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On the presence of a pustulated temnospondyl in the Lower Triassic of southern Brazil

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The fossil record of temnospondyls in South America has been greatly expanded in the last 10 years, increasing their overall significance. They occur in Argentina, Brazil, and Uruguay, and range from the Guadalupian to the Late Triassic. The Early Triassic temnospondyl record in southern Brazil is mainly composed of fragmentary specimens, usually represented by dermal skull bones from the Sanga do Cabral Formation. Some of these fragments were tentatively referred to Lydekkerinidae and Rhytidosteidae based on their characteristic ridge-grooved “spider-web” pattern of ornamentation. In this contribution we report, for the first time, a temnospondyl skull fragment with pustulated sculpturing pattern, which is tentatively ascribed to Plagiosauridae. This new record could indicate the presence of a new temnospondyl taxon for the Lower Triassic of South America.

Key words: Temnospondyli, Plagiosauridae, paleobiogeography, Sanga do Cabral Formation, Lower Triassic, western Gondwana.

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Introduction

The Early Triassic temnospondyl record in southern Brazil is scarce and fragmentary, and, to the present, it is only represented by *Sangaia lavinae*, an undoubted rhytidosteid stereospondyl from the Sanga do Cabral Formation (Dias-da-Silva and Marsicano 2006; Dias-da-Silva et al. 2006). Other Brazilian specimens were attributed to Temnospondyli incertae sedis, Stereospondyli incertae sedis, and putative “lydekkerinids”, and rhytidosteids (Lavina and Barberena 1985; Dias-da-Silva et al. 2005). Except for the recent description of postcranial temnospondyl remains (see Dias-da-Silva and Schultz 2008) most of the specimens from the Sanga do Cabral Formation comprise dermal skull fragments which display a reticulate pattern of ornamentation, the so-called “spider web” pattern sensu Cosgriff and Zawiskie (1979) typical of most temnospondyls. This pattern consists of pitting at the bone ossification centers, which becomes a ridge-grooved pattern peripherally. In rhytidosteids, the pattern of ornamentation is quite diverse, with nodules or pustules present at points of junction and bifurcation of ridges and sulci (see Cosgriff and Zawiskie 1979).

This contribution is a preliminary report of a temnospondyl fragment from the Sanga do Cabral Formation with a rare pustular sculpturing, where neither crest nor ridges are present. While it seems reasonable to consider the presence of a new temnospondyl group for the Sanga do Cabral For-

mation, more complete specimens will be needed to erect a new taxon.

Institutional abbreviations.—MCN, Museu de Ciências Naturais da Fundação Zoobotânica do Estado do Rio Grande do Sul; PV, Paleovertebrates collection.

The temnospondyl record in South America

Occurrences of temnospondyls in South America can be summarized as follows: Permo-Triassic strata from the Buena Vista Formation in Uruguay have yielded a poorly preserved dvinosaurid (Marsicano et al. 2000; Piñeiro et al. 2007c), the laidleriid *Uruiella liminea* and still unnamed mandibular specimens attributed to Mastodontosauridae (Piñeiro et al. 2007a, b). In Argentina, five Late Triassic occurrences were reported, all ranging from Carnian to Norian: the poorly preserved mastodontosaurid *Promastodontosaurus bellmanni* from the Ischigualasto Formation, Ischigualasto Basin (Bonaparte 1963), the chigutisaurids *Pelorocephalus mendonzensis* and *P. cacheutensis* (Marsicano 1999), a still unnamed mandibular fragment of a brachyopid from the Cacheuta Formation, Cuyana Basin (Marsicano 2005), and *P. tenax*, from the Rio Blanco Formation, Cuyana Basin (Marsicano 1999). The temnospondyl record in Brazil ranges from the Guadalupian

