EARLY TRIASSIC POSTCRANIAL TEMNOSPONDYL REMAINS FROM SOUTHERN BRAZIL (SANGA DO CABRAL FORMATION, PARANÁ BASIN)

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ABSTRACT – Postcranial temnospondyl remains have been, as a general trend, neglected by paleontologists. In South America, most published temnospondyl material generally consists of cranial elements, excepting for brachyopoid postcranial material from Argentina. This work provides the first survey of temnospondyl postcranial bones recovered from the south Brazilian Lower Triassic Sanga do Cabral Formation. The reduced ossification of the bones, among other characters, point to the presence of aquatic temnospondyls in this unit. As the highly fragmentary nature of most materials constrains an accurate taxonomic identification, some of them are assigned to Temnospondyli *insertae sedis*. Other bones, however, display a morphology which is consistent with well-described aquatic Mesozoic stereospondyls. This preliminary assessment on temnospondyl postcranial skeleton could be an important contribution for future comparative research in order to increase our knowledge about this interesting group of basal tetrapods, which achieved a worldwide distribution during the Mesozoic. In the absence of cranial elements, postcranial features can be very useful in the identification of temnospondyl remains and investigation on this topic should be encouraged.

Key words: Temnospondyli, Stereospondyli, postcranial skeleton, Lower Triassic, Paraná Basin.

RESUMO – Restos pós-cranianos de temnospôndilos tem sido, via de regra, negligenciados pelos paleontólogos. Na América do Sul, a maioria dos trabalhos publicados sobre esse grupo geralmente consistem de elementos cranianos, excetuando materiais pós-cranianos de braquiopóides da Argentina. Este trabalho fornece o primeiro levantamento de ossos pós-cranianos de temnospôndilos provenientes da Formação Sanga do Cabral (Triássico Inferior brasileiro). A ossificação reduzida dos ossos, entre outras características, evidencia a presença de temnospôndilos aquáticos nesta unidade. Uma vez que a natureza fragmentária da maioria dos materiais impede uma identificação taxonômica mais exata desses materiais, alguns deles são identificados como Temnospondyli *insertae sedis*. Outros ossos, contudo, apresentam uma morfologia consistente com formas já descritas de estereospôndilos aquáticos mesozóicos. Este estudo preliminar de restos pós-cranianos é uma importante contribuição para futura pesquisa comparativa, na intenção de aumentar nosso conhecimento acerca deste interessante grupo de tetrapods basais que atingiu distribuição mundial durante o Mesozóico. Na ausência de elementos craniais, características pós-craniais podem ser muito úteis na identificação de restos de Temnospôndilos e as investigações neste assunto devem ser encorajadas.

Palavras-chave: Temnospondyli, Stereospondyli, esqueleto pós-craniano, Triássico Inferior, bacia do Paraná.

INTRODUCTION

The short temporal distribution of most temnospondyls has led several authors to claim them as useful biostratigraphic markers (Cosgriff, 1969, 1984; Anderson & Cruickshank, 1978; Kitching, 1978; Shishkin, 1994; Groenewald & Kitching, 1995). In fact, they are among the commonest tetrapods in continental deposits during the Triassic. Moreover, the characteristic pattern of ornamentation found

in the dermal bones of stereospondyls makes their identification (at least in a more inclusive level) easier than in other groups (Schoch & Milner, 2000). Most South American stereospondyls exhumed in Triassic and Permo-Triassic units consist of cranial remains (Lavina & Barberena, 1985; Marsicano, 1999, 2005; Marsicano *et al.*, 2000; Dias-da-Silva *et al.*, 2005, 2006a,b; Dias-da-Silva & Marsicano, 2006; Piñeiro *et al.*, 2007a, b, c), whereas postcranial materials are rare excepting for an almost complete postcranial skeleton of a

