

THE FIRST PALEOZOIC TEMNOSPONDYL POSTCRANIAL SKELETON FROM SOUTH AMERICA

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ABSTRACT - New postcranial materials of a temnospondyl amphibian are described, represented by two specimens with almost complete skeletons associated with part of their skulls. These specimens were collected from the Serra do Cadeado area (Paraná State) in the Rio do Rasto Formation, which is considered of Late Permian age. Despite the scarcity of cranial information, the material is tentatively assigned to the long-snouted rhinesuchid temnospondyl *Australerpeton cosgriffi* Barberena, 1998, which was originally described based only on cranial material. The specimens described here present vertebrae with predominant intercentra and small pleurocentra that are firmly attached to the neural arches, showing an advanced rhachitomous organization in the vertebral column. The light curvature of the ribs is interpreted as evidence for a flattened body and hence this amphibian was a shallow water dweller. On the other hand, the robustness of the shoulder girdle and the limbs, as well as the presence of ossified carpals and tarsals, suggests an ability to walk.

Key words: Temnospondyli, paleobiology, Late Permian, Rio do Rasto Formation.

RESUMO - Um novo material pós-craniano de um anfíbio temnospôndilo é descrito. Este consiste de dois esqueletos quase completos, exceto pela falta, em ambos, de quase todo o crânio. O material em questão foi coletado na região da Serra do Cadeado, na Formação Rio do Rasto, a qual é considerada de idade Neopermiana. Apesar da pouca quantidade de informações cranianas, o material foi tentativamente atribuído ao rinesuquídeo de rosto longo *Australerpeton cosgriffi* Barberena, 1998, cuja descrição original está baseada apenas em materiais cranianos. Os espécimes apresentam vértebras com intercentro predominante e pleurocentros menores que estão firmemente ligados aos arcos neurais, gerando uma coluna vertebral do tipo raquitome avançado. A pouca curvatura das costelas foi interpretada como evidência de um corpo achatado e para inferir que este anfíbio provavelmente habitava águas rasas. Por outro lado, a robustez das cinturas e dos membros, bem como a presença de carpais e tarsais ossificados, sugerem a capacidade de caminhar.

Palavras-chave: Temnospondyli, paleobiologia, Neopermiano, Formação Rio do Rasto.

INTRODUCTION

The Permian temnospondyls of Brazil are known from at least three main localities. From the northeast of Brazil is known *Prionosuchus plummeri* Price, 1948, an archegosaurid from the Early Permian Pedra do Fogo Formation (Price, 1948; Cox & Hutchinson, 1991). From the south of Brazil two localities are known, both in the Rio do Rasto Formation. In the Paraná State, remains of the rhinesuchid *Australerpeton cosgriffi* Barberena, 1998, and another still unnamed rhinesuchoid taxon (Barberena & Dias, 1998). In Rio Grande do Sul State is known the archegosaurid *Bageherpeton longignathus* Dias & Barberena, 2001. All of these taxa are known from cranial and mandibular materials only.

Traditionally, most of the authors emphasize the skull anatomy in the description of the of fossil vertebrates, and it is not different for temnospondyls, which skulls are very well known in contrast with the postcranium skeleton. Detailed descriptions of the postcranium of these basal amphibians are scarce in the literature (*e. g.* Kozhukova, 1955; Carroll, 1967; Howie, 1970; Moulton, 1974; Dutuit, 1976; Warren & Hutchinson, 1983; Warren & Snell, 1991; Marsicano, 1993; Schoch, 1999).

This study describes the postcranium material of a temnospondyl tentatively referred to *Australerpeton cosgriffi*, resulting in a more integral knowledge of this taxon and allowing ecological interpretations that cannot be provided by the cranial anatomy alone. This is the first complete

description of the postcranium skeleton of a Paleozoic South American temnospondyl.

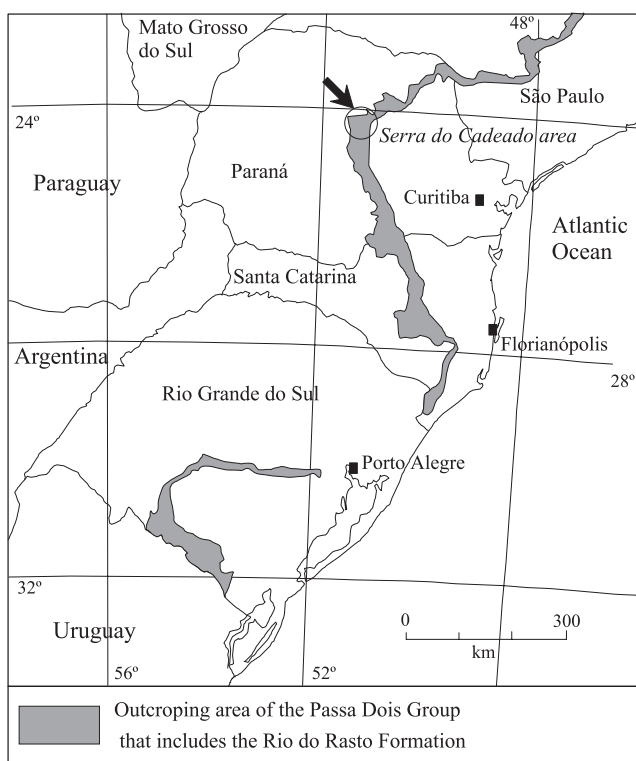


Figure 1. Map showing the geographic location of the Serra do Cadeado (arrow).

The studied material belongs to the vertebrate collection of the Universidade Federal do Rio Grande do Sul (UFRGS-PV) Porto Alegre, and was collected in the Rio do Rasto Formation outcropping in the Serra do Cadeado area, Paraná State, Brazil (Figure 1), during expeditions led by Dr. Mario C. Barberena in the 1970's and 1980's. It consists of two individuals (UFRGS-PV0319P, UFRGS-PV0320P) comprising parts of the skulls and almost complete articulated postcranial skeletons.

UFRGS-PV0319P comprises a small fragment of the skull table, a fragment of a mandibular ramus, 18 complete trunk and five caudal vertebrae, some isolated vertebral elements, ribs, bones of the shoulder girdle and forelimb, some hand bones, and incomplete bones of the pelvic girdle, hind limb and foot (Figures 2, 3). Many articulated and isolated dermal scales are also preserved.

UFRGS-PV0320P comprises a fragment of the left posterior portion of the skull, at least 20 trunk vertebrae, some presacral ribs, a complete left shoulder girdle, and an almost complete forelimb. Only a fibula is present of the hindlimb. This specimen also has many isolated dermal scales (Figures 4, 5) already studied by Dias & Richter (2002).

The outcrops where the material was collected are vertical railroad cuttings of very difficult access. The embedding rocks are very hard mudstones, making the fieldwork complicated and with arduous extraction conditions (M.C. Barberena, *personal communication*). A combination of

weathering and taphonomic features such as compression and skeletal disarticulation often results on incomplete specimens. Nevertheless, both specimens described here were found partially articulated.

Specimen UFRGS-0319P presents its cervical region with disarticulated ribs and vertebrae. The fragment of a mandibular ramus and the posterior fragment of the skull are preserved near the scattered cervicals. Most of the trunk vertebrae and ribs, as well as the sacral rib, are articulated. Only six anteriormost caudal vertebrae are articulated but there are also some isolated caudal vertebrae elements preserved posteriorly. Both girdles, as well as the fore and hind limbs, are preserved close to their original positions. The interclavicle is badly preserved and almost completely covered by other bones. The clavicles were not found. The pelvic girdle was damaged by compression and by difficulties of preparation. Most of the lost portions, such as the distal caudal vertebrae and most of the skull, were lost during railroad construction or eroded.

In UFRGS-0320P, the preserved portion of the skull is attached to the vertebral column without evidence of disarticulation. The cervical vertebrae, with the exception of the atlas, are well preserved and articulated. Anterior left ribs and shoulder girdle are nearly in their original positions and only the distal elements of the left manus are not preserved. The degree of disarticulation increases posteriorly, with trunk vertebrae and ribs becoming gradually more disarticulated. No evidence of pelvic girdle, hind limb and caudal elements were found. This may indicate a delay in burial for the sacral and caudal regions. The anterior region and the right side of the skull, the atlas, and most of the right shoulder girdle and right fore limb, may have been lost during railroad construction and subsequent erosion.

