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On a new stereospondylomorph temnospondyl from the Middle–Late Permian of Southern Brazil

ADRIANA STRAPASSON, FELIPE L. PINHEIRO, and MARINA B. SOARES



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A new temnospondyl is described from the Middle–Upper Permian sequence of the Paraná Basin (Rio do Rasto Formation) in southern Brazil. The material consists of disarticulated cranial and postcranial elements, preserved in association. The cranial elements include part of the orbital region of the skull roof, the basicranium, a number of endocranial elements, stapes and a right hemimandible. The postcranial elements include vertebrae, ribs, pectoral girdle elements, a right femur and a cluster of scales. The new species displays a rhinesuchid pattern, which is similar to the South African rhinesuchids from the Upper Permian Beaufort Group of the Karoo Basin, but differs from them by the presence of a robust and elongated epipterygoid with a blade-like anterior process in addition to elongated and deeper muscular pockets on the parasphenoid, which allow the assignment of this specimen to a new species. However, the phylogenetic analysis grouped the material described herein and *Australerpeton cosgriffi* inside Stereospondylomorpha, in a transitional position between the Laurasian assemblages and South African temnospondyls. This result supports a connection between the Brazilian and Eastern European Permian fauna and provides important data for future biostratigraphic studies.

Key words: Amphibia, Temnospondyli, Stereospondylomorpha, Permian, Rio do Rasto Formation, Brazil.

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Introduction

The Rio do Rasto Formation, a Middle–Upper Permian sequence from the Paraná Basin that crops out in southern Brazil (Holz et al. 2010), presents a typical continental fossil assemblage that includes an increasing number of temnospondyl amphibians. The fossil material originates from three distinct tetrapod local faunas (Fig. 1A).

Recent study of the Brazilian Upper Permian basal tetrapods started in the early 1970s, with the discovery of a supposed *Platyops* sp. specimen (Barberena and Daemon 1974), a temnospondyl from Paraná State, which belongs to the Serra do Cadeado Local Fauna. This specimen was subsequently reinterpreted and described by Barberena (1998) as a new rhinesuchoid, *Australerpeton cosgriffi* (Barberena, 1998), and following works added more information (Dias and Richter 2002; Dias and Schultz 2003; Ramos and Vega 2011; Eltink and Langer 2014). Nevertheless, the taxonomic affinity of *A. cosgriffi* remains uncertain, with it having

been regarded as a stereospondylomorph platyoposaurine (Werneburg and Schneider 1996; Schoch and Milner 2000) and as a rhinesuchid (Dias and Schultz 2003), in addition to a recent phylogenetic analysis that positioned it as a basal stereospondyl (Eltink and Langer 2014). Adding to the tetrapod diversity of the Serra do Cadeado Local Fauna, a short-snouted skull was briefly described by Barberena and Dias (1998) as a “*Rhinesuchus*-like” form, and recent discoveries under study have revealed a very diverse temnospondyl fauna from this state (AS, Cristina S. Vega, and MBS unpublished material; Karine L. Azevedo, Cristina S. Vega, and MBS unpublished material). The other two Brazilian Upper Permian tetrapod-bearing sites are located in Rio Grande do Sul State. An incomplete lower jaw of *Bageherpeton longignathus*, tentatively assigned to the Platyoposaurinae by Dias and Barberena (2001), was recovered from the Aceguá Local Fauna, and a lower jaw (Malabarba et al. 2003), in addition to an incomplete skull of a probable melosaurine (Dias-da-Silva 2012), both still

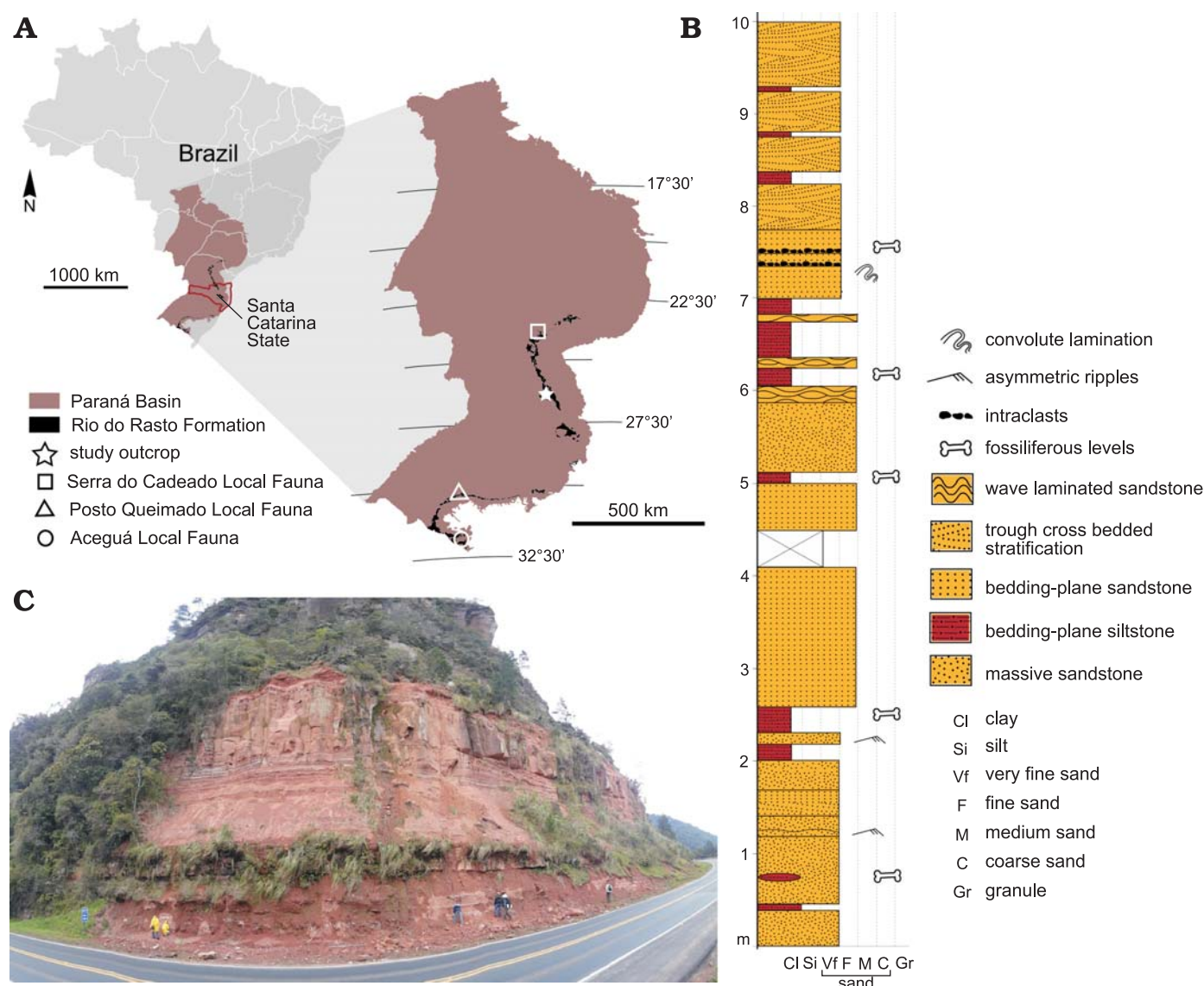


Fig. 1. **A.** Geographic map with the location of the study outcrop in Santa Catarina State within Paraná Basin, Brazil. **B.** Profile of the study outcrop with fossiliferous levels. **C.** Photo of the outcrop.

lacking formal description, are recorded from the Posto Queimado Local Fauna.

Here we present the description of a new genus and species of a stereospondylomorph temnospondyl, the first material to be described from a new Brazilian Upper Permian tetrapod-bearing site, located in Santa Catarina State. The specimen UFRGS-PV-0355-P was collected in the early 1980s by a team headed by Mário C. Barberena, a former researcher at Universidade Federal do Rio Grande do Sul (UFRGS) and is housed at the Laboratório de Paleontologia de Vertebrados of UFRGS.

