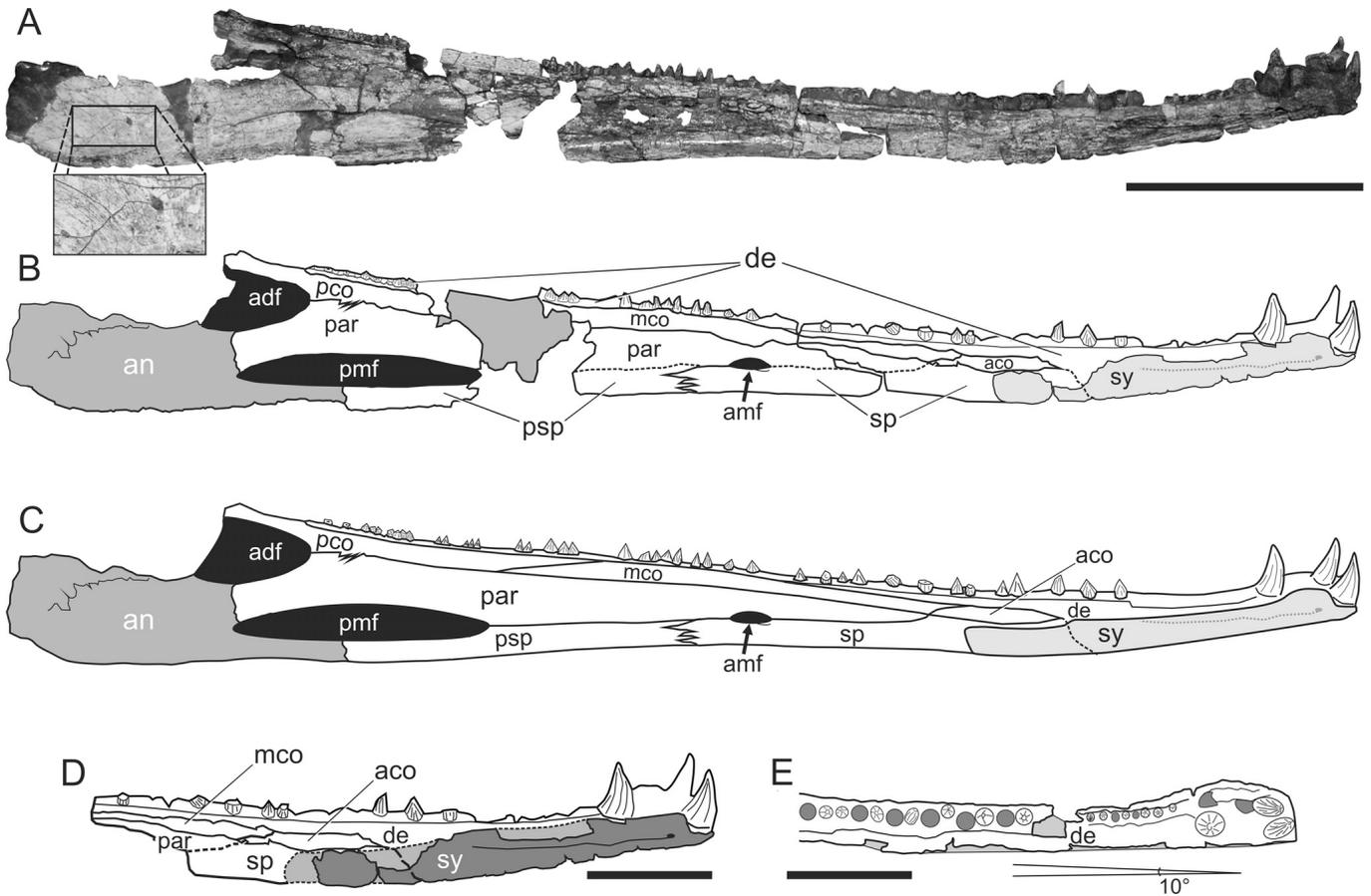


FIGURE 3. *Australerpeton cosgriffi*, LPRP/USP-0011, left mandible, in lingual (A–D) and dorsal (E) views. A, photograph of preserved parts; B, drawing of the preserved bones (dashed lines indicates inferred bone boundary); C, reconstruction; D, detail of the symphyseal region (dark gray indicates the preserved surface, light gray indicates the probable area occupied by the symphysis); E, detail of the symphysis, showing the angle formed by the lingual surface of the symphysis and main axis of the mandible. Abbreviations: aco, anterior coronoid; adf, adductor fossa; amf, anterior Meckelian fenestra; an, angular; de, dentary; mco, middle coronoid; par, prearticular; pco, posterior coronoid; pmf, posterior Meckelian fenestra; psp, postsplenial; sp, splenial; sy, symphysis. Scale bars equal 10 cm (A–C) and 5 cm (D and E).

**Dentary**—This is the largest and only tooth-bearing bone of the mandible. It does not reach the ventral margin except at the anterior part of the symphysis. Its posterior-most extension is not entirely preserved (Fig. 2B, dashed lines). The anterior part of its dorsal margin bulges to accommodate tusks. There are 76 alveoli and 48 preserved teeth. An evident posterior reduction in tooth size occurs in the posterior three-quarters of the bone. The teeth are conical, mostly curved posteriorly, with a rounded cross-section. These show typical temnospondyl sculpturing, with longitudinal grooves on the surface and labyrinthodont infolding in transverse section. Anteriorly, there are three large fangs, two of which are closer to each other than to the third (Fig. 3E). Immediately posterior, 8–12 small alveoli (five with preserved teeth) are seen near the incomplete labial margin of the bone.

In lateral view, the dentary forms the anterior one-fifth of the mandible. Its height decreases posteriorly above the angular and surangular. A wedged-shaped process (behind the last tooth) may have been present, but the posterior tip of the bone is missing. Lingually, its contact with the splenial is enclosed in the symphysis. Posterior to that, the dentary forms a dorsoventrally narrow bar above the coronoids, only interrupted by the middle coronoid reaching the dorsal margin of the mandible (Fig. 3B, C). The suture with the posterior coronoid is deeply marked, resembling a furrow.

**Splenial**—This is a wedge-shaped bone in labial profile, narrowing posteriorly (Fig. 2B, dashed lines) to meet the postsplenial along a posterolingually oriented suture. The boundary with the prearticular forms a straight line, parallel to the ventral margin of the jaw, enclosing the anterior Meckelian fenestra. The anterior portion of the anterior Meckelian fenestra is bordered ventrally by a short crest on the splenial (Fig. 3B, C).

**Postsplenial**—This bone appears on both lingual and labial sides, forming the midlength portion of the mandible floor. Anteriorly, the postsplenial contacts the dentary and splenial in a ‘zigzag’ pattern (Fig. 3; UFRGS-PV-224-P); posteriorly, the bone is dorsally covered by the angular (labially) and prearticular (lingually). The postsplenial has a prominent labioventral border and forms the anteroventral margin of the posterior Meckelian fenestra.

**Angular**—The angular is relatively thicker than the other mandibular bones. Laterally, its anterior half is wedged between the dentary and postsplenial. Ventrally, its anterior half contacts the postsplenial, and a convex suture marks its dorsal contact with the dentary.

**Surangular**—Only the anterior part is preserved, which is divided into dorsal and ventral portions by the dentary (Fig. 2B).

**Coronoid Series**—The anterior coronoid is exposed only on the lingual side. It is anteroposteriorly elongated, with tapering

extremities and a trapezoid shape. A posterodorsally oriented, oblique line appears anteriorly at the dorsal contact with the dentary. The contact with the middle coronoid slopes posteroven- trally (Fig. 3). The elongated middle coronoid appears exclusively on the lingual side of the jaw, forming its dorsal margin sandwiched between the posteriorly narrowing dentary and prearticu- lar. Lingually, the posterior coronoid forms a longitudinal ventral suture with the prearticular with a 'zigzag' pattern im- mediately anterior to the adductor fossa. The posterior coronoid forms the anterodorsal margin of the adductor fossa (Fig. 3B, C), and appears on the labial side of the jaw, covering the den- tary/surangular contact. There is no dentigerous structure on the occlusal surface of the coronoids, just as there is no dentigerous structure in UFRGS-PV-229-P.

**Prearticular**—The prearticular forms a long strip at midheight on the lingual surface of the jaw. Posteriorly, it separates the posterior Meckelian and the adductor fossae, but tapers more

anteriorly to reach the contact between the anterior and middle coronoids (Fig. 3C). Ventrally, it contacts the splenial and postsplenial.

