



ELSEVIER

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

Reassessing the affinities of vertebral remains from Permo-Triassic beds of Gondwana



Réévaluation des affinités des restes vertébraux des lits permo-triassiques du Gondwana

Graciela Piñeiro^{a,*}, Jorge Ferigolo^b, Ana María Ribeiro^b, Pablo Velozo^b^a Departamento de Evolución de Cuencas, Facultad de Ciencias, Iguá 4225, CP. 11400, Montevideo, Uruguay^b Seção de Paleontologia, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Rua Salvador França, 1427-90 690-000, Porto Alegre, RS, Brazil

ARTICLE INFO

Article history:

Received 13 June 2014

Accepted after revision 24 February 2015

Handled by Michel Laurin

Keywords:

Seymouriamorph

Diadectid

Pareiasaur

Sanga do Cabral Formation

Permian

? Triassic

Brazil

ABSTRACT

The Sanga do Cabral Formation of southern Brazil has a rich fossil tetrapod assemblage and is suggested to have an Early Triassic age mainly based on the presence of the parareptile *Procolophon trigoniceps*. However, a Permo-Triassic age can be also suggested for this unit taking into account the presence of putative Permian taxa and some previous stratigraphic assessments. We describe here several large vertebrae from the Sanga do Cabral Formation that display a distinctive morphology that includes the presence of a transverse distance across postzygapophyses more than twice the transverse width of the centrum, and accessory articulation structures in the neural arch that remind the hyposphene and hypantrum present in some basal parareptiles and diadectomorphs. Vertebrae with a similar large size and morphology had been previously reported from the same locality as belonging to the genus *Procolophon* based on their parareptile appearance (mainly the presence of a swollen neural arch) and the fact that the vertebrae were collected at the same locality where a large fragmentary skull assigned to this taxon was found. However, these vertebrae lack a comparable consistent morphology with those of *Procolophon* and basic statistical analyses demonstrate that these vertebrae are significantly larger than those expected in the largest known *Procolophon* skulls of South Africa. The morphology of these vertebrae is consistent with that present in seymouriamorphs, pareiasaurs and diadectomorphs, but the absence of exclusive diagnostic characters precludes an assure assignation to either of these taxa. According to their current stratigraphic range, seymouriamorphs are the most plausible postulation, as their younger representatives are known from Late Permian deposits of Russia, but the other candidates cannot be excluded. The presence of any representative of those groups in the Sanga do Cabral Formation would be important because: (1) they would represent the first and only known record of seymouriamorphs or diadectomorphs in Gondwana, regarding the characters that the described vertebrae share with these groups; (2) they would suggest a survivorship for pareiasaurs up to the Latest Permian or through the Permian-Triassic boundary, according to geochronological data currently available for this unit; (3) they might also suggest a Late Permian age for at least part of the Sanga do

* Corresponding author.

E-mail addresses: fossil@fcien.edu.uy (G. Piñeiro), jorgeferigolo@gmail.com (J. Ferigolo), amaria_ribeiro@fzb.rs.gov.br (A.M. Ribeiro), pablovelozod@gmail.com (P. Velozo).

Cabral Formation if the intraformational conglomerates that yielded the vertebrae resulted from the rejuvenation of older levels of the same unit, and they do not include reworking of stratigraphically older strata.

© 2015 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

R É S U M É

Mots clés :

Seymouriamorphes
Diadectidés
Paréisaures
Formation Sanga do Cabral
Permien
? Trias
Brésil

La formation de Sanga do Cabral, dans le Sud du Brésil, possède un riche assemblage fossile de tétrapodes et est supposée avoir un âge Trias inférieur, principalement en raison de la présence du parareptile *Procolophon trigoniceps*. Cependant, un âge Permo-Triasique peut également être suggéré pour cette unité, si l'on prend en compte la présence possible de taxons permien et certaines assertions stratigraphiques antérieures. Les auteurs décrivent ici, dans la formation Sanga do Cabral, de grandes vertèbres qui présentent une morphologie caractéristique, incluant la présence d'une distance transversale au travers des postzygapophysys représentant plus du double de la largeur transversale du centre, et des structures accessoires d'articulation qui rappellent l'hyposphène et l'hypantrum, présents dans certains parareptiles et diadectomorphes. Les vertèbres avec une grande taille et une morphologie similaires ont été signalées, dans la même localité, comme appartenant au genre *Procolophon*, sur la base de leur apparence de parareptile (surtout par la présence d'un arc neural gonflé) et du fait que les vertèbres ont été collectées dans la même localité que celle où a été trouvée une large portion de crâne assigné à ce taxon. Cependant, ces vertèbres n'ont pas une morphologie compatible avec celles observées dans le genre *Procolophon*, et les analyses statistiques de base démontrent que ces vertèbres ont une taille significativement plus grande que celle qu'on pourrait attendre dans le cas des plus grands crânes connus de *Procolophon* connus en Afrique de Sud. La morphologie de ces vertèbres est compatible avec ce que l'on observe chez les seymouriamorphes, les paréisaures et les diadectomorphes, mais l'absence de caractères diagnostiques exclusifs empêche une assignation assurée à l'un ou l'autre de ces taxons. D'après leur domaine stratigraphique courant, les seymouriamorphes sont les postulants les plus plausibles, étant donné que leurs plus jeunes représentants sont connus à partir du Permien supérieur de Russie ; mais d'autres candidats ne peuvent être exclus. La présence de quelque représentant que ce soit de ces groupes dans la formation de Sanga do Cabral serait importante, car : (1) ils représenteraient le premier enregistrement et le seul connu de seymouriamorphes ou diadectomorphes dans le Gondwana, en ce qui concerne les caractères que les vertèbres décrites partagent avec ces groupes ; (2) ils suggéreraient une survivance des paréisaures jusqu'à la fin du Permien ou à la frontière Permien-Trias, d'après les données géochronologiques couramment disponibles pour cette unité ; (3) ils pourraient aussi suggérer un âge fini-Permien pour au moins une partie de la formation Sanga do Cabral, si les conglomérats intraformationnels qui ont fourni les vertèbres résultent du rajeunissement de plus anciens niveaux de la même unité et ne comportent pas le remaniement de strates stratigraphiquement plus anciennes.

© 2015 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

1. Introduction

The Sanga do Cabral Formation crops out in southernmost Brazil as part of the Paraná Basin, an intracratonic sedimentary basin that extends over the current territories of Brazil, Uruguay, Paraguay and Argentina (Fig. 1). It is usually considered to represent the oldest lithostratigraphic unit of the Brazilian Triassic sequence, underlying the Santa Maria and Caturrita formations (Andreis et al., 1980).

The depositional environment suggested for the Sanga do Cabral Formation is related to the activity of braided fluvial systems characterized by ephemeral channels, interdigitated by sandy aeolian facies deposited under warm conditions (Holz and Scherer, 1998). Bodies of red sandstones are predominant through the entire formation, but levels of claystones and intraformational conglomerates are interbedded, in particular at the lower portion of the unit. Sandstones are medium to fine-grained and

present primary sedimentary structures, including planar and cross-bedding stratification and also calcareous nodules (Andreis et al., 1980). The Sanga do Cabral Formation overlies discordantly the early Upper Permian Rio do Rasto Formation. Both units represent the Permo-Triassic sequence in Brazil, which has been interpreted as being stratigraphically equivalent to the upper part of the Yaguari and the overlying Buena Vista formations of Uruguay (Andreis et al., 1980; Azevedo et al., 1985) (see Fig. 2). The Brazilian and the Uruguayan sequences are lithostratigraphically equivalent, more evidently accentuated between the Sanga do Cabral and the Buena Vista formations.

Most of the Sanga do Cabral and Buena Vista formations fossil content come from the conglomerates, but both faunas appear not to be taxonomically and biostratigraphically equivalent (Piñeiro et al., 2007a, 2012). Several conglomerate levels are exposed in the Buena Vista

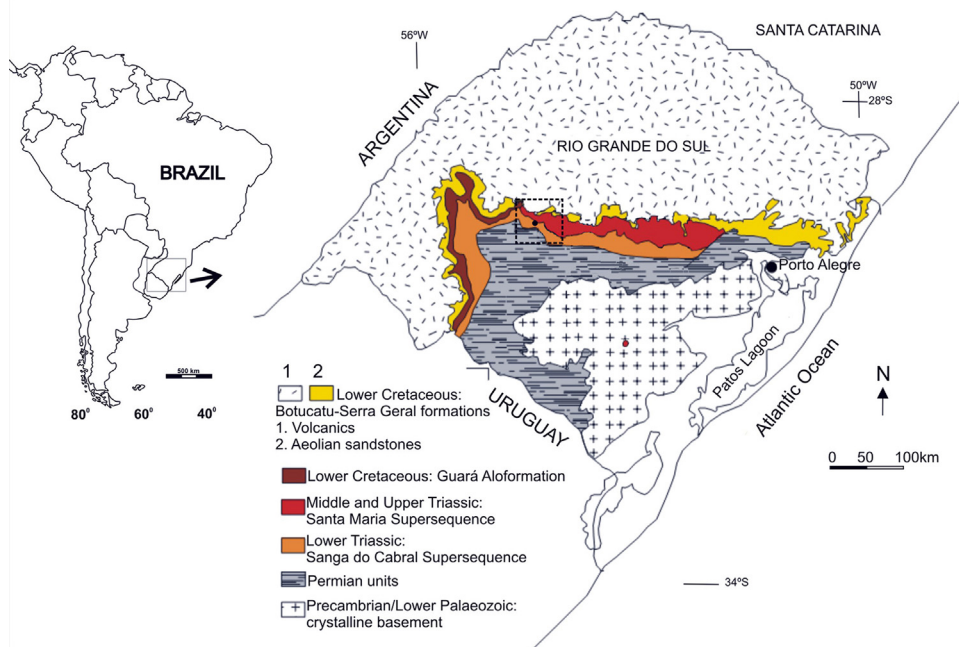


Fig. 1. (Color online.) The Sanga do Cabral Formation and its stratigraphic relation to older and younger units that comprise the Paraná Basin. The square indicates the location area of the outcrops that yielded the described vertebral specimens.

Fig. 1. (Couleur en ligne.) La formation Sanga do Cabral et sa relation stratigraphique avec des unités plus anciennes ou plus récentes du bassin du Parana. Le carré indique la localisation des affleurements qui ont fourni les échantillons de vertèbres décrits.

Modified from Zerfass, 2003.