to the Late Triassic. Guadalupian temnospondyls comprise two long snouted archegosaurids: *Prionosuchus plummeri*, from the Pedra de Fogo Formation, Paranaíba Basin, Northern Brazil (Price 1948; Cox and Hutchinson 1991) and *Bageherpeton longignathus*, from the Morro Pelado Member, Rio do Rasto Formation, Paraná Basin, Southern Brazil (Dias and Barberena 2001); also, two rhinesuchids, the long snouted *Australerpeton cosgriffi* and an unnamed short-snouted rhinesuchid, both from the locality of Serra do Cadeado, Rio do Rasto Formation (Barberena 1998; Barberena and Dias 1998; Dias and Schultz 2003); and an indeterminate mandible which was included with the other records from southern Morro Pelado Member (Malabarba et al. 2003). Early Triassic temnospondyls are recognized in Southern Brazil (Sanga do Cabral Formation, Paraná Basin) comprising dermal skull fragments tentatively attributed to lydekkerinid and rhytidosteid stereospondyls (Lavina and Barberena 1985; Dias-da-Silva et al. 2005) and the rhytidosteid *Sangaia lavinai* (Dias-da-Silva et al. 2006; Dias-da-Silva and Marsicano 2006). The Late Triassic temnospondyl record in Brazil is restricted to the occurrence of a single interclavicular element tentatively attributed to Mastodonsauroidea (Dias-da-Silva et al. 2009). To the present, temnospondyls are still not reported in the Middle Triassic of Brazil and Argentina (Dias-da-Silva et al. 2009) and the presence of Middle Triassic strata in Uruguay are not reported so far.

Geological and stratigraphical setting

The Triassic infilling of the Paraná Basin in southern Brazil (Rosário do Sul Group) is non-marine (Pierini et al. 2002; Zeffass et al. 2003). The Lower Triassic Sanga do Cabral Formation is a 50 to 100 m thick unit that crops out in southern Brazil (for the location of the main outcrops, see Dias-da-Silva et al. 2006) and unconformably covers the Rio do Rasto and Pirambóia formations (Andreis et al. 1980; Scherer et al. 2000). Massive to trough cross-bedded intraformational conglomerates and horizontally bedded sandstones are present and are interpreted as deposited by braided river systems with poorly confined channels that were developed on a low gradient alluvial plain. Argillaceous lenses in the sequence provide evidence of lakes and ponds related to the alluvial plains (Zeffass et al. 2003). The bone-bearing levels correspond to intraformational conglomerates that yield disarticulated and fragmented tetrapods. The Early Triassic age of the Sanga do Cabral Formation was based on the presence of the procolophonids *Procolophon pricei*, *P. brasiliensis*, and a definite rhytidosteid (*Sangaia lavinai*), which are present in both southern Brazil and South Africa (Lavina 1983; Cisneros and Schultz 2002; Dias-da-Silva et al. 2006; Dias-da-Silva and Marsicano 2006). Recently, Cisneros (2008) reevaluated the taxonomic status of *P. pricei* and *P. brasiliensis* and considered both taxa junior synonyms of *P. trigoniceps*, a procolophonid

widespread in Lower Triassic Gondwanan deposits. Therefore, only *P. trigoniceps* occurs in Lower Triassic deposits from Gondwana (Cisneros 2008). Regarding rhytidosteid stereospondyls, this monophyletic group is almost completely composed of Early Triassic taxa. The sole exception is *Trucho-saurus major*, a Late Permian rhytidosteid from Australia (see Marsicano and Warren 1998; Schoch and Milner 2000).

Material and methods

MCN PV 1999a (Fig. 1A), a dermal skull fragment that includes four dorsoventrally compressed partial bones (Figs. 1A, 2) and MCN PV 1999b (Fig. 1B) a natural cast which partially fits MCN PV 1999a. MCN PV 1999a, b are partially embedded in the enclosing rock and comprise thin dermal elements. Mechanical preparation of the specimens was avoided, since the surrounding rock provide a good support and reinforcement to the slender and delicate bones.

Systematic paleontology

Temnospondyli von Zittel, 1888

Stereospondylomorpha Yates and Warren, 2000

?Stereospondyli von Zittel, 1888

?Plagiosauroida Kuhn, 1965

?Plagiosauridae Abel, 1919

?Plagiosauridae indet.

Figs. 1, 2.

Locality and horizon: 6.4 km from the beginning of the BR 158 (a federal highway), that connects the municipalities of Santa Maria and Rosário do Sul (Coordinates 29°42'59.45"S 53°54'01.76"W). *Lystrosaurus* Assemblage Zone, Sanga do Cabral Formation, Lower Triassic, Brazil.

Material.—MCN PV 1999a, a dermal skull fragment including four dorsoventrally compressed partial bones, and MCN PV 1999b, a natural cast which partially fits MCN PV 1999a.