### Pelvic Girdle

The pelvis is described with the acetabulum facing laterally and the ventral rim of the puboischial lamina aligned horizontally (as in Schoch, 1999). It is totally ossified in LPRP/USP-0011 (Fig. 4A, C), except for the base of the ilium and the top of the puboischial blade, which were probably cartilaginous. The pelvis is massive and coossified in LPRP/USP-0011, as is typical for Permian tem- nospondyls (Warren and Snell, 1991). The ventral part of the con- tact between pubis and ischium is fused, without any evidence of suture (Fig. 4B).

**Ilium**—The ilium is a thin bone, with the blade correspond- ing to two-thirds of its total height. Its convex ventral margin

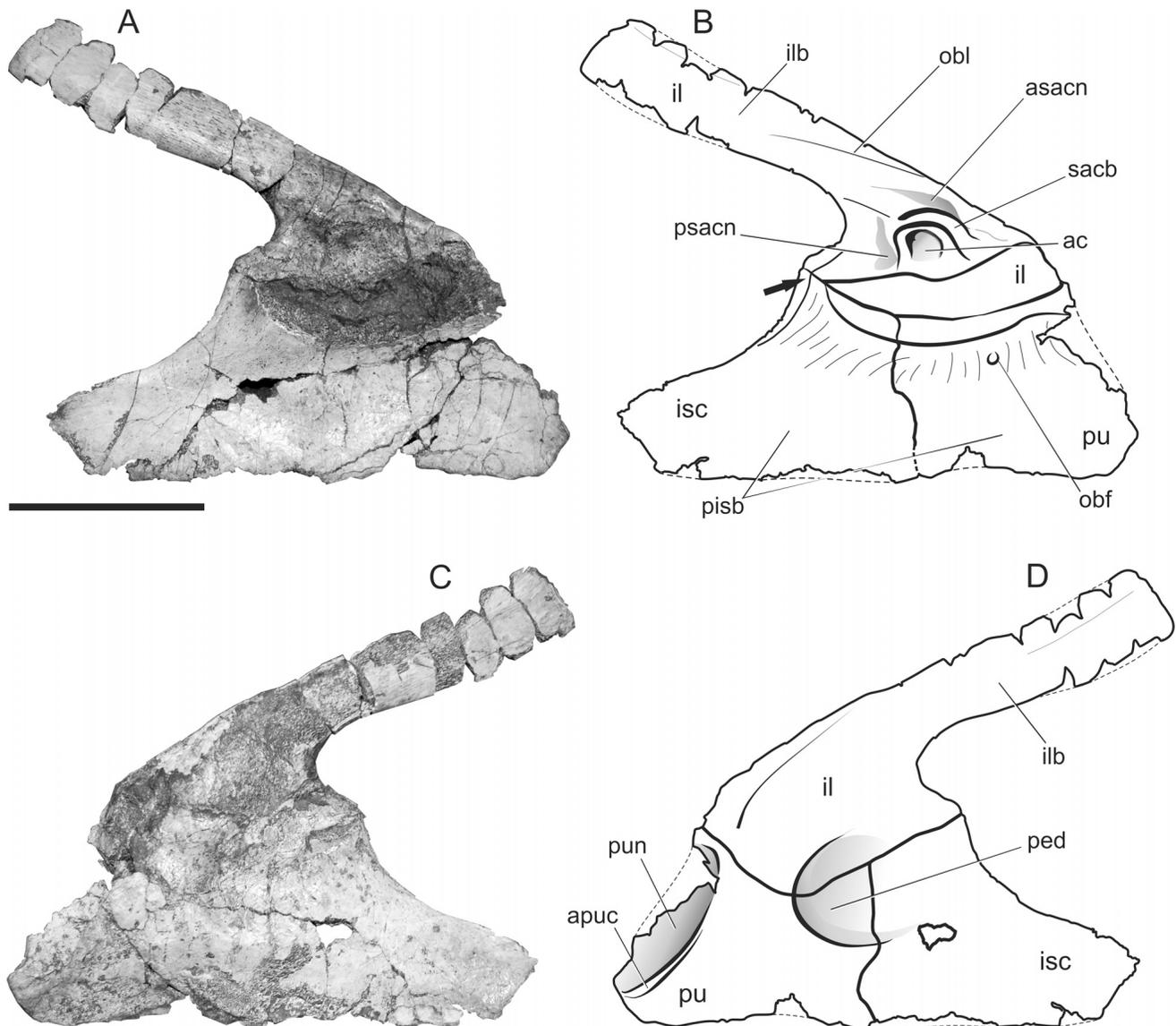


FIGURE 4. *Australerpeton cosgriffi*, LPRP/USP-0011, right pelvis. **A**, photograph of lateral view; **B**, reconstitution of lateral view (the arrow indicates a posterodorsal projection of the pelvis that is accompanied by a lateral furrow along the border); **C**, photograph of medial view; **D**, reconstruction of medial view. **Abbreviations:** ac, acetabulum; apuc, anterior pubic crest; asacn, anterior supracetabular notch; il, ilium; ilb, iliac blade; isc, ischium; obf, obturator foramen; obl, oblique line; ped, pelvic depression; pis, pubo-ischial blade; psacn, posterior supracetabular notch; pu, pubis; pun, pubic notch; sacb, supracetabular buttress. Scale bar equals 5 cm.

meets the puboischiac blade and a furrow extends along the posterior border of the bone. The acetabulum was probably composed mostly of cartilage, as indicated by unfinished bone in the center of the pelvis. Its dorsal margin is ossified, forming a round depression totally enclosed in the ilium. The supraacetabular buttress is laterally projected, and thicker anteriorly. Two notches bound the acetabulum, the anterior and posterior supraacetabular notches: the former is slender and more dorsally placed (Fig. 4B). The iliac blade is mostly smooth laterally, but bears some muscle scars at midlength (Fig. 4A). The shaft is oval in cross-section, flattening lateromedially and broadening dorsally along its length (and slightly curved dorsally). An oblique line is present on the lateral surface of the blade (Fig. 4B).

**Ischium**—The ischium has a trapezoid outline (Fig. 4), with a longer ventral border. The lateral surface is smooth, whereas the medial surface has some roughness near the ventral margin and close to the symphysis. The contact with the ilium is oblique, the anterior two-thirds of this contact was probably covered (laterally) by cartilage. The posterior one-third represents the posterodorsal projection, and is accompanied by a lateral furrow along the border of the pelvis (Fig. 4B, arrow). The dorsal margin of the ischium is gently concave; the posterior margin is straight and forms an angle of approximately 130° to the equally straight ventral margin. The anterodorsal portion of the bone is thicker than the rest of the ischium and bears muscle scars.

**Pubis**—The pubis is also trapezoid in lateral and medial views. The ventral margin is straight, the anterior rim is rounded, and the dorsal rim forms a slightly concave contact with the ilium. The bulging of the dorsal and anterior margins results in a laterally concave bone. The obturator foramen is totally enclosed near the dorsal margin of the pubis. Medially, the pubis encloses the larger portion (anteroventral) of a depression located in the center of the pelvis (Fig. 4D). Also medially, the anterior margin is excavated by a shallow notch, posteriorly bounded by the arched pubic crest.

### Hind Limb

The orientation and identification of the appendicular bones follow Romer (1922), Bystrow and Efremov (1940), Coates (1996), and Pawley and Warren (2006), unless noted otherwise. The femur is mediolaterally oriented, so that the adductor crest faces ventrally and the adductor lamina anteriorly. The tibia and fibula have their extensor and flexor surfaces dorsally and ventrally oriented, respectively.

**Femur**—Although well preserved, the right femur of LPRP/USP-0011 lacks the fourth trochanter, part of the ventral crest, and the anterodistal extremity of the tibial condyle (Fig. 5). In addition, the articular surfaces are unfinished. In dorsal view, the femur shows a concave posterior margin and a straight anterior margin. In proximal view, the head has a teardrop-like outline, narrowing posteriorly (Fig. 6A, B). The femoral head bears an anterior oval bulge, which corresponds to the internal trochanter. The most anteroproximal point of the femoral head corresponds to the acetabular torus, as seen in *Metoposaurus diagnosticus krasiejowensis* (Sulej, 2007:fig 64). The posterior trochanter is close to the proximal articulation and extends distally, continuous with the blade of the adductor crest. The insertion of the *M. pubischiofemoralis internus* is seen in dorsal view, near the acetabular torus (Fig. 5H). Posterioventrally on the femoral head, the intertrochanteric fossa forms a shallow depression (Fig. 5B, D), the posterior intertrochanteric ridge is very pronounced proximally, extending distally to form the adductor crest.