Anatomical abbreviations. **c** - clavicle; **ca** - carpals; **cb** - coracoid blade; **cl** - cleithrum; **diap** - diapophysis; **f** - femur; **fi?** - probably a fibula; **fil** - fossa for the intervertebral ligament; **fp** - fossa poplitea; **ft** - fossa tendinalis; **h** - humerus; **i** - intercentrum; **ic** - interclavicle; **mca** - metacarpals; **mts** - metatarsals; **nc** - neural canal; **parap** - parapophysis; **pd** - pedicel; **ple** - pleurocentrum; **poz** - postzygapophysis; **prz** - prezygapophysis; **ra** - radius; **r** - rib; **rup** - ribs with uncinat process; **sc** - scapula; **sk** - skull; **sr** - sacral rib; **tb** - tibia; **tr** - trochanter; **ts** - tarsal; **ul** - ulna; **vc** - ventral crest; v.4 - fourth vertebra.

DESCRIPTION

AMPHIBIA Linnaeus, 1758 [*sensu* Gauthier *et al.*, 1988]

TEMNOSPONDYLI Zittel, 1890 [*sensu* Milner, 1993]

RHINESUCHIDAE Watson, 1919 [*sensu* Schoch & Milner, 2000]

Australerpeton cosgriffi Barberena, 1998

(Figures 2-5)

Diagnosis (from Barberena, 1998). Supratemporal not bordering the otic notch (as in Lydekkerinidae); sutural contact between pterygoid and parasphenoid firm and moderately extended; parasphenoid corpus does not

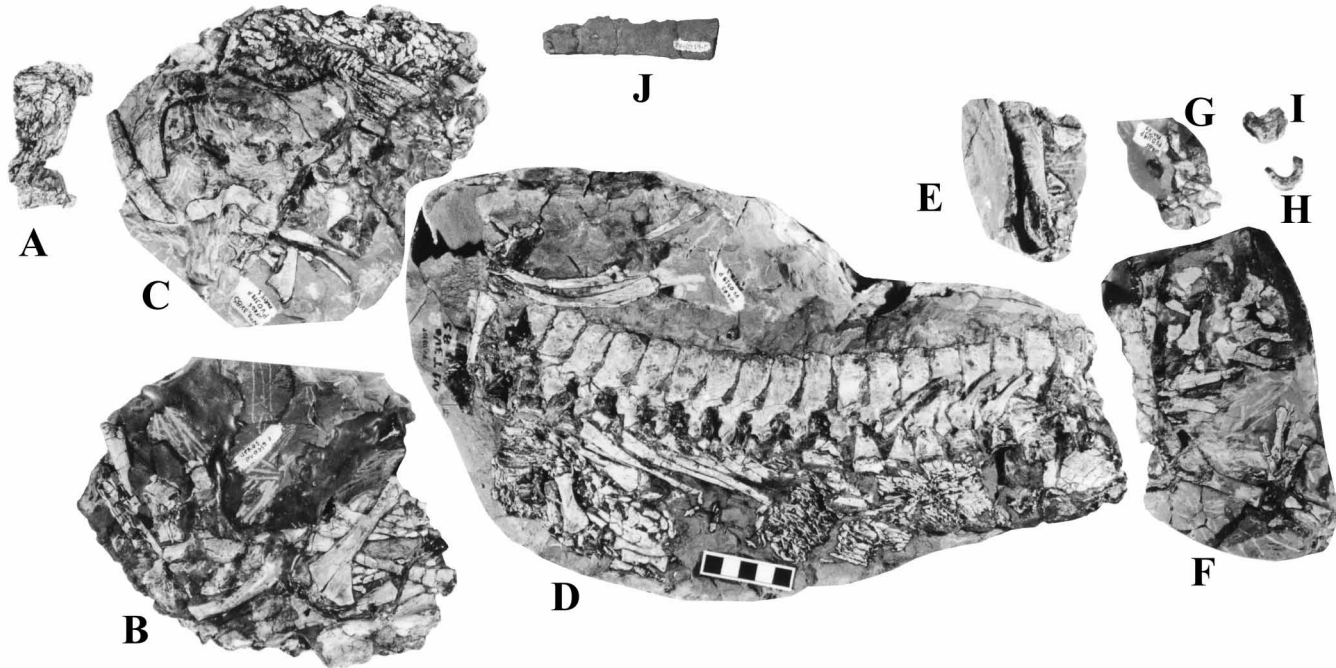


Figure 2. Photographic composition of the sub-adult specimen of *Australerpeton cosgriffi* (UFRGS-PV0319P). All parts were merge to show the complete specimen. **A.** Fragment of the skull; **B** and **C.** left and right side of the same block; **D.** left side of the trunk region; **E.** - Right femur preserved on the right side of the block **D**; **F.** - Left hind limb and some caudal vertebrae; **G, H** and **I.** isolated caudal intercentra; **J.** Fragment of the lower jaw. Scale bar = 5 cm.

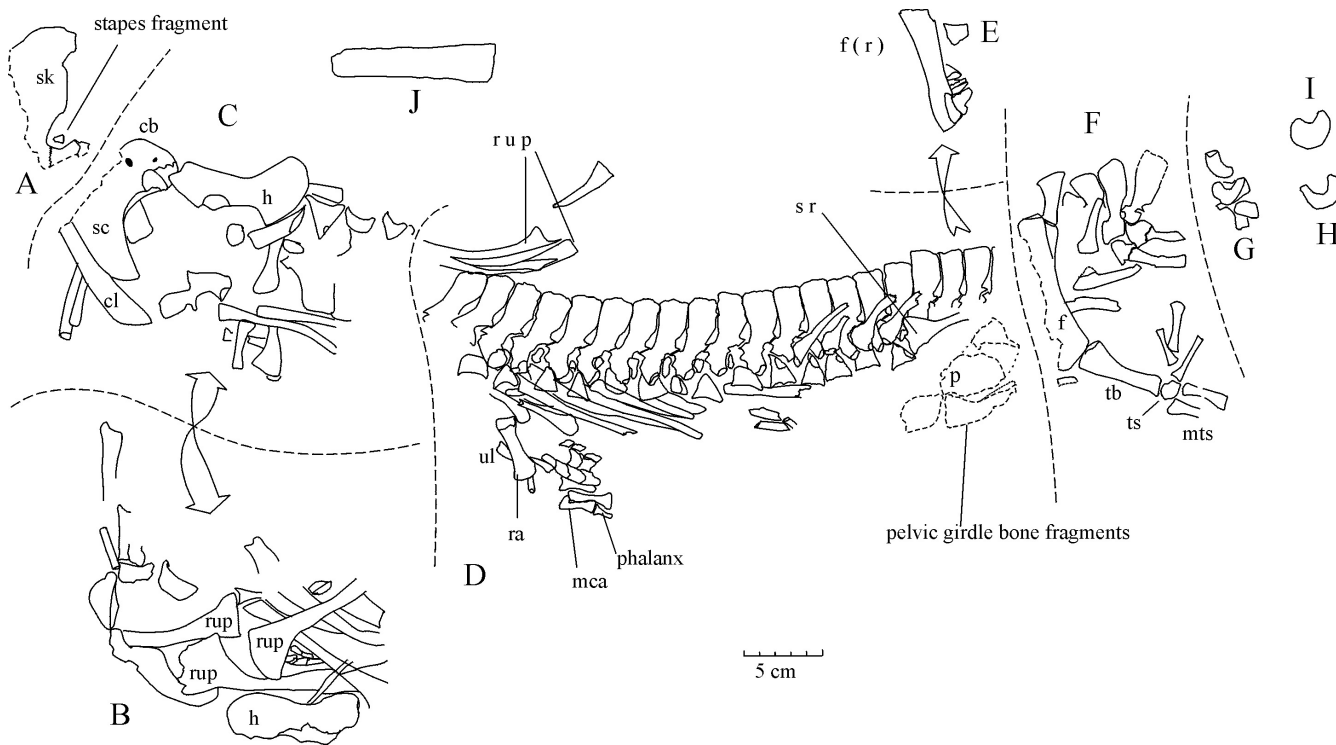


Figure 3. Composition drawing of the sub-adult specimen of *Australerpeton cosgriffi* (UFRGS-PV0319P). All parts were merge to show the complete specimen. Most of the ventral scales were omitted. **A.** Fragment of the skull; **B** and **C.** Left and right side of the same block; **D.** Left side of the trunk region; **E.** Right femur preserved on the right side of the block **D**; **F.** Left hind limb and some caudal vertebrae; **G, H** and **I.** isolated caudal intercentra; **J.** Fragment of the lower jaw.

underplate exoccipital condyles; basioccipital briefly exposed on palatal surface; occipital condyles well separated, with no basioccipital connecting them (not as in *Rhinesuchus*, *Muchocephalus* and *Rhineceps*); unossified opisthotic on paroccipital bar (not as in *Rhinesuchus*); orbits dorsally placed; quadrates lying behind exoccipital condyles level; well developed parasphenoid “pockets” for the insertion of vertebro-occipitalis muscles; the almost entire occipital surface of a rhinesuchid pattern with particular emphasis on the well developed, vertically descending flange of the paroccipital portion of the tabular.