Description.—MCN PV 1999b (Fig. 1B) is a partial natural cast of MCN PV 1999a. Therefore, only MCN PV 1999a is herein described, since MCN PV 1999b does not present any sign of sutures or other features which could be useful in the present study. An arenaceous layer of rock covers the ventral surface of MCN PV 1999a. As a result, only its dorsal view was examined. Four dermal bones can easily be observed, since their sutures are clearly visible through the use of stereoscopic microscope. The overall surface of MCN PV 1999a is covered by a dense pustular field (Fig. 1A, C). There is no sign of concentric crests or peripheral ridges and grooves away from the centre of ossification. Due to the conspicuous presence of pustules, only tiny round grooves can be observed among them (Fig. 1C). However, the pustules of MCN PV 1999a are not as conspicuous as those found, for instance, in the plagiosauroid *Gerrothorax pulcherrimus*

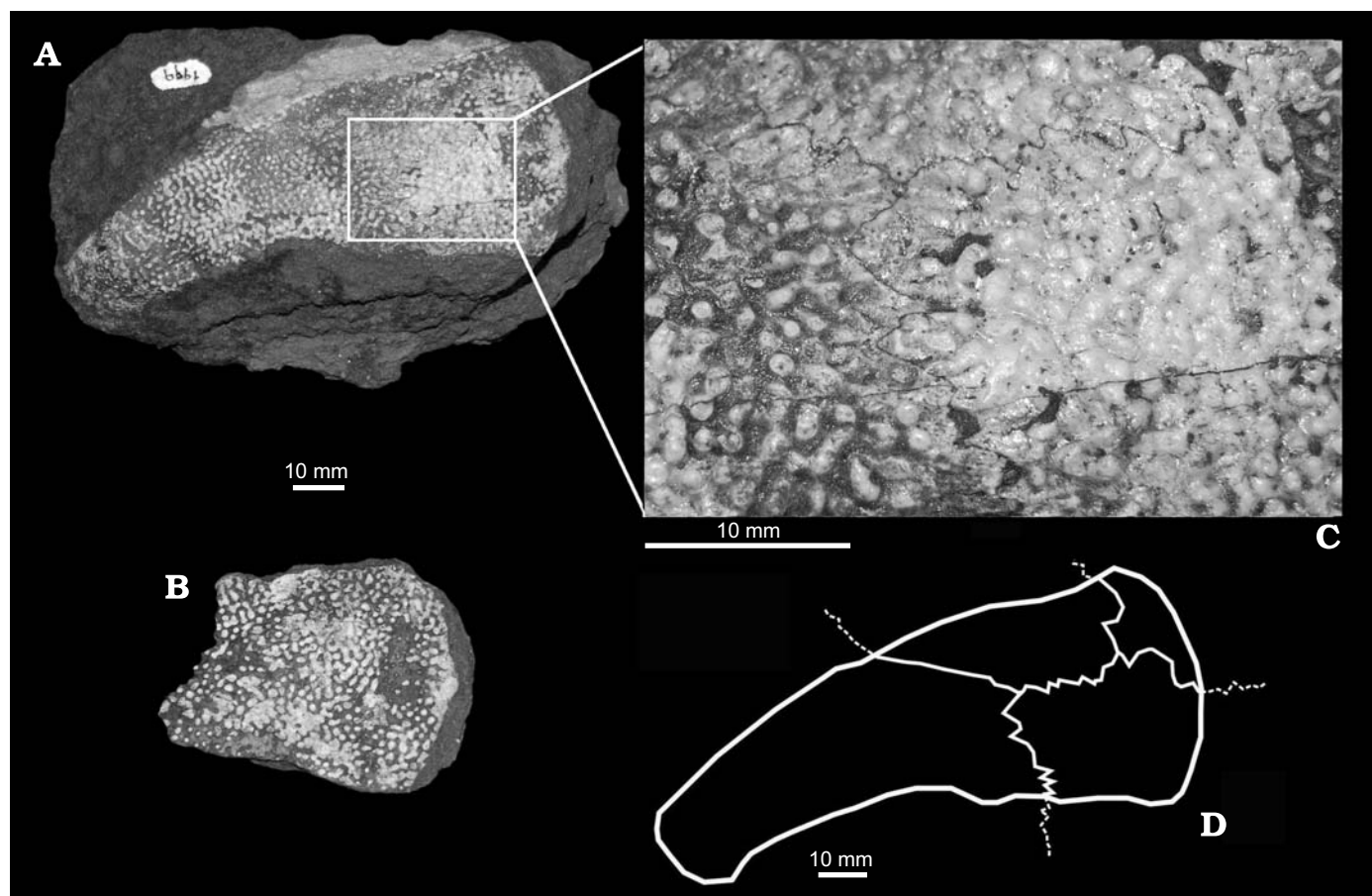


Fig. 1. **A.** MCN PV 1999a, a pustulated temnospondyl from the Lower Triassic Sanga do Cabral Formation (Paraná Basin, Southern Brazil). **B.** MCN PV 1999b, a natural cast that partially fits MCN PV 1999a. **C.** Magnification of PV 1999a, where the pustular ornamentation can be observed in detail. **D.** Schematic drawing showing the sutural contact between the bones of the Brazilian specimen.