brachyopoid from the Upper Triassic of Argentina (Rusconi, 1951; Marsicano, 1993). According to Warren & Snell (1991), early paleontologists frequently left temnospondyl postcranial materials in the field, collecting and describing only cranial remains. This situation generated a great deal of information regarding cranial material and, as a result, axial and appendicular elements remained largely underestimated. The best known exceptions are the contributions by Watson (1917, 1919, 1926), Nilsson (1937), Bystrow & Efremov (1940), Romer (1947), Cosgriff (1974), Warren & Hutchinson (1983), Warren & Snell (1991), Schoch & Milner (2000), Dias & Schultz (2003), and Pawley & Warren (2005). Intense collecting, particularly in Lower Triassic levels of the Paraná Basin in the last years, has produced hundreds of cranial stereospondyl remains (mostly represented by dermal skull fragments), whereas clearly identifiable postcranial bones attributed to this group are fewer than fifty pieces, all of them undescribed. Therefore, it is reasonable to assume that differential preservation of postcranial bones compared to cranial remains could be due to taphonomic processes instead of collecting bias.

The aim of this short paper was to provide the first comprehensive survey of temnospondyl postcranial remains recovered from the Sanga do Cabral Formation, Lower Triassic of the Paraná Basin, southern Brazil.

GEOLOGICAL SETTING

The Lower Triassic Sanga do Cabral Formation crops out in southern Brazil, and it is a 50- to 100-m thick unit that unconformably covers the Guadalupian ("Middle Permian") Rio do Rasto (Langer, 2000; Malabarba *et al.*, 2003; Cisneros *et al.*, 2005) and the Permo-Triassic Pirambóia formations (Andreis *et al.*, 1980; Scherer *et al.*, 2000). According to Andreis *et al.* (1996), this unit also occurs in Uruguay, where the deposits are locally included in the Buena Vista Formation. However, according to Piñeiro *et al.* (2003, 2004, 2007a, b, c), the presence of varanopid pelicosaurids, basal procolophonids and non-stereospondyl temnospondyls provide evidence for the inclusion of the Buena Vista Formation close to the Permo-Triassic boundary. Moreover, and according to Piñeiro *et al.* (2007c), the faunal content of the Colonia Orosco Local Fauna (Buena Vista Formation) appears to represent early stages of the turnover evidenced in the communities of continental tetrapods at the Permo-Triassic Boundary. Recently, Dias-da-Silva *et al.* (2006b) questioned the presence of Permian strata in the Buena Vista Formation, arguing that the varanopid material was probably misidentified, and also because owenettid procolophonids range from Upper Permian to Lower Triassic. More recently, however, new data published by Piñeiro *et al.* (2007c) and a careful reading of the descriptions of Uruguayan temnospondyls provided arguments to convince the present authors that the Buena Vista Formation is likely Permo-Triassic in age as previously stated. Therefore, the Sanga do Cabral Formation is younger than the Uruguayan

unit because the faunal components of Sanga do Cabral Formation occur in Lower Triassic deposits worldwide (*e.g.*, through the presence of *Procolophon*, thrinaxodontid cynodonts, a rhytidosteid stereospondyl, a single protorosaurid vertebra, and a doubtful lystrosaurid stapes; see Langer & Schultz, 1997; Langer & Lavina, 2000; Cisneros & Schultz, 2002; Abdala *et al.*, 2002; Dias-da-Silva *et al.*, 2006a,b). The Sanga do Cabral Formation consists of massive to trough cross-bedded intraformational conglomerates and horizontally bedded sandstones which are interpreted as deposited by braided river systems with poorly confined channels that were developed on a low gradient alluvial plain. The presence of argillaceous lenses in the sequence provides evidence of lakes and ponds related to the alluvial plains (Zerfass *et al.*, 2003). The bone-bearing levels correspond to intraformational conglomerates that provided mostly disarticulated and fragmented vertebrate remains. Hence, both the sedimentology of the unit and some taphonomic features of the vertebrates collected (scattered, disarticulated, fragmented, etc.) suggest that intense reworking took place during the deposition of these bone-bearing levels.

Preservation of tetrapods in the neighboring Buena Vista Formation from Uruguay is quite similar. This unit is also characterized by reddish fine sandstones interbedded with lenticular clay layers and bone-bearing intraformational conglomerates (Bossi & Navarro, 1991; Goso *et al.*, 2001; Piñeiro *et al.*, 2003).