Convergent and parallel characters can be also detected in *Australerpeton*, such as: elongated triangular skull with narrow snout; postorbital region longer than in other rhinesuchoids; cheek area deeper than in other rhinesuchoids, but not as deep as in trematosauroids; narrow contact between palatines and pterygoids; elongate interpterygoid vacuities; keeled cultriform process of parasphenoid (as in Trematosauridae and Capitosauridae).

Revised diagnosis. Tabular does not contact the squamosal and Supratemporal bordering the otic notch, as already figured by Werneburg & Schneider (1996) and Schoch & Milner (2000), although without seen the type series.

Emended diagnosis. The association of the following characters diagnoses the postcranial skeleton of *Australerpeton cosgriffi*: Vertebrae composed of intercentra that are wedge-shaped in lateral view, crescent-shaped in anterior and posterior views and also opened dorsally, indicating that the notochord was uninterrupted. Pleurocentra reduced and not well ossified in younger specimens but well developed and strongly attached to the neural arch in the adult. Adult neural arches with pedicels that go downward making the neural canal totally enclosed in the trunk vertebrae. Ribs with large distal laminar portion associated with large uncinat processes. The ventral blade of the clavicles is elongated, about 2.5 times longer than wide, and the anterior process of the interclavicle follows the elongation of the clavicle. Cleithrum rod-like and scapular blade axe-shaped. Humerus with prominent deltoid and supinator process. The carpals and tarsals are ossified.

Axial skeleton

Vertebrae. As in other Temnospondyli the vertebrae are composed of four basic bone elements: a neural arch, one intercentrum anteriorly and two pleurocentra posteriorly. This description is based on 18 vertebrae preserved articulated in lateral view in the sub-adult specimen (UFRGS-PV0319P) and 20 vertebrae preserved in various positions of the adult (UFRGS-PV0320P). The vertebrae of both specimens show little morphological variation along the column (except the 4th cervical).

The neural arches, as with the other vertebral elements, are similar in size and shape along the trunk vertebrae. The sub-adult (UFRGS-PV0319P) has more than 15 well preserved neural arches, all exposed in lateral view, and most belonging to the trunk vertebrae (Figures 2, 3). Neural spines are laterally compressed with small variation in their height.

The neural spines are rectangular in lateral view, comprising almost two thirds of the total height of the neural arch. In lateral view, the dorsal half of the neural spine shows straight anterior and posterior edges, while in its ventral half, the posterior edges are curved forward just dorsally to the zygapophyses. In both specimens, the lateral surfaces of the neural spines show irregular protuberances for insertion of axial muscles and ligaments (Figures 7, 8). They are more conspicuous in the anterior trunk vertebrae. In the sub-adult specimen, these protuberances are present throughout the whole vertebral column forming lateral ridges in some vertebrae. In the cervical and anterior trunk vertebrae these ridges face forward and in the posterior trunk vertebrae they face backward. This orientation change seems to be marked by a middle trunk vertebra without a conspicuous ridge.

The zygapophyses of the sub-adult specimen, seen only in lateral view, have articular surfaces inclined at about 30° in relation to the body axis. Each zygapophysis (both pre and post) continues dorsally into a crest that merges in the upper half of the neural spine to form a single crest which runs until the tip of the neural spine. These crests are the borders of the axial cavities, which are the *fossae* for the inter-vertebral ligaments (Figure 7).

The transverse processes, better seen in some well-preserved neural arches of the adult specimen, extend laterally in a right angle from the sagittal plane. Their ventral edges are rounded, comprising approximately a quarter of a circle in anterior view. The diapophyses are notches in the posterior facets of the transverse processes, not seen in anterior view (Figure 7). Ventrally, the transverse processes form two pedicels. In the adult specimen, the medial portion of the arch's pedicel and small portions of the dorsal surface of the pleurocentra enclose the neural canal ventrally.

Of the atlas-axis complex only the neural arch of the axis is preserved in the adult. It is compressed over the third arch but seems to have an expanded spine as in the trunk vertebrae. The fourth vertebra of *Australerpeton cosgriffi* presents a reduced neural spine with an anteroposteriorly narrow lance-shaped tip (Figure 5). The zygapophyses of the fourth vertebrae are badly preserved. The cervical neural arches have a more constant shape as in the trunk vertebrae.

The intercentra of the trunk vertebrae of both specimens have, in lateral view, the shape of an equilateral triangle. Their ventral and lateral faces are slightly concave. In anterior and posterior views the intercentra are crescent-shaped with a dorsal concavity for the notochord. This persistent portion of the notochord should be thicker in the sub-adult specimen and thinner in the adult, but never enclosed by the intercentra. The intercentra vary in size and thickness according to the age of the animal and their heights are 1/3 of the total height of a vertebra (Figures 2, 8). In the sub-adult specimen, the intercentra seem to articulate with adjacent vertebral elements by ample portions of cartilage, whereas in the older specimen it is attached to the pedicel of the neural arch and to the corresponding pleurocentra. The proximity to the vertebral elements of adjacent vertebrae seems close suggesting there was little cartilage.

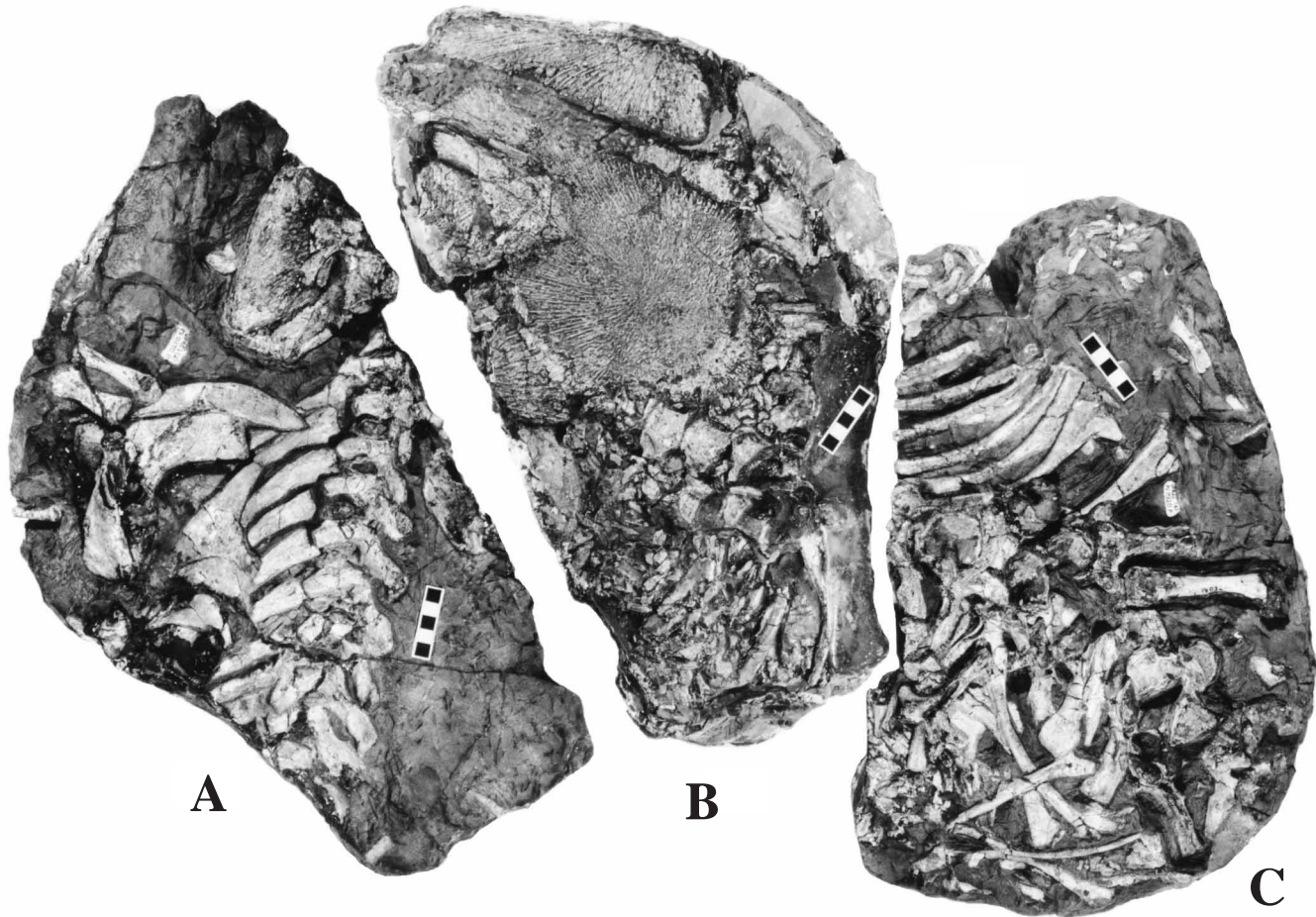


Figure 4. Photographic composition of the adult specimen - UFRGS-PV0320P(a, b). A.- Dorsal view of the block a (anterior part); B. ventral view of the block a; C. Ventral view of the block b (posterior part). Scale bar = 5 cm.