(Jenkins et al. 2008) and the chroniosuchian *Chroniosaurus dongusensis* (Golubev 1998), because MCN PV 1999a probably belonged to a subadult specimen, so its pustules were not fully developed. Also, the preserved bones are very thin, which is a common ontogenetic feature in juvenile temnospondyls. In spite of the incompleteness of MCN PV 1999a, a cautious examination was carried out in order to gather useful anatomic information regarding the likely taxonomic position of this material. Unfortunately, it is not possible to be totally confident regarding the completeness of each bone, since most of their margins are embedded in the matrix. Nonetheless, the sutures of MCN PV 1999a are clearly visible and four partial bones are surely present (Fig. 1D). Comparisons of MCN PV 1999a with *Peltobatrachus pustulatus* and plagiosaurid skulls lead us to the proposition of six alternative bone configurations for the Brazilian material. As a result, a description of each one of these six spatial arrangements seems to be pointless, because any particular choice of bone arrangement would be purely speculative. However, for the sake of accuracy, they are provided in Figure 2. MCN PV 1999a fits in two and four possible positions in the skull table of *Peltobatrachus pustulatus* (Fig. 2C, D) and *Gerrothorax pulcherrimus* (Fig. 2E–H), respectively.

Discussion.—This contribution presents a pustulated temnospondyl specimen from the Lower Triassic of Brazil, increasing the significance of this worldwide group of basal tetrapods in western Gondwana. It is important to point out that a pustulated pattern of sculpturing in dermal bones of temnospondyls is known in non-directly related taxa, such as *Peltobatrachus pustulatus*, Plagiosauridae, Amphibamidae (*Micropholis stowi*), Rhytidosteidae, and also in chroniosuchians (Chroniosuchidae) (Panchen 1959; Cosgriff and Zawiskie 1979; Golubev 1998; Schoch and Rubidge 2005; Jenkins et al. 2008; Witzmann and Soler-Gijón 2008). Based solely on the pustular pattern of ornamentation, we could ascribe MCN PV 1999a, b to either *Peltobatrachus* or Plagiosauridae, because in rhytidosteids and chroniosuchians pustules and well-developed crests and ridges are present (Cosgriff and Zawiskie 1979; Golubev 1998). In the “rhytidosteid” pattern of ornamentation (sensu Cosgriff and Zawiskie 1979) pustules are present in the points of junction and bifurcation of crests and ridges of dermal elements of the skull and shoulder girdle in a radiate concentric pattern. We consider this feature a valid argument to exclude the possibility that MCN PV 1999 (which lacks a radiate concentric sculpturing) may represent a new rhytidosteid specimen. A similar situation occurs regarding Late Permian chro-