Formation and, as a result, a careful stratigraphic control can be taken. By contrast, just one or two fossiliferous conglomeratic levels are common in most of the studied localities of the Sanga do Cabral Formation. Intriguingly, therapsids were not found in the Buena Vista Formation, and scarce remains were reported by the Sanga do Cabral Formation (Abdala et al., 2002; Da-Rosa et al., 2009; Langer and Lavina, 2000). On the other hand, fragmentary remains attributed to basal synapsids are present in both of them (Ferigolo et al., 2013; Piñeiro et al., 2003). The scarcity of therapsids in the Sanga do Cabral Formation (Catuçaba Fauna) and their absence in the Buena Vista Formation (Colonia Orozco Fauna) preclude the establishment of confident biostratigraphic correlations with other Permo-Triassic sequences elsewhere where therapsids are very common. Abdala et al. (2002) reported the presence of cynodont-like therapsids from the Sanga do Cabral Formation, but the materials that they described are very fragmentary and bad preserved, so that is difficult to identify the diagnostic structures. The poor preservation is so marked that the described proximal femoral end fragments display and overall morphology that also fits with that of sphenacodontid and basal diapsid proximal humeral heads (see Peabody, 1952; Romer, 1956). In this context, it is difficult to see the diagnostic structures that the authors described; the trochanter major, for instance, is not visible on the posterior views of any of the photographs in Abdala et al. (2002), and it is not discernible from the drawings. The trochanter major is characteristically present in therapsid and mammal femora [although it is also present in

pareiasaurids (Lee, 1995)]. Similar controversial interpretations occur with other of the described materials as the distal end of femur and humerus. While the distal femur was related to cynodonts because of the different development of the medial and lateral condyles, this condition is not exclusive of that taxon but it also characterizes several basal synapsids, particularly sphenacodonts, and other therapsids like the dicynodont *Lystrosaurus* (see Surkov et al., 2005). The morphology of the fragmentary distal portion of the humerus described in Abdala et al. (2002) does not fit in any of the described *Lystrosaurus* humerus. A notorious difference is the position of the entepicondylar foramen, which in *Lystrosaurus* (as well as in some basal synapsids) pierces a ridge that is the ventral extension of the deltopectoral crest (Reisz and Laurin, 2004; Surkov et al., 2005). That crest is not visible on the Abdala et al. (2002) figured distal humerus and the inferred placement of the entepicondylar foramen is somewhat speculative. However, it is possible that the humerus displays a similar feature as that observed in varanopid eupelycosaur: the trochlear and capitular articulation facets are poorly developed and the distal condyles are almost equally developed, thus differing from the condition in *Lystrosaurus* and other basal therapsids in which the entepicondyle is more robust and more developed than the posterior ectepicondyle (see Campione and Reisz, 2010; Surkov et al., 2005, for comparison).

No biostratigraphic markers relate both communities (Catuçaba and Colonia Orozco Faunas), but they display a similar taxonomic composition dominated by

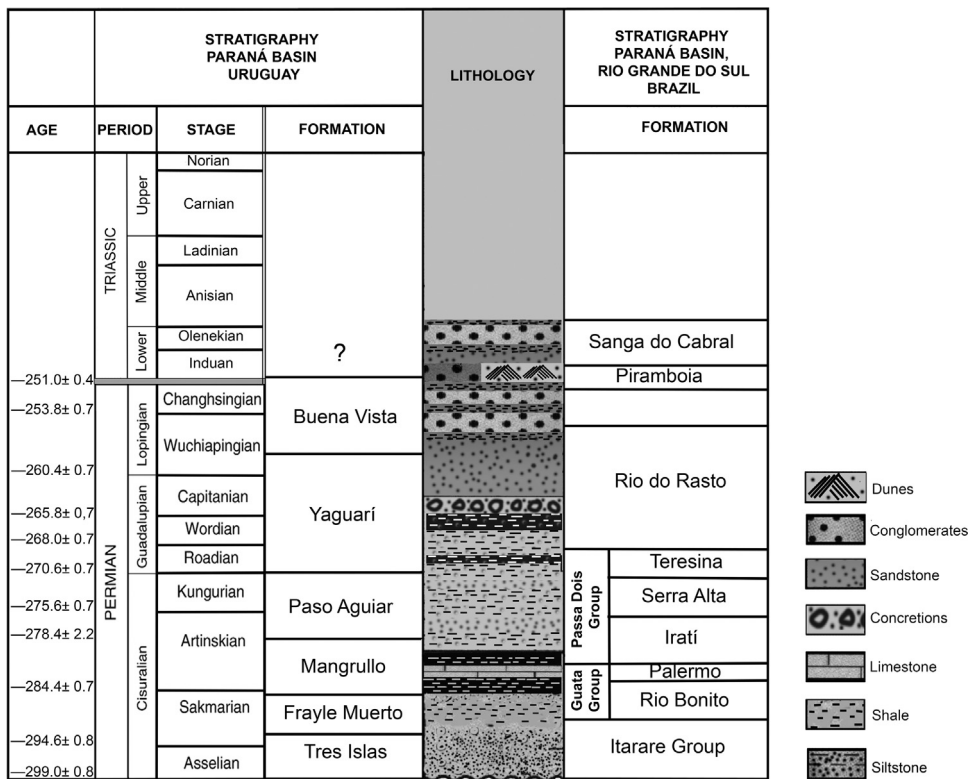


Fig. 2. Stratigraphic synthesis that combines the most recent hypotheses of correlation between Uruguayan and Brazilian Permian and probable Early Triassic units at the Paraná Basin. Radiometric data and stratigraphic arrangement are based on Piñeiro, 2002; Piñeiro and Ubilla, 2003; Santos et al., 2006; Milani et al., 2007, and Piñeiro et al., 2012.

Fig. 2. Synthèse stratigraphique combinant les plus récentes hypothèses de corrélation avec les unités uruguayennes et brésiliennes permienues et vraisemblablement Trias inférieur du bassin du Paraná. Les données radiométriques et la colonne stratigraphique sont basées sur Piñeiro, 2002; Piñeiro et Ubilla, 2003; Santos et al., 2006 et Piñeiro et al., 2012.

temnospondyls, procolophonoids and a minor component of diapsid archosauromorphs. Concerning the Catuçaba fauna, we may include eventually the therapsids if more complete material finally can demonstrate their presence in the Sanga do Cabral Formation more confidently. While temnospondyls pertaining to the Catuçaba Fauna possibly represent groups that characterize well established Early Triassic communities as rhytidosteids and lydekkerinids (Dias-da-Silva and Marsicano, 2006; Lavina and Barberena, 1985), those from the Colonia Orozco fauna show affinities with Permian taxa (Da-Rosa et al., 2009; Piñeiro, 2002; Piñeiro and Ubilla, 2003; Piñeiro et al., 2007a,b,c, 2012). The procolophonoids from the Brazilian fauna were assigned to *Procolophon* (Lavina, 1983, Cisneros, 2008; Cisneros and Schultz, 2002), a taxon well represented in the South African Early Triassic *Lystrosaurus* Assemblage Zone (Groenewald and Kitching, 1995; Rubidge, 2005). Procolophonoids from Uruguay are represented by *Pintosaurus magnidentis*, a basal procolophonoid (Piñeiro et al., 2004), but its affinities are being reassessed on the light of recently discovered more complete specimens. The archosauromorphs from the Colonia Orozco Fauna (Buena Vista Formation) are currently being studied and they are represented by non-archosauriform and proterosuchid-grade archosauromorphs (Ezcurra et al., 2015). Despite the fragmentary nature of the specimens,

the Buena Vista archosauromorphs were related to the *Archosaurus-Proterosuchus* clade (Nesbitt, 2011), as they share several characters with basal archosauromorphs as *Proterosaurus feneri* and *Archosaurus rossicus* from the Late Permian of Germany and Russia respectively, as well as with species of *Proterosuchus* from the Earliest Triassic of South Africa. Thus, the Colonia Orozco Fauna suggests a latest Permian or Permo-Triassic age for the Buena Vista Formation (Piñeiro, 2002; Piñeiro and Ubilla, 2003; Piñeiro et al., 2007a,b,c, 2012), an older age than that suggested for the Catuçaba assemblage at the Sanga do Cabral Formation, which is thus placed in the Late Induan-Early Olenekian by most authors (e.g., Abdala et al., 2002; Dias-da-Silva et al., 2006a,b; Lavina and Barberena, 1985; Zeffass et al., 2003).

However, as mentioned above, the Triassic age of the Sanga do Cabral Formation (Catuçaba Fauna) has been inferred mainly on the presence of the parareptile genus *Procolophon* (Lavina, 1983) which is represented by fragmentary but well preserved specimens. The taxonomic affinities of other specimens recovered from that formation resulted controversial because of their fragmentary nature. The description of a putative pareiasaurid partial skull represents one of the records of a Palaeozoic-restricted group in the Sanga do Cabral Formation (Schultz and Dias-da-Silva, 1999). However, this assignment was subsequently questioned by Cisneros et al. (2005), although they did

not provide an alternative hypothesis for the affinities of the specimen. Similarly, the presence of rhytidosteid and lydekkerinid temnospondyls was originally based on skull fragments that displayed ornamentation reminiscent of these taxa. A subsequently discovered skull confirmed the presence of rhytidosteids in the Sanga do Cabral Formation (Dias-da-Silva and Marsicano, 2006a; Dias-da-Silva et al., 2006b). These last taxa characterize the upper levels of the *Lystrosaurus* Assemblage Zone of South Africa and have been used to suggest biostratigraphic equivalences between the Brazilian and South African continental communities (Barberena et al., 1985a). In recent years, *Procolophon pricei* and *P. brasiliensis* were synonymized with *P. trigoniceps* because they were thought to fit within the individual and/or ontogenetic variation present in the latter species (Cisneros, 2008). This taxonomic scheme would bolster an Early Triassic age for Sanga do Cabral Formation. The therapsids reported for Sanga do Cabral Formation include isolated stapes attributed to dicynodonts and tentatively assigned to *Lystrosaurus* by Schwanke and Kellner (1999) and Langer and Lavina (2000). It is currently known that the genus *Lystrosaurus* is not exclusively restricted to the Triassic, being found in the Upper Permian of Zambia and in the Permian-Triassic South African Karoo succession (King and Jenkins, 1997; Ward et al., 2005). Moreover, some fragmentary postcranial remains were assigned to putative non-mammalian cynodonts (Abdala et al., 2002), but such assignation is not well supported with the available specimens, as discussed previously. The fossils that we describe here consist of four large, isolated and almost complete dorsal vertebrae found in conglomerate levels of the Sanga do Cabral Formation at the Rincão dos Weiss locality (Fig. 1). A few years ago, vertebrae with a similar morphology and size were reported from the same locality and assigned to the procolophonid genus *Procolophon* (Dias-da-Silva et al., 2006b), mainly based on the fact that the vertebrae were collected in the same locality, although not in close association, with a relatively large skull that they assigned to *Procolophon* sp. Even though Dias-da-Silva et al. (2006b) asserted that the dimensions of the neural arch in the vertebra that they described are similar to those of pareiasaurs, diadectomorphs and seymouriamorphs, they dismissed potential affinities to these groups. Comparative anatomical analyses of the vertebrae described here, including a statistic study of the relationship between skull and vertebral proportions among procolophonids, cast doubts in the assignment of the vertebrae by Dias-da-Silva et al. (2006b) to *Procolophon* sp. Thus, we present an alternative hypothesis suggesting that these relatively large vertebrae from the Sanga do Cabral Formation belong to a seymouriamorph, a pareiasaur-like parareptile, or even to a diadectomorph, although the older known stratigraphic range of this last group in the Lower Permian makes this last alternative less plausible. Preliminary biostratigraphic and palaeobiogeographic analyses about the implications of the new taxonomic interpretation are also attempted.

Institutional Abbreviations. MCN-PV: Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil. NHMUK: Natural History Museum, United Kingdom.