Institutional abbreviations.—UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Other abbreviations.—CI, consistency index; RI, retention index.

Geological setting

UFRGS-PV-0355-P was recovered from an outcrop located on the BR 116 highway, Serra do Espigão, Santa Catarina State, Brazil, between the Monte Castelo and Santa Cecília municipalities (UTM 22J 567876.5/7040838.5).

The studied outcrop belongs to the Middle–Upper Permian sequence of the Rio do Rasto Formation, Paraná Basin (Holz et al. 2010). In Brazil, this sequence extends across the Paraná, Rio Grande do Sul and Santa Catarina states (Fig. 1A). The Rio do Rasto Formation was divided into two members by Gordon (1947): the lower Serrinha Member and the upper Morro Pelado Member. According to Rohn (1994), the Serrinha Member is represented by typical lacustrine deposits related to wetter climatic conditions and a maximum rainfall, with increased occurrences of aeolian



Fig. 2. Preserved elements of *Parapytanga catarinensis* gen. et sp. nov. (holotype, UFRGS-PV-0355-P) from the Santa Catarina State (Brazil), Middle–Upper Permian.

sandstone towards the top, which indicate the beginning of a dry climate, with greater aridity, culminating in the fluvio-lacustrine deposits of the Morro Pelado Member, the most severe phase of aridity recorded in the Rio do Rasto Formation.

The outcrop (Fig. 1B, C) presents a sequence related to the upper portion of the Morro Pelado Member, in which it is possible to observe at its top an abrupt erosive contact with the overlying aeolian sandstone of the Botucatu Formation, of Jurassic to Early Cretaceous age (Milani et al. 2007). It displays a succession composed of dominant layers of fine- to medium-grained sandstone, interbedded with siltstone layers with bedding-parallel stratification at the base. At the top of the outcrop, sandstones with tangential cross bedding of typical sigmoidal geometry are present (Fig. 1B). This succession reflects a delta-front depositional

environment. Fragments of bone elements were found in five different levels of the outcrop, mainly in the siltstone strata and fine- to medium-grained massive or bedding-parallel stratified sandstone.

Systematic palaeontology

Temnospondyli Zittel, 1888

Stereospondylomorpha Yates and Warren, 2000

Genus *Parapytanga* nov.

Etymology: From the Tupi language (spoken by the indigenous Tupi tribes, native to the Brazilian coast) *parapytanga*, red river, reflecting the red colour of the fossil rock matrix, which was formed in a fluvial-lacustrine environment of the Rio do Rasto Formation.

Type species: *Parapytanga catarinensis* sp. nov., monotypic; see below.

Diagnosis.—As for the type species.

Parapytanga catarinensis sp. nov.

Figs. 2–6.

Etymology: In reference to Santa Catarina State, where the fossil was found.

Holotype: UFRGS-PV-0355-P, an incomplete skeleton composed of the orbital region of the skull roof, the basicranium, some endocranial elements, a left stapes, and a right hemimandible, in addition to vertebrae and ribs, bones from the pectoral girdle, a right femur and a cluster of scales.

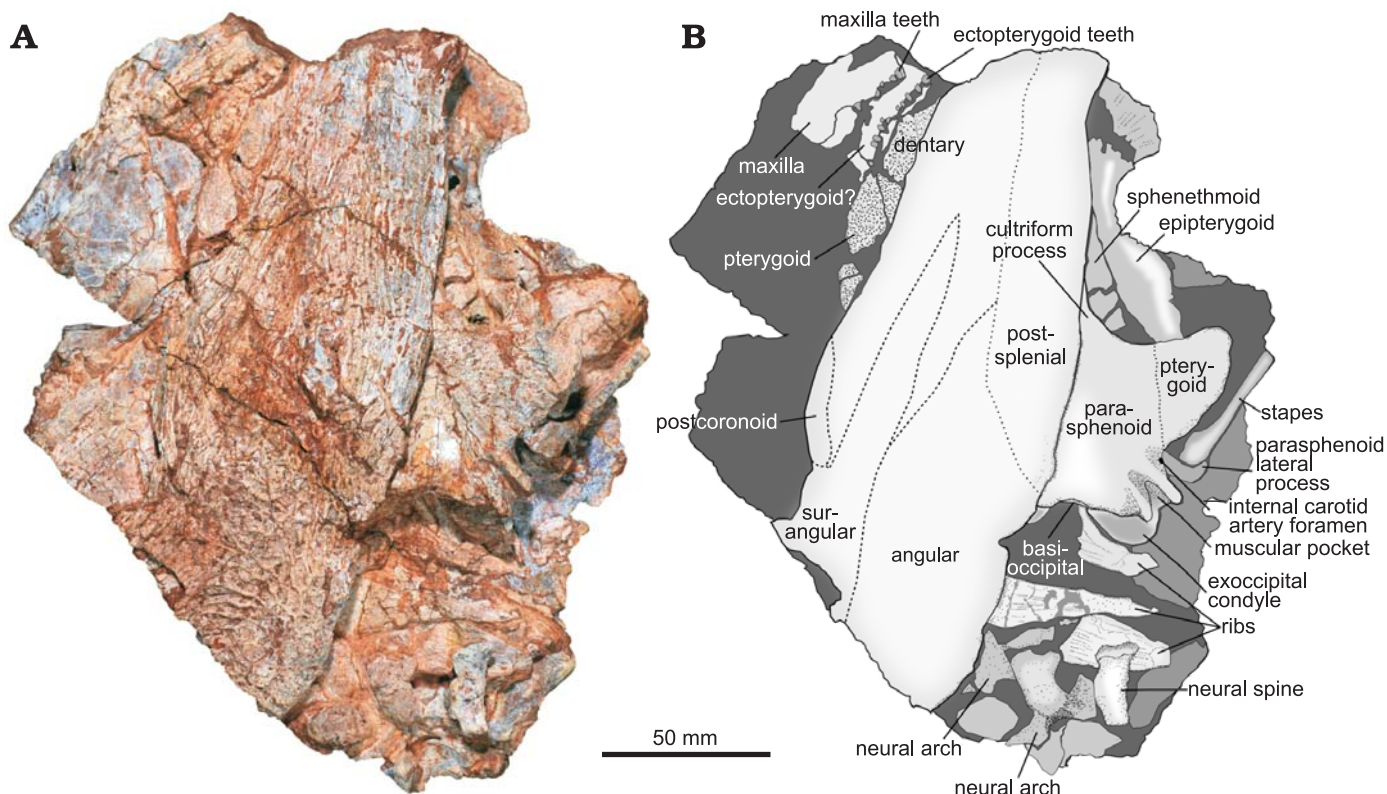


Fig. 3. Stereospondylomorph temnospondyl *Parapytanga catarinensis* gen. et sp. nov. (holotype, UFRGS-PV-0355-P) from the Santa Catarina State (Brazil), Middle–Upper Permian. Side of the sample containing the skull in palatal view (elements from palate and braincase); stapes; right hemimandible in labial view; fragments of vertebrae and ribs. Photo (A) and interpretative drawing (B).