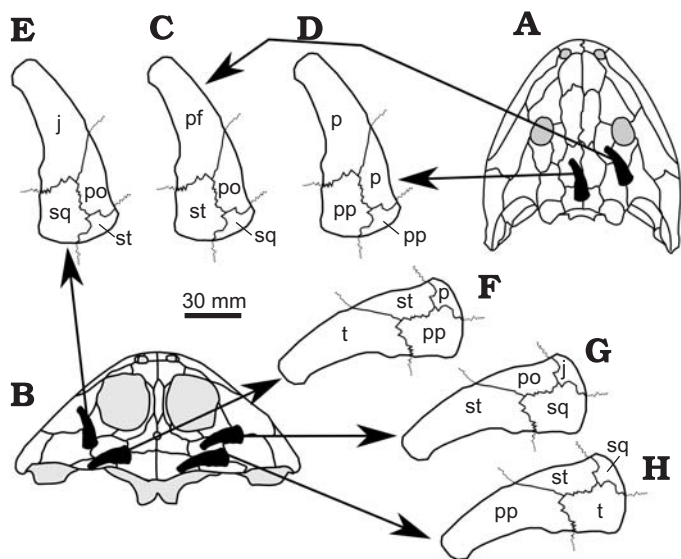


Fig. 2. Schematic drawings showing alternative bone arrangements of MCN PV 1999a. **A.** *Peltobatrachus pustulatus* (skull not to scale, modified from Panchen, 1959). The black areas show two alternative positions of MCN PV 1999a in *P. pustulatus*, enlarged in **C** and **D**. **B.** *Gerrothorax pulcherrimus* (skull not to scale, modified from Jenkins et al. 2008). The black areas show four alternative positions of MCN PV 1999a in *G. pulcherrimus*, enlarged in **E**, **F**, **G**, and **H**. Abbreviations: j, jugal; p, parietal; pf, prefrontal; po, postorbital; pp, postparietal; sq, squamosal; st, supra-temporal; t, tabular.

niosuchians. However, chroniosuchians present pustules along the ridges and not in the points of junction and bifurcation of crests and ridges (Golubev 1998 and personal observation of high resolution photographs of *Chroniosaurus dongusensis*). In the amphibamid *Micropholis stowi*, dermal sculpturing consists of isolated tubercles and short radial ridges (Boy 1985; Schoch and Rubidge 2005). Regarding the hypothesis of a close relationship of MCN PV 1999 with the amphibamid *Micropholis stowi*, it is important to point out that dissorophoid temnospondyls were quite common and diverse during the Early Permian of Laurasia (Yates and Warren 2000; Schoch and Rubidge 2005). However, several small specimens of *Micropholis stowi* represent a relictual occurrence in rocks of the Early Triassic *Lystrosaurus* Assemblage Zone (Beaufort Group; Karoo Supergroup) where a significant number of stereospondyl genera are currently recognized (Schoch and Milner 2000; Yates and Warren 2000). To the present *Micropholis stowi*, the smallest of the Karoo amphibians, is the sole non-stereospondyl South African taxon which, according to Schoch and Rubidge (2005: 502), “has long been referred as a ‘generalized’ small temnospondyl” (see Watson 1913, Romer 1947). According to Schoch and Rubidge (2005), miniaturization was a critical factor in the amphibamid evolution, and, in fact, all current representatives of Amphibamidae (*Amphibamus*, *Eoscopus*, *Platyrhinops*, *Doleserpeton*, and the Early Triassic South African *Micropholis*) are tiny sized individuals, with complete skulls hardly reaching 45 mm in length. MCN PV 1999 is clearly a medium-sized temnospondyl (a giant specimen in comparison with amphibamids).

Also, its pattern of pustular ornamentation is quite different from *Micropholis*, as in this last taxon it consists of isolated tubercles surrounded by short radial ridges. Therefore, we exclude any possibility of an amphibamid assignment to MCN PV 1999. Additional biostratigraphic and phylogenetic information also narrow down the assignment of the Brazilian specimen to Plagiosauridae. *Peltobatrachus pustulatus* is a Late Permian temnospondyl from Tanganyika (Karoo Supergroup). It was firstly regarded as a plagiosauroid (Panchen 1959). However, a further phylogenetic investigation placed it at the base of Stereospondyli, and away from the highly derived Plagiosauridae (Yates and Warren 2000). The size of *Peltobatrachus pustulatus* is consonant with that of the Brazilian specimen MCN PV 1999. However, *P. pustulatus* has a short temporal distribution (early Late Permian) and there is no record of this taxon even remotely close to the Permo-Triassic boundary.

Unless new findings of *Peltobatrachus* increase its temporal range, it seems unreasonable to associate MCN PV 1999 with it, since a tentative taxonomic assignment of the Brazilian taxon to Plagiosauridae is better supported by the available data. Plagiosauridae is a Triassic family of trematosaurian stereospondyls sensu Yates and Warren (2000) and according to Hellrung (2003) it is subdivided into three subfamilies, Plagiosaurinae, Plagiosuchinae, and Plagiosterninae. The first two present a pustular ornamentation, but the third one (Plagiosterninae) presents a reticular pattern of sculpturing. Therefore, the putative Brazilian plagiosaurid might belong to either Plagiosaurinae or Plagiosuchinae.