The popliteal fossa is deeper distally, but muscle scarring is heavier more proximally. Two excavations are seen proximal to the popliteal crests. The tibial condyle has half of the thickness (dorsoventrally) of the fibular condyle. In dorsal view, the anterior border of the fibular condyle extends for about the distal one-

third of the femur. The moderately deep intercondylar fossa also occupies the distal one-third of the bone. Dorsally, the fibular fossa mirrors the length of the ventral bifurcation of the adductor crest. The fibular condyle is somewhat more projected posteriorly. It is divided into ventral and dorsal 'subcondyles,' separated by the fibular fossa (Fig. 5A, B). In distal view, the former has a rectangular shape, whereas the latter bears a faint ridge; a short, rugose ridge on the ventral surface of this, described for *Trimerorhachis insignis* as the femoral fibular ridge (Pawley, 2007), is also seen in LPRP/USP-0011 (Fig. 5B, arrow).

**Tibia**—This is a dorsoventrally flattened bone with smooth dorsal and ventral surfaces, and proximal and distal surfaces of unfinished bone. The head is expanded and transversally rounded, the shaft is narrow, and the distal extremity is weak expanded. In proximal view, the articular surface is divided into a thicker anterior part that articulates with the tibial condyle of the femur, and a posterior part that articulates with the fibular condyle (Fig. 7). Dorsally, the cnemial crest is convex, and extends along the proximal one-third of the bone. Its surface is grained, as in the articular areas, and a marked tuberosity is seen on its posterior side. The cnemial sulcus corresponds to a distal continuation of the intercondylar fossa. More distally, a conspicuous rectangular, longitudinally oriented protuberance is located on the anterior margin of the bone. Its texture resembles that of the cnemial tuberosity and it is probably related to muscle insertion. Distal to the cnemial crest, the dorsal surface of the tibia is convex. The distal tip has a weak expansion and a number of muscle scars. Three flexor crests are seen on the ventral surface; the anterior and posterior tibial flexor crests are more proximal, separated by a triangular flattened surface. Distally, the crests meet to form the distal tibial flexor crest (Fig. 7).

**Fibula**—The fibula is slender, dorsoventrally flattened, and as long as the tibia. The proximal articular surface has a trapezoid outline, and both extremities have an unfinished (grained) appearance. The proximal head has a rectangular outline and the anterior border is concave. The distal margin has a sigmoid outline, formed by the intermedial (concave) and fibular (convex) facets. On the proximal half, the extensor fibular ridge forms a rugose, mound-like structure and is not elongated as in *E. megacephalus* (Pawley and Warren, 2006:fig. 10). The anterior fibular ridge extends along the proximal one-third of the bone, parallel to its anterior margin (Fig. 8A, B). Distally, scars are radially arranged (fan-like) and most probably were related to extensor muscles of the foot.

Ventrally, the well-developed posterior fibular ridge extends along the entire posterior margin of the bone (Fig. 8D). This is bound anteriorly by a furrow and posteriorly by an elevated surface formed by two small parallel ridges. The fibular sulcus forms a longitudinal concave line (Fig. 8C, D), extending from the distal margin of the shaft to the middle of the intermedial facet. It defines a triangular anterodistal projection of the fibula. Some muscle scars, probably involved in the flexion of the foot, extend along the fibular sulcus.

### PHYLOGENETIC ANALYSIS

In order to access the affinities of *A. cosgriffi*, the taxon was scored into a data matrix of 133 characters (Supplementary Data, Appendix S1). To encompass the taxa set of previous suggested phylogenetic positions of *A. cosgriffi*, which range from the stereospondylomorph Archegosauridae (Platyoposaurinae) to stereospondyl Rhinesuchidae, a number of taxa (analyzed firsthand) covering these groups were included (Supplementary Data, Appendix S2). All representatives of the major groups comprising Eutemnospondyli (Dissorophoidea, Eryopoidea, Trimerorhachoidea, and 'higher' Stereospondyli) were included. *Dendrerpeton acadianum* (Holmes et al., 1998) was used as the outgroup. This generalized temnospondyl is

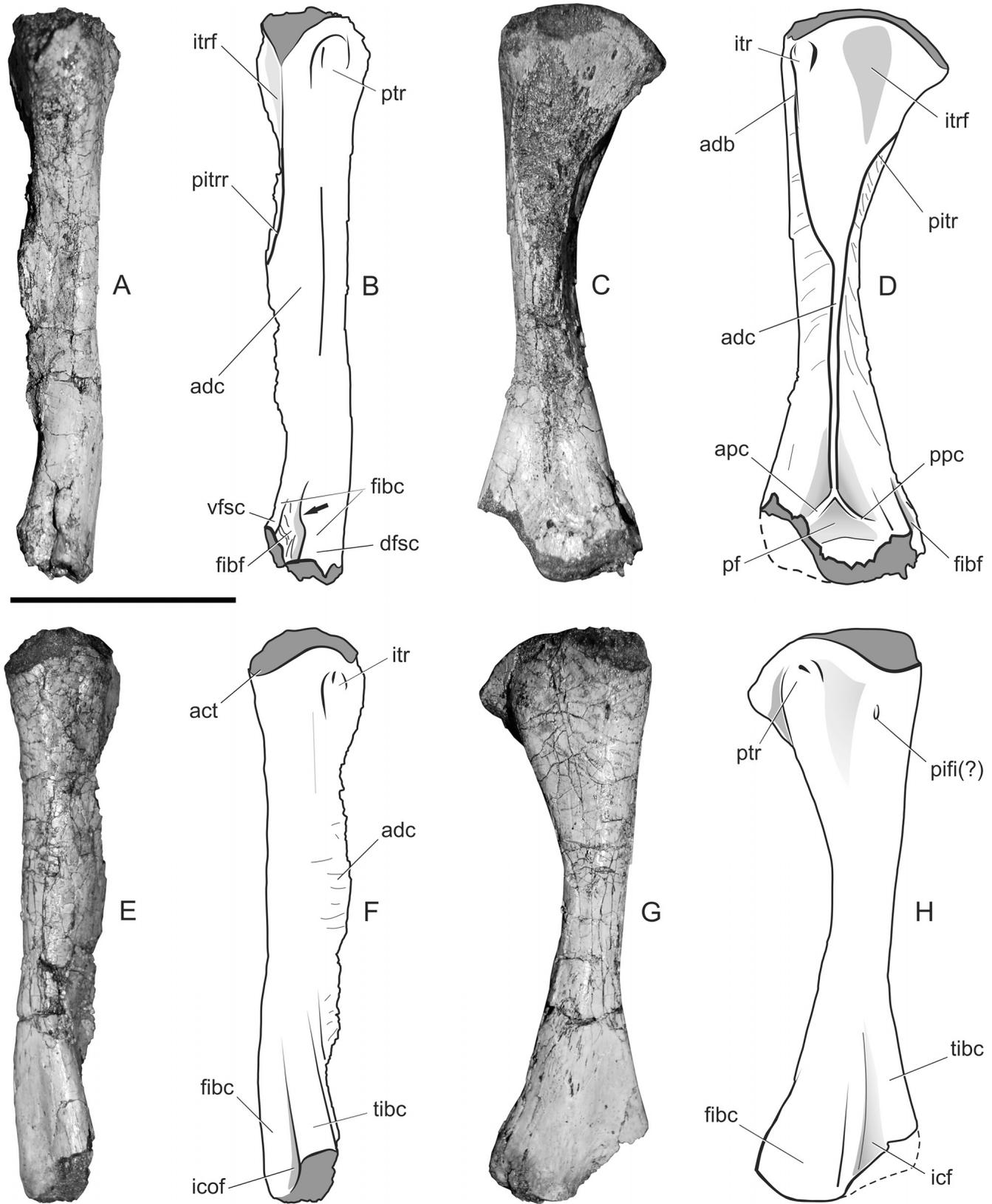


FIGURE 5. *Australerpeton cosgriffi*, LPRP/USP-0011, right femur. **A**, photograph of posterior view; **B**, reconstruction of posterior view (the arrow indicates the femoral fibular ridge); **C**, photograph of ventral view; **D**, reconstruction of dorsal view; **E**, photograph of anterior view; **F**, the reconstruction of anterior view; **G**, photograph of dorsal view; **H**, reconstruction of dorsal view. **Abbreviations:** **act**, acetabular torus; **adb**, adductor blade; **adc**, adductor crest; **apc**, anterior popliteal crest; **dfsc**, dorsal fibular 'subcondyle'; **fibc**, fibular condyle; **fibf**, fibular fossa; **icf**, intercondylar fossa; **itr**, internal trochanter; **ptr**, posterior trochanter; **pitrr**, posterior intertrochanteric ridge; **ppc**, posterior popliteal crest; **pifi**, M. pubischiiofemoralis internus insertion; **tibia**, tibial condyle; **vfsc**, ventral fibular 'subcondyle.' Scale bar equals 5 cm.