Table 1. Temnospondyl postcranial elements from Sanga do Cabral Formation.

Specimen	Osteological identification
UFRGS PV0326T	Distal fragment of a femur
UFRGS PV0331T	A complete left stereospondyl humerus
UFRGS PV0332T; UFRGS PV0339T	Distal fragments of humeri
UFRGS PV0353T; UFRGS PV0375T	Distal fragments of femora
UFRGS PV0369T	Proximal fragment of a femur
UFRGS PV0387T	A cleithrum
UFRGS PV0499T	A complete right stereospondyl ilium
UFRGS PV0357T; UFRGS PV0358T	Radial fragments
UFRGS PV0236T to UFRGS PV0238T; UFRGS PV0253T; UFRGS PV0255T to UFRGS PV0258T; UFRGS PV0330T; UFRGS PV0333T to UFRGS PV0338T; UFRGS PV0362T to UFRGS PV0365T; UFRGS PV0386T; UFRGS PV0402T; UFRGS PV0351T to UFRGS PV0352T; UFRGS PV0354T to UFRGS PV0355T; UFRGS PV0359T; UFRGS PV0370T to UFRGS PV0374T; UFRGS PV0376T	Appendicular fragments

Figure 1. UFRGS PV 0331 T, a stereospondyl left humerus in dorsal (A) and ventral (B) views. **Abbreviations:** **dc**, deltoid crest; **ect**, ectepicondyle; **ects**, ectepicondylar sulcus; **ent**, entepicondyle; **sch**, attachment of scapulo-humeralis anterior muscle; **sp**, supinator process. Scale bar = 10 mm.

MATERIALS AND METHODS

The described material is housed in the fossil collection of the Universidade Federal do Rio Grande do Sul (UFRGS), in Porto Alegre. Several remains tentatively assigned to appendicular elements of temnospondyls were examined during the present study and a complete list can be accessed in Table 1. From the materials listed in this Table, those better preserved that could be helpful for taxonomic identification are herein described: a left humerus (UFRGS PV0331T), a right ilium (UFRGS PV0499T), a cleithrum (UFRGS PV0387T), two radial fragments (UFRGS PV0357T and UFRGS PV0358T), and finally, two femoral fragments (UFRGS PV0369T and UFRGS PV0326T).

All specimens were recovered on different field trips to outcrops in several localities from the central region (central depression) of the state of Rio Grande do Sul (see Dias-da-Silva *et al.*, 2006a:fig. 1). They were found scattered and isolated, and therefore, none can be linked to the same individual. For the same reason, it is difficult to directly ascribe them to any already known taxon, since they were erected mainly based on cranial morphology.

The specimens UFRGS PV0331T, UFRGS PV0499T, and UFRGS PV0387T (humerus, ilium and cleithrum, respectively) are well preserved and most features can easily be observed. The remaining postcranial elements are broken fragments,

and consequently, they provide limited information when compared with the well-preserved ones. All elements were found already detached from rocks and no laboratory preparation was necessary.

DESCRIPTION

UFRGS PV0331T. This left humerus (Figure 1) is relatively short and slightly dorsoventrally compressed. The proximal and distal ends are expanded and separated by a short diaphysis, and are twisted at an angle of approximately 60 degrees. In dorsal view, the distal extremity is more expanded than the proximal one and its articular surface is slightly curved and continuous. The supinator process, ectepicondylar sulcus (misinterpreted as an entepicondylar sulcus by Santana, 1992), ectepicondyle, and entepicondyle are poorly developed. The entepicondylar foramen is not present as in all stereospondyls (Schoch & Milner, 2000; Yates & Warren, 2000). On the anterior border of the proximal extremity, a tubercle for muscular insertion is present, probably for the attachment of the scapulo-humeralis anterior muscle. In ventral view a well-developed deltoid crest is present.