The supposed presence of plagiosaurids in western Gondwana raises interesting paleobiogeographic implications regarding the stereospondyl evolution and their worldwide distribution, particularly across South America. According to Yates and Warren (2000) plagiosaurids have a sister-group relationship with the terrestrial South African stereospondyl *Laidleria gracilis* (Cynognathus Assemblage Zone, Beaufort Series, Karoo Supergroup), a taxon also regarded as having a close relationship with the Uruguayan non-stereospondyl temnospondyl *Uruiella liminea* (Piñeiro et al. 2007a). Plagiosaurids have been recorded in Germany, Greenland, Russia, Spitsbergen, and possibly in the Upper Triassic of Thailand (Suteethorn et al. 1988; Hellrung 2003; Jenkins et al. 2008). The oldest record of this group was reported from the Early Triassic of Eastern Europe (Shishkin 1967). The well-known and well represented *Gerrothorax* is a long-lived genus, ranging from Ladinian of Kupferzell to the “Rhaetic” of Sweden (Hellrung 2003). Plagiosauridae was long thought as being an exclusive Laurasian clade until Warren (1985) reported plagiosaurid remains (vertebral and mandibular fragments) from the Lower Triassic of Australia (Arcadia Formation, Rewan Group), but later, she withdrew the hypothesis of a plagiosaurid presence in Gondwana by questioning her previous assignment, arguing that the Australian material is fragmentary and of uncertain taxonomy (Warren 2000). Therefore, the putative plagiosaurid found in Brazil could suggest that this group of temnospondyls sur-

vived in Gondwanan habitats. Moreover, the Brazilian material also implies that plagiosaurids were already widespread in the Early Triassic, since there are reports of their presence in Eastern Europe, and putative remains in Australia and Brazil. Indeed, Yates and Warren (2000), pointed out that the Gondwanan region of Pangea could have been a safety area for temnospondyls and other groups. Also, Piñeiro et al. (2007b) stated that plagiosaurids could have ghost lineages well deep into the Upper Permian, then surviving to the Permo-Triassic extinction event. The convergence of pustular ornamentation in different temnospondyls constrains a more accurate identification of the fragmentary specimen herein presented, but still, the unusual pustular pattern present in the dermal bones of MCN PV 1999 strongly suggests the presence of a new taxon in South America, because exclusively pustular ornamentation was never reported before in this part of Gondwana. In conclusion, further prospecting efforts are needed in order to find more complete material to corroborate the presence of plagiosauroids in Lower Triassic deposits from Brazil.