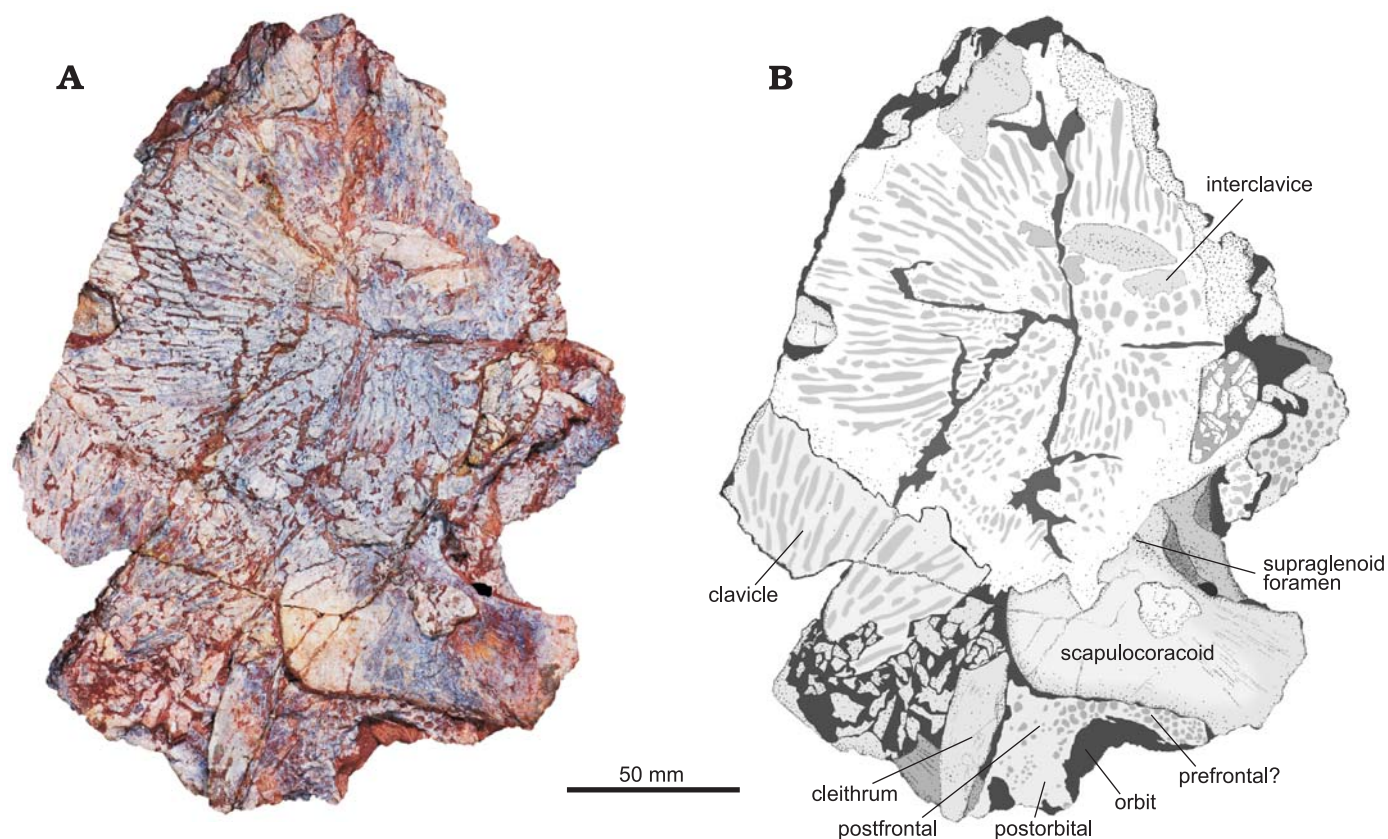


Fig. 4. Stereospondylomorph temnospondyl *Parapytanga catarinensis* gen. et sp. nov. (holotype, UFRGS-PV-0355-P) from the Santa Catarina State (Brazil), Middle–Upper Permian. Side of the sample containing skull elements in dorsal view; interclavice and right clavicle in ventral view; right scapulocoracoid and cleithrum in lateral and medial view, respectively. Photo (A) and interpretative drawing (B).

Type locality: Serra do Espigão, Santa Catarina State, Brazil, between Monte Castelo and Santa Cecília municipalities (UTM 22J 567876.5/7040838.5).

Type horizon: Middle–Upper Permian, Rio do Rasto Formation, Morro Pelado Member, Paraná Basin.

Material.—Holotype only.

Diagnosis.—Distinguished from all other temnospondyl taxa by the following combination of characters: epipterygoid robust with an elongated blade-like anterior process; broad sutural contact between the parasphenoid and pterygoid; elongated muscular “pockets” on the parasphenoid, anterolaterally limited by very developed and sharp muscular crests that extend upwards, over the lateral side of the exoccipital condyles; small basioccipital ossification, visible only in occipital view, contributing to the exoccipital condyles; shagreen on the pterygoids and parasphenoid; the foramen for the internal carotid artery lying at the posterolateral corner of the parasphenoid, posterior to the pterygoid articulation.

Description.—The specimen (UFRGS-PV-0355-P) consists of an incomplete skeleton composed of several disarticulated cranial and postcranial elements (Fig. 2). The cranial elements include part of the orbital region of the skull roof, the basicranium, and some neurocranial and palatoquadrate ossifications, in addition to a left stapes and an incomplete right hemimandible. The postcranial elements include

vertebrae, ribs and pectoral girdle bones (the interclavice, the right clavicle, the right scapulocoracoid, and the right cleithrum), in addition to a right femur and a cluster of scales (Figs. 3, 4). The material is altered by biostratinomical factors, such that the skeleton is disarticulated and incomplete. The preserved elements lie in association, slightly displaced from their anatomical position and with a high degree of compression, displaying some fragmentation. The material has a large number of small fractures, and the dermal bone ornamentation is badly damaged, making visualisation of the sutures between the bones difficult.

Skull roof: The dorsal surface of the skull (Fig. 4B) is almost hidden by pectoral girdle elements, although part of the posteromedial border of the right orbit is preserved in this view. The orbit has an elliptical outline in which the margin is raised above the skull plane, being dorsally placed close to the sagittal plane. As the skull is not completely preserved, it is not possible to infer the position of the orbits relative to the midlength of the skull, nor even the width of skull at the interorbital level; however, the skull table seems to be short. The dorsal surface of the skull is covered by dermal ornamentation displaying a pattern of uniformly small pits enclosed by a network of ridges.

Only a small fragment from the posterior part of a right prefrontal is preserved, and it sutures posteriorly with the postfrontal, participating in the anteromedial orbital mar-

gin. The postfrontal is posteriorly incomplete, contacting the postorbital laterally. The postfrontal forms part of the posteromedial margin of the orbit and sutures with the prefrontal anteriorly. The postorbital contributes to the posterior margin of the orbit. However, the incomplete preservation prevents the recognition of its limits.

Palate: In palatal (Fig. 3B) and occipital (Fig. 5A, B) views, only the posterior part of the skull is preserved, mostly covered by a large incomplete hemimandible. The posteromedial margin of the right interpterygoid vacuity is preserved and is formed medially by the cultriform process of the parasphenoid and posteriorly by the parasphenoid and part of the pterygoid. It is possible to infer that the interpterygoid vacuity is long and expanded anteriorly.

The basal plate of the parasphenoid lies at the posterior end of the skull, in palatal view. It has a quadrangular shape in the sagittal plane, posteriorly suturing with the basioccipital. At the posterolateral corner of the basal plate, a suture with the exoccipital is present. The slender cultriform process is anteriorly fragmented and almost completely covered by the hemimandible. The ventral surface of the parasphenoid is covered anterolaterally by many small denticles, forming a shagreen (“area asperae”), which extends laterally across the suture with the pterygoid and also covers the whole preserved extension of this element, as in many stereospondyls (Yates and Warren 2000). The foramen for the internal carotid artery lies at the posterolateral corner of the parasphenoid, posterior to the pterygoid articulation.

At the posterior end of the ventral surface of the parasphenoid plate, only one well-developed “pocket” can be observed, but it is possible to infer that both “pockets” are widely separated from each other by at least 25 mm. This structure comprises a very elongated and deep depression, anterolaterally limited by a strong and high muscular crest, suggesting a well-developed vertebro-occipitalis musculature. The pockets extend upwards, over the lateral side of the exoccipital condyles.

The parasphenoid has a wide lateral sutural contact with the pterygoid, approximately 33 mm long, almost as long as the basal plate, which is typical of Stereospondyli (Yates and Warren 2000). A lateral process from the parasphenoid lies posterior to the parasphenoid–pterygoid suture, providing attachment for the footplate of the stapes.