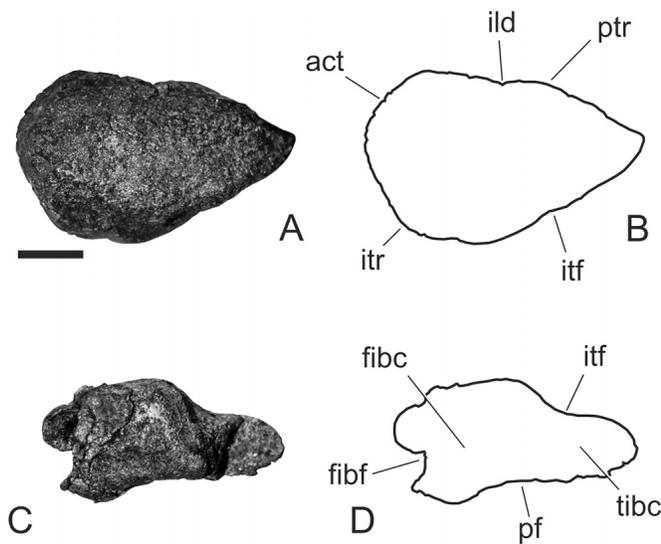


FIGURE 6. *Australerpeton cosgriffi*, LPRP/USP-0011, right femur. **A**, photograph of proximal view; **B**, outline of proximal view; **C**, photograph of distal view; **D**, outline of distal view. **Abbreviations:** act, acetabular torus; fibc, fibular condyle; fibf, fibular fossa; ild, iliac depression; itr, intertrochanteric fossa; ptr, posterior trochanter; tunc, tibial condyle. Scale bar equals 1 cm.

relatively complete and considered a basal temnospondyl (Holmes, 2000). *Australerpeton cosgriffi* was first scored solely on the basis of the specimens described by Barberena (1998) and Dias and Schultz (2003). In a second step, the anatomical information provided by the specimen described here (LPRP/USP-0011) was included. The searches were performed using TNT ver-

sion 1.1 (Goloboff et al., 2008) under the implicit enumeration algorithm ('traditional search'), and resulted in two most parsimonious trees of length 351 steps (consistency index = 0.435; rescaled consistency index = 0.280; retention index = 0.644). The strict consensus tree of the analysis, including Bremer support values and bootstrap proportions, is shown in Figure 9.

*Australerpeton cosgriffi* was recovered as a basal member of Stereospondyli, more derived than *Peltobatrachus pustulatus* and basal to Rhinesuchidae. The position contradicts previous hypothesis supporting its affinity with either the more basal archeosaurids or the rhinesuchids. The autapomorphies identified for *A. cosgriffi* were (1) the intertemporal absent with a postorbital-parietal suture; (38) the posterior face of quadrate ramus of the pterygoid with a large sharp edged oblique ridge; (63) elongate posteromedial process of the palatine extending posterior to the most anterior ectopterygoid tooth; (77) posterolateral ramus of the vomer extending posterior to the palatine tusks; (87) coronoids without any denticle fields; and (127) choana slit-like. Likewise, the synapomorphies recovered to Stereospondyli (including *Peltobatrachus* and *A. cosgriffi*) were (42) tabular and exoccipital articulating in the paroccipital process; (50) parasphenoid articulates with the corpus of the pterygoid forming a broad contact along the lateral margins of the parasphenoid plate; (56) internal carotid and the palatine and intracranial branches pass through the dorsal surface of the parasphenoid plate, either leaving foramina where they pass below the surface or grooves where they lie upon it; and (65) parasphenoid denticle field enlarged to a transverse 'belt' extending between the pterygoid-parasphenoid articulations.

DISCUSSION

Comparisons

Among the material referred to *A. cosgriffi*, two skulls are associated with mandibles (UFRGS-PV-0224-P and UFRGS-PV-0229-P). The mandible of UFRGS-PV-0224-P is attached to the

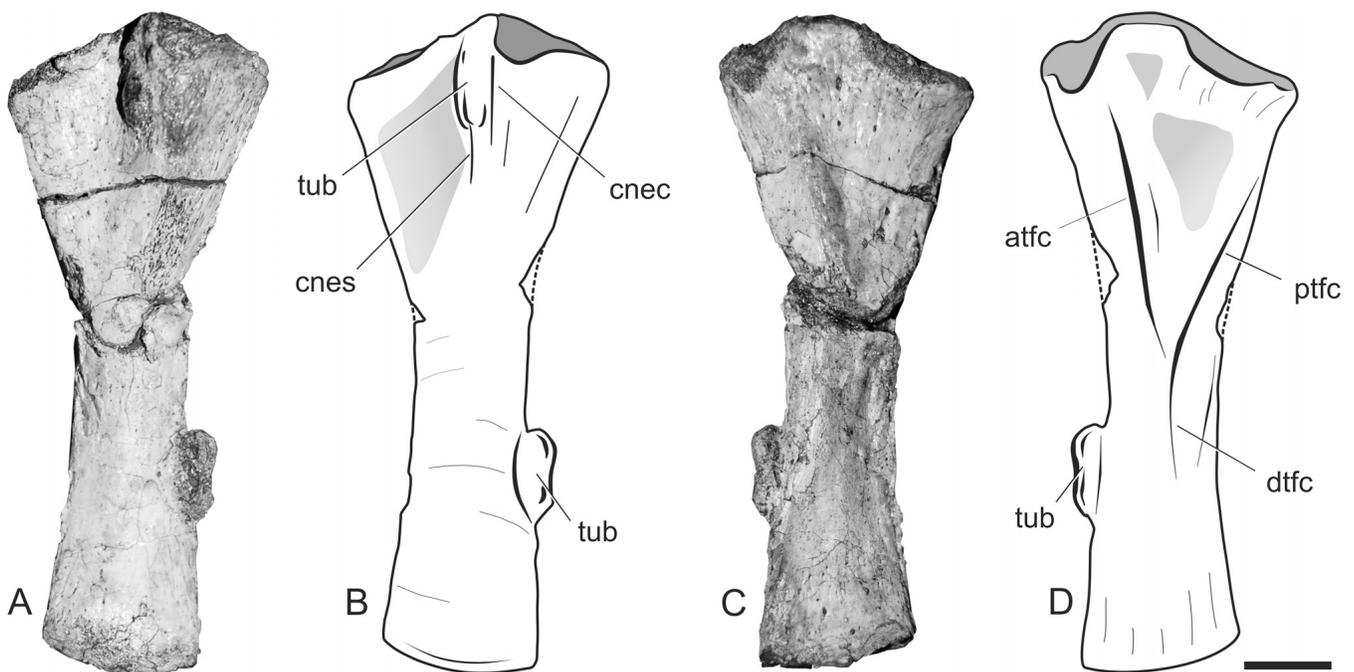


FIGURE 7. *Australerpeton cosgriffi*, LPRP/USP-0011, right tibia. **A**, photograph of dorsal view; **B**, reconstruction of dorsal view; **C**, photograph of ventral view; **D**, reconstruction of ventral view. **Abbreviations:** atfc, anterior tibial flexor crest; cneec, cnemial crest; cnes, cnemial sulcus; dtfc, distal tibial flexor crest; ptfc, posterior tibial flexor crest; tub, tuberosity. Scale bar equals 1 cm.