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References

- Andreis, R., Bossi, G.E., and Montardo, D.K. 1980. O Grupo Rosário do Sul (Triássico) no Rio Grande do Sul. *Anais do XXXI Congresso Brasileiro de Geologia, Camboriú, Santa Catarina* 1309: 659–673.
- Barberena, M.C. 1998. *Australerpeton cosgriffi* n.g., n.sp., a Late Permian Rhinesuchoid amphibian from Brazil. *Anais da Academia Brasileira de Ciências* 70: 125–137.
- Barberena, M.C. and Dias, E.V. 1998. On the presence of a short-snouted rhinesuchoid amphibian in the Rio do Rasto Formation (Late Permian of Paraná Basin, Brazil). *Anais da Academia Brasileira de Ciências* 70: 465–468.
- Bonaparte, J.F. 1963. *Promastodonsaurus bellmanni* n. g. et n. sp., capitosáurio del Triásico Medio de Argentina (Stereospondyli – Capitosauroidae). *Ameghiniana* 3: 67–78.
- Boy, J.A. 1985. Über *Micropholis*, den letzten Überlebenden der Dissorophioidea (Amphibia: Temnospondyli; Unter-Trias). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 1985: 29–45.
- Cisneros, J.C. and Schultz, C.L. 2002. *Procolophon brasiliensis* n. sp., a new procolophonid reptile from the Lower Triassic of southern Brazil. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 11: 641–648.
- Cisneros, J.C. 2008. Taxonomic status of the reptile genus *Procolophon* from the Gondwanan Triassic. *Palaeontologia Africana* 43: 7–17.
- Cosgriff, J.W. and Zawiskie, J.M. 1979. A new species of the Rhytidosteidae from the *Lystrosaurus* Zone and a review of the Rhytidosteioidea. *Palaeontologia Africana* 22: 1–27.
- Cox, C.B. and Hutchinson, P. 1991. Fishes and amphibians from the Late Permian Pedra do Fogo Formation of Northern Brazil. *Palaeontology* 34: 561–573.
- Dias, E.V. and Barberena, M.C. 2001. A temnospondyl amphibian from the Rio do Rasto Formation, Upper Permian of Southern Brazil. *Anais da Academia Brasileira de Ciências* 73: 135–143. doi:10.1590/S0001-37652001000100011
- Dias, E.V. and Schultz, C.L. 2003. The first Paleozoic temnospondyl postcranial skeleton from South America. *Revista Brasileira de Paleontologia* 6: 29–42.
- Dias-da-Silva, S. and Marsicano, C. 2006. *Sangaia*, a replacement generic name for the rhytidosteid temnospondyl *Cabralia*, a preoccupied name. *Journal of Vertebrate Paleontology* 26: 1004. doi:10.1671/0272-4634(2006)26[1004:SARGNF]2.0.CO;2
- Dias-da-Silva, S. and Schultz, C.L. 2008. Early Triassic postcranial Temnospondyl remains from southern Brazil (Sanga do Cabral Formation, Paraná Basin). *Revista Brasileira de Paleontologia* 11: 51–58. doi:10.4072/rbp.2008.1.05
- Dias-da-Silva, S., Dias, E.V., and Schultz, C.L. 2009. First record of stereospondyls (Tetrapoda, Temnospondyli) in the Upper Triassic of Southern Brazil. *Gondwana Research* 15: 131–136. doi:10.1016/j.gr.2008.07.002
- Dias-da-Silva, S., Marsicano, C., and Schultz, C.L. 2005. Early Triassic temnospondyl skull fragments from southern South America (Paraná Basin, Brazil). *Revista Brasileira de Paleontologia* 8: 165–172.
- Dias-da-Silva, S., Marsicano, C., and Schultz, C.L. 2006. Rhytidosteid Temnospondyls in Gondwana: A New Taxon from the Lower Triassic of Brazil. *Palaeontology* 49: 381–390. doi:10.1111/j.1475-4983.2006.00545.x
- Golubev, V.K. 1998. Revision of the Late Permian chroniosuchians (Amphibia, Anthracosauromorpha) from Eastern Europe. *Paleontological Journal* 32: 390–401.
- Hellrung, H. 2003. *Gerrothorax pustuloglomeratus*, ein Temnospondyle (Amphibia) mit knöcherner Branchialkammer aus dem Unteren Keuper von Kupferzell (Süddeutschland). *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* 330: 1–130.
- Jenkins, F.A. Jr., Schubert, N.H., Gatesy, S.M., and Warren, A. 2008. *Gerrothorax pulcherrimus* from the Upper Triassic Fleming Fjord Formation of East Greenland and a reassessment of head lifting in temnospondyl feeding. *Journal of Vertebrate Paleontology* 28: 935–950. doi:10.1671/0272-4634.28.4.935
- Lavina, E.L. 1983. *Procolophon pricei* sp. n., um novo réptil procolofonídeo do Triássico do Rio Grande do Sul. *Iheringia, Série Geologia* 9: 51–78.
- Lavina, E.L. and Barberena, M.C. 1985. Anfíbios rítidostéideos e lídekerínídeos da Formação Sanga do Cabral (Triássico Inferior do Rio Grande do Sul) Implicações bioestratigráficas e geocronológicas. *Iheringia, Série Geologia* 10: 19–27.
- Malabarba, M.C., Abdala, F., Weiss, F., and Perez, P.A. 2003. New data on the Late Permian Fauna of Posto Queimado, Rio do Rasto Formation, Southern Brazil. *Revista Brasileira de Paleontologia* 6: 49–54.
- Marsicano, C.A. 1999. Chigutisaurid Amphibians from the Upper Triassic of Argentina and their Phylogenetic Relationships. *Paleontology* 42: 545–565. doi:10.1111/1475-4983.00084
- Marsicano, C.A. 2005. A new temnospondyl record from the Upper Triassic of Argentina. *Ameghiniana* 42: 501–504.
- Marsicano, C.A. and Warren, A.A. 1998. The first Palaeozoic rhytidosteid: *Truheosaurus major* (Woodward, 1909) from the late Permian of Australia, and a reassessment of the Rhytidosteidae (Amphibia, Temnospondyli). *Bulletin Natural History Museum of London (Geology)* 54: 147–154.