Remarks. Santana (1992) compared the material with the humerus of the mastodonsaurid *Parotosuchus pronus*, and she found them to be very similar. However, as similar humeri were already known for rhytidosteids, trematosaurids and

Figure 2. UFRGS PV0499T, a stereospondyl right ilium in medial (A) and lateral (B) views. Scale bar = 10 mm.

mastodontosaurids, Santana (1992) assigned the Brazilian material to *Temnospondyli incertae sedis*. Nonetheless, the loss of the entepicondylar foramen in UFRGS PV0331T clearly relate it to Stereospondyli, as this condition is considered a diagnostic character of that group (Schoch & Milner, 2000). Additionally, the presence of an angle of less than 90 degrees between the two ends, an adaptation to an aquatic habit, is found in all non-terrestrial stereospondyls (Warren & Snell, 1991; Schoch & Milner, 2000). Moreover, according to several authors (Warren & Snell, 1991; Schoch & Milner, 2000; Pawley & Warren, 2005), stereospondyls with weakly developed processes for muscle attachment and poorly ossified articulation surfaces, as occur in UFRGS PV0331T, were likely to have been primarily aquatic animals.

UFRGS PV0499T. Right ilium (Figure 2). It is a slender bone with an anteroposteriorly expanded dorsal blade. Its distal end, also anteroposteriorly expanded, bears the dorsal part of the acetabulum. It is slightly sigmoid in anterior and posterior views and posteriorly inclined.

Remarks. Ilium structure is very conservative among stereospondyls, as also occurs with the humeri. Thus, it is not useful for taxonomic purposes. For example, UFRGS PV0499T is quite similar to those attributed to the putative rhytidosteid *Acerastea* (Warren & Hutchinson, 1987:fig. 12), but this morphology is also comparable to that described for the mastodontosaurid *Parotosuchus* (Warren & Snell, 1991: fig. 9). The only exception is the ilium of the metoposaurids, in which the dorsal blade is unexpanded anteroposteriorly and massive in cross section (see Warren & Hutchinson, 1987; Warren & Snell, 1991). Thus, as previously mentioned for the humerus UFRGS PV0331T, the described ilium cannot be assigned to any taxonomic level more specific than Stereospondyli.

UFRGS PV0387T. UFRGS PV0387T (Figure 3) is a nearly complete cleithrum which is a triangular rod in cross section that possesses an expanded head and pointed tail with facets for articulation with the scapulocoracoid and clavicle. The

tip of the tail is broken, but it is reasonable to assume that at least two thirds of its extension is preserved. The posteroventral portion of the head is also fractured and it is subdivided into two flanges unequally developed, one following the line of the external surface of the head and

Figure 3. UFRGS PV0387T, a cleithrum in medial (A) and lateral (B) views. Scale bar = 10 mm.

Figure 4. Appendicular elements: UFRGS PV0369T, a proximal femoral fragment in dorsal (A) and ventral (B) views; UFRGS PV0326T, distal femoral fragment in dorsal (C) and ventral (D) views; UFRGS PV0358T, a proximal radial fragment in dorsal (E) and ventral (F) views; UFRGS PV0372T, a proximal radial fragment in dorsal (G) and ventral (H) views. Scale bar = 10 mm.

other continuous with its inner surface along with the ridge that delineates the scapulocoracoid articular area and the clavicular articulation area (lamina suprascapularis sensu Bystrow & Efremov (1940). The recess of both flanges holds the anterodorsal part of the scapula.

Remarks. UFRGS PV0387T resembles cleithra present in Triassic stereospondyls such as *Bentosuchus sushkini* (Bystrow & Efremov, 1940), *Parotosuchus pronus* (Howie, 1970). However, the lack of distinctive cleithral characters among different temnospondyls constrains a more accurate identification. In the comprehensive study of stereospondyls, Schoch & Milner (2000) affirm that the cleithrum is only known in a few species, and appears to be quite conservative throughout the group. Therefore, UFRGS PV0387T is assigned to *Stereospondyli incertae sedis*, mainly due to biostratigraphic reasons, since most non-stereospondyl temnospondyls did not survive the Permo-Triassic mass extinction.