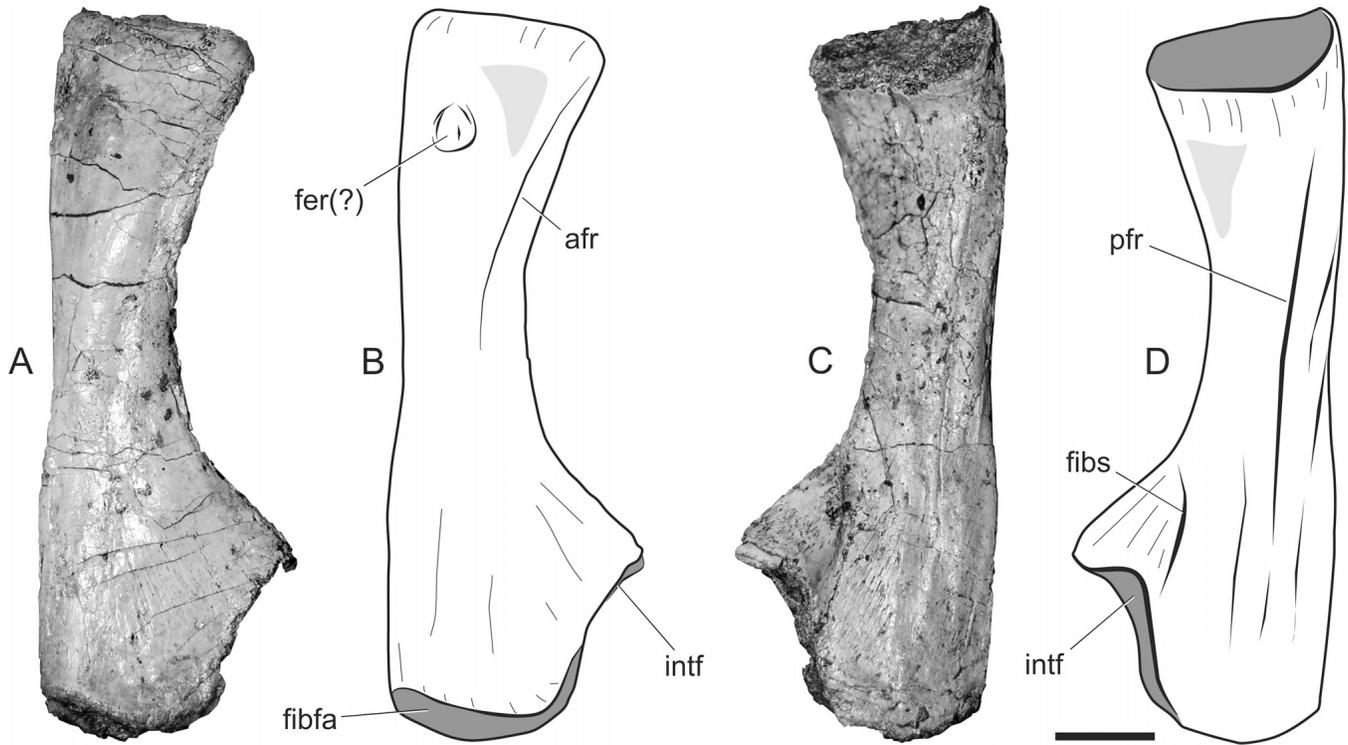


FIGURE 8. *Australerpeton cosgriffi*, LPRP/USP-0011, right fibula. **A**, photograph of dorsal view; **B**, reconstruction of dorsal view; **C**, photograph of ventral view; **D**, reconstruction of ventral view. **Abbreviations:** afr, anterior fibular ridge; fer, fibular extensor ridge; fibfa, fibular facet; fibs, fibular sulcus; intf, intermedial facet; pfr, posterior fibular ridge. Scale bar equals 1 cm.

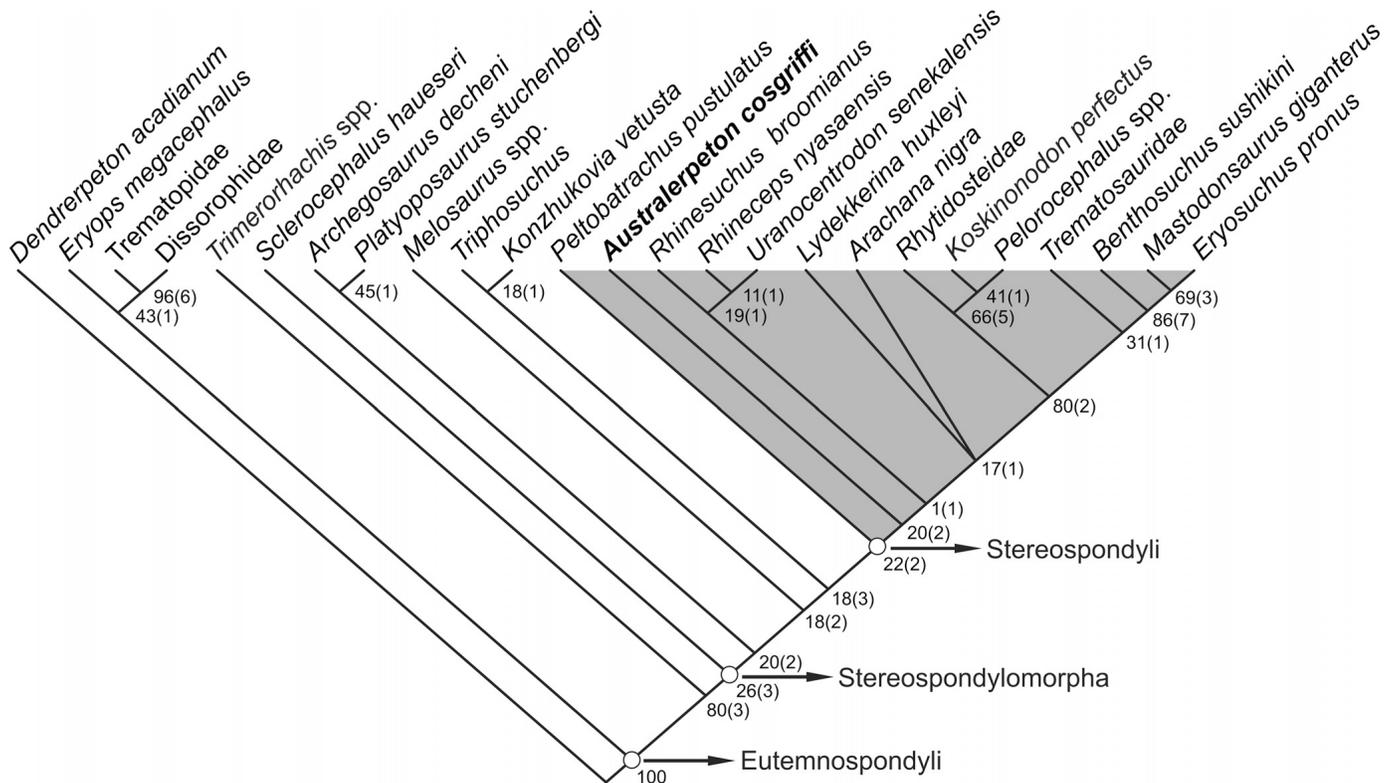


FIGURE 9. Strict consensus tree of two most parsimonious trees depicting the phylogenetic position of *Australerpeton cosgriffi*. Tree length = 351 steps; consistency index = 0.435; rescaled consistency index = 0.280; retention index = 0.644. Bremer support (in parentheses) and bootstrap values are indicated for each node.

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skull. Few features of the mandible are visible, particularly in the glenoid area (not preserved in LPRP/USP-0011). Nevertheless, an anteriorly extended prearticular, and the diagnostic contact between the splenial and postsplenial in a 'zigzag' pattern, can be seen. Like LPRP/USP-0011, the mandible of UFRGS-PV-0229-P bears coronoids without denticles or teeth, and the posterior coronoid merges with the adductor fossa anteriorly. The symphysis is quite elongate, bearing the conspicuous anterior foramen, which is posteriorly extended as a deep furrow.

LPRP/USP-0011 has a more gracile lower jaw in comparison with other slender-headed temnospondyls, such as Intasuchidae. Comparably elongated symphyses are seen only in the long-snouted temnospondyls belonging to Lonchorhynchinae and Platyoposaurinae. The symphyseal height/length ratio is approximately 0.15 in LPRP/USP-0011, approaching the condition in *Platyoposaurus stuckenbergi* (0.13) and *Archegosaurus decheni* (0.20). LPRP/USP-0011 has the anterior Meckelian fenestra positioned dorsal to the splenial and ventral to prearticular. This condition differs from that of *Eryops megacephalus* (Sawin, 1941:pl. 5), *Glanochthon latirostre* (Boy, 1993:fig. 4), *Scleurocephalus haeuseri* (Schoch and Witzmann, 2009:fig. 4), *A. decheni* (Witzmann, 2005:fig. 21), and *Uralosuchus tverdochlebovae* (Gubin, 1993:figs. 3, 4), which is composed by the postsplenial, or totally embedded into the bone. It differs from *P. stuckenbergi* (Gubin, 1991:fig. 20), *Tryphosuchus paucidens* (Gubin, 1991:fig. 24), *Rhineceps nyasaensis* (Watson, 1962:fig. 8), and *Lydekkerina* (Hewison, 2007:fig. 34), which have two or three foramina in the postsplenial.