- Marsicano, C.A., Perea, D., and Ubilla, M. 2000. A new temnospondyl amphibian from the Lower Triassic of South America. *Alcheringa* 24: 119–123. doi:10.1080/03115510008619528
- Panchen, A.L. 1959. A new armoured amphibian from the Upper Permian of East Africa. *Philosophical Transactions of the Royal Society of London B* 242: 207–281. doi:10.1098/rstb.1959.0005
- Pierini, C., Mizusaki, A.M., Scherer, C.M.S., and Alves, D.B. 2002. Integrated stratigraphic and geochemical study of the Santa Maria and Caturrita formations (Triassic of the Paraná Basin), southern Brazil. *Journal of South American Earth Sciences* 15: 669–681. doi:10.1016/S0895-9811(02)00114-1
- Piñeiro, G., Marsicano, C., and Damiani, R. 2007a. Earliest record of mastodonsaurids (Tetrapoda, Temnospondyli) from South America: Permo-Triassic of Uruguay. *Acta Palaeontologica Polonica* 52: 695–703.
- Piñeiro, G., Marsicano, C., and Lorenzo, N. 2007b. A New Temnospondyl from the Permo-Triassic Buena Vista Formation of Uruguay. *Palaeontology* 50: 627–640. doi:10.1111/j.1475-4983.2007.00645.x
- Price, L.I. 1948. Um anfíbio labirintodonte da Formação Pedra do Fogo, Estado do Maranhão. *Boletim do Ministério da Agricultura – Departamento Nacional de Produção Mineral, divisão de Geologia e Mineralogia* 124: 7–32.
- Romer, A.S. 1947. Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology, Harvard University* 99: 1–353.
- Scherer, C.M., Ferruccio Faccini, U., and Lavina, E.L. 2000. Arcabouço estratigráfico do Mesozóico da Bacia do Paraná. In: M. Holz and L.F. De Ros. (eds.), *Geologia do Rio Grande do Sul*. 445 pp. CIGO/UFRGS, Porto Alegre, Brazil.
- Schoch, R.R. and Milner, A.R. 2000. Stereospondyli. In: P. Wellnhofer (ed.), *Handbuch der Paläoherpertologie, Encyclopedia of Paleoherpertology – Stereospondyli, Part 3B*, 1–203. Verlag Dr. Friedrich Pfeil, München.
- Schoch, R.R. and Rubidge, B.S. 2005. The amphibamid *Micropholis stowi* from the Lystrosaurus Assemblage Zone of South Africa. *Journal of Vertebrate Paleontology* 25: 502–522. doi:10.1671/0272-4634(2005)025[0502:TAMFTL]2.0.CO;2
- Shishkin, M.A. [Šiškin, M.A.] 1967. Plagiosauroids from the Triassic of the USSR [in Russian]. *Paleontologičeskij žurnal* 1967 (1): 86–92.
- Suteethorn, V., Janvier, P., and Morales, M. 1988. Evidence for a plagiosauroid amphibian in the Upper Triassic Huai Hin Lat Formation of Thailand. *Journal of Southeast Asian Earth Science* 2: 185–187. doi:10.1016/0743-9547(88)90029-3
- Warren, A.A. 1985. Triassic Australian plagiosauroid. *Journal of Paleontology* 59: 236–241.
- Warren, A.A. 2000. Secondarily aquatic temnospondyls of the Upper Permian and Mesozoic. In: H. Heatwole and R.L. Carroll (eds.), *Amphibian Biology, Vol. 4, Palaeontology: The Evolutionary History of Amphibians*, 1121–1149. Surrey Beatty and Sons, Chipping Norton.
- Watson, D.M.S. 1913. *Micropholis stowi*, Huxley, a temnospondylous amphibian from South Africa. *Geological Magazine* 10: 340–346. doi:10.1017/S0016756800127001
- Witzmann, F. and Soler-Gijón, R. 2008. The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*. *Acta Zoológica*. doi:10.1111/j.1463-6395.2008.00385.x
- Yates, A.M. and Warren, A.A. 2000. The phylogeny of the “higher” temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyls. *Zoological Journal of the Linnean Society* 128: 77–121. doi:10.1111/j.1096-3642.2000.tb00650.x
- Zerfass, H., Lavina, E.L., Schultz, C.L., Garcia, A.J.V., Faccini, U.F., and Chemale, F. Jr. 2003. Sequence stratigraphy of continental Triassic strata of southernmost Brazil: a contribution to southwestern Gondwana palaeogeography and palaeoclimate. *Sedimentary Geology* 161: 85–105. doi:10.1016/S0037-0738(02)00397-4
- Zittel, K. von 1887–1890. *Handbuch der Paläontologie. I. Abteilung, Paläozoologie. 3. Vertebrata (Pisces, Amphibia, Reptilia)*. 1890 pp. Verlag R. Oldenbourg, München.