The right pterygoid is very fragmented, such that the palatine and the quadrate rami are not preserved. The corpus of the pterygoid is totally covered with denticles on the ventral surface, forming a continuous shagreen field with the parasphenoid plate. The suture between the pterygoid and the exoccipital is not visible in ventral view.

On the left side of the specimen, only a small part of a very fragmented palatine ramus of the left pterygoid rises from below the hemimandible. Its ventral surface is totally covered by small denticles that are circular in cross-section. The palatine ramus is elongated and extends anteriorly, possibly contacting the ectopterygoid.

A small fragment of the ectopterygoid is preserved. It is possible to recognise a toothrow with 11 badly preserved labyrinthodont teeth, some preserved in cross-section and others in longitudinal section, revealing the labyrinthine infolding of the dentine. These elements are poorly preserved, and the marginal dentition shows apparent homogeneity, being composed of small equidistant teeth. No ectopterygoid tusk is preserved. The ectopterygoid contacts the maxilla laterally and the pterygoid medially.

In ventral view, the maxilla lies laterally to the ectopterygoid and forms the lateral margin of the skull. Only a slender fragment of this element is preserved. This bone is displaced, and thus, it is preserved only in lateral view, and its lateral ornamentation can be observed. Five small and fragmented teeth are badly preserved, preventing the observation of the type of tooth in cross-section.

Occiput: In occipital view (Fig. 5A, B), only the exoccipitals and the basioccipital can be observed, as all the other dorsal bones are covered by the rock matrix.

The exoccipitals are large and robust bones, sited dorsally to the basioccipital, and forming two massive and well-defined condyles in occipital view, which is characteristic of more derived temnospondyls than edopsoids (Romer 1947). The condyles are circular structures separated by the basioccipital, which participates in a small medial portion of the condyle formation. The exoccipital condyles form the lateral border of the foramen magnum and face inwards and downwards. In lateral view, the subtympenic process of the exoccipital is preserved, being a short dorsolateral extension. Lateral to the exoccipital condyles, the foramina for nerves XII and IX (sensu Bystrow and Efremov 1940) can be observed.

The basioccipital is a well-ossified element, with a triangular shape in occipital view. It participates in the posteroventral margin of the skull, suturing extensively with the parasphenoid plate. The basioccipital contacts the exoccipitals dorsolaterally, where it has a small participation in the occipital condyles and forms the ventral border of the foramen magnum.

Braincase: The braincase (Fig. 3B) seems to be well ossified, as in advanced stereospondyls (Schoch and Milner 2000), with the already mentioned basioccipital and the exoccipital preserved, in addition to the sphenethmoid and the epipterygoid. The sphenethmoid as well as the epipterygoid are very fragmented elements that have been slightly displaced.

The sphenethmoid lies medially to the epipterygoid, right above the cultriform process of the parasphenoid. This element is very fragmented to an extent that prevents detailed analysis. A posterolateral expansion of the sphenethmoid is present and becomes a thin blade that contacts the epipterygoid dorsolaterally, a character thus far only observed in mastodonsaurids (Schoch 2002).

The epipterygoid is a robust, elongated and fragmented element that lies laterally to the sphenethmoid. Its basal process contacts the pterygoid and the basisphenoid pos-

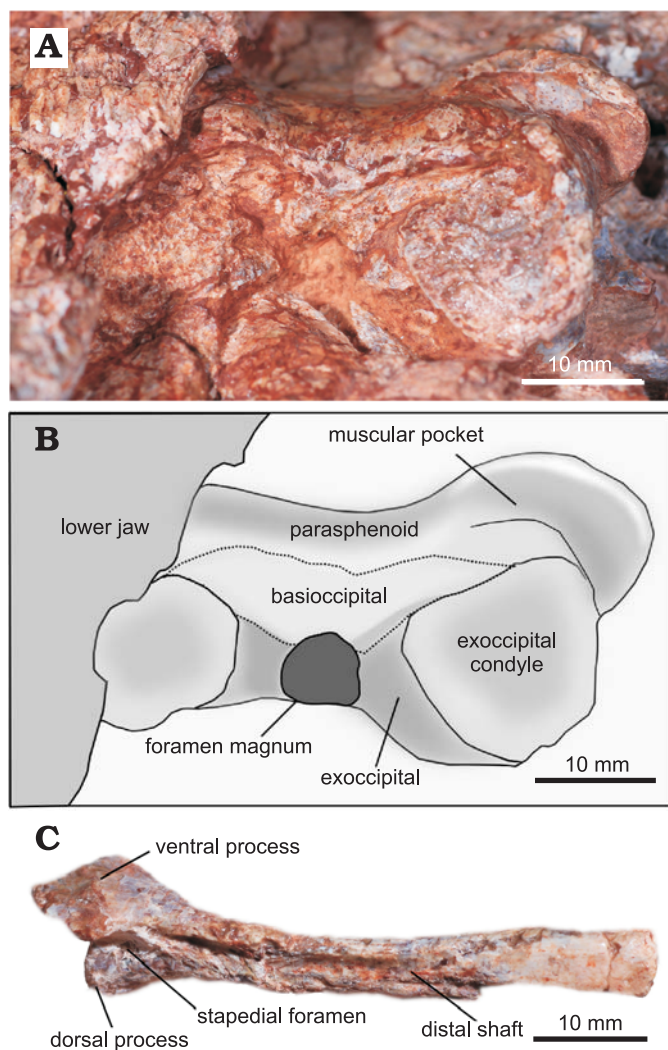


Fig. 5. Cranial elements of stereospondylomorph temnospondyl *Parapytanga catarinensis* gen. et sp. nov. (holotype, UFRGS-PV-0355-P) from the Santa Catarina State (Brazil), Middle–Upper Permian. Photo (A) and interpretative drawing (B) of the skull in occipital view. C. Photo of the left stapes in postero-medial view.

terovertrally. It extends anteriorly as an extensive blade of approximately 60 mm in length, forming the anterior process of the epipterygoid, which contacts the sphenethmoid dorsomedially. Anterodorsally, it contacts the skull roof in a round dorsal process.

Stapes: Only the left stapes is preserved (Figs. 3B, 5C) and is completely exposed in posterior and ventral view, being slightly displaced from its anatomical position. It is a slender and elongated element, measuring approximately 53 mm long, with a very long distal shaft slightly curved dorsodistally, and quadrangular in cross section, following anteroposterior compression. Its shaft apparently has a small quadrate process on the ventral surface that is almost completely fragmented. The proximal end of the stapes has two heads, similar to those observed in stereospondyls (Schoch and Milner 2000). The stapes attaches to the parasphenoid, and the other head is configured as a rounded dorsal process that points into the fenestra vestibuli. The ventral process is

a blade that extends from the shaft. A stapedial foramen is present medially to its heads.

Mandible: An incomplete right ramus of the lower jaw is preserved in labial view (Fig. 3B). This element is robust and broad, and becomes narrower throughout its anterior region. In this view, all the bone elements have a characteristic dermal ornamentation formed by reticulate ridges of various sizes. The mandible is badly preserved, displaying a large number of fractures that have damaged the dermal ornamentation, which makes observation of sutures between the bones difficult. Unfortunately, the most diagnostic regions of the mandible are not preserved, such as the symphyseal area, the glenoid and post-glenoid area.

The angular is incomplete posteriorly. It sutures dorsally with the surangular along an extensive contact and extends anteriorly, where it contacts the dentary anterodorsally and the postsplenial anteroventrally.

The surangular is posteriorly fragmented, placed dorsally to the angular, and sutures with the postcoronoid anterodorsally and with the dentary anteroventrally.

The dorsal surface of the postcoronoid is preserved in labial view of the mandible and lies in the posterodorsal region, where it makes contact posteriorly with the surangular and ventrally with the dentary. There are no teeth preserved.