2. Materials and methods

The specimens described here include four isolated, well preserved and almost complete dorsal vertebrae found at the Rincão dos Weiss locality of the Sanga do Cabral Formation, southern Brazil (Fig. 1). This locality is characterized by the presence of several undescribed procolophonoid cranial and postcranial remains, some temnospondyl bones and putative varanopid and sphenacodontid vertebrae, and cranial and postcranial therapsid bones. All the described specimens belong to the collection of fossil tetrapods housed at the Museu de Ciências Naturais of the Fundação Zoobotânica do Rio Grande do Sul (MCN-PV), Porto Alegre, Brazil. All the specimens were found isolated from each other and, subsequently, prepared using manual mechanical tools and a ZEISS binocular microscope.

3. Systematic palaeontology

Tetrapoda *incertae sedis* (sensu Hatschek and Cori, 1896)

Figs. 3, 4, 6.

Description: the studied specimens (MCN-PV 2722, 2723, 20000, 20001) consist of four isolated, well preserved and almost complete vertebrae (Fig. 3). A brief description of the general morphology of the vertebrae is provided to facilitate the recognition of diagnostic characters, and is followed by a more detailed description of each specimen.

Most of the vertebrae seem to be variably squeezed to the left probably because of postmortem distortion. This feature might suggest that the vertebrae belong to the same animal or it may be just a casual fact. Centra are amphicoelous, notochordal and spool-shaped, with outward expanded ends to form thick subcircular rims. Vertebral centra are anteroposteriorly short when compared with the diameter of their terminal articular surfaces. The diameter of the anterior articular surface of the centrum is in general larger than the posterior. The centra are slightly beveled, suggesting that proportionally small intercentra may have been present, but they are lost. The lateral surface of the centra is deeply excavated and the ventral margin is slightly anteroposteriorly concave or straight. There are not accessory articulations on the centra. The pedicles of the neural arch are dorsoventrally short and form the walls of sub-oval neural canals. The ventral surface of a few centra is mainly flat (maybe due to preparation) or in most vertebrae possesses a median longitudinal stout ridge that delimits shallow depressions.

The neural arches of all the vertebrae are swollen, and the zygapophyses extend laterally well beyond the lateral margin of the centrum, resembling the condition present in diadectomorphs, seymouriamorphs and pareiasaurs (Sumida and Modesto, 2001). In all of the specimens, the neural arch is fused to the centrum, without trace of suture. The transverse processes are robust, wing-like structures in anterior and posterior views. In lateral view, the transverse processes are anteroventrally-to-posterodorsally oriented and extend from the point of mid-height on the anterior margin of the centrum to the posterior portion of the base of the prezygapophysis. The transverse processes do not extend laterally beyond the

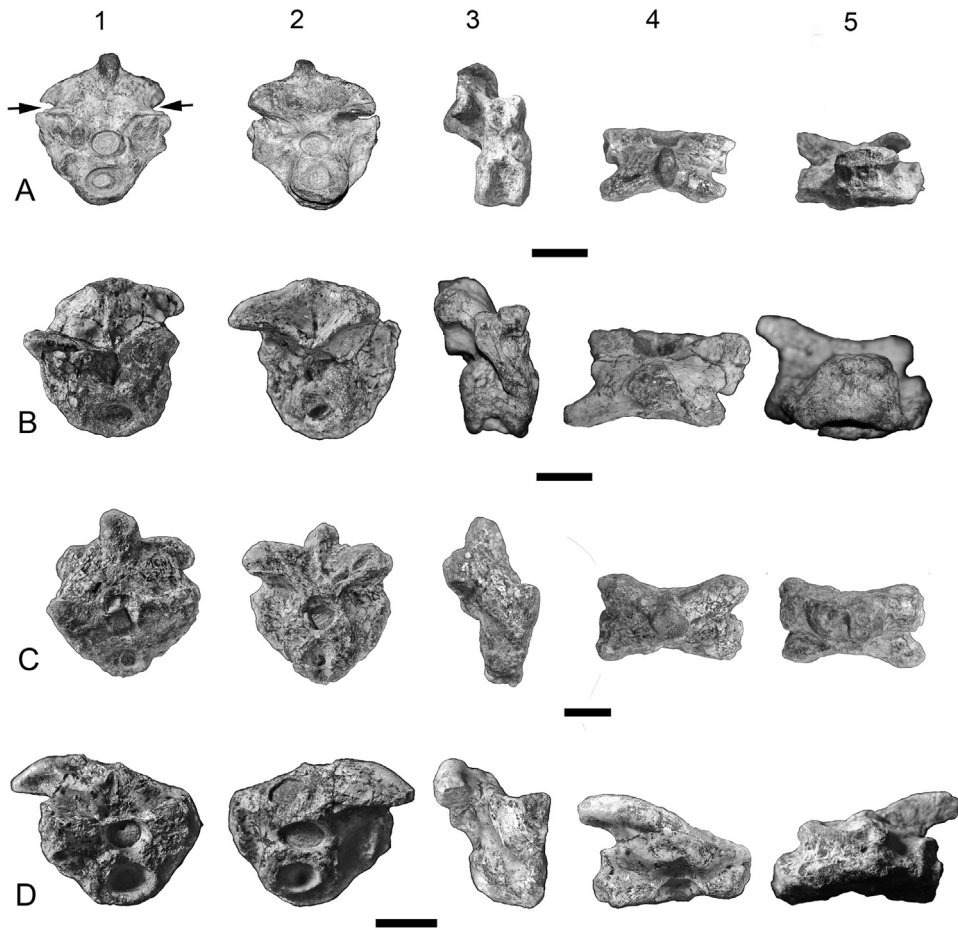


Fig. 3. Dorsal vertebrae from the Sanga do Cabral Formation. A. Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil (MCN-PV) 2722. B. MCN-PV 2723. C. MCN-PV 20000. D. MCN-PV 20001 in anterior (1), posterior (2), right lateral (3), dorsal (4) and ventral (5) views. Scale bars: 10 mm. **Fig. 3.** Vertèbres dorsales de la formation Sanga do Cabral. A. Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil (MCN-PV) 2722. B. MCN-PV 2723. C. MCN-PV 20000. D. MCN-PV 20001 en vues antérieure (1), postérieure (2), latérale droite (3), dorsale (4) et ventrale (5). Barres d'échelle = 10 mm.

level of lateral projection of the zygapophyses. This condition and the probably short neural spine suggest that the vertebrae may pertain to middle-posterior elements of the trunk region. The distal end of the transverse processes lodges well-developed articular rib facets. Some of these facets have a kidney-shaped contour (e.g., MCN-PV 2722, 2723), with a central constriction that clearly defines tubercular and capitular areas. By contrast, other vertebrae possess an inverted teardrop facet that lacks a constriction. The postzygapophyses extend laterally usually beyond the level of the lateral margin of the prezygapophyses and the transverse distance between both postzygapophyses is more than twice the diameter of the centrum. This character distinguishes diadectomorph and pareiasaur vertebrae from all other known tetrapods (Sumida, 1990). The prezygaphophyseal facets are slightly tilted dorsomedially and those of the postzygapophyses are slightly ventrolaterally facing. Small accessory articulations are placed below the level of the prezygapophyses in at least two vertebrae (MCN-PV 2722 and 2723; the last not shown), but they seem to have suffered severe damage and, as a result, it is

difficult to provide a detailed description of such structures. In the specimens with almost complete neural spines, these structures are proportionally short, being dorsoventrally shorter than the height of its respective centrum, resembling the condition present in the vertebrae described by Dias-da-Silva et al. (2006b), seymouriamorphs (Sumida, 1990) and tseajaiids (e.g., *Tseajaia campi*: Moss, 1972). By contrast, in *P. trigoniceps* and some diadectids the neural spines are proportionally tall, being at least as tall as the rest of the neural arch and centrum combined (deBraga, 2003; Sumida, 1990). The neural spines of the Brazilian specimens possess sharp anterior and posterior edges that generate a rhomboidal contour of the neural spine in cross-section.

3.1. MCN-PV 2722

This specimen is an almost complete, deeply amphicoelous vertebra, missing the distal end of the neural spine (Fig. 3A1–5). The anterior exit of the notochordal canal is inflated and forms a dome-shaped structure, resembling the condition present in the anterior and posterior

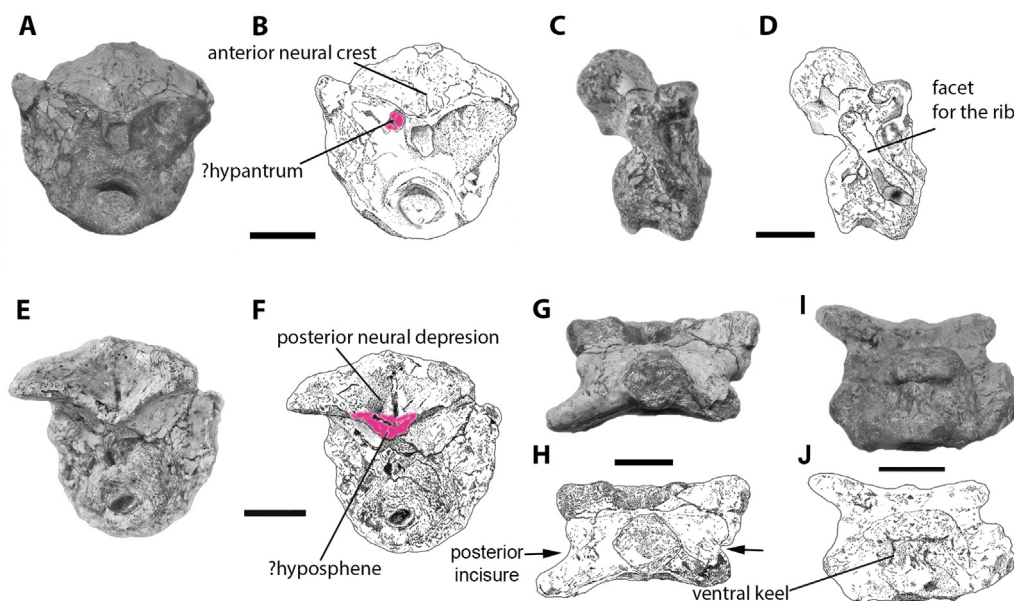


Fig. 4. Accessory articulation structures in Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil (MCN-PV) 2723 (shown in pink color). Photographs in anterior (A), lateral (C), posterior (E), dorsal (G) and ventral (I) views and corresponding drawings in B, D, F, H, J. Arrows point to the lateral incisions between the anterior portion of the neural arch and the base of the postzygapophyses (see text). Scale bars: 10 mm.

