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

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Abstract: We describe a large, fragmentary procolophonid skull, and three large vertebrae from the Sanga do Cabral Formation, Paraná Basin, Lower Triassic of Brazil. Cranial and dental morphology allow us to refer the skull to the genus *Procolophon*; the fragmentary nature of the specimen, however, does not permit identification to species. The vertebrae are tentatively assigned to *Procolophon*. They are of a size expected for an individual represented by the skull, although the cranial and postcranial elements were not directly associated. The vertebrae are unusual for a procolophonid in exhibiting neural arches that are twice as broad as they are long, a dimension seen elsewhere among parareptiles only in pareiasaurs. A comparison of the manner of tetrapod preservation between the Sanga do Cabral and Katberg formations reveals that tetrapods in the former occur within conglomerates, whereas in the latter they are recovered mainly from mudstones. This taphonomic disparity may account for the absence in South America of the nearly cosmopolitan synapsid *Lystrosaurus*. The recent recognition of Permian tetrapods from the Buena Vista Formation of Uruguay, regarded widely to be a lateral equivalent of the Sanga do Cabral Formation, is assessed. We conclude that there is no compelling evidence of Permian tetrapods from the Buena Vista Formation, and that the available information is suggestive of a Lower Triassic age for that formation.

Introduction

Procolophonoids are small to medium-sized parareptiles that achieved cosmopolitan distributions during the Triassic. The eponymous genus *Procolophon* Owen, 1876 is one of the most familiar basal tetrapod taxa because of the detailed descriptions published by Broili and Schröder (1936), Kemp (1974), Carroll and Lindsay (1985), Hamley and Thulborn (1993), and deBraga (2003). *Procolophon* is also the most widespread procolophonoid genus, with materials collected from the Lower Triassic of South Africa (Watson 1914; Broili and Schröder 1936), Antarctica (Colbert and Kitching 1975), and South America (Lavina 1983; Cisneros and Schultz 2002).

South American *Procolophon* materials are locally abundant in the Lower Triassic Sanga do Cabral Formation of Brazil, and have allowed the recognition of two species, *P. pricei* (Lavina 1983) and *P. brasiliensis* (Cisneros and Schultz 2002). The nature of preservation of the tetrapods, particularly the procolophonoid materials, in intraformational conglomerates of the Sanga do Cabral Formation has resulted in the collection of fragmentary specimens. This is in sharp contrast to the collection from the coeval Katberg Formation of South Africa of more complete *Procolophon* materials, usually skulls but in many cases nearly complete skeletons, from mudstones. The Antarctic material described by Colbert and Kitching (1975) resembles the South African material in terms of relative completeness and preservation in mudstone matrix. The Sanga do Cabral procolophonoid materials, therefore, are all the more interesting because of their mode of preservation when considered with the taxonomic diversity that these materials imply for the genus *Procolophon*.

Despite the observation that procolophonoid materials are the most common tetrapod elements in the Sanga do Cabral Formation (Cisneros and Schultz 2002), both *P. pricei* Lavina, 1983 and *P. brasiliensis* Cisneros and Schultz, 2002 are known only from their respective holotypes. Accordingly, any new procolophonoid material from this formation is of great interest. We provide here a description of an unusually large partial skull from the Sanga do Cabral Formation. This specimen was mentioned briefly by Dias-da-Silva (1998) and Langer and Lavina (2000). Large specimens of the Early Triassic genus *Procolophon* were known heretofore only from the South African Katberg Formation. Although the fragmentary nature of the skull prohibits a confident identification to the level of species, what is preserved allows us to refer the skull to the genus *Procolophon*. In addition, three unassociated procolophonoid vertebrae that were collected from the same outcrop are described here for the first time. These vertebrae are remarkable for their large size and neural arch morphology.

We discuss the implications of the new *Procolophon* materials from the Sanga do Cabral Formation for the age of this rock unit, and the biostratigraphic implications of the manner of preservation of procolophonoids and other tetrapods in the Sanga do Cabral Formation for the Buena Vista Formation of Uruguay. The latter formation has been considered to be a lateral equivalent of the former (Andreis et al. 1980; Bossi and Navarro 1991). Piñeiro et al. (2003, 2004), however, have suggested that the Uruguayan formation is Late Permian, based upon their work on tetrapods from conglomerates of the middle part of the Buena Vista Formation.