UFRGS PV0369T. Proximal femoral fragment (Figure 4A, B). This material is badly preserved in ventral view, where the periosteal layer of bone was lost. It will be discussed together with UFRGS PV0326T (see below).

UFRGS PV0326T. Distal femoral fragment (Figure 4C, D).

This fragment is bigger compared to UFRGS PV0369T, and indicating it belongs to a larger individual. The head for tibial and fibular articulation is slender and slightly bifurcated, and ventrally, the beginning of a poorly developed Y-shaped system of adductor ridge and trochanters can be observed.

Remarks. Warren & Hutchinson (1983) pointed out that femoral elements of temnospondyls do not vary greatly within the group and differences occur mainly in the slenderness of the shaft and the degree of development of the ventral adductor crest and the internal trochanter. Warren & Snell (1991) could not find differences to define femoral patterns among different families. Hence, UFRGS PV0326T and UFRGS PV0369T are assigned to *Temnospondyli incertae sedis*.

UFRGS PV0358T and UFRGS PV0372T. Two proximal radial fragments (Figure 4E-H). UFRGS PV0372T is larger than UFRGS PV0358T and therefore belongs to a more robust or a more mature individual. Both ends are subcircular.

Remarks. According to Warren & Snell (1991), few radial elements were described for Mesozoic temnospondyls, and therefore, any range of variation is unknown. Thus, these fragments cannot be assigned to any taxonomic level more specific than *Temnospondyli*.

DISCUSSION

Excepting for the diagnostic humerus, ilium, and cleithrum, it is important to point out that the taxonomic assignment of the remaining fragments (*Temnospondyli incertae sedis*) is tentative and based on their large size when compared with the previously described basal amniotes recorded to FSC. Protorosaurids, procolophonids and non-mammalian cynodonts, and ?lystrosaurids from this unit belong to relatively smaller taxa. In other words, from the Lower Triassic, only temnospondyls are consistent (so far) with the size of the elements described here.

In spite of the small number of postcranial elements known from the Sanga do Cabral Formation, several identifiable specimens described here strongly suggest an aquatic mode of life. The humerus UFRGS PV0331T certainly presents anatomical features found in non-terrestrial stereospondyls (e.g., humeral twisting angle less than 90 degrees and poorly developed processes). Moreover, the slenderness and small degree of ossification present in the remaining materials (UFRGS PV0499T, UFRGS PV0387T, and UFRGS PV0357T) are consistent with those found in well-described Mesozoic postcranial skeletons of aquatic stereospondyls. Unfortunately, it is not possible to provide a less inclusive taxonomy for the material herein presented, since most temnospondyl taxa either did not preserve postcranial skeletons, or in such cases, the present postcranial elements do not provide informative characters due to the great deal of ecologic convergence. This situation produced, within temnospondyls, similar postcranial skeletons in different lineages (see ecomorphic discussion by Defaw, 1989). So far, the exceptions are the highly apomorphic postcranial skeletons of both metoposaurids (see Warren & Snell, 1991), and the more terrestrial *Lydekkerina huxleyi* (Pawley & Warren, 2005). The remaining fragments (UFRGS PV0358T, UFRGS PV0369T, UFRGS PV0326T and UFRGS PV0372T) are assigned to *Temnospondyli incertae sedis*, due to their lack of informative taxonomic features.

CONCLUSION

The purpose of the present contribution was to provide information about temnospondyl postcranial elements from the Sanga do Cabral Formation of southern Brazil. Previously, only cranial materials were described and published from that unit. Some of the specimens studied are assigned to *Stereospondyli incertae sedis*, although others are referred to *Temnospondyli incertae sedis*. It is important to point out that the lack of knowledge regarding postcranial temnospondyl remains should not be an obstacle in studying such materials. A good example of the usefulness of temnospondyl postcrania can be observed in the family Metoposauridae, where the well-known skeleton possesses several autapomorphic characters that are useful for taxonomic purposes when

cranial elements are absent. Unfortunately, apart from this family, our knowledge of postcranial elements is very scarce. Therefore, efforts to enhance information on this topic should be encouraged.

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