Fig. 4. Structures accessoires d'articulation au Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil (MCN-PV) 2723 (présentées en rose). Photographies en vues antérieure (A), latérale (C), postérieure (E), dorsale (G) et ventrale (I) correspondant aux dessins B, D, F, H, J. Les flèches pointent en direction des incisions latérales entre la portion antérieure de l'arc neural et la base des postzygapophyses (voir texte). Barres d'échelle = 10 mm.

ends of the dorsal vertebral centra of *Limnoscelis dynatis* (Berman and Sumida, 1990). These structures do not represent accessory articulations. The ventral surface of the centrum apparently possesses two median longitudinal, blunt ridges that delimitate a central groove, which split anteriorly, but the area is rather damaged in this specimen. Paired, longitudinal keels on the ventral surface of the centrum have been reported in dorsal vertebrae of *L. dynatis* (Berman and Sumida, 1990), but they are also present in other basal tetrapods. The pedicel of the base of the neural arch is almost as long dorsoventrally as the centrum and possesses a gentle posterior emargination. The ventrolateral extension of the transverse process up to almost the mid-height of the anterior rim of the centrum weakly differentiates it from the neural arch, as in the dorsal vertebrae of *T. campi* (Moss, 1972; Sumida, 1990) and limnoscelids (Berman and Sumida, 1990). By contrast, the transverse process only extends up to the dorsal portion of the anterior rim of the centrum and is restricted to the base of the prezygapophysis in the posterior dorsals of diadectids (Berman et al., 1998). The rib facet is ventrolaterally and posteriorly facing. Both prezygapophyses are rather damaged at their distal ends, particularly the left one. However, it can be determined that they are anterolaterally directed and their articular facets tilt dorsomedially approximately 10° from the horizontal plane. The surface of the articular facets is flat, smooth and subtriangular, with a medially facing apex, differing from diadectomorphs where the articular facets show concentric growth ridges (Sumida, 1990, Plate 3; Sumida, personal communication, 2014). The postzygapophyses are robust, strongly swollen and posterolaterally projected. The articular facet of the

postzygapophyses is oval and less tilted from the horizontal plane than that of the prezygapophyses. Right and left pre- and postzygapophyses are connected with each other through a thin, transverse bony shelf situated immediately above the roof of the neural canal. Between both postzygapophyses, the shelf projects ventrally and forms a median, transversely broad process that extends well below the level of the postzygapophyses. The distal end of this process is broken off and, as a result, is not possible to determine the presence of articular surfaces on this structure. Similar processes have been reported in the dorsal vertebrae of *Limnoscelis* and they possess accessory articulation structures (Lewis and Vaughn, 1965). Even though in *Limnoscelis*, a wedge-shaped shelf is present between the zygapophyses, the median posterior process is less developed (Langston, 1966; see also Wideman et al., 2005) than in the vertebrae from the Sanga do Cabral Formation. A median, vertical ridge between both postzygapophyses has been reported in the dorsal vertebrae of *Seymouria* (Sumida, 1990: 45, fig. 21e). The neural arch of MCN-PV 2722 has a deep, subtriangular depression immediately above the transverse shelf that connects both postzygapophyses, resembling the condition present in some diadectids and seymouriamorphs (Sumida, 1990), although this can be a size-effect character. This depression is interrupted by a weak, median vertical ridge that disappears before reaching the base of the neural spine. The anterior surface of the neural arch possesses a dorsomedially facing facet that connects the prezygapophyses with the lateral wall of the neural canal. Although an articular surface cannot be discerned, probably because of poor preservation, this structure seems to have received the median

ventral process situated between both postzygapophyses, resembling the rudimentary accessory articulation structures (i.e. hyposphene-hypantrum) present in diadectids (Case, 1910; Romer, 1956) and *Seymouria* (Sumida, 1990: fig. 21g). Dorsal to the prezygapophyses, the neural arch is convex and faces almost vertically. A median crest separates two small, oval and well delimited fossae between the bases of both prezygapophyses. As mentioned above, there are small posterior incisures (emarginations) between the anterior portion of the neural arch and the base of the postzygapophyses (see Fig. 3 A1 and Fig. 4H), which resemble the shallow fossa present on the anterior surface of the postzygapophyses of *L. dynatis* (Berman and Sumida, 1990). The neural spine is broken off at its base and possesses the rhomboidal contour in cross-section described above, with a well-defined posterior sharp edge that extends ventrally to the low median, vertical ridge situated immediately above the roof of the neural canal.

3.2. MCN-PV 2723

This specimen consists of an almost complete dorsal vertebra, lacking most of the neural spine and part of the right postzygapophysis (Fig. 3B1–5 and Fig. 4). Although this vertebra is very similar to MCN-PV 2722, it presents some morphological differences. MCN-PV 2723 is slightly smaller than MCN-PV 2722 but its centrum is markedly anteroposteriorly longer. Both anterior and posterior articular facets possess subequal diameters. In lateral view, the ventral margin of the centrum is almost straight and the ventral surface possesses a pair of longitudinal ridges that delimitate a median, shallow groove as in MCN-PV 2722. The transverse processes extend from the base of the prezygapophyses to the mid-height of the anterior margin of the centrum; they are short and do not surpass the lateral level of the zygapophyses. The rib facet is placed at the end of the process and is large and slightly constricted at mid-length, but it does not form well-defined tubercular and capitular areas. The anterior surface of the neural arch is almost vertical at its lower portion, but slants slightly posterodorsally through all of its extension. The depressions observed on the anterior surface of the neural arch of MCN-PV 2722 are also present in this specimen, and the surface is flat and laterally, it is crossed by two low ridges that connect the base of the neural spine with the medial margin of the prezygapophyses. The transverse bony shelf that connects both prezygapophyses is less evident in this vertebra, as well as the posterior emarginations, that are small incisures in this specimen. Accessory vertebral articulations are clearly present in this specimen; they can be seen as small projections at the base of the anterior prezygapophyses, well identified at the right side, which displays the characteristic hypantrum structure. The posterior surface of the neural arch possesses a rhomboidal median depression between both postzygapophyses, which is deeper than that present in MCN-PV 2722. This fossa is subdivided by a low median vertical ridge that connects the base of the neural spine with a wedge-shaped transverse bony shelf that bridges both postzygapophyses (hyposphene). The transverse shelf possesses a ventrally projected, median process that closely

resembles that present in MCN-PV 2722 and probably represents an accessory vertebral articulation. Contrary to what occurs in MCN-PV 2722, articular facets can be distinguished, even though the specimen is not well preserved at this area. The incisures present between the anterior portion of the neural arch and the base of the postzygapophyses are anteroposteriorly shorter and less extended medially than those present in MCN-PV 2722. The prezygapophyseal facets are tilted ventromedially at approximately 20° from the horizontal plane; the posterior zygapophyses start almost horizontal and slant gradually ventrolaterally to contact each other at the midline forming the presumed posterior hypantrum. The neural spine has a diamond-shaped base as in MCN-PV 2722 but its posterior edge does not extend onto the posterior depression of the neural arch. This spine reminds that of the pareiasaur *Bradysaurus* from the Middle-Late Permian of South Africa (Boonstra, 1935; Romer, 1956).

3.3. MCN-PV 20000

This specimen consists of an almost complete dorsal vertebra, lacking most of the neural spine and the left postzygapophysis (Fig. 3C1–5). This vertebra is slightly larger than the other described specimens, except MCN-PV 2722, which is of almost the same size. There is no dome-like structure at the opening of the notochordal canal. The ventral surface of the centrum is severely damaged, as in MCN-PV 2722; thus, it is difficult to ascertain the presence of longitudinal ridges in this specimen. The neural arch of MCN-PV 20000 is transversely broader and dorsoventrally lower than those of the other described vertebrae. The neural canal is oval, with a transverse main axis, but this condition may result from artificial compression during fossilization. The posterior emarginations are as poorly marked as in MCN-PV 2723. The postzygapophyses extend farther laterally than those of the remaining vertebrae. Although the bony shelf that connects both postzygapophyses is eroded away, the median ventral process is present, finishing slightly posterior to the level of the articular facets of the zygapophyses, as occurs in MCN-PV 2722, 2723 and 20001 (see below). The pre- and postzygapophyseal facets are tilted in a similar fashion as in the previously described vertebrae, but the posterior facets are straighter. There is a subcircular depression on the left side of the neural arch that might be pathological or a taphonomic artifact. If pathological, it could have represented a constraint to the development of the neural spine, which position is not clearly visible at this specimen. The ventral margin of the articular facet for the rib is placed at level with the dorsal border of the anterior surface of the centrum. The facet has an inverted teardrop contour and lacks distinct tubercular and capitular areas. A subtriangular and deep depression is present only on the anterior surface of the neural arch and a delicate vertical ridge subdivides it. No accessory articulations can be observed anteriorly in the neural arch of MCN-PV 20000, but a shelf connecting the postzygapophyses is present as in the other described vertebrae.

3.4. MCN-PV 20001

This almost complete specimen is the smallest one (Fig. 3D1–5). As in most described specimens, there is no dome-like structure at the opening of the notochordal canal. The centrum is oval with the transverse diameter larger than the dorsoventral one. There are no ridges at the ventral surface of MCN-PV 20001, but the surface is somewhat weathered. The neural arch is similar to that of MCN-PV 2723, but appears less robust. Posteriorly it has a deep depression divided by a median crista, which is a ventral projection of the posterior sharp edge of the neural spine. The lateral emarginations are well marked, especially the right one, where it appears as a shallow notch partially enclosed by a posteroventrally extension of the zygapophysis. The zygapophyseal planes are similarly tilted as in the other vertebrae. The rib facet is medially constricted, delimitating well-defined tubercular and capitular areas. There are no visible accessory articulations on the neural arch, but it is not possible to be sure that they were not originally present. The neural spine is longitudinally oval in cross-section, with the main axis anteroposterior; however, as in the previously described vertebrae, anterior and posterior sharp wedges are present.

4. Discussion

4.1. Morphological comparisons

All the vertebrae, as well as those previously attributed to *Procolophon* by Dias-da-Silva et al. (2006b), have a similar general morphology and proportions with each other. Although all these vertebrae come from the same locality, it is not possible to determine if they belong to the same animal, although it is probable that they belong to the same taxon, given their similarity. The observed differences in morphology are possibly related with different positions in the vertebral column. The cervical and dorsal vertebrae of diadectomorphs have different ratios between the length of the centrum and its diameter through the axial series (Berman and Sumida, 1990; Sumida, 1990). This ratio may be useful to determine the region of the column to which the described vertebrae pertain. Moreover, the morphology and degree of development of the transverse processes and the height of the neural spine can also help in determining the location of the vertebrae through the axial series (Sullivan and Reisz, 1999). Therefore, whereas in dorsal vertebrae of diadectids, *Tseajaia* and seymouriamorphs the length of the centrum increases posteriorly (Sumida, 1990), as also could occur in procolophonids (Martin Ezcurra, pers. comm. 2014), limnoscelids exhibit exactly the opposite pattern (Berman and Sumida, 1990; Berman et al., 1998; Case, 1910; Case and Williston, 1913). Thus, the length/diameter ratio of the centrum is different in cervical and dorsal vertebrae in these taxa. By contrast, in the dorsal vertebrae of limnoscelids, the width of the centrum strongly exceeds its length (Berman and Sumida, 1990; Berman et al., 1998) (see Table 1). In the Sanga do Cabral vertebrae the width of the centrum is slightly larger or subequal to its length, resembling the condition present in the dorsal vertebrae of diadectids, *Tseajaia*

and seymouriamorphs, as well as those of the Late Carboniferous limnoscelids (Carroll, 1967). Additionally, the laterally short transverse processes, in which they do not exceed the lateral extension of the postzygapophyses, are also congruent with that observed in the dorsal posterior vertebrae of most diadectomorphs. However, the Sanga do Cabral vertebrae lack zygapophyseal surfaces showing concentric growth rings, which are extraordinarily clear in limnoscelids and diadectids (Sumida, 1990; Sumida, personal communication, 2014). The neural spines of the Sanga do Cabral Formation vertebrae seem to be short, even though most are broken off at their bases, and none of the completely preserved spines is tall.