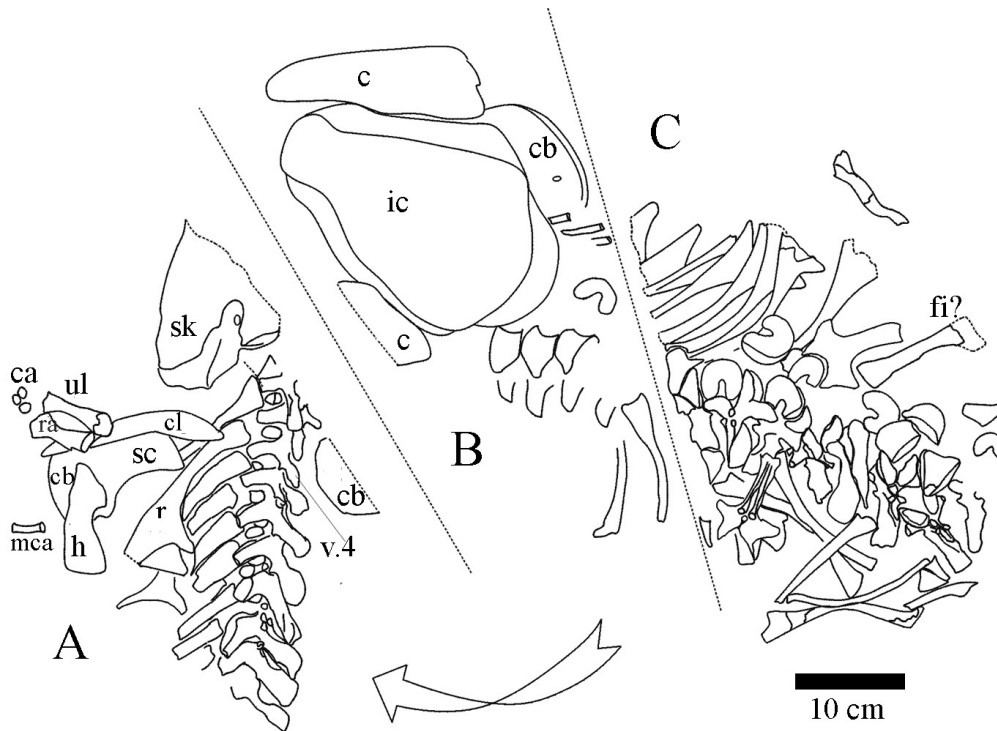


Figure 5. Drawing of the adult specimen - UFRGS-PV0320P (a, b). A. Dorsal view; B. ventral view of the block a (anterior part); C. Ventral view of the block b (posterior part).

The parapophyses, visible on both specimens, are small projections of the posterior dorsolateral surface of the intercentra and are projected posteriorly. The sub-adult specimen shows the intercentrum of the sacral vertebra with a notch in its posterior face as a distinct parapophysis (Figures 2, 3). The neural arch of the sacral vertebra is not completely visible because the sacral and the preceding rib covers it.

The intercentra of the caudal vertebrae, seen in the sub-adult specimen, are fused with the corresponding haemal arches. These haemal arches are shorter in height than the corresponding neural arches, and they are directed backward (Figure 3F).

In the sub-adult specimen the pleurocentra are small, irregular bones of uncertain shape, not very well preserved, probably because they were not well ossified. The contact between the pleurocentrum and the neural arch is not visible.

In the adult specimen, the pleurocentra are chestnut-shaped and completely ossified (Figures 7, 8), with fully developed articulations with all surrounding bones (neural arch and intercentra). Their dorsal anterior region has a very close articulation with the pedicels of the corresponding neural arch. Their lateral surfaces are slightly concave following the same feature of the intercentra; the ventral anterior region is a straight facet which articulates the dorso-posterior portion of the anterior intercentrum; the posterior facet is rounded, being the articulation surface for the dorso-anterior portion of the posterior intercentrum. Internally, the pleurocentra are slightly rounded to accommodate the dorsal portion of the notochord. Its dorsomedial portion also contributes to enclose part of the neural canal.

Comparisons. The vertebrae of *A. cosgriffi* can be classified as typically rhachitinous due to the presence of one crescent-shaped ventral intercentrum and two dorsal pleurocentra (Romer, 1956, 1966). One may also call it advanced rhachitinous because of the expanded pleurocentra which are firmly attached to the pedicels of the neural arch, and close articulation with the anterior and posterior intercentra. The neural canal, ventrally enclosed by the expansion of the neural arch peduncle and by the dorsal portion of the pleurocentra, also indicates an advanced rhachitinous condition. The sub-adult would have larger spaces between the vertebral elements with larger cartilaginous portions due to the ossification delay of the pleurocentra. Otherwise, the close attachments of the vertebral elements in the adult show that these spaces were smaller with little cartilaginous portions. Moulton (1974) has observed it in *Eryops* but, judging by his illustrations, the adult specimen of *Australerpeton cosgriffi* has smaller articulation spaces, suggesting less cartilage between the pleurocentra and the pedicels. This continuous articulated axis of bone and cartilage makes a strengthened vertebral

column. As observed by Moulton (1974), *Eryops megalcephalus* presents an almost ordinary axis neural arch but the fourth vertebrae dorsal extremity is reduced. *Australerpeton cosgriffi* presents a similar configuration with the fourth neural arch tip lance-shaped. This lance-shaped tip is related to the head mobility, compensating restrictions in movement at the occiput (Moulton, 1974). The distribution of this character among other temnospondyls needs a careful evaluation.

Ribs. The ribs bear a laminar distal portion associated with an uncinat process as their main feature (Figures 9, 10). The tuberculum and capitulum of the anterior trunk ribs are more conspicuous than in the posterior ones. This is easily observed in the adult specimen in which the capitulum is an expanded, flat structure. In the cervical region and also in some posterior trunk vertebrae of the sub-adult specimen, the tuberculum is a short, condyle-like structure, slightly straight and not well separated from the capitulum.

The ribs present flattened heads and rod-like medial portions. The ribs are slightly curved down and backward