Jupp and Warren (1986) distinguished the families Uranocentrodontidae (Rhinesuchidae sensu Schoch and Milner, 2000), Benthosuchidae, Capitosauridae, and Trematosauridae by a posterior Meckelian fenestra with its midpoint posterior to the anterior edge of the adductor fossa, a condition also seen in the derived archegosaur *P. stuckenbergi* (PIN 3968/1) and in the melosaurids *Melosaurus kamaensis* (PIN 683/1), *U. tverdochlebovae* (PIN 4405/1), and *Tryphosuchus paucidens* (PIN 157/112). In contrast, in LPRP/USP-0011, as well as in the rhinesuchid *R. nyasaensis* (CAMZM T.259), the midpoint is located more anteriorly. Likewise, most Triassic temnospondyls have the posterior Meckelian fenestra located at midheight (dorsoventrally) of the mandible (Jupp and Warren, 1986), whereas this fenestra is more ventral in LPRP/USP-0011 and other Permian taxa (e.g., *P. stuckenbergi*, *M. kamaensis*, *U. tverdochlebovae*, *T. paucidens*, and *R. nyasaensis*).

The postsplenial does not reach the posterior Meckelian fenestra in Permian taxa such as *S. haeuseri*, *G. latirostre*, and *P. stuckenbergi*. In contrast, in the derived stereospondylomorphs, the anteroventral margin of the fenestra is formed by the postsplenial (Schoch and Milner, 2000), as seen in LPRP/USP-0011 and the taxa *U. tverdochlebovae*, *T. paucidens*, and *R. nyasaensis*. The angular of LPRP/USP-0011 has a straight ventral margin and a posteroventral corner forming an angle of 150°. This set of features resembles those of *U. tverdochlebovae* (PIN 4405/1), but differs from the ventrally concave angular of *P. stuckenbergi* (PIN 3968/1). An anteriorly extensive prearticular (reaching the midpoint of the middle coronoid) is a plesiomorphic condition (Yates and Warren, 2000) shared by LPRP/USP-0011, *G. latirostre*, and *A. decheni*, whereas a shorter prearticular is seen in *P. stuckenbergi*, Lydekkerinidae (a synapomorphy according to Hewison, 2007), and most Mesozoic temnospondyls (Jeannot et al., 2006).

The plesiomorphic tetrapod lower jaw dentition includes one symphyseal fang and a replacement pit (see Ahlberg and Clack, 1998), whereas basal Stereospondylomorphs (e.g., *G. latirostre*) have two replacement pits, usually with three or four symphyseal fangs. This is seen in LPRP/USP-0011. In LPRP/USP-0011, the total number of teeth is at least 76. Other long-snouted temnospondyls, such as Trematosauridae, have no more than 40–50 teeth. The only temnospondyl that approximates the condition of

LPRP/USP-0011 is *P. stuckenbergi* (PIN 3968/1), with about 60 mandibular teeth. The absence of coronoid denticles is a derived condition among temnospondyls (Yates and Warren, 2000), as seen in Capitosauridae and Trematosauridae. Coronoid denticles are retained in some stereospondylomorphs, such as *S. haeuseri* and *G. latirostre*, the archegosaurids *A. decheni* and *P. stuckenbergi*, and even in *R. nyasaensis*. In LPRP/USP-0011, there are no denticles on the coronoids.

The iliac blade of LPRP/USP-0011 is not bifurcated, as also seen in *Konzhukovia vetusta* (PIN 520/8), whereas a clearly expanded blade occurs in *P. stuckenbergi* (PIN 164-1/6) or a dichotomic process occurs in *Tryphosuchus kinelensis* (PIN 272/52). The iliac shaft is more inclined posterodorsally in LPRP/USP-0011 than in *T. kinelensis* (PIN 272/52) and *P. stuckenbergi* (PIN 164-1/6). The pelvis of LPRP/USP-0011 resembles that of the indeterminate melosaurid described by Gubin (1991) in its supraacetabular notches, the trapezoid shape of the ischium, and the posterodorsal projection between ilium and ischium bearing a posterolateral dorsal furrow. As in the indeterminate melosaurid (PIN 2255/6), the pubis of LPRP/USP-0011 has a straight ventral margin, but the suture to the ischium is sigmoid instead of straight.

The femur of LPRP/USP-0011 has a popliteal area that is comparatively smaller than those of *A. decheni* (MB.Am 298), *Prionosuchus plummeri* (DGM 320-R; NHMUK R12005), *P. stuckenbergi* (PIN 2255/2), and *Platyoposaurus vjuschkovi* (PIN 272/57). However, the popliteal ridges are only well defined in LPRP/USP-0011 and *Platyoposaurus* (above), as is the case of the presence of a fibular condyle that is extended more than the tibial condyle. The fibular and intercondylar fossae are deeper in LPRP/USP-0011 than in *P. vjuschkovi* (PIN 272/57). In contrast to *A. decheni* (MB.Am 298) and *Platyoposaurus* (PIN 2255/2, PIN 272/57), the internal trochanter of LPRP/USP-0011 is separated from the adductor blade. The posterior sharp projection on the femoral head is comparable to those seen in *P. vjuschkovi* only.

The tibia of LPRP/USP-0011 is typically temnospondyl, but it is not as robust and expanded in the extremities as in *E. megacephalus*. Instead, it is more slender, as in *T. insignis* (Pawley, 2007:fig. 14). The subparallel tibial extremities differ from the rotated condition of *T. insignis* and *Lydekkerina huxleyi* (Hewison, 2008:fig. 13). Ventrally, the 'Y'-shaped flexor crests of LPRP/USP-0011 are also seen in *E. megacephalus* and *T. insignis*, but not in *L. huxleyi*, which bears three parallel crests, and in *A. decheni*, which has a posterior crest extending along the whole length of the bone. The cnemial structures are more evident in LPRP/USP-0011 than in *T. insignis*, *L. huxleyi*, and *E. megacephalus*. The fibula of LPRP/USP-0011 differs from that of *E. megacephalus*, in its expanded distal tip that is only slightly twisted relative to the proximal portion of the bone (about 25°). Its posterior margin is not concave as in *T. insignis*, approaching the condition of *A. decheni*. The posterior fibular ridge of LPRP/USP-0011 is similar to that of *A. decheni*, and much longer than that of *E. megacephalus*. In the distal margin, the fibular facet is rounded and not flattened as in *A. decheni*, and the intermedial facet is not convex as in *L. huxleyi*.

#### Ontogenetic Stage of LPRP/USP-0011

The only preserved pubis of *A. cosgriffi* is attributed to a juvenile with an open obturator foramen (Dias and Schultz, 2003). We assume a late ontogenetic stage for LPRP/USP-0011, because a closed obturator foramen indicates maturity (Pawley and Warren, 2006). This is also inferred from the entirely cartilaginous pubis, which is usually one of the latest bones to ossify in temnospondyls. Indeed, even the largest specimens of *Archegosaurus decheni* are known to lack an ossified pubis (Witzmann and Schoch, 2006). Also, an oblique line, seen only in adult

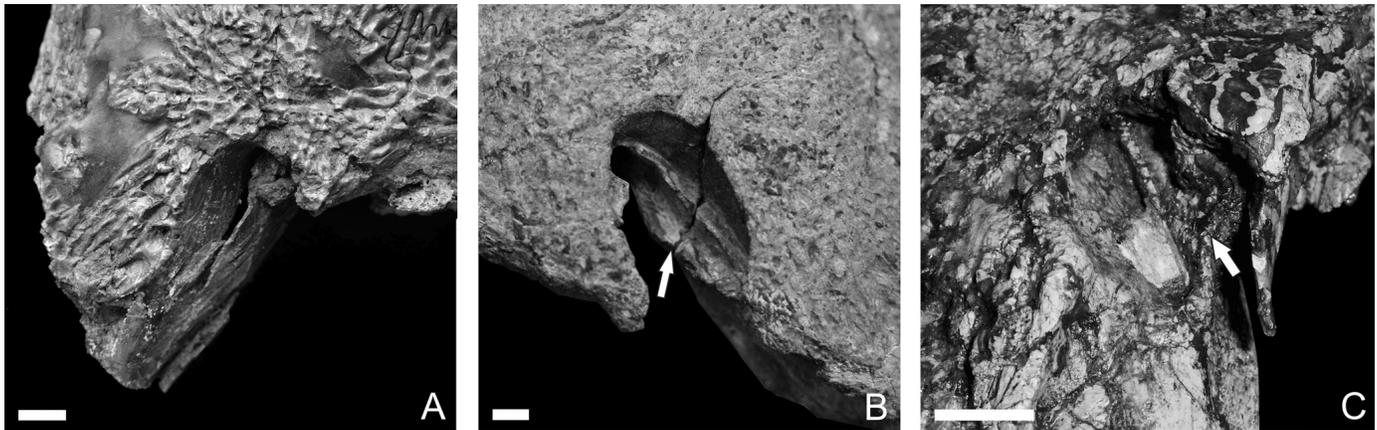


FIGURE 10. Temnospondyl otic notches in dorsal view (A, B) and dorsolateral view (C). A, photograph of the left otic notch of *Platyposaurus watsoni* (PIN 161/20); B, photograph of the right otic notch of *Rhineceps nyasaensis* (CAMZM T.259); C, photograph of the left otic notch of *Australerpeton cosgriffi* (UFRGS-PV-229-P). The white arrows indicate the oblique ridge on the medial surface of the ascending ramus of pterygoid. All scale bars equal 1 cm.