The apparent presence of rudimentary accessory articulations on the neural arch and the presence of a transverse bony shelf connecting the postzygapophyses, closely resembles the condition present in the diadectid *Diasparactus zenos* (Case, 1910). Indeed, with exception of *Stephanospondylus pugnax* and *Diadectes absitus* (Berman et al., 1998; Kissel, 2010), the presence of such accessory articulation structures is distinctive for diadectids, although they were also recently described in pareiasaurids (Xu et al., in press). These structures are absent in limnoscelids, but there is a wedge of bone connecting the posterior zygapophyses in some taxa (Langston, 1966, but see also Wideman et al., 2005). Their presence in *Tseajaia* cannot be ascertained (Moss, 1972), and seymouriamorphs have accessory articulation structures on the centrum (Sumida, 1990), which are absent in all the vertebrae from the Sanga do Cabral Formation. A poorly developed shelf of bone unites the posterior zygapophyses in procolophonids and captorhinomorphs, but these structures were never described as representing the presence of neural accessory articulations in these groups.

4.2. Taxonomic assignment

Seymouriamorphs and diadectomorphs are reptile-like early tetrapods. They are mainly known from the Late Carboniferous (only diadectomorphs) to Early Permian of Laurasia (Berman et al., 1992, 1997, 2000) although some possible fragmentary diadectomorph specimens and very well preserved seymouriamorphs are also known from the Late Permian of Russia (e.g., Bulanov, 2003; Ivachnenko, 1973). Diadectomorphs are defined as the last common ancestor of diadectids, limnoscelids and *Tseajaia* and all their descendants (Laurin and Reisz, 1997). The group is particularly interesting because early and recent workers have described multiple characters shared between diadectomorphs and amniotes, leading several researchers to consider Diadectomorpha and, particularly, diadectids as early amniotes (e.g., Berman et al., 1992; Case, 1910; Lee and Spencer, 1997; Modesto, 1992; Olson, 1947; Sumida et al., 1992). However, most of the recent phylogenetic studies do not support the inclusion of diadectomorphs within Amniota but as their closest relatives (e.g., Berman et al., 1997; Gauthier et al., 1988; Kissel and Reisz, 2004; Laurin and Reisz, 1997, 1999).

Pareiasaurs, a group of large, herbivorous parareptiles are known from the Middle–Late Permian times (Tsuji et al., 2013). They achieved an almost world-like distribution at

Table 1

Proportions of dorsal vertebrae from diadectomorphs, seymouriamorphs and large specimens of *Procolophon trigoniceps* for comparison to the specimens described herein (MCN-PV 2722, 2723, 20000 and 20001). Data for limnoscelids are from Williston, 1911; Langston, 1966; Carroll, 1967; Berman and Sumida, 1990, and Wideman et al., 2005; for *Diasparactus zenos* and *Diadectes maximus* from Case, 1910, for *Diadectes absitus* from Berman et al., 1998, *Pareiasauria* indet., from Jalil and Janvier, 2005; for *Procolophon trigoniceps* from deBraga, 2003 and a specimen housed at the National History Museum from United Kingdom (NHMUK R4088); for *Seymouriamorpha* from Sullivan and Reisz, 1999; Berman et al., 2000. Measurements in mm.

Tableau 1

Proportion de vertèbres dorsales de diadectomorphes, de seymouriamorphes et de grands spécimens de *Procolophon trigoniceps* pour la comparaison avec les spécimens décrits ci-dessus (MCN-PV 2722, 2723, 20000 et 20001). Les données pour les limnoscéliés sont de Williston, 1911; Langston, 1966; Carroll, 1967; Berman et Sumida, 1990, et Wideman et al., 2005; pour *Diasparactus zenos* et *Diadectes maximus*, de Case, 1910; pour *Diadectes absitus*, de Berman et al., 1998; pour *Pareiasauria* indet., de Jalil et Janvier, 2005; pour *Procolophon trigoniceps*, de deBraga, 2003 et d'un spécimen (NHMUK R4088) conservé au National History Museum (Royaume-Uni); pour *Seymouriamorpha*, de Sullivan et Reisz, 1999; Berman et al., 2000. Les mesures sont en mm.

Taxon	Centrum width	Centrum length	Maximum width at the level of postzygapophyses
<i>Limnoscelis dynatis</i>	30	20	50
<i>Limnoscelis paludis</i>	5	3.5	12
<i>Limnoscelis</i> sp.	16	11	–
<i>Limnoscelis</i> sp.	18	19	42
<i>Limnoscelis</i> sp.	8	8	12.5
<i>Diasparactus zenos</i>	4.5	4	16.5
<i>Diadectes maximus</i>	31	–	77.5
<i>Diadectes absitus</i>	–	36	75
<i>Pareiasauria</i> indet.	25	41	90
<i>Procolophon trigoniceps</i> (deBraga, 2003)	18.9	12	16.8
<i>Procolophon trigoniceps</i> (NHMUK R4088)	4.7 (middle dorsal)	4.5 (middle dorsal)	7
	5.9 (posterior dorsal)	5.3 (posterior dorsal)	7.4
<i>Seymouria sanjuanensis</i>	–	10	30
<i>Seymouria</i> sp.	18	19	40
MCN-PV 2722	13.7	7.1	30
MCN-PV 2723	9.2	9	27 (inferred)
MCN-PV 20000	13.1	11	36 (inferred)
MCN-PV 20001	9	8	24

MCN-PV: Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil.

the beginning of the Late Permian (Lee, 1997) and apparently, they were severely affected by the end Guadalupian extinction event and they are not known above the Permian-Triassic boundary (see Sennikov, 1996a,b).

The main characters that preclude the assignment of the vertebrae described here and those described by Dias-da-Silva et al. (2006b) to *Procolophon* are the pronounced swollen neural arch and the strong lateral expansion of postzygapophyses beyond the level of the lateral surface of the centrum, and the apparently short neural spines. The width across both postzygapophyses is more than twice transverse width of the centrum (two and half times in MCN-PV 2722 and 2723, and almost three times in MCN-PV 2000). According to several authors (e.g., Berman and Sumida, 1990; Sumida, 1990; Sumida and Modesto, 2001), swollen neural arches are present in most anapsids, but they are never wider than they are long, excepting pareiasaurids. Thus, such wider than long neural arches is a feature shared by diadectomorphs, seymouriamorphs and pareiasaurs, and was also noted in the vertebrae described by Dias-da-Silva et al. (2006b). Even in large specimens of *Procolophon trigoniceps* this condition is absent, and the neural arches are as wide as they are long, even though this interpretation may be unreliable when vertebrae are fully articulated (see Colbert and Kitching, 1975; deBraga, 2003, and Fig. 5). Pareiasaur vertebrae possess a similar general morphology to those of diadectomorphs and to the vertebrae described from the Sanga do Cabral Formation.

However, pareiasaurs differ from the latter because the width across postzygapophyses is almost four times the centrum diameter, and the centra are longer, laterally compressed and bear sharp longitudinal keels on their ventral surface, which progressively disappear to the posterior-most dorsals (see Jalil and Janvier, 2005 and Table 1). Moreover, according to Gow and Rubidge (1997) pareiasaur centra are not notochordal, contrasting with the condition in all the described vertebrae from the Sanga do Cabral Formation. However, this character is not easily observed when vertebrae are articulated; thus, the non-notochordal nature of the pareiasaur centrum needs to be confirmed. Finally, the dorsal vertebrae of *Procolophon* may differ from those of seymouriamorphs, diadectomorphs, and pareiasaurs by the absence of full co-ossification between centrum and neural arch, as shown by the presence of a persistent neurocentral suture. Evidence of this is that very often typical representative vertebrae of *P. trigoniceps* from the Sanga do Cabral Formation preserve just the neural arch and lack the centrum (Fig. 5C–D). This may mean that diagenetic processes favored the preservation of isolated neural arches. That condition seems also to be present in large specimens of this taxon from South Africa, although some complete vertebrae have been described in well preserved, almost complete specimens (deBraga, 2003, Fig. 5B). However, these vertebrae were figured as having well marked, neurocentral sutures. Thus, it is possible that the presence of neurocentral suture, which persists

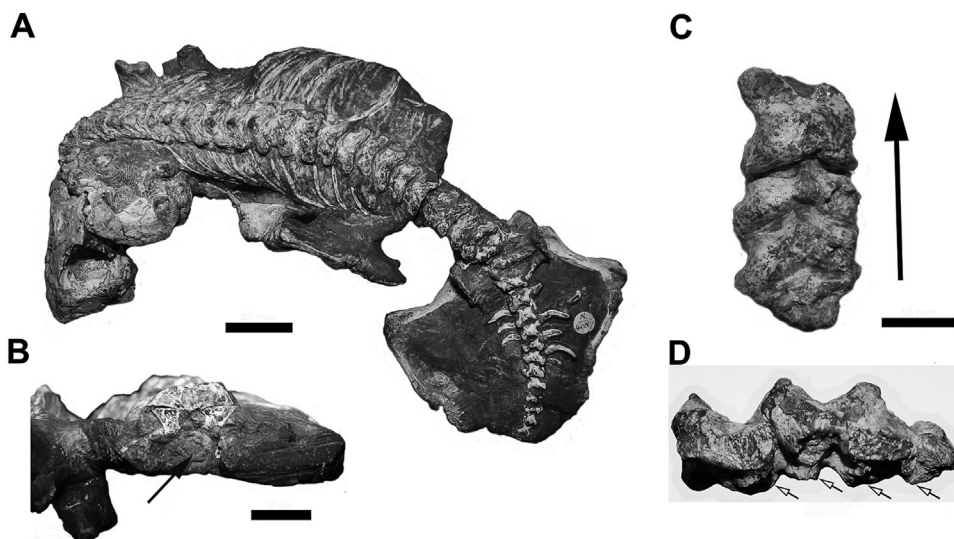


Fig. 5. *Procolophon trigoniceps*. A. National History Museum from United Kingdom (NHMUK) R4088, an almost complete skeleton of a large adult specimen from the Early Triassic of South Africa, showing the shape of the vertebrae in dorsal view, which in natural articulation suggests that neural arches that are wider than long, thus superficially resembling those of diadectomorphs. Scale bar: 20 mm. B. NHMUK R4088, posterior dorsal vertebra in transversal posterior view. Arrow points at the centrum preserved as an external mold. Scale bar: 10 mm. C. Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil (MCN-PV) 20019, dorsal view of four articulated, large dorsal vertebrae from the Sanga do Cabral Formation. Recall the shape of the neural arch in the most anterior vertebra, which is as wide as it is long, representing the common feature for procolophonoids. Arrow points to cranial direction. D. MCN-PV 20019 in lateral view. Arrows show the poorly ossified centrum in all these vertebrae. Scale bar: 10 mm.