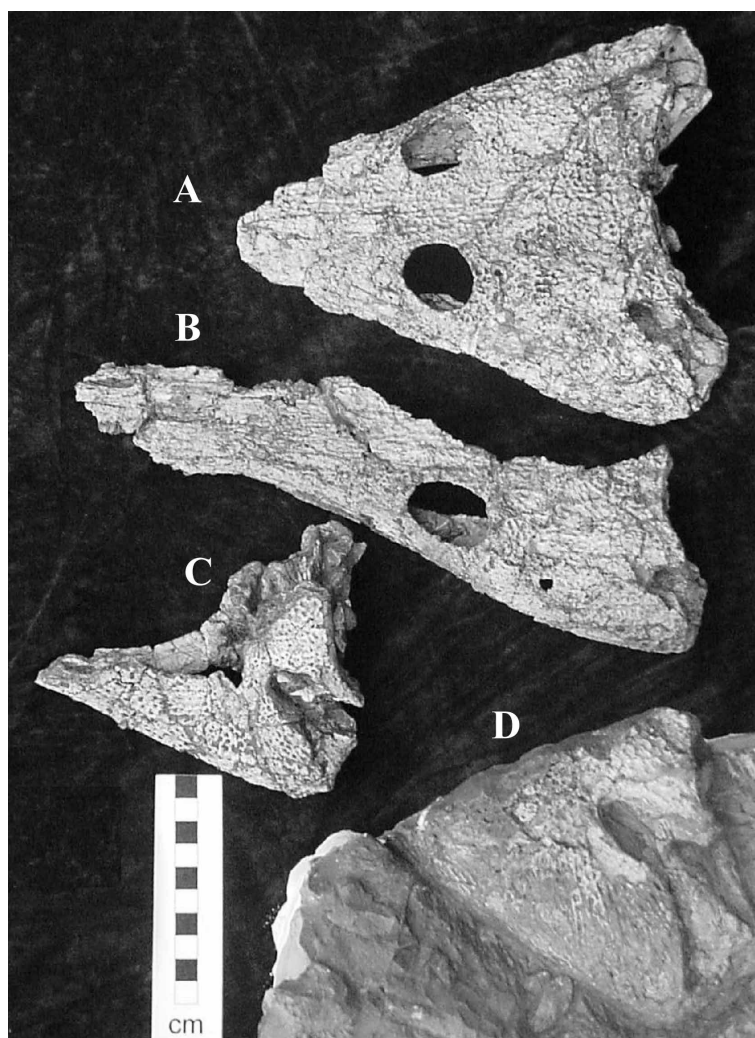


Figure 6. Skulls of the type series of *Australerpeton cosgriffi*: **A.** UFRGS-PV0229P; **B.** UFRGS-PV0227P (holotype); **C.** UFRGS-PV0230P. Skull portion of the adult specimen tentatively assigned to *Australerpeton cosgriffi*; **D.** UFRGS-PV0320P.

(Figure 9), becoming laterally flattened distally, thus forming a laminar portion in its posterior side while the anterior side remain rod-like, as seen in many primitive tetrapods, such as *Ichthyostega* (Jarvik, 1980). These laminar portions of the abdominal ribs are ample triangles in lateral view, where the uncinatous process projects backward in a rounded projection (Figure 10). The uncinatous processes are placed in a medial position in the anterior trunk ribs and become more distally placed posteriorly. Therefore, the median trunk ribs have the uncinatous process in the distal extremity of the rib and the posterior trunk ribs have only a small distal laminar portion where the uncinatous process became reduced. In the sub-adult specimen, the uncinatous processes are similarly well developed, as seen in some isolated trunk ribs. The laminar portion and the uncinatous process are structures usually related to increment on the body wall resistance, improving the support and protection for internal organs.

In the sub-adult specimen the proximal portion of a sacral rib is preserved. This rib differs from others by its enlarged head that is at least two times larger than the immediately anterior ones (Figure 2). The distal portion should be robust but unfortunately is not preserved. It shows two very well developed articulation facets, one for the neural arch and another for the intercentrum.

Comparisons. The light curvature of the ribs indicates that *A. cosgriffi* was a flattened animal (Figure 9) and could be a shallow water dweller. This flat body could also improve buoyancy allowing to swim on open waters. This hypothesis is compatible with the presumed sedimentary environment of the Rio do Rasto Formation, which consisted mainly of freshwater shallow lakes and rivers (Ragonha, 1989). This kind of rib shape probably gave little ventral protection for the visceral organs, so it could have presented difficulties on a terrestrial habitat. *Eryops megalcephalus*, which is considered a terrestrial temnospondyl, does not have a flattened body and its ribs are strongly curved downward, giving protection for the lungs and other visceral organs. The well-developed cover of dermal scales in *A. cosgriffi*, which could provide mechanical protection for the abdominal organs, can also be interpreted as a counter-balance for hydrostatic equilibrium, as discussed by Dias & Richter (2002). This reinforces its tendency to an aquatic way of life.

Appendicular Skeleton

Shoulder girdle and forelimb. The shoulder girdle has its dermal elements better preserved in the adult specimen (UFRGS-PV0320P). In the sub-adult specimen (UFRGS-0319P), the cleithrum is partially preserved and other dermal elements of the shoulder girdle are badly preserved.

The interclavicle of *Australerpeton cosgriffi* (Figures 4, 11), as in many temnospondyls, is a flat, rhomboidal bone plate with the two anterior sides larger than the two posterior ones. Its longitudinal axis is about 1.5 times longer than the transverse axis. The ossification centre is about 1cm posterior to the intersection of these axes. The transverse axis divides the bone in two parts, the anterior portion being two

times longer than the posterior one. The anterior region is composed by thin dermal bone with the anterior end as a round spatula-shaped or duck-beak shaped structure, ventrally ornamented with almost parallel short ridges. Romer (1947) interpreted this ornamentation as insertions for the longitudinal muscles of the throat. The two anterolateral margins of the interclavicle show a chamfer where the clavicles overlap ventrally. The posterior margin is almost rounded and short, corresponding to the posterior third of the bone and forming a semicircle. Dermal ornament is very conspicuous on almost all the ventral surface of the interclavicle. It is composed of pits and ridges radiating from the ossification centre, where the pits are completely closed and, towards the bone margins, become open distally and then run to the margin as long ridges and furrows with little transverse bridges.

The ventral part of the clavicle of *Australerpeton cosgriffi* (Figures 4, 11) is an elongated bone plate. The ascending process is not preserved. Its ornamentation pattern is similar to that of the interclavicle, composed of some shallow pits in

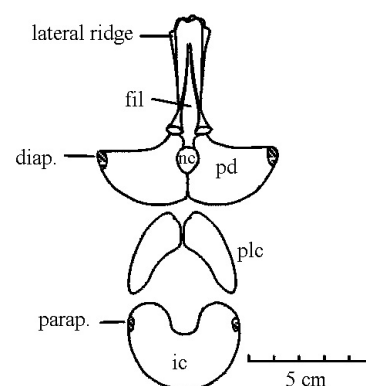


Figure 7. Composition of an adult trunk vertebra in posterior view with the elements splitted. Drawing based on several trunk vertebrae.

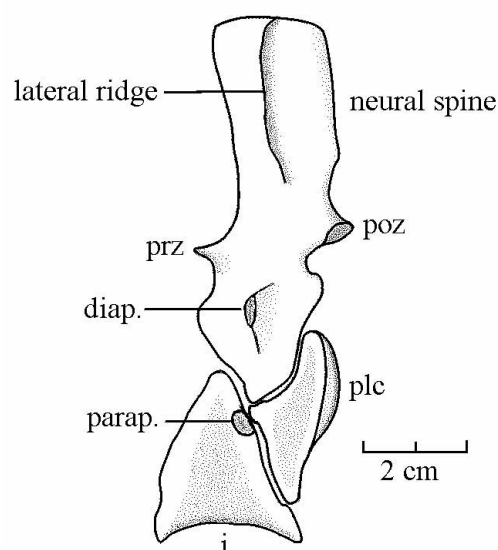


Figure 8. Reconstruction of an adult vertebra in lateral view, showing the articulation of vertebral elements. Drawing based on better preserved portions of several trunk vertebrae.

the ossification centre that become open distally and radiate to the anterior extremity of the bone, where they become just ridges and furrows almost without bridges. The medial side of the clavicle overlaps the interclavicle anterolaterally, covering the anterior two thirds of interclavicle in the overlap area (Figure 11).

In both specimens, the scapula and the coracoid are fused into a single scapulocoracoid bone, without a clear suture zone (Figures 12, 13). Compared to some more terrestrial temnospondyls, *Eryops* for instance, the scapulocoracoid of *Australerpeton cosgriffi* is proportionally short. Its height is about 75 mm in the sub-adult and 127 mm in the adult specimen. The scapulocoracoid length in the adult is 130 mm and uncertain in the sub-adult since it is not completely preserved. The scapula is an axe-shaped bone in which the leading edge is the antero-dorsal border of the bone, which contacts the cleithrum. The coracoid is a small plate that turns a little inward below the glenoid region. It presents an anteroventral supracoracoid foramen and a posteroventral coracoid foramen. The supracoracoid is at the level of the suture between the scapula and coracoid bones and is larger than the coracoid foramen. In the sub-adult specimen the anterior portion of the scapular blade is not preserved and in the older one it is partially covered by the attached preserved humerus, radius and ulna. There is a prominent dorsal articular glenoid facet in both specimens, but a complete glenoid cavity is not preserved. Dorsal to the glenoid cavity, the scapular edge is divided in to two crests forming the supraglenoid buttress, between which there is a deep furrow, the supraglenoid fossa. Inside this fossa is the supraglenoid foramen. The crests join dorsally enclosing the furrow to make the single edged dorsal scapular blade. In internal view, the coracoid of the adult specimen show a large and thick portion just anterior to the coracoid foramen, forming an internal buttress which crosses the coracoid ventrodorsally.