The dentary is a very elongated element that extends anteriorly along the full dorsal surface of the mandible. This element is dorsally and anteriorly fragmented, and the teeth are not preserved. It contacts the postcoronoid and the surangular posteriorly, the angular ventrally and the postsplenial anteroventrally.

The postsplenial lies anteriorly to the angular and is fragmented in its anterior portion, such that its contact with the presplenial is not preserved.

Axial skeleton: Only two neural arches are preserved in posterior view (Fig. 3B) with their neural spines and transverse processes. In addition, one fragmented and isolated neural spine, preserved in lateral view, can be observed. All these elements are disarticulated and displaced from their anatomical positions. The neural spines have a rectangular shape in lateral view. The zygapophyses of the neural arches are absent. The transverse processes are fragmented on their distal ends, and examination of their orientation and position of the diapophysis is not possible.

Only three fragments probably belonging to cervical ribs are preserved, but they are disarticulated and displaced. These ribs are thin bones, with confluent proximal heads.

Pectoral girdle: The pectoral girdle (Fig. 4B) consists of well-developed and ossified elements, formed by an interclavicle articulated with the right clavicle. In addition, the right cleithrum and the scapulocoracoid are preserved, slightly displaced from their anatomical positions. The pectoral girdle is intensely ornamented.

The interclavicle is a robust flat bone preserved in ventral view, with a rhomboidal shape, as is typical in temnospondyls (Schoch 2013). Its ornamented main body is better preserved, and only a narrow strip of the unornamented

border can be observed, being largely fragmented along the interclavicle margin. Thus, the left clavicular facet is not preserved, and the right one is covered by the articulated right clavicle. The interclavicle has the anterior and posterior portions fragmented. The anterior edges are longer than the posterior ones.

The ornamentation of this element is remarkable, being formed by pits and grooves. The pits are agglomerated in the ossification centre, which lies just posterior to the line of maximum width. From the centre of ossification, the ornamentation elongates and radiates towards the margins of the interclavicle, forming elongated grooves. The grooves are robust and deep, ranging from 2–4 mm in depth.

Only the ventral blade of an incomplete right clavicle is preserved in ventral view. It is a wide and robust element, with a triangular shape. This element lies on the clavicular facet of the interclavicle, overlapping the interclavicle broadly. The clavicle ornamentation displays a reticulated pattern that radiates from the centre of ossification to the anteromedial margins of the clavicle.

The cleithral shaft is preserved medially. This element is a narrow bar that wedges posteriorly, with a teardrop-shaped cross-section, typical of temnospondyls (Pawley and Warren 2005). The cleithrum is posteriorly fragmented, and this portion bears an expanded dorsal head: the dorsal cleithral process.

The scapula is co-ossified with the coracoid. Only the right scapular blade of the scapulocoracoid is preserved in lateral view, the coracoid portion being covered by the interclavicle. The scapular blade is almost three times longer than wide. The supraglenoid foramen is present.

Hind limb: Only the distal portion of a right femur is preserved (Fig. 6A–C). This element was found disarticulated and not associated with the other materials. In ventral view, a shallow and wide popliteal fossa is preserved, occupying the major portion of this view. In dorsal view, the intercondylar fossa is a large and deep triangular depression. The fibular condyle is divided into ventral and dorsal “subcondyles” (see Eltink and Langer 2014), between which is a small and moderately deep triangular fibular fossa. A small part of the shaft is preserved, being anteroposteriorly flattened and elliptical in cross-section.

Squamation: Among the three general types of dermal ossification of temnospondyls defined by Pawley (2006), the ventral scutes are the only type preserved in our specimen (Fig. 6D, E). A great number of ventral dermal scales lie posteriorly to the pectoral girdle elements and some lie disarticulated and isolated over the other bone elements.

These ventral scutes are large and vary in size, with their length ranging from 15–35 mm and their width from 5–8 mm. They are elongated structures with a ridge along their longitudinal axes, displaying a typical spindle shape. One of the scales shows a possible impression of growth rings. The ventral scutes are intensively agglomerated, making it difficult to determine the real arrangement of the complete squamation. Some scutes lie aligned to each other, in

which a medial groove on the dorsal side of the scute forms an internal articular process for overlapping scales.

Remarks.—The basicranium and occiput of *Parapytanga catarinensis* gen. et sp. nov. have a rhinesuchid pattern that encompasses the association of a broad sutural contact between the lateral margins of the parasphenoid and the corpus of the pterygoid, well-developed muscular pockets on the parasphenoid, and the foramen for the internal carotid artery located at the posterolateral corner of the parasphenoid, in addition to a double occipital condyle with a reduced basioccipital contribution (Yates and Warren 2000; Schoch and Milner 2000). Furthermore, *Parapytanga catarinensis* gen. et sp. nov. displays extensive palatal shagreen that covers part of the parasphenoid and pterygoid, and that distinguishes the Rhinesuchidae from the Capitosauridae, Stenotosauridae and Cyclotosauridae (Shishkin and Rubidge 2000), although widespread shagreen is also observed on the parasphenoid and pterygoids of *Lydekkerina huxleyi* (Warren and Black 1985; Jeannot et al. 2006). However, the main synapomorphies of the Rhinesuchidae—including cheek deeply recurved in occipital view, otic notch deep with parallel margins, prefrontal posterolaterally constricted, tabular ventrally extended to give a nearly horizontal paroccipital process, tabular horn posteriorly extended and present without dermal sculpturing, and shagreen on vomers and precoronoids (Schoch and Milner 2000)—are not preserved in *Parapytanga catarinensis* gen. et sp. nov. So a precise attribution to Rhinesuchidae is not possible, but cannot be discarded either.

Parapytanga catarinensis gen. et sp. nov. differs from other Permian temnospondyls already described from the Rio do Rasto Formation, supporting the erection of the new taxon. The most complete temnospondyl described from the Brazilian Upper Permian is *Australerpeton cosgriffi* (Barberena, 1998), the taxonomic affinity of which remains uncertain. *A. cosgriffi* shows a posterior extension of the parasphenoid in ventral view, which has a rectangular shape in the sagittal plane, but this element does not entirely cover the basioccipital, such that it is briefly exposed in ventral view (UFRGS-PV-0229-P and UFRGS-PV-0230-P) (Fig. 8A). This condition differs from *Parapytanga catarinensis* gen. et sp. nov., which bears a relatively less-posteriorly elongated parasphenoid, composing a shorter posterior portion of the skull in ventral view (Fig. 8B). Moreover, the basioccipital of *A. cosgriffi* (UFRGS-PV-0229-P and UFRGS-PV-0230-P) does not participate in the structure of the occipital condyles, which are composed entirely by the exoccipitals, elements that lie well separated from each other and are totally visible in ventral view. On the other hand, in *Parapytanga catarinensis* gen. et sp. nov., the basioccipital is larger than in *A. cosgriffi* and connects the exoccipitals, participating medially in the more robust occipital condyles. In addition, the new taxon has more elongate and shallower muscular pockets, differing from the circular and deeper pockets observed in *A. cosgriffi*. This character, although present in a number temnospondyl taxa (Yates and Warren