Fig. 5. *Procolophon trigoniceps*. A. National History Museum from United Kingdom (NHMUK) R4088, squelette presque complet d'un spécimen adulte du Trias inférieur d'Afrique du Sud, montrant la forme des vertèbres en vue dorsale qui, dans le cas de l'articulation naturelle, suggère que les arcs neuraux sont plus larges que longs, donc ressemblent superficiellement à ceux des diadectomorphes. Barre d'échelle = 20 mm. B. NHMUK R4088, vertèbre postérieure dorsale en vue postérieure transversale. La flèche pointe vers le centre préservé sous forme de moulage externe. Barre d'échelle = 10 mm. C. Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil (MCN-PV) 20019, vue dorsale de quatre grandes vertèbres dorsales articulées de la formation de Sanga do Cabral. Se remémorer la forme de l'arc neural dans la vertèbre la plus antérieure, qui est aussi large que long, représentant le trait commun des procolophonidés. La flèche pointe en direction du crâne. D. MCN-PV 20019 en vue latérale. Les flèches montrent le centre faiblement ossifié de toutes ces vertèbres. Barre d'échelle = 10 mm.

into adulthood in *P. trigoniceps* and other procolophonoids, is characteristic of these taxa.

The ratio between the size of the vertebrae and the length of the skull in *Procolophon* may also shed light on the affinities of the vertebrae from Sanga do Cabral. The largest figured *Procolophon* skull is approximately 75 mm long (see Colbert and Kitching, 1975; deBraga, 2003), and the vertebrae that belong to this individual are significantly smaller than the specimens described here (see Table 1).

The skull described by Dias-da-Silva et al. (2006b), which putatively belongs to the same taxon as the large vertebrae that they described, belongs to a rather robust animal with a bizarre morphology, when compared to the common, *Procolophon* structural plan (see Carroll and Lindsay, 1985). The quadratojugal is very well-developed and forms a rounded horn that extends directly posteriorly in lateral view, contrasting with the more delicate, posterolateral projection present in small and large *Procolophon* specimens (Colbert and Kitching, 1975). Besides, the skull is proportionally dorsoventrally lower than that expected for a large-sized *Procolophon*. It is possible that these differences indicate the presence of a different, undescribed new taxon. Thus, we disagree with the assignment of Dias-da-Silva et al. (2006b). Conversely, our study indicates that the vertebrae described by Dias-da-Silva et al. (2006b) and the vertebrae described here from the Sanga do Cabral Formation

could belong to an indeterminate seymouriamorph (see Fig. 6), although we cannot exclude also the possibility of vertebrae belonging to a pareisaur or even to a diadectomorph, according to the similar general morphology observed among the dorsal series in these taxa (see Fig. 7).

4.3. Biostratigraphic and palaeobiogeographic considerations

The Early Triassic age of the Brazilian Sanga do Cabral Formation is mainly supported by the presence of the procolophonid *P. trigoniceps* (Barberena et al., 1985a,b; Lavina, 1983). As we previously mentioned, most records from this unit are very fragmentary and some attributions are questionable and may thus not be very reliable stratigraphic markers. At the moment, *P. trigoniceps* is the only procolophonid species present in the Sanga do Cabral Formation because of the recent synonymy of the previously described species (Cisneros, 2008). *Sangaia lavinae* is a second taxon that supports an Early Triassic age for the Sanga do Cabral Formation (Dias-da-Silva and Marsicano, 2006; Dias-da-Silva et al., 2006a). This taxon is a basal rhytidosteid that possesses some characters not previously reported in any other Triassic member of the group, such as the presence of a lacrimal bone, which, instead, occur in the only known putative Permian rhytidosteid *Trucheosaurus major*

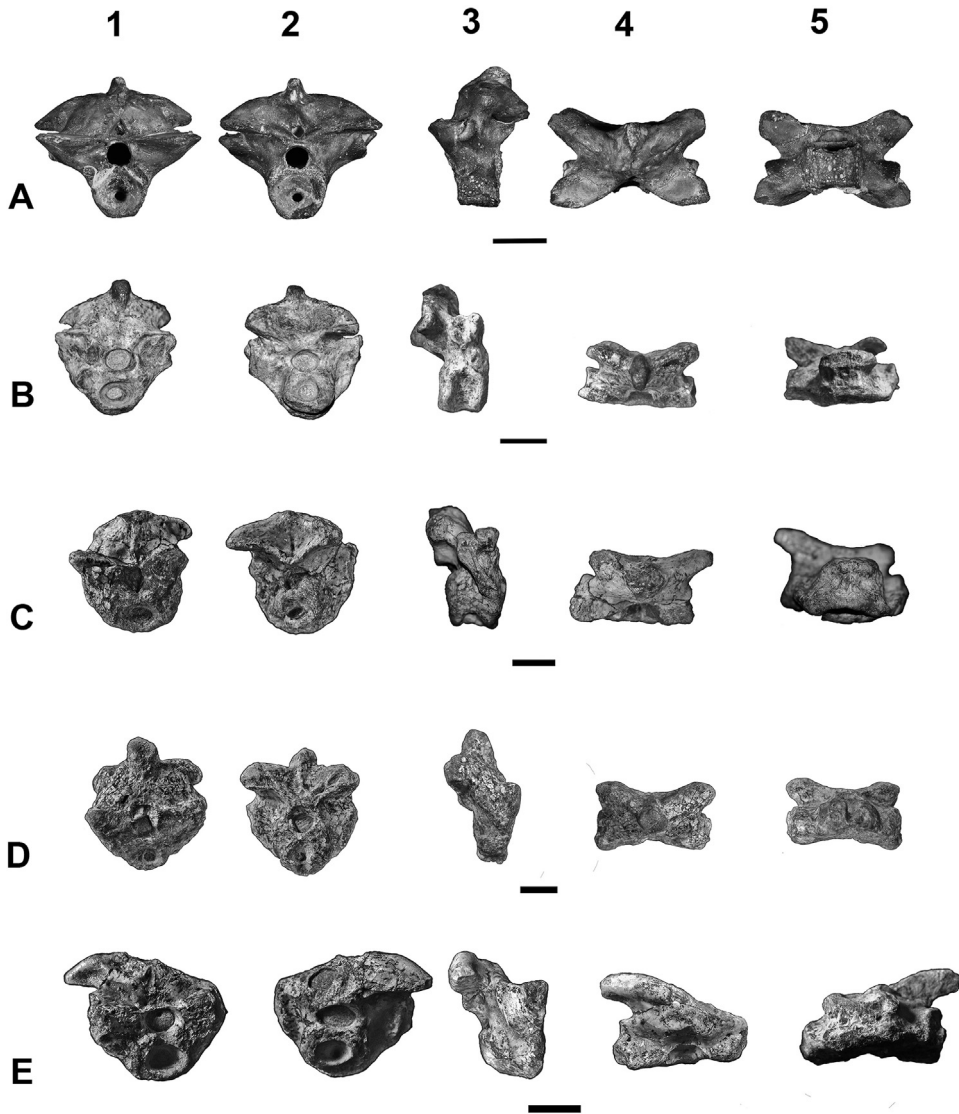


Fig. 6. Dorsal vertebra of *Seymouria* (A, 1–5) (courtesy of Robert Reisz) and the described vertebrae from the Sanga do Cabral Formation, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil (MCN-PV 2722) (B, 1–5), 2723 (C, 1–5), 20000 (D, 1–5) and 20001 (E, 1–5) showing their general similar morphology. Particularly notable is the posterolateral developing of the postzygapophyses in all the figured vertebrae. Scale bars: 10 mm.
Fig. 6. Vertèbre dorsale de *Seymouria* (A, 1–5) (avec la permission de Robert Reisz), et les vertèbres décrites en provenance de la formation Sanga do Cabral, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil (MCN-PV) 2722 (B, 1–5), 2723 (C, 1–5), 20000 (D, 1–5) et 20001 (E, 1–5), montrant leurs morphologies générales similaires. À noter en particulier le développement postéro-latéral des postzygapophyses dans toutes les vertèbres figurées. Barres d'échelle = 10 mm.

(Marsicano and Warren, 1998). If the putative presence of basal synapsids and pareiasaurs could be confirmed in the fossiliferous conglomerates of the Sanga do Cabral Formation, it would weaken the case for an Early Triassic age of the Brazilian unit. In this regard, a transitional Permo-Triassic age has been also previously suggested for the Sanga do Cabral Formation based on stratigraphic data (Faccini, 1989; Nowatzki and Klein, 2001), although subsequently, Faccini (2007) supported the proposed Early Triassic age. As a result, the described vertebrae, which may indicate the presence of seymouriamorphs, an exclusively Permian taxon [although reaching the Late Permian, (Bulanov, 2003; Laurin, 2000)] in the Sanga do Cabral

Formation, requires a reappraisal of the geological age of this unit. The vertebrae described here are also compatible with the presence of two diachronic communities of continental tetrapods in the Sanga do Cabral conglomerates, or with a taxonomically complex, transitional Permo-Triassic biota, resembling that recorded in the Buena Vista Formation of Uruguay, its historically proposed stratigraphic equivalent unit (see Bossi and Navarro, 1991; Piñeiro et al., 2007a, 2012). Survivorship of seymouriamorphs, pareiasaurs or even diadectomorphs in Gondwana until the end of the Permian or the beginning of the Triassic is conceivable, but considering that the fossiliferous levels of the Sanga do Cabral Formation are intraformational

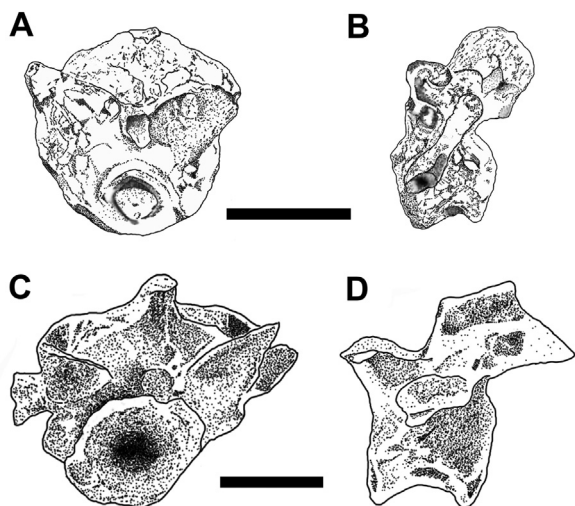


Fig. 7. Morphological comparison between Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil (MCN-PV) 2723 (A–B) and an anterior dorsal vertebra of *Limnoscelis* sp. (C–D) modified from Sumida (1990, Plate 3A, B), in anterior and lateral view, respectively. The different development of the transverse processes and the anteroposterior length of the centrum, as well as the unlike morphology of the facet for the rib could be related to the different position of the vertebrae in the vertebral column.

Fig. 7. Comparaison morphologique entre Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil (MCN-PV 2723) (A–B) et une vertèbre dorsale antérieure de *Limnoscelis* sp. (C–D), modifié d'après Sumida (1990, Planche 3A, B) en vues antérieure et latérale respectivement. Le développement différent des processus transverses et la longueur antéro-postérieure du centre, de même que la morphologie dissemblable de la facette pour la côte pourraient être reliés à la position différente des vertèbres dans la colonne vertébrale.

conglomerates, a rejuvenation of the materials described here due to reworking of stratigraphically lower levels cannot be dismissed. However, it is possible that the Buena Vista conglomerates originated by the reworking of claystone levels intercalated in the main sandstone of the same unit, as there is still no evidence that the fossils come from older strata.