The cleithrum is an elongated, rod-like bone with a small expansion in its dorso-posterior extremity, while its ventral end is a thin bone leaf. It overlaps laterally the scapula, from

the anterior to the dorsal edge of that bone (Figures 12, 13). There are three almost completely preserved humeri, two from the sub-adult specimen (UFRGS-PV0319P) and one from the older one (UFRGS-PV0320P) (Figures 2, 5). The humerus is an almost flat bone with two expanded extremities twisted, in the sub-adult specimen 40° in the right humerus and 60° in the left one, and in the older specimen, 80°. We assume that the humerus which presents an angle of 60° of twist is the closest to reality because the other two seem to be much distorted by compression. The posterior border has a strong proximal deltoid process, although not well preserved in any of the specimens, and a very prominent distal supinator process (Figure 12). The anterior edge is a very lightly curved without conspicuous structures.

The radius and ulna of the older specimen are preserved almost attached to the humerus (Figure 13). In the sub-adult, the right radius, ulna, and some hand bones are spread but preserved in their correct anatomical sequence (Figure 12). Although, the description is based mainly on the bones of the older specimen, whose metapodial bones are better preserved. The ulna is slightly cylindrical proximally and flat distally, having a concave articular surface in the proximal extremity. This articular surface is quite concave and presents a proximal extension that corresponds to the olecranon process, which comprises 20% of the ulna length. The proximal extremity of the ulna has also two small medial processes with a short shallow furrow between them, the antero-superior notch of Dutuit (1976). The radius also has a cylindrical proximal extremity and a flat distal one, the distal being larger than the proximal.

Hand fragments are present in both specimens. In the older specimen, there are three small rounded carpal bones and only a single metacarpal. In the sub-adult specimen there are some articulated hand elements including, two carpals, three metacarpals and also one attached phalanx. The metacarpal extremities are two times larger than the diaphysis. The fourth digit is not preserved.

Pelvic girdle and hindlimb. All pelvic girdle and hindlimb

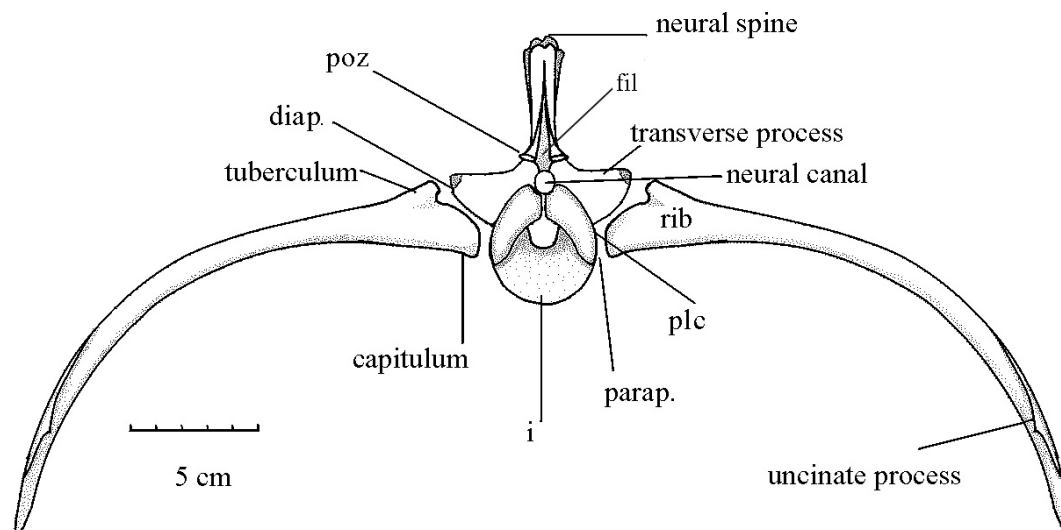


Figure 9. Composition with ribs and vertebra in posterior view. A possible life position.

bones preserved are incomplete and belong to the sub-adult specimen (Figures 2, 3). Portions of the pubis and the ischium are badly preserved. The pubis seems to be an anteriorly square blade of bone with an anterior notch that could be the obturator foramen. The ischium is a more wide bone but its posterior limit is missing. The ilium is not preserved. The sacral rib shows an enlarged head and it is articulated with a very well developed parapophysis in the corresponding intercentrum. The transverse processes of the sacral vertebra are partially covered by the large head of its own sacral rib but it seems to be of similar size to the other trunk vertebrae, probably with a distinct diapophysis.

The femur, known only in the sub-adult specimen UFRGS-PV0319P, is incompletely preserved (Figures 2, 3, 14). The right femur has incomplete extremities and can only be observed in anterior view since it is difficult to isolate it from the matrix without damage to other surrounding bones (Figure 14A). The left femur has the proximal extremity better preserved, in which the ventral trochanter is a thick bone projection directed down and backward, with a slender portion between itself and the head of the femur (Figure 14D). It becomes smaller distally (Figure 14B, D) and continues to form the ventral crest (*Crista aspera femoris* or adductor ridge) that runs throughout the two thirds of the bone and shows a smoothly serrated edge. The alignment of the trochanter and the ventral crest presents an angle around 150° (Figure 14C). At the distal end, two main condyles are separated by a shallow *fossa poplitea* ventrally and an equally shallow dorsal triangular depression, the *fossa tendinalis* (or external dorsal gutter of Dutuit, 1976). The trochanter and ventral crest in the femur of *Australerpeton cosgriffi* are similar to that of *Platyoposaurus stuckenbergi* and *Platyoposaurus vjuschkovi* (Gubin, 1991), but none of the latter species displays the angle between the trochanter and the ventral crest as seen on UFRGS-PV-0319-P. It is important to remark that this angle is not a result of taphonomic distortion, since it is observed on both right and left femora.

The tibia, preserved in UFRGS-PV0319P, has an expanded proximal extremity and a narrow, rod-like distal one that articulates with the ossified tarsals. The precise identification of each preserved tarsal was difficult due to the poor preservation. The tibia is preserved only on the sub-adult specimen and is similar to that found in many temnospondyls. The expanded proximal portion is twice as large as the distal portion, which is almost cylindrical. The femur and tibia shows a proportion of 1/0.6, which is a similar to ratio that found for humerus and ulna of the forelimb.

The fibula is incompletely preserved on both specimens. That of UFRGS-PV0319P has only the distal portion, badly preserved. The UFRGS-PV0320P has its extremities broken. It is flattened at the distal portion with the lateral face straight and the medial face curved or concave.

Comparisons. Most of the differences between sub-adult and adult specimens are related to growth in size and ossification of the skeletal elements. The Table 1 presents some selected measurements of appendicular elements of the skeleton, where these proportions can be obtained.

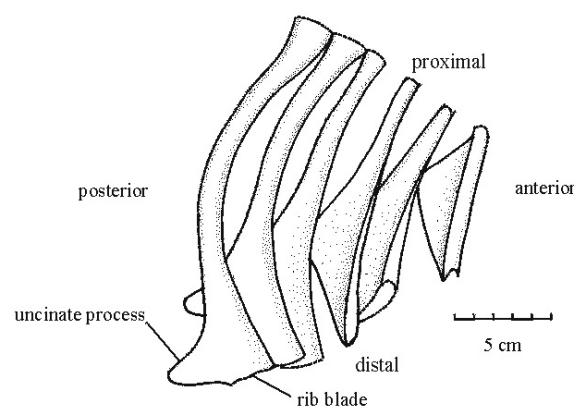


Figure 10. Drawing of a sequence of incomplete trunk ribs of the adult specimen.

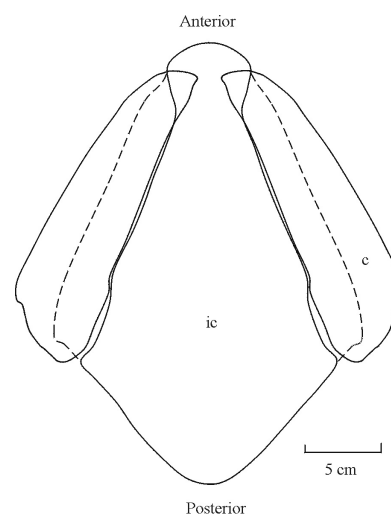


Figure 11. Reconstruction of the dermal shoulder girdle in ventral (UFRGS-PV0320P).