specimens of *A. decheni*, is present on the lateral surface of the iliac blade. In a subadult specimen of *A. cosgriffi* (UFRGS-PV-0319-P), the femoral head projects anteroposteriorly and the fourth trochanter is represented by a rugose area. This arrangement is typical of juvenile temnospondyls and differs from that of LPRP/USP-0011. Some osteological indicators of maturity supporting the late ontogenetic stage of the femur include the well-developed intertrochanteric fossa, prominent adductor blade and internal trochanter, distinct intercondylar fossa, and clearly defined popliteal area and crests (Pawley and Warren, 2006). All of these characteristics are clearly seen in the femur of LPRP/USP-0011 (Fig. 5). The same indicators of maturity appear in the tibia, in which the proximal head is expanded to twice the size of the distal head, the cnemial crests are evident with a deep cnemial sulcus, and a clearly 'Y'-shaped system of flexor crests is present (Fig. 7). The fibula of larval temnospondyls lacks expanded extremities, as in *T. insignis*. This condition differs from LPRP/USP-0011, in which the fibula bears an expanded distal margin with a sigmoid contour, formed by the intermedial (concave) and fibular (convex) facets.

#### Inclusion of *Australerpeton cosgriffi* in Stereospondyli

Two of the three unambiguous synapomorphies of Stereospondyli sensu Yates and Warren (2000) are seen in *A. cosgriffi*: (1) palatine ramus of the pterygoid posteriorly retracted, exposing the palatine in the interpterygoid vacuity; and (2) pterygoid with a flat, broad internal process that articulates with most of the lateral edge of the parasphenoid plate (Barberena, 1998:fig. 4). Yates and Warren (2000) also considered an ornamented ventral pterygoid surface as apomorphic for Stereospondyli, but this condition is absent in *A. cosgriffi*, as well as in Rhinesuchidae and *Mastodonsaurus giganteus* (Schoch, 1999:fig. 8). Among supporting synapomorphies mapped on Stereospondyli, Schoch (2013) listed (1) the rounded otic notch confined to the dorsomedial part of squamosal; (2) squamosal with a convex projection, referred to as the falciform crest; (3) tooth bases of the marginal dentition forming transversely broadened ovals; (4) transverse processes of vertebrae distally extended with diapophysis pointing laterally; and (5) interclavicle (anterior margin) smooth. With the exception of the dentition, where the tooth bases are clearly rounded in *A. cosgriffi*, all of these features are present in *A. cosgriffi*.

The fact that *A. cosgriffi* is found to be more derived than *P. pustulatus*, but more basal than Rhinesuchidae, could suggest

that *A. cosgriffi* and *P. pustulatus* are not stereospondyls. Applying the node-based phylogenetic definition for Stereospondyli (Schoch, 2013), which corresponds to the most inclusive clade containing *Uranocentrodon senekalensis* and *M. giganteus*, but not *E. megacephalus*, both *A. cosgriffi* and *P. pustulatus* are not stereospondyls. The relationships of *P. pustulatus* are not well established (Schoch et al., 2007). However, the stereospondyl condition of *P. pustulatus* is supported in some other works (Yates and Warren, 2000; Pawley and Warren, 2005; Piñeiro et al., 2012) and coupled with the clear stereospondyl characteristics seen in *A. cosgriffi*, has led us to conclude that *A. cosgriffi* is a basal member of Stereospondyli. As a long-snouted temnospondyl, *A. cosgriffi* bears resemblance to the archegosaur *Platyposaurus*, but this similarity seems conditioned by the general conformation of the skull (Dias and Schultz, 2003), and is here interpreted as an evolutionary convergence for a fish-eating habit. Convergent evolution of long-snouted forms appears to be relatively common, as seen among Crocodyliformes (Brochu, 2001).

The occipital and posterior palatal regions of *A. cosgriffi* resemble those of rhinesuchids much more than those of platypososaurs. For instance, there is the clear oblique ridge on the ascending ramus of the pterygoid (Fig. 10). Other characteristics seen in *A. cosgriffi* are typical of basal stereospondyls, including the posterior retraction of the palatine ramus of the pterygoid; the many teeth on both the ectopterygoid and palatine; the clasping of the anterior cultriform process by the vomers; the larger vomerine tusks; a transverse 'belt' of denticles on the base of cultriform process; an extensive suture between the parasphenoid and pterygoid; double occipital condyles with no contribution from the basioccipital; the large and round otic notches; the contact between the tabular and exoccipital; tabular horns that are ventrally directed; the falciform crest on the squamosal; discontinuous crista muscularis on the ventral surface of the parasphenoid; and conspicuous notches ('pockets' for the insertion of musculature) on the posterolateral surface of the parasphenoid body.

The presence of the stereospondyl *A. cosgriffi* in the late Permian of Brazil corroborates a proposal advocated by Ruta et al. (2007), which suggested a radiation of the group in the late Permian. The presence of *A. cosgriffi* increases basal stereospondyl diversity outside Africa. Other Permian Stereospondyli are the rhinesuchid *Gondwanasaurus bijoriensis* and the dubious *Lysipterigium risinense* (Schoch and Milner, 2000), both from India (Werneburg and Scheneider, 1996), and the rhytidosteid *Trucheosaurus major* (Warren and Marsicano, 1998;