Because of the fragmentary nature of the specimens, we cannot make a firm taxonomic identification; thus, we should be cautious about possible palaeobiogeographic implications of our findings. Nevertheless, if the vertebrae belong to an unknown seymouriamorph, which is the hypothesis that fits best the currently prevailing biostratigraphic scheme, they represent the first evidence of this group in Gondwana. If so, the Sanga do Cabral vertebrae may represent relictual forms that persisted in Gondwana until the Late Permian or even the beginning of the Triassic, thus briefly surviving the Permo-Triassic extinction event.

Acknowledgements

We thank Andrey Sennikov, Robert Reisz, Valery Golubev and Valery Bulanov for valuable references and images that contribute to the comparative study of the specimens, and Martín Ezcurra for supply interesting suggestions and comments to the manuscript. Stuart Sumida and Robert Reisz made useful comments that highly

improved the manuscript. The research was supported by the grant ANII-FCE 2011.6450 to GP.

References

- Abdala, F., Dias-da-Silva, S., Cisneros, J.C., 2002. First record of non-mammalian cynodonts (Therapsida) in the Sanga do Cabral Formation (Early Triassic) of southern Brazil. *Palaeont. Afr.* 38, 92–97.
- Andreis, R.R., Bossi, G.E., Montardo, D.K., 1980. O Grupo Rosário do Sul (Triássico) no Rio Grande do Sul, Brasil. *An. XXXI Congr. Bras. Geol., Florianópolis* 2, 659–673.
- Azevedo, S.A., Lavina, E.L., Barberena, M.C., Ferrando, L., Andreis, R., 1985. Evidências de correlação entre a Formação Yaguari (Uruguai) e as Formações Rio do Rasto e Sanga do Cabral (Rio Grande do Sul-Brasil). *Pesquisas* 17, 112–121.
- Barberena, M.C., Araújo, D.C., Lavina, E.L., 1985a. Late Permian and Triassic tetrapods of southern Brazil. *Nat. Geo. Res.* 1, 5–20.
- Barberena, M.C., Araújo, D.C., Lavina, E.L., Azevedo, S.A., 1985b. O estado atual do conhecimento sobre os tetrápodes Permianos e Triássicos do Brasil Meridional. *MME-DNPM. Colêctanea Trabalhos Paleont. Ser. Geol.* 27, 21–28.
- Berman, D.S., Sumida, S.S., 1990. A new species of *Limnoscelis* (Amphibia: Diadectomorpha) from the Late Pennsylvanian Sangre de Cristo Formation of Central Colorado. *Anns. Carnegie Mus.* 59, 303–341.
- Berman, D.S., Sumida, S.S., Lombard, R.E., 1992. Reinterpretation of the temporal and occipital regions in *Diadectes* and the relationship of diadectomorphs. *J. Paleontol.* 66, 481–499.
- Berman, D.S., Sumida, S.S., Lombard, R.E., 1997. Biogeography of primitive amniotes. In: Sumida, S.S., Martin, K.L.M. (Eds.), *Amniote Origins: Completing the Transition to Land*. Academic Press, London, pp. 85–139.
- Berman, D.S., Sumida, S.S., Martens, T., 1998. *Diadectes* (Diadectomorpha: Diadectidae) from the Early Permian of central Germany, with description of a new species. *Anns. Carnegie Mus.* 67, 53–93.
- Berman, D.S., Henrici, A.C., Sumida, S.S., Martens, T., 2000. Redescription of *Seymouria sanjuanensis* (Seymouriamorpha) from the Lower Permian of Germany based on complete, mature specimens with a discussion of paleoecology of the Bromacker Locality Assemblage. *J. Vertebr. Paleontol.* 20, 53–268.
- Boonstra, L.D., 1935. On a pareiasaurian reptile from South Africa, *Bradysaurus whaitsi*. *Am. Mus. Nov.* 770, 1–4.
- Bossi, J., Navarro, R., 1991. *Geología del Uruguay*. Departamento de Publicaciones Universidad de la República, Montevideo (970 p.).
- Bulanov, V.V., 2003. Evolution and systematics of seymouriamorph parareptiles". *Paleont. J.* 37 (Supplement 1), 1–105.
- Campione, N.E., Reisz, R.R., 2010. *Varanops brevirostris* (Eupelycosauria: Varanopidae) from the Lower Permian of Texas, with discussion of varanopid morphology and interrelationships. *J. Vertebr. Paleontol.* 30 (3), 724–746.
- Carroll, R.L., 1967. A *Limnoscelid* Reptile from the Middle Pennsylvanian. *J. Paleont.* 41 (5), 1256–1261.
- Carroll, R.L., Lindsay, W., 1985. The cranial anatomy of the primitive reptile *Procolophon*. *Can. J. Earth Sci.* 22, 1571–1587.
- Case, E.C., 1910. New or little known reptiles and amphibians from the Permian (?) of Texas. *Bull. Am. Mus. Nat. Hist.* 28, 163–182.
- Case, E.C., Williston, S.W., 1913. Description of a nearly complete skeleton of *Diasparactus zenos* Case. *Publ. Carnegie Inst.* 8, 17–35.
- Cisneros, J.C., 2008. Taxonomic status of the reptile genus *Procolophon* from the Gondwanan Triassic. *Palaeont. Afr.* 43, 7–17.
- Cisneros, J.C., Schultz, C.L., 2002. *Procolophon brasiliensis*, n. sp., a new procolophonid reptile from the Lower Triassic of southern Brazil. *Neues Jb. Geol. Paläont. Monatshefte* 11, 641–648.
- Cisneros, J.C., Abdala, F., Malabarba, M.C., 2005. Pareiasaurids from the Rio do Rasto Formation, southern Brazil: biostratigraphic implications for Permian faunas of the Paraná Basin. *Rev. Bras. Paleont.* 8, 13–24.
- Colbert, E.H., Kitching, J.W., 1975. The Triassic reptile *Procolophon* in Antarctica. *Am. Mus. Novitates* 2566, 1–23.
- Da-Rosa, A.A., Piñeiro, G., Dias-da-Silva, S., Cisneros, J.C., Feltrim, F.F., Witek-Neto, L., 2009. "Sítio Bica São Tomé", um novo sítio fossilífero para o Triássico Inferior do sul do Brasil. *Rev. Bras. Paleont.* 12, 67–76.
- deBraga, M., 2003. The postcranial skeleton, phylogenetic position, and probable lifestyle of the Early Triassic reptile *Procolophon trigoniceps*. *Can. J. Earth Sci.* 40, 527–556.
- Dias-da-Silva, S., Marsicano, C., 2006. *Sangaia*, a replacement generic name for the rhytidosteid temnospondyl *Cabralia*, a preoccupied name. *J. Vertebr. Paleontol.* 26, 1004. <http://dx.doi.org/10.1671/0272.4634>.