The femur does not vary greatly in temnospondyls, any differences being in slenderness of the shaft and the degree of development of the ventral crest and the shape of the trochanter (Warren & Hutchinson, 1983). The following comparisons were carried out based on some better described or illustrated femora, independently of the group. The femur of *Metoposaurus ouazzoui* (Dutuit, 1976) resembles, in some features, the femur of UFRGS-PV0319-P, such as the shallow triangular *fossa tendinalis* and the shallow *fossa poplitea*. However, the trochanter and the head in that species are slightly distinct in shape and aligned to the ventral crest. The femur of *Platyoposaurus stuckenbergi* (Gubin, 1991 figure 35) has the distal extremity enlarged, has a deep *fossa tendinalis*, the trochanter is aligned with to the ventral crest and is well separated from the head, and the well developed intertrochanteric. *Prionosuchus plummeri* and *Australerpeton cosgriffi* share similar proportions of body size. However, *Platyoposaurus stuckenbergi* has a femur proportionally smaller than these long-snouted species.

TAXONOMY

At present, only two temnospondyl morphotypes, both belonging to Rhinesuchidae, are known within the fossil assemblage of the Rio do Rasto Formation in the Serra do Cadeado area: the long-snouted *Australerpeton cosgriffi*, which is represented by several skulls (Barberena, 1998), and an undescribed short-snouted taxon, represented by a single specimen with a partial skull with the lower jaws UFRGS-PV0352P (Barberena & Dias, 1998), some isolated lower jaws (UFRGS-PV0235P, UFRGS-PV0347P, UFRGS-PV0348P, UFRGS-PV0349P, UFRGS-PV0350P), preliminarily studied by Dias & Kroeff (2002), and some associated postcranial material UFRGS-PV0356P.

The skull portion preserved on specimen UFRGS-PV0320P fits exactly with the corresponding region of the skull of the long-snouted morphotype and was the base for tentatively assign it to *Australerpeton cosgriffi* (Figure 6). At the otic notch region, the vertically descending flange of the paroccipital process of the tabular and the otic flange of the quadrate ramus of the pterygoid are features observed on UFRGS-PV0320P that are conspicuous on the type series of *Australerpeton cosgriffi* and its configuration is the same of that observed in the specimen UFRGS-PV0229P.

The contact between tabular and squamosal was used by Barberena (1998) for the diagnosis of the species. However, a revision of the type series of *Australerpeton cosgriffi* revealed that the tabular does not contact squamosal and the supratemporal participates on the otic notch. This condition is also present on specimen UFRGS-PV0320P, reinforcing its assignment to *A. cosgriffi*.

Besides, the clavicle and interclavicle of UFRGS-PV0320P

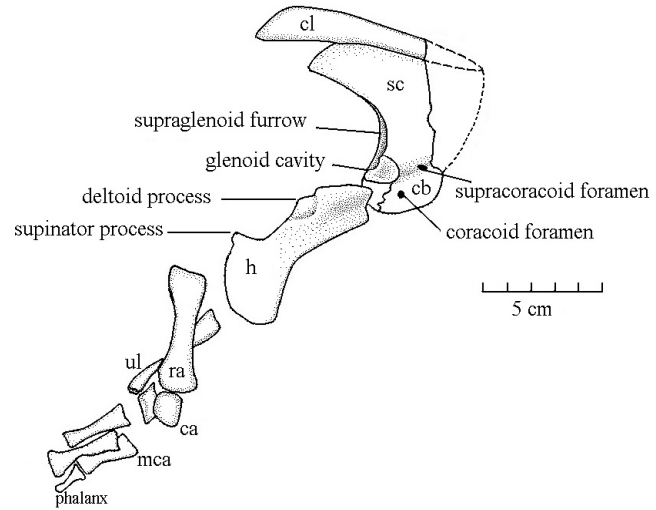


Figure 12. Drawing of the right shoulder girdle and forelimb bones of the sub-adult specimen (UFRGS-PV0319P).

are anteroposteriorly elongated, and differ from the clavicle of the short-snouted taxa of the Rio do Rasto Formation UFRGS-PV0356P, which is much anteroposteriorly shorter. The clavicle and interclavicle elongated is also present in other long-snouted taxa such as *Aphaneramma* (Romer, 1947), in which the elongation of the anterior portion of the interclavicle was related to a more elaborate muscular apparatus for mouth opening with an elongated lower jaw, since it is the insertion site of longitudinal throat muscles (Romer, 1947). A very similar pattern is observed in the UFRGS-PV0320P. These conditions indicates that UFRGS-PV0320P was a long-snouted animal.

Table 1. Selected measurements (mm) of the postcranial elements of *Australerpeton cosgriffi*.

Bone	Length		Width	
	sub-adult	adult	sub-adult	adult
Cleithrum	?	176	15	24
Humerus	78	103	26 17 34	41 proximal 27 diaphysis 51 distal
Ulna	45	70	11 ? ?	20 proximal 10 diaphysis 17 distal
Radius	45	62	12 7 15	20 proximal 14 diaphysis 24 distal
Metacarpals	24, 27, 21	36		
Phalanx	12			
Femur	90		12 proximal head 24 proximal head plus trochanter	
Tibia	53		21 proximal 9 diaphysis 11 distal	
Fibula	109		13 diaphysis	
Metatarsals	22, 31, 29			

Specimen UFRGS-PV0319P presents a small fragment of the posterior portion of the skull table and a mandibular ramus which provide little anatomical information. Even so bad preserved it was possible to recognize the descending flange of the paroccipital process of the tabular and the otic flange of the quadrato ramus of the pterygoid. The tabular also does not contact the squamosal and the supratemporal participates on the otic notch. The fragment of mandibular ramus is elongated, narrow and low, clearly of a long-snouted morphotype.

The femur of specimen UFRGS-PV0319P is much more slender than that associated with the short-snouted morphotype UFRGS-PV036P, which has a strong finger-shaped trochanter and a more wide femur head. The anatomical similarity of many postcranial elements with that of specimen UFRGS-PV0320P such as ribs, vertebrae, scapula and fore limb also provide evidences to relate both specimens the same taxon. Most of the distinct features can be attributed to the ontogenetic development. Following these evidences the specimen UFRGS-PV0319P was also tentatively assigned to *Australerpeton cosgriffi*, the long-snouted taxon known for these levels of Rio do Rasto Formation on the Serra do Cadeado area.

As we can exclude the possibility that the specimens described here belongs to the short-snouted morphotype from the Serra do Cadeado area, the tentative assignment of them to *A. cosgriffi* seems most likely. In addition, the distinct geographic and stratigraphic positions of *Bageherpeton*

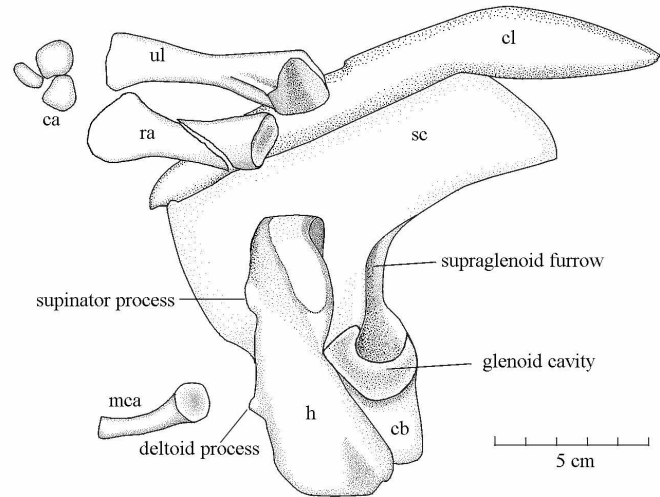


Figure 13. Drawing of the left shoulder girdle of the adult specimen (UFRGS-PV0320P).

longignathus Dias & Barberena, 2001 (the other long-snouted species temnospondyl from the Rio do Rasto Formation, Upper Permian of Rio Grande do Sul State), and *Prionosuchus plummeri* Price, 1948 (a long-snouted from the Pedra do Fogo Formation, Early Permian of northeastern Brazil: Price, 1948; Barberena, 1972; Cox & Hutchinson, 1991), suggests that the studied material cannot be assigned to these taxa. Another possibility is that the specimens belong to a new taxon.