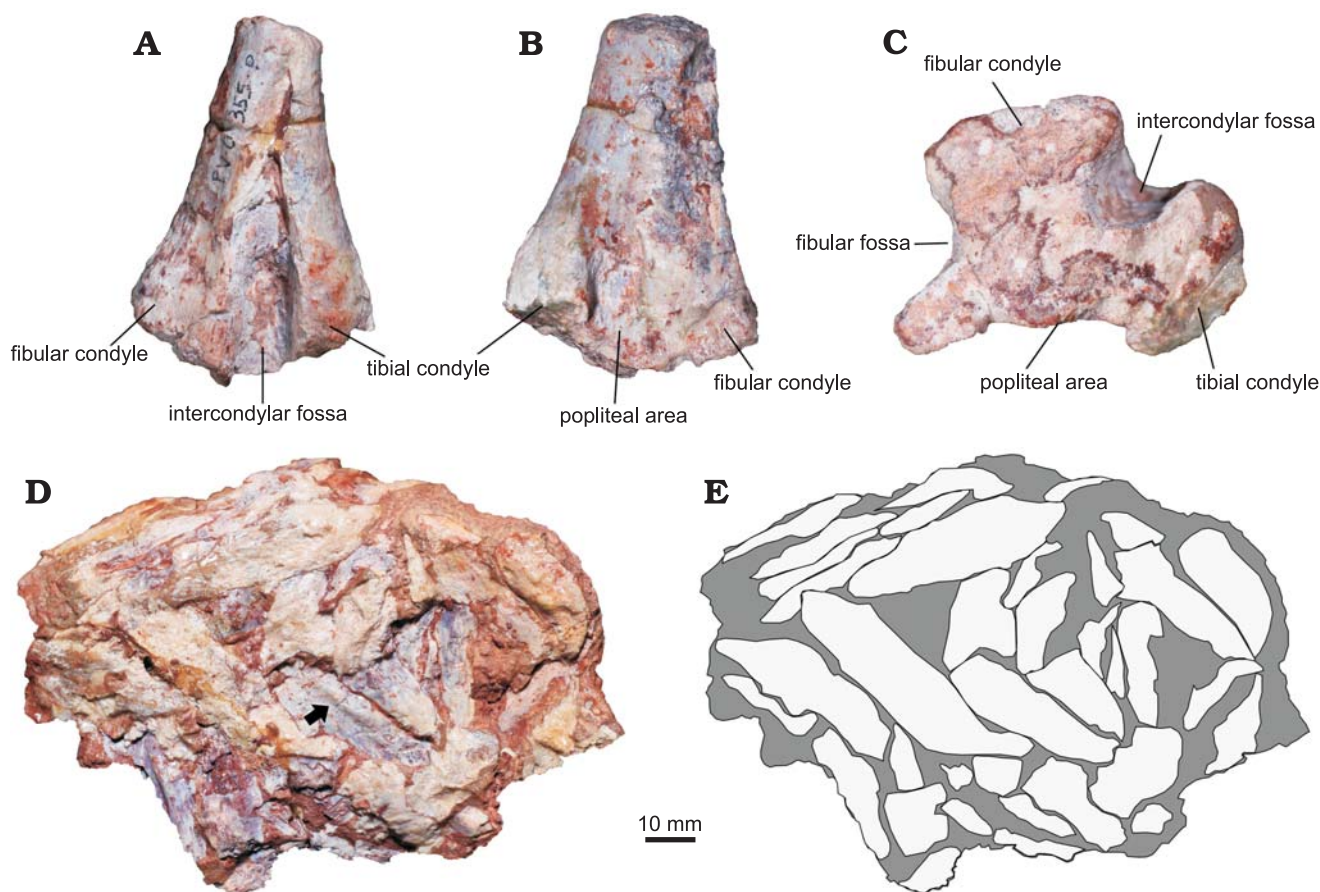


Fig. 6. Postcranial elements of stereospondylomorph temnospondyl *Parapytanga catarinensis* gen. et sp. nov. (holotype, UFRGS-PV-0355-P) from the Santa Catarina State (Brazil), Middle–Upper Permian. Photos of the right femur in dorsal (A), ventral (B), and distal (C) views. Photo (D) and interpretative drawing (E) of the ventral scutes. The arrow indicates the internal articular process of a scute.

2000), is unique to *Parapytanga catarinensis* gen. et sp. nov., in which the well-developed and sharp muscular crests is visible in occipital view and appears to be an autapomorphy.

The poor preservation of the short-snouted rhinesuchid amphibian from the Rio do Rasto Formation, preliminarily described by Barberena and Dias (1998), makes comparisons with *Parapytanga catarinensis* gen. et sp. nov. difficult. The lower jaws of these two taxa differ, as the postcoronoid of the 1998 specimen does not present denticles or teeth; in addition, the region of the hemimandible that extends anteriorly to the postcoronoid is proportionally higher and much more robust in size than the hemimandible. Preserved elements of the other two Permian archegosaurids from Brazil, *Prionosuchus plummeri* (Price, 1948) and *Bageherpeton longignathus* Dias and Barberena, 2001, do not show overlaps with *Parapytanga catarinensis* gen. et sp. nov. Long-snouted temnospondyls are known to have slender, lower and gracile mandibles (Schoch and Milner 2000), different from that observed in UFRGS-PV-0355-P. This suggests that *Parapytanga catarinensis* gen. et sp. nov. is most likely a short-snouted form, with a robust and high mandible.

Some basicranial and occipital features of *Parapytanga catarinensis* gen. et sp. nov. also show some affinity to South African Upper Permian rhinesuchids, in particu-

lar *Rhinesuchus whaitsi* (Watson, 1962), which also has a broad, posteriorly extended parasphenoid that meets the exoccipitals laterally and a triangular basioccipital laterally sutured with the exoccipital and participating in the rounded condyles. In addition, *Parapytanga catarinensis* gen. et sp. nov. shares with rhinesuchids an extension of the muscular pockets of the parasphenoid over the lateral side of the exoccipital condyles, in addition to the distribution pattern of the denticles that cover the parasphenoid and pterygoid (Yates and Warren 2000). On the other hand, *Parapytanga catarinensis* gen. et sp. nov. differs from *R. whaitsi* in the shape of the muscular pocket, which is much more elongated and deeper, and positioned in the posterior corner of the parasphenoid, such as is observed in *Arachana nigra*, a rhinesuchid-like temnospondyl from the Permo-Triassic of Uruguay (Piñeiro et al. 2012). Moreover, *Parapytanga catarinensis* gen. et sp. nov. has a robust and enlarged epipterygoid, different to that observed in the South African rhinesuchids (Watson 1962).

The well-ossified braincase of *Parapytanga catarinensis* gen. et sp. nov. is similar to that of the capitosauroids *Eryosuchus* (Schoch, 2008) and *Mastodonsaurus* (Schoch, 2002), displaying a massive and robust epipterygoid that bears a blade-like anterior process, is anteriorly expanded,