- Dias-da-Silva, S., Marsicano, C., Schultz, C.L., 2006a. Rhytidosteid temnospondyls in Gondwana: a new taxon from the Lower Triassic of Brazil. *Palaeontology* 49, 381–390.
- Dias-da-Silva, S., Modesto, S.P., Schultz, C.L., 2006b. New material of *Procolophon* (Parareptilia: Procolophonoidea) from the Lower Triassic of Brazil, with remarks on the ages of the Sanga do Cabral and Buena Vista formations of South America. *Can. J. Earth Sci.* 43, 1685–1693.
- Ezcurra, M.D.E., Velozo, P., Meneghel, M., Piñeiro, G., 2015. Early archosauromorph remains from the Permo-Triassic Buena Vista Formation of north-eastern Uruguay. *Peer J.* 3, e776, <http://dx.doi.org/10.7717/peerj.776>.
- Faccini, U.F., 1989. O Permo-Triássico do Rio Grande do Sul. Uma análise sob o ponto de vista das seqüências deposicionais. Curso de Pós-Graduação em Geociências, Dissertação de Mestrado. Universidade do Rio Grande do Sul (unpublished) (121 p.).
- Faccini, U.F., 2007. Tectonic and climatic induced changes in depositional styles of the Mesozoic sedimentary record of southern Paraná Basin, Brazil. In: Iannuzzi, R., Boardman, D.R. (Eds.), *Problems in western Gondwana Geology I*. Gramado, pp. 42–45 (Extended abstracts).
- Ferigolo, J., Ribeiro, A.M., Piñeiro, G., 2013. First record of a Brazilian “pelycosaur”-grade synapsid. In: XIII Congr. Bras. Paleont. Gramado, Brazil. *Paleontologia em Destaque/Boletim de Resumos*, 225 p.
- Gauthier, J., Kluge, A.G., Rowe, T., 1988. The early evolution of the Amniota. In: Benton, M.J. (Ed.), *The Phylogeny and Classification of the Tetrapods*, No. 1: Amphibians, Reptiles, Birds. Clarendon Press, Oxford, pp. 103–155.
- Gow, C.E., Rubidge, B.S., 1997. The oldest procolophonoid (Amniota: Parareptilia)—new discovery from the Lower Beaufort of South Africa. *Palaeont. Afr.* 34, 49–53.
- Greenewald, G.H., Kitching, J.W., 1995. Biostratigraphy of the *Lystrosaurus* Assemblage Zone. In: Kitching, J.W. (Ed.), *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*, Biostratigraphic Series 1. South African Committee for Stratigraphy, South Africa, pp. 35–40.
- Hatschek, B., Cori, C.J., 1896. *Elementarcus der Zootomie in fünfzen Vorlesungen*. Gustav Fischer, Jena.
- Holz, M., Scherer, C.M., 1998. Sedimentological and paleontological evidence of paleoclimatic change during the Southbrazilian Triassic: the register of a global trend towards a humid paleoclimate. *Zent. Geol. und Paläont. Teil 1* 11–12, 1589–1609.
- Ivachenko, M., 1973. New Cisuralian cotylosaurs. *Paleont. Zhur* 2, 131–134.
- Jalil, N.O., Janvier, P., 2005. Les pareiasaures (Amniota: Parareptilia) du Permien supérieur du Bassin d’Argana, Maroc. *Geodiversitas* 27, 35–132.
- King, G.M., Jenkins, I., 1997. The dicynodont *Lystrosaurus* from the Upper Permian of Zambia: evolutionary and stratigraphical implications. *Palaeontology* 40 (1), 149–156.
- Kissel, R., 2010. Morphology, Phylogeny, and Evolution of Diadectidae (Cotylosauria: Diadectomorpha). University of Toronto Press, Toronto, 185 p. (hdl:1807/24357).
- Kissel, R.A., Reisz, R.R., 2004. *Ambedus pusillus*, new genus, new species, a small diadectid (Tetrapoda: Diadectomorpha) from the Lower Permian of Ohio, with a consideration of diadectomorph phylogeny. *Anns. Carnegie Mus.* 73, 197–212.
- Langer, M.C., Lavina, E.L., 2000. Os amniotas do Neopermiano e Eotriássico da Bacia do Paraná – répteis e “répteis mamaliformes”. In: Holz, M., De Ros, L.F. (Eds.), *Paleontologia do Rio Grande do Sul*. Universidade Federal do Rio Grande do Sul – CIGO – Centro de Investigação do Gondwana, pp. 210–235.
- Langston, J.R., 1966. *Limnosceloides brachycoles* (Reptilia: Captorhinomorpha) a new species from the Lower Permian of New Mexico. *J. Paleontol.* 40, 690–695.
- Laurin, M., 2000. Seymouriamorphs. In: Heatwole, H., Carroll, R.L. (Eds.), *Amphibian Biology*. Surrey Beatty & Sons, Chipping Norton, pp. 1064–1080.
- Laurin, M., Reisz, R.R., 1997. A new perspective on tetrapod phylogeny. In: Sumida, S.S., Martin, K.L.M. (Eds.), *Amniote Origins: Completing the Transition to Land*. London Academic Press, London, pp. 9–59.
- Laurin, M., Reisz, R.R., 1999. A new study of *Solenodonsaurus janenschii*, and a reconsideration of amniote origins and stegocephalian evolution. *Can. J. Earth Sci.* 36, 1239–1255.
- Lavina, E.L., 1983. *Procolophon pricei* sp. n., um novo réptil procolofonídeo do Triássico do Rio Grande do Sul. *Iheringia, Ser. Geol.* 9, 51–78.
- Lavina, E.L., Barberena, M., 1985. Anfíbios ritidosteídeos y lidekkerinídeos da Formação Sanga Do Cabral (Triássico inferior do Rio Grande do Sul) Implicações bioestratigráficas y geocronológicas. *Iheringia, Ser. Geol.* 10, 19–27.
- Lee, M.S.Y., 1995. Historical burden in systematics and the interrelationships of “parareptiles”. *Biol. Rev.* 70, 459–547.
- Lee, M.S.Y., 1997. A taxonomic revision of pareiasaurian reptiles: implications for Permian terrestrial palaeoecology. *Mod. Geol.* 21, 231–298.
- Lee, M.S.Y., Spencer, P.S., 1997. Crown-clades, key characters and taxonomic stability: when is an amniote not an amniote? In: Sumida, S.S., Martin, K.L.M. (Eds.), *Amniote Origins: Completing the Transition to Land*. London Academic Press, London, pp. 61–84.
- Lewis, G.E., Vaughn, P.P., 1965. Early Permian vertebrates from the Cutler Formation of the Placerville Area Colorado. *United State Geol. Survey Prof. Pap.* C 503, 1–46.
- Marsicano, C.A., Warren, A.A., 1998. The first Palaeozoic rhytidosteid: *Trucheosaurus major* (Woodward, 1909) from the Late Permian of Australia, and a reassessment of the Rhytidosteidae (Amphibia, Temnospondyli). *Bull. Nat. Hist. Mus. London (Geol.)* 54, 147–154.
- Milani, E.J., Gonçalves de Melo, J.E., Alves de Souza, P., Fernandes, L.A., França, A.B., 2007. Bacia do Paraná. *B. Geoci. Petrobras* 15 (2), 265–287.
- Modesto, S.P., 1992. Did herbivory foster early amniote diversification? *J. Vertebr. Paleontol.* 12, 44A.
- Moss, J.L., 1972. The morphology and phylogenetic relationships of the Lower Permian tetrapod *Tseajaia campi* Vaughn (Amphibia: Seymouriamorpha). *Univ. Calif. Publ. Geol. Sci.* 98, 1–72.
- Nesbitt, S.J., 2011. The early evolution of archosaurs: relationships and the origin of major clades. *Am. Mus. Nat. Hist. Bull.* 352, 1–292, <http://dx.doi.org/10.1206/352.1>.
- Nowatzki, C.H., Klein, C., 2001. A Formação Sanga do Cabral na Região de São Leopoldo, Rio Grande do Sul, Brasil. *Geol. Colombiana* 26, 45–57.
- Olson, E.C., 1947. The family Diadectidae and its bearing on the classification of reptiles. *Fieldiana Geol.* 11, 1–53.
- Peabody, F.E., 1952. *Petrolacosaurus kansensis* Lane, a Pennsylvanian reptile from Kansas. *Vertebrata* 1, 1–41 (University of Kansas. Paleontological contributions).
- Piñeiro, G., (MSc Thesis, PEDECIBA) 2002. Paleofaunas del Pérmico-Eotriássico de Uruguay. Universidad de Montevideo, Uruguay (208 p. + 28 figs.).
- Piñeiro, G., Ubilla, M., 2003. Unidades Permo-Triássicas en la Cuenca Norte: paleontología y ambientes. In: Veroslavsky, G., Ubilla, M., Martinez, S. (Eds.), *Cuencas sedimentarias de Uruguay: Mesozoico*. D.I.R.A.C., Montevideo, pp. 33–49.
- Piñeiro, G., Verde, M., Ubilla, M., Ferigolo, J., 2003. First basal synapsids (“pelycosaur”) from the Upper Permian-Lower Triassic of Uruguay, South America. *J. Paleontol.* 77, 389–392.
- Piñeiro, G., Rojas, A., Ubilla, M., 2004. A new procolophonoid (Reptilia: Parareptilia) from the Upper Permian of Uruguay. *J. Vertebr. Paleontol.* 24, 814–821.
- Piñeiro, G., Marsicano, C., Goso, C., Morosi, E., 2007a. Temnospondyl diversity of the Permian-Triassic Colonia Orozco Local Fauna (Buena Vista Formation) of Uruguay. *Rev. Bras. Paleont.* 10, 169–180.
- Piñeiro, G., Marsicano, C., Lorenzo, N., 2007b. A new temnospondyl from the Late Permian-Early Triassic of Uruguay. *Palaeontology* 50, 627–640.
- Piñeiro, G., Marsicano, C., Damiani, R., 2007c. Mandibles of mastodontosaurid temnospondyls from the Upper Permian-Lower Triassic of Uruguay. *Acta Palaeont. Pol.* 52, 695–703.
- Piñeiro, G., Ramos, A., Marsicano, C., 2012. A rhinesuchid-like temnospondyl from the Permo-Triassic of Uruguay. *C. R. Palevol.* 11, 65–78.
- Reisz, R.R., Laurin, M., 2004. A reevaluation of the enigmatic Permian synapsid *Watongia* and of its stratigraphic significance. *Can. J. Earth Sci.* 41, 377–386.
- Romer, A.S., 1956. *The osteology of Reptiles*. University Chicago Press, Chicago (772 p.).
- Rubidge, B.S., 2005. Re-uniting lost continents—fossil reptiles from the ancient Karoo and their wanderlust. *South Afr. J. Geol.* 108, 135–172.
- Santos, R.V., Souza, P.A., Alvarenga, C.J.S., Dantas, E.L., Pimentel, E.L., Oliveira, C.G., Araújo, L.M., 2006. Shrimp U–Pb Zircon Dating and Palynology of Bentonitic Layers from the Permian Irati Formation Parana Basin, Brazil. *Gondwana Res.* 9, 456–463.
- Schultz, C.L., Dias-da-Silva, S., 1999. A possible new pareiasaurid in the Sanga do Cabral Formation, Lower Triassic of southern Brazil. *Paleont. em Destaque* 26, 49.
- Schwanke, C., Kellner, A.W.A., 1999. Sobre o primeiro registro de Synapsida no Triássico basal do Brasil. In: XVI Congresso Brasileiro de Paleontologia, Boletim de Resumos, p. 101.
- Sennikov, A.G., 1996a. Evolution of the Permian and Triassic tetrapod communities of Eastern Europe. *Palaeoclimatol. Palaeogeogr. Palaeoecol.* 123, 31–351.
- Sennikov, A.G., 1996b. Evolution of the Permian and Triassic communities of Eastern Europe. *Palaeoclimatol. Palaeogeogr. Palaeoecol.* 120, 331–351.

- Sullivan, C., Reisz, R.R., 1999. First record of *Seymouria* (Vertebrata, Seymouriamorpha) from the Early Permian fissure fills at Rikchard Spur, Oklahoma. *Can. J. Earth Sci.* 36, 1257–1266.
- Sumida, S.S., 1990. Vertebral morphology, alternation of neural spine height, and structure in Permo-Carboniferous tetrapods, and a reappraisal of primitive modes of terrestrial locomotion. University of California Press, California (129 p. + 3 plates).
- Sumida, S.S., Modesto, S.P., 2001. A phylogenetic perspective on locomotory strategies in early amniotes. *Am. Zool.* 41, 586–597.
- Sumida, S.S., Lombard, E.R., Berman, D.S., 1992. Morphology of the atlas-axis complex of the Late Palaeozoic tetrapod suborders Diadectomorpha and Seymouriamorpha. *Phil. Trans. R. Soc. Lond.* 336, 259–273.
- Surkov, M.V., Kalandadze, N.N., Benton, M.J., 2005. *Lystrosaurus georgi*, a dycinodont from the Lower Triassic of Russia. *J. Vertebr. Paleontol.* 25 (2), 402–413.
- Tsuji, L.A., Sidor, C.A., Steyer, J.S., Smith, R.M., Tabor, N.J., Ide, O., 2013. The vertebrate fauna of the Upper Permian of Niger—vii. Cranial anatomy and relationships of *Bunostegos akokanensis* (Pareiasauria). *J. Vert. Paleont.* 33 (4), 747–763.
- Ward, P.D., Botha, J., Buick, R., De Kock, M.O., Erwin, D.H., Garrison, G.H., Kirschvink, J.L., Smith, R., 2005. Abrupt and gradual extinction among Late Permian land vertebrates in the Karoo Basin, South Africa. *Science* 307, 709–714.
- Wideman, N.K., Sumida, S.S., O'Neil, M., 2005. A reassessment of the taxonomic status of the materials assigned to the Early Permian tetrapod genera *Limnosceloides* and *Limnoscelops*. *New Mexico Mus. Natl. Hist. Sci. Bull.* 30, 358–362.
- Williston, S.W., 1911. A new family of Reptiles from the Permian of New Mexico. *Am. J. Sci.* 4, 378–398.
- Xu, L., Li, X-W., Jia, S-H., Liu, J., in press. The Jiyuan tetrapod Fauna of the Upper Permian of China—1. New pareiasaur material and the reestablishment of *Honania complicidentata*. *Acta Palaeontologica Polonica*. doi.org/10.4202/app.00035.2013 (available online 14 January, 2014).
- Zerfass, H., 2003. História tectônica e sedimentar do Triássico da Bacia do Paraná (Rio Grande do Sul, Brasil) e comparação Geológica com as bacias de Ischigualasto e de Cuyo (Argentina) (PhD. Thesis). Universidade Federal do Rio Grande do Sul. Instituto de Geociências. Programa de Pós-graduação em Geociências, Porto Alegre, Brasil (191 p.).
- Zerfass, H., Lavina, E.L., Schultz, C.L., Garcia, A.J.V., Faccini, U.F., Chemale Jr., F., 2003. Sequence stratigraphy of continental Triassic strata of southernmost Brazil: a contribution to southwestern Gondwana palaeogeography and palaeoclimate. *Sediment. Geol.* 161, 85–105.