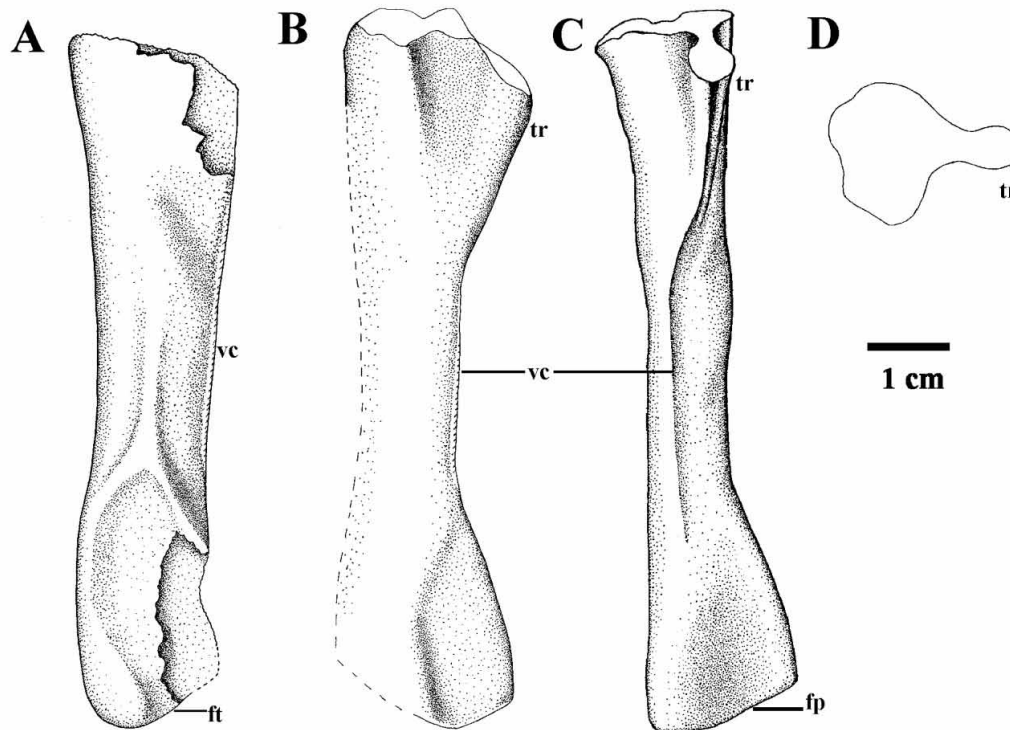


Figure 14. Drawing of the femura of the sub-adult specimen of *Australerpeton cosgriffi*. **A.** right in anterior view; **B.** left in posterior view of the femur; **C.** left in ventral view; **D.** outline of the proximal extremity.

However, this is problematic because one must assume that no material of this new taxon had been collected until now, as well as no postcranium of *A. cosgriffi*. Besides, the ecological niche occupied by these amphibians (the same as crocodiles today) does not fit with such high diversity among them. So, the most parsimonious hypothesis, in this case, is to attribute the specimens to *A. cosgriffi*.

The type series of *Australerpeton cosgriffi* is represented by specimens of distinct sizes (Barberena, 1998), suggesting a thaphocoenosis composed of individuals of different ages. UFRGS-PV0319P is here considered a sub-adult specimen and UFRGS-PV0320P as an adult.

DISCUSSION

Barberena (1998) created the new family Australerpetonidae within the Superfamily Rhinesuchoidea to include *Australerpeton cosgriffi*. This systematic scheme was not completely accepted, thus, Werneburg & Schneider (1996) and Schoch & Milner (2000) included *A. cosgriffi* within the archegosaurids. This misunderstanding is due to the fact that many characters of *A. cosgriffi* can, at first sight, be similar with platypososaurs, especially concerning the general skull shape. In fact, *Australerpeton cosgriffi* shares many similarities with the platypososaurs like the double anterior palatal vacuity and the elongation of the clavicle and snout, but, in many others they are distinct.

Now, a new evaluation of the material was done and many characters listed by Schoch & Milner (2000) for Rhinesuchidae were found in *Australerpeton cosgriffi*: skull table recurved in occipital view, otic notch deep and broad, with almost parallel margins, prefrontal posterolaterally constricted and does not participating on the lateral border of the orbit, tabular ventrally extended to give a nearly horizontal paroccipital process, tabular horn extending posteriorly and with little dermal ornamentation, vomer showing a denticle row medial to the coana. Some other features are shared with all other Stereospondyli (*sensu* Schoch & Milner, 2000), like the suture between pterygoid and parasphenoid well developed (absent in platypososaurs); presence of conspicuous adjacent pockets in the posterior portion of the parasphenoid (like rhinesuchids and other capitosaurids); and absence of a contact between pterygoid and vomer (like in lydekkerinids), whose presence is very clear in platypososaurs.

Thus, it would be preferable to keep *A. cosgriffi* closer related to the Rhinesuchidae than to Archegosauridae. Further systematic discussions about *A. cosgriffi* is beyond the scope of this work and will be done in future papers. However, following Warren & Snell (1991), most of the anatomical variation on temnospondyl humeri and femora are related to adaptations for a terrestrial or an aquatic habitat, and seem to be of little use for systematics. Thus, probably, many of the cranial and postcranial similarities between *A. cosgriffi* and the platypososaurs may be attributed to convergence due to a similar semi-aquatic life style, as discussed below.

A common feature for aquatic temnospondyls is the absence of ossified carpals and tarsals, since they do not have to support the body weight. Based on *Metoposaurus ouazzoui*, Dutuit (1976) proposed that carpal and tarsal bones should be entirely cartilaginous in aquatic temnospondyls. Thus, DeFauw (1989) classified metoposaurs as fully aquatic, freshwater temnospondyls.

The presence of ossified carpal and tarsal bones in the specimens here assigned to *Australerpeton cosgriffi* points to the possibility that this temnospondyl could crawl in the bottom of lakes and occasionally walk on land, requiring for this more strengthened hands and feet. This land-walking ability is possible even in the sub-adult specimen which also presents ossified carpals and tarsals. The femur is not weak enough to preclude this ability and the well developed shoulder girdle, with a relatively strengthened humerus showing strong muscles attachment sites, on both specimens, also points to a land walking condition. But, this condition was probably limited, since the appendicular skeleton described for *Australerpeton cosgriffi* is distinct from that of some fully terrestrial temnospondyls such as *Eryops megalocephalus*, which has a much more powerful appendicular skeleton with more conspicuous muscle attachment areas (Carroll, 1988).

In general, *A. cosgriffi* shares similarities with *Platyposaurus stuckenbergi* on the femur anatomy and the presence of ossified carpals, even so, *P. stuckenbergi* was reconstructed as an aquatic temnospondyl (Gubin, 1991). In this point of view, these shared similarities are probable convergences.

The elongated skull shape is probably the most efficient design for a piscivorous animal since it allow to minimize the shock waves produced by fast lateral movements of the head and consequently reducing the perception of the fish's lateral line system. Thus, the long-snouted cranial morphology is the most important feature pointing to an aquatic condition for *Australerpeton cosgriffi* and based on this feature alone, one can conclude that it was a fully aquatic animal with a mainly piscivorous diet, as has been proposed for other temnospondyls, such as, *Platyposaurus stuckenbergi*, *Aphaneramma*, *Prionosuchus plummeri* and *Bageherpeton longinathus*. Notwithstanding, postcranial features suggest that *Australerpeton cosgriffi* also could walk on land even during limited incursions, and this interpretation could also be extended at least to *Platyposaurus stuckenbergi*.

The fossil fish fauna of the Rio do Rasto Formation is composed of paleoniscids (Dias, 1996; Vega-Dias *et al.*, 2000), dipnoans and xenacanthodians (Ragonha, 1989), representing sufficient diversity to supply *Australerpeton cosgriffi*.

The flat body outline could improve buoyancy of *Australerpeton cosgriffi* indicating that it lived in shallow waters or even swim on open waters. This interpretation is compatible with the sedimentological analyses and fossil record of the

Rio do Rasto Formation, that suggest a deposition in a freshwater environment (Barberena *et al.*, 1985; Ragonha, 1989; Rohn & Roesler, 2000; Rohn & Stollhofen, 2000; Stollhofen *et al.*, 2000). However, levels of mud cracks indicates that the environment was periodically dryness. Growth lines present on the dermal scales of *A. cosgriffi* (Dias & Richter, 2002) can be result of this seasonal climate. Thus, the walking ability of *Australerpeton cosgriffi* should be primordial to find wet places.

All these features suggest that *Australerpeton cosgriffi* was a semi-aquatic or even a temporary fully aquatic freshwater temnospondyl, which is compatible with the classification proposed by DeFauw (1989) that rhine-suchids are semi-aquatic freshwater (SAF) and fully aquatic freshwater (FAF) ecomorphic types.

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