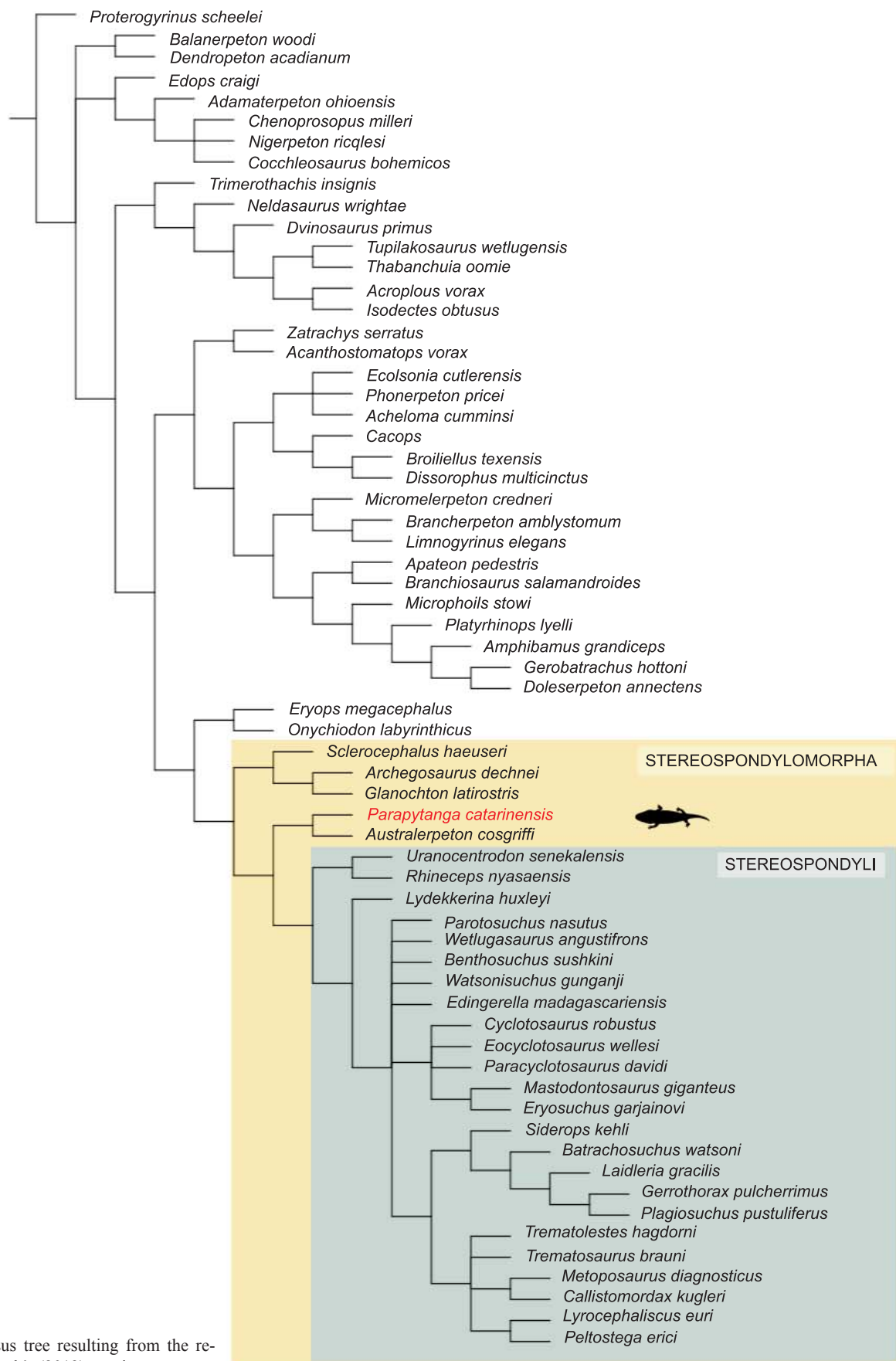


Fig. 7. Strict consensus tree resulting from the reduced analysis of Schoch's (2013) matrix.

and sutures anteromedially with a well-ossified and large sphenethmoid. The posterior region of the anterior process of the epipterygoid is curved and medially concave, similar to the anterior process of the epipterygoid of the mastodonsauroid *Cyclotosaurus* (Damiani 2001), but differing by the presence of a blade-like anterior extension, which confers a proportionally larger epipterygoid.

Preserved postcranial elements of *Parapytanga catarinensis* gen. et sp. nov. present some plesiomorphic characters. The femur, for instance, resembles that of *Lydekkerina huxleyi* and *Eryops megacephalus* (Pawley and Warren 2006), with an enlarged, deep and well-defined intercondylar fossa. The well-developed articulation surface of the femur could suggest some terrestrial adaptation, like that observed in *E. megacephalus* (Pawley and Warren 2006). The preserved portion of the scapulocoracoid shows a general morphology similar to that of *E. megacephalus* (Pawley and Warren 2006), with a robust and laterally flattened scapular blade. However, this element is proportionally shorter in *Parapytanga catarinensis* gen. et sp. nov. than in *E. megacephalus*, having a similar size compared with the sub-adult scapulocoracoid of *Australerpeton cosgriffi* (Dias and Schultz 2003). The interclavicle is smaller in our material (approximately 140 mm in width) than in *A. cosgriffi*, which is 200 mm in width in UFRGS-PV-0320-P (Dias and Schultz 2003), even if the dermal bone ornamentation of the former is more marked and robust than in the latter. The spindle-shaped scales of *Parapytanga catarinensis* gen. et sp. nov. differ from the trapezoid-shaped scales of juvenile specimens of *A. cosgriffi*, as well as from the ellipsoid scales of adult individuals (Dias and Richter 2002), being more similar to the ventral scales observed on a South African rhinesuchid described by Pawley and Warren (2004).

Geographic and stratigraphic range.—Type locality and horizon only.

Phylogenetic analysis

To assess the phylogenetic relationships of *Parapytanga catarinensis* gen. et sp. nov., the new taxon was scored using the datasets from Schoch (2013), both the expanded and short versions of the matrix. This dataset was chosen because of its inclusive nature.

Cladistic analyses were conducted using TNT v. 1.1 (Goloboff et al. 2003). All searches were performed with equally weighted parsimony through the branch swapping (TBR) heuristic option. The analysis of the Schoch's (2013) dataset is based on 212 characters and 73 terminal taxa (72 from the published dataset, plus *Parapytanga catarinensis* gen. et sp. nov.). Character number 68 was set as additive (see Schoch 2013). In addition, the studied material was scored on the reduced, preferred matrix proposed by Schoch (2013). The reduced matrix is composed of the same characters as the expanded one but with the exclusion of nine

problematic terminal taxa. The *Parapytanga catarinensis* gen. et sp. nov. scores based on Schoch (2013) are presented in Appendix 1 here.

The Schoch (2013) expanded dataset resulted in 176 equally parsimonious trees of 683 steps (CI = 0.34, RI = 0.79). The strict consensus also depicts a strong polytomy, with low resolution of *Parapytanga catarinensis* gen. et sp. nov. This result is attributed to the small number of scored characters, as well as the inclusion of problematic taxa (mostly incomplete specimens or taxa only known from skull material). After the exclusion of the problematic taxa, the Schoch's (2013) reduced dataset resulted in 67 equally parsimonious trees of 633 steps (CI = 0.36, RI = 0.8). The strict consensus is better resolved and displays the same general pattern of the Schoch's (2013) reduced phylogeny (Fig. 7). The clade Edopoidea and the grade "Dendrerpetontidae" were recovered as the most basal Temnospondyli Zittel, 1888, and the clade Eryopiformes as the most derived, encompassing eryopids + stereospondylomorphs + Stereospondyli.

Several changes concerning the relationships occurred within and among some clades. The grade "Dendrerpetontidae", weakly supported in the Schoch's (2013) analysis (bootstrap 59; Bremer support 1), was positioned outside Eutemnospondyli and grouped with Edopoidea at the base of the tree. As stated by Schoch (2013), the dendrerpetontids were already considered less derived than edopoids by Milner (1990). In addition, the analysis places *Cochleosaurus*, *Nigerpeton*, and *Chenoprosopus* in a polytomy inside Edopoidea. The short-snouted Palaeozoic temnospondyls, which include Divinosauria + (Zatracheidae + Dissorophoidea), display many changes, with Divinosauria placed outside Rhachitomi, the Olsoniformes positioned at the base of the Dissorophoidea, and a polytomy formed of *Ecolsonia* + *Phonerpeton* + *Acheloma*. As mentioned by Schoch (2013), olsoniforms are mostly found as a separate clade in recent analyses, in which amphibamids are more closely related to micromelerpetontids than branchiosaurids. The greatest changes occurred with Stereospondylomorpha Yates and Warren, 2000 and between Capitosauria and Trematosauria. Stereospondylomorpha was recovered as a paraphyletic group. A polytomy was formed with Capitosauria + Capitosauroida + Trematosauria.

Finally, the phylogenetic analysis grouped *Parapytanga catarinensis* gen. et sp. nov. and *Australerpeton cosgriffi* (Barberena, 1998) in a clade inside Stereospondylomorpha, being the most derived group inside this clade, with the exception of Stereospondyli.