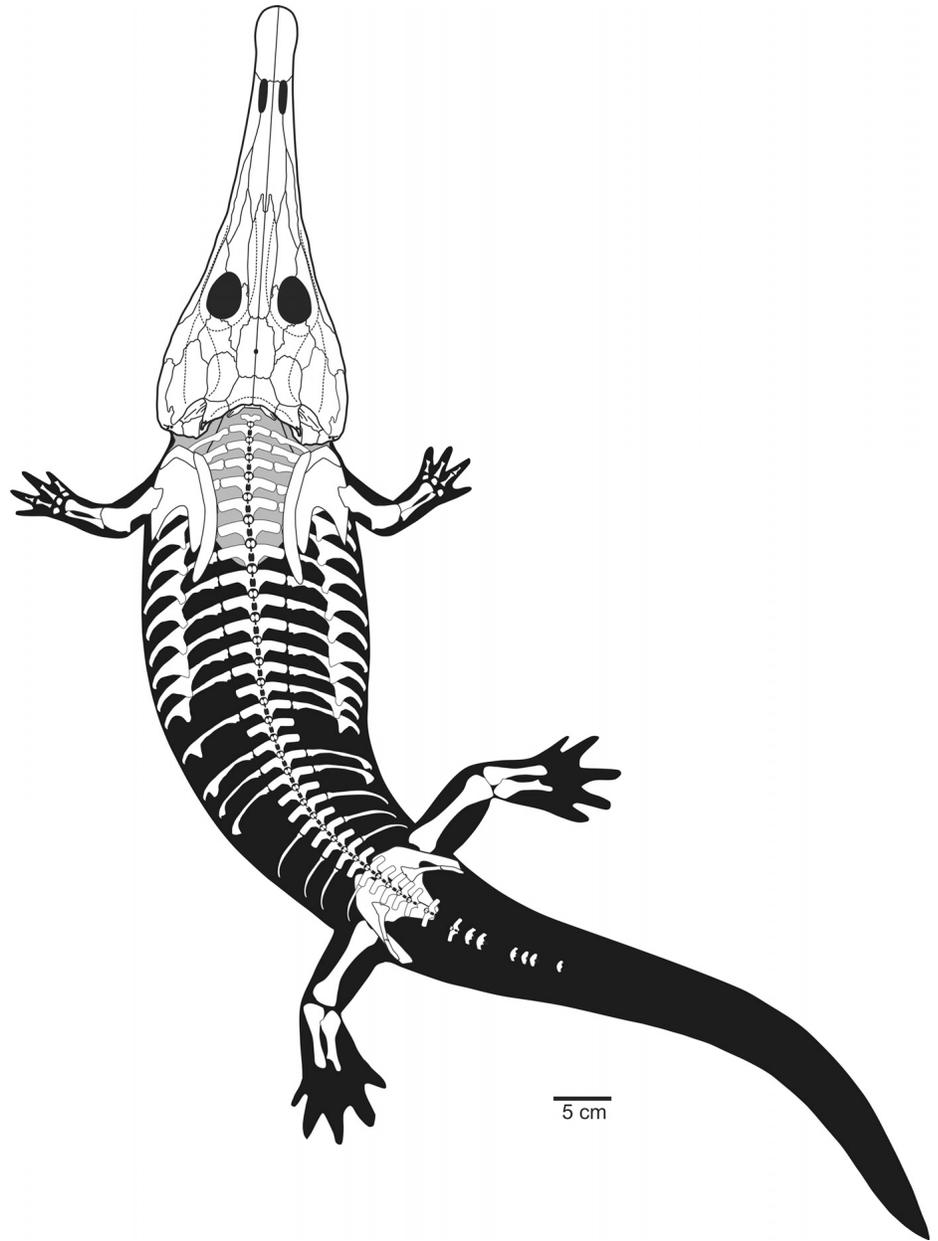


FIGURE 11. *Australerpeton cosgriffi*. Skeletal reconstruction of preserved parts in dorsal view.

Dias-da-Silva and Marsicano, 2011) and the probable brachyopomorph *Bothriceps australis* (Warren and Marsicano, 1998, 2000), both from Australia.

(3) The stereospondyl affinity of *A. cosgriffi* places the Paraná Basin within the possible ancestral range of the clade, within southern Pangea, before the end-Permian extinction.

#### CONCLUSIONS

- (1) Preserved lower jaws of *A. cosgriffi* are rare and the weak ossification of the temnospondyl postcranium renders their preservation generally uncommon. The well-ossified LPRP/USP-0011, a clearly adult specimen, is important for the better understanding of these anatomical parts. With these new data (see also Barberena, 1998, and Dias and Schultz, 2003), a near-complete skeletal reconstruction of *A. cosgriffi* is possible (Fig. 11).
- (2) Phylogenetic analysis indicates that *A. cosgriffi* corresponds to a basal stereospondyl, more derived than *P. pustulatus* and closer to the higher stereospondyls, but more basal than Rhinesuchidae.

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APPENDIX 1. Terminal taxa used in this analysis with specimens and literature from which the information was gathered; (\*) indicates specimens examined by authors.

*Dendrerpeton acadianum* (Holmes et al., 1998)

### Trematopidae

*Anconastes vesperus* (Berman et al., 1987)  
*Phonerpeton pricei* (Dilkes, 1990)

### Dissorophidae

*Dissorophus multicinctus* (DeMar, 1968)  
*Tersomius texensis* (Carroll, 1964)  
*Eryops megaloccephalus* (Sawin, 1941; Moulton, 1974; Pawley and Warren, 2006)  
*Trimerorhachis* spp. (Williston, 1915; Case, 1935)  
*Trimerorhachis sandovalensis* (Berman and Reisz, 1980)  
*Trimerorhachis insignis* (Pawley, 2007)  
\**Sclerocephalus haueseri* (MB.Am 1345, MB.Am 985 [cast], SMNS 51395, SMNS 52462, SMNS 81791, SMNS 90055, SMNS 91280 [cast], SMNS 91282 [cast], SMNS 91283 [cast], SMNS 91295; Boy, 1988; Schoch and Witzmann, 2009)  
\**Archeogosaurus decheni* (hundreds of specimens at MB; GPIT Am.00020, GPIT Am.00034, GPIT Am.00685, NHMUK R1787, NHMUK R1298, NHMUK R1785, NHMUK OR35804, NHMUK OR35805, NHMUK OR42754, NHMUK OR42806, CAMZM T.128, CAMZM T.130, CAMZM T.222, CAMZM T.256 [cast], CAMZM T.131; Witzmann, 2005; Witzmann and Schoch, 2006)

- \**Platyoposaurus stuckenbergi* (PIN 49/1, PIN 49/2, PIN 49/3, PIN 49/4, PIN 49/18, PIN 49/19, PIN 49/20, PIN 49/21, PIN 49/29, PIN 49/30, PIN 49/31, PIN 164-1/3, PIN 164-1/4, PIN 164-1/5, PIN 164-1/6, PIN 164-1/7, PIN 2255/2, PIN 161/103, PIN 3968/1, PIN 3968/3; Gubin, 1991)  
\**Triphosuchus paucidens* (PIN 157/100, PIN 157/101, PIN 157/102, PIN 157/105, PIN 157/108, PIN 271/159, PIN 157/112; Gubin, 1991)  
\**Triphosuchus kinelensis* (PIN 272/52, PIN 272/54, PIN 272/8, PIN 272/71; Gubin, 1989)  
\**Melosaurus kamaensis* (PIN 3968/2, PIN 683/1, PIN 683/2; Gubin, 1991)  
\**Melosaurus* sp. (PIN 2255/6, PIN 157/139, PIN 271/100, PIN 271/14; Gubin, 1991)  
\**Konzhukovia vetusta* (PIN 520/1, PIN 520/8, PIN 520/10, PIN 520/11, PIN 4273/1; Gubin, 1991)  
\**Peltobatrachus pustulatus* (CAMZM T.267, CAMZM T.269, CAMZM T.270, CAMZM T.271, CAMZM T.272, CAMZM T.276, CAMZM T.277, CAMZM T.286; Panchen, 1959)  
\**Australerpeton cosgriffi* UFRGS-PV-0224-P, UFRGS-PV-0225-P, UFRGS-PV-0227-P, UFRGS-PV-0228-P, UFRGS-PV-0229-P, UFRGS-PV-0230-P, UFRGS-PV-0319-P, UFRGS-PV-0320-P; LPRP/USP 0011; Barberena, 1998; Dias and Schultz, 2003)  
\**Rhinesuchus broomianus* (GPIT/Am. 722; Huene, 1931)  
\**Rhineceps nyasaensis* (CAMZM T.259; Watson, 1962)  
*Uranocentron senekalensis* (R. Schoch, pers. comm.; Van Hoepen, 1915; Broom, 1930; Watson, 1962)  
*Arachana nigra* (Piñeiro et al., 2012)  
\**Lyddekerina huxleyi* (NHMUK R504, NHMUK R506, NHMUK R507, NHMUK R508, NHMUK R5482, CAMZM T.238, CAMZM T.110; Pawley and Warren, 2005; Jeannot et al., 2006; Hewison, 2007, 2008)

### Rhithosteidae

*Arcadia myriadens* (belonging to *Rewana* according to Schoch and Milner [2000]; Warren and Black, 1985)  
*Pellostega* cf. *erici* (Janvier, 1983)  
*Pneumatostega potamia* (Cosgriff and Zawiske, 1979)  
*Pelorocephalus* spp. (Marsicano, 1993, 1999; Warren and Marsicano, 2000)  
*Koskinonodon perfectus* (Sawin, 1945)

### Trematosauridae

*Trematosaurus brauni* (Jaekel, 1922)  
*Lyrocephaliscus euri* (Mazin and Janvier, 1983)  
*Hyperokynodon keuperinus* (Hellrung, 1987)  
*Trematolestes hagdorni* (Schoch, 2006)  
*Benthosuchus sushikini* (Bystrow and Efremov, 1940)  
*Eryosuchus pronus* (Howie, 1970; Damiani, 2001)  
\**Mastodonsaurus giganteus* (SMNS 54675, SMNS 54677, SMNS 80879, SMNS 80887, SMNS 80890, SMNS 81212, SMNS 81265, SMNS 81267, SMNS 81305, SMNS 81316, SMNS 81330, SMNS 81343, SMNS 81347, SMNS 81360, SMNS 81361, SMNS 81966, SMNS 82015, SMNS 82017, SMNS 84140, SMNS 84141, SMNS 84142, SMNS 84147, SMNS 84214; Schoch, 1999)