Discussion

Parapytanga catarinensis gen. et sp. nov. shows a high degree of ossification and extensive development of the endocranial ossifications, which according to Boy (1974), suggest an adult ontogenetic stage. In addition, its pectoral

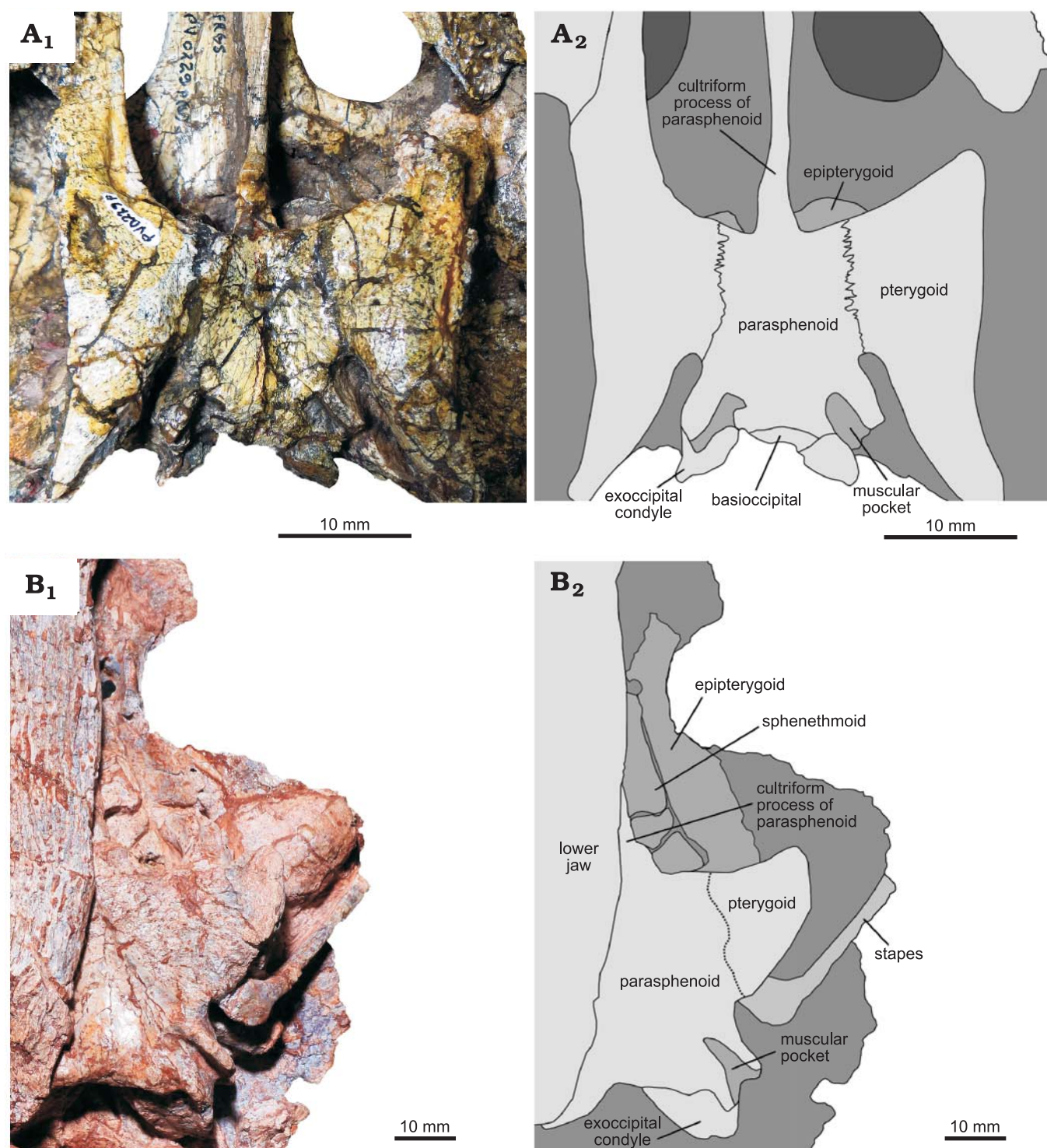


Fig. 8. Comparison between the posterior part of the skull of temnospondyl *Australerpeton cosgriffi*, (Barberena, 1998) (UFRGS PV 0229 P in ventral view) from the Paraná State (Brazil), Upper Permian (A) and the stereospondylomorph temnospondyl *Parapytanga catarinensis* gen. et sp. nov. (holotype, UFRGS-PV-0355-P in ventral view) from the Santa Catarina State (Brazil), Middle–Upper Permian (B). Photos (A₁, B₁) and interpretative drawings (A₂, B₂).

girdle dermal bones present robust ornamentation, which also implies an adult age (Steyer 2000).

Parapytanga catarinensis gen. et sp. nov. shares many similar features with South African rhinesuchids; however, the phylogenetic analysis presented here does not recover the new taxon within Rhinesuchidae. This may reflect the

high amount of missing data for *Parapytanga catarinensis* gen. et sp. nov. Until now, rhinesuchid temnospondyls have been found only in the Late Permian to Early Triassic of Gondwana (Damiani and Rubidge 2003), being recorded in southern Africa, where they are very widespread, as well as Madagascar (Schoch and Milner 2000), Malawi

(Watson 1962) and India (Werneburg and Schneider 1996). In addition, they have been dubiously reported from South America, with the occurrence of *Australerpeton cosgriffi* in Brazil (Barberena 1998; Barberena and Dias 1998). Their occurrence is quite expected in the Permian of Brazil. If *A. cosgriffi* is indeed a rhinesuchid, as proposed by Dias and Schultz (2003), added to another most likely short-snouted rhinesuchid not formally described yet (Barberena and Dias 1998), *Parapytanga catarinensis* gen. et sp. nov. would be a new record of Rhinesuchidae from South America, revealing a widespread and diverse family.

The cladistic analysis positioned *Parapytanga catarinensis* gen. et sp. nov. as a sister-taxon of *A. cosgriffi* (Barberena, 1998), being the most derived group inside Stereospondylomorpha Yates and Warren, 2000, with the exception of Stereospondyli. This transitional position of *Parapytanga catarinensis* gen. et sp. nov. between the stereospondylomorph Archegosauridae from the Laurasian assemblages and the stereospondyl Rhinesuchidae from South Africa, in combination with the presence of two further archegosaurid platyoposaurines, *Prionosuchus plummeri* (Price, 1948) and *Bageherpeton longignathus* Dias and Barberena, 2001, besides a probable melosaurine (Dias-da-Silva 2012) in the Permian of Brazil, favours a connection between the Brazilian Permian fauna and the Eastern European fauna, as already stated by Dias-da-Silva (2012). This faunal relationship also supports the existence of a barrier-free connection between Laurasia and Gondwana that allowed the migration of the temnospondyls and other Permian tetrapods across Pangaea, as previously proposed by Schoch (2000) and Cisneros et al. (2012). In addition, the presence of a derived stereospondylomorph with close affinity to *A. cosgriffi* and great resemblance to the South African Rhinesuchidae also supports Eltink and Langer's (2014) suggestion of a Southern Brazilian ancestral range for the stereospondyl clade (more precisely inside the Paraná Basin) and subsequent radiation of the group to the African continent during the Late Permian.

Conclusions

A new temnospondyl taxon, *Parapytanga catarinensis* gen. et sp. nov., is described from the Rio do Rasto Formation (Paraná Basin), southern Brazil. Although very similar in anatomy to the South African Upper Permian rhinesuchids from the Beaufort Group of the Karoo Basin, cladistic analysis grouped the new taxon with *Australerpeton cosgriffi* (Barberena, 1998) inside Stereospondylomorpha Yates and Warren, 2000 (sensu Schoch 2013). However, this may be because of the high amount of missing data for the new taxon.

The position of *Parapytanga catarinensis* between the Eastern European and South African forms could provide new data for future biogeographic and biostratigraphic studies. Moreover, *Parapytanga catarinensis* gen. et sp. nov. is the first fossil material described from a new tetrapod-

-bearing locality from the Rio do Rasto Formation in Brazil, the Serra do Espigão, which is still poorly explored. Therefore, further discoveries of more complete specimens may be expected.

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Appendix 1

Parapytanga catarinensis gen. et sp. nov. scores included to Schoch's (2013) dataset.

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