Geological Setting

Triassic rocks of the Paraná Basin of southern Brazil are entirely nonmarine. The oldest unit is the Lower Triassic Sanga do Cabral Formation (Andreis et al. 1980; Scherer et al. 2000). This 50–100 m thick formation lies unconformably over the Upper Permian Rio do Rasto and Pirambóia formations. It consists of massive to trough cross-bedded intraformational conglomerates and horizontally-bedded sandstones, which are interpreted as being deposited by braided river systems with poorly confined channels that developed on a low gradient alluvial plain. Interbedded, laminated mudstone lenses are present towards the top, and have been related to deposition in small ponds and lakes (Scherer et al. 2000; Zerfass et al. 2003). The intraformational conglomerates are the bone-bearing beds, where vertebrate remains are generally found scattered, disarticulated, and fragmented. This mode of preservation suggests extensive post-mortem exposure and transport, as well as intense reworking in these deposits.

The Sanga do Cabral Formation is regarded as Upper Induan/Lower Olenekian (Dias-da-Silva et al. 2005), and thus lowermost Triassic strata are not present in the Paraná Basin. The formation is correlated with the "impoverished zone" (*Procolophon* Subzone sensu Neveling et al. 1999) of the *Lystrosaurus* Assemblage Zone of Karoo Basin, South Africa (Abdala et al. 2002; Cisneros and Schultz 2002; Dias-da-Silva et al. 2005, 2006), because of the presence of the procolophonoid reptiles *Procolophon pricei* and *P. brasiliensis* (Cisneros and Schultz 2002); thrinaxodontid cynodonts (Abdala et al. 2002); a definite rhytidosteid stereospondyl (Dias-da-Silva et al. 2006) and fragments of temnospondyls tentatively assigned to Rhytidosteidae (Dias-da-Silva et al. 2005); a single protorosaurian vertebra (Langer and Schultz 1997); and a doubtful lystrosaurid stapes (Langer and Lavina 2000).

Until recently, the Sanga do Cabral Formation was thought to crop out in northern Uruguay, where the deposits are assigned to the Buena Vista Formation (Andreis et al. 1996). Piñeiro et al. (2003) regarded the age of the most productive fossiliferous conglomerate bed of the Buena Vista Formation as Permian, on the basis of vertebrae that they identifed as belonging to the basal synapsid clade Varanopidae. The other tetrapod materials that have been described from the Buena Vista conglomerates (Marsicano et al. 2000; Piñeiro et al. 2004), however, are not strongly indicative of a Permian age for that formation.

Institutional abbreviations

BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; CGP, Council for Geoscience, Pretoria, South Africa; MCT/PUCRS, Museu de Ciência e Tecnologia da Pontitícia Universidade Católica do Rio Grande do Sul, Brazil; UFRGS PV, Paleovertebrates collection, Universidade Federal do Rio Grande do Sul, Brazil.

Material and Methods

The material consists of a partial skull (UFRGS PV 0494 T) and three isolated vertebrae (UFRGS PV 0252 T, UFRGS PV 0498 T, and MCT/PUCRS 3790). The specimens were recovered from sediments that crop out along a secondary route that crosses the highway BR 287, in the locality of Rincão dos Weiss, municipality of Mata (central region of Rio Grande do Sul State, see Dias-da-Silva et al. 2006, fig. 1). All of the specimens exhibit erosional damage to some degree. The specimens were prepared primarily with an air scribe, with additional cleaning by pin vises.

Description

UFRGS PV 0494 T is a partial skull comprising the posterior right corner of the skull roof and adjoining regions of the palate; the snout, braincase, and most of the skull roof are missing. Only the supratemporal is entirely preserved among the skull table elements. For this reason, the skull is figured and illustrated only in ventral and right lateral views (Figs. 1, 2). The degree of preservation of the skull roof and palate is poor, and most sutures cannot be clearly observed.

The vertebrae (UFRGS PV 0252 T, UFRGS PV 0498 T and MCT/PUCRS 3790) were collected from the same outcrop, but they were not directly associated with one another or with the skull. They are all approximately the same size, however, and together they are of a size appropriate for the individual represented by the skull. MCT/PUCRS 3790 and UFRGS PV 0252 T are both missing the neural spine, but are otherwise well preserved. Apart from damage to its pleurocentrum, UFRGS PV 0498 T is well preserved.

Skull

Fig. 1 near here

The preserved portion of UFRGS PV 0494 T represents a skull that is approximately 50 percent larger than the skull of *Procolophon trigoniceps* reconstructed by Carroll and Lindsay (1985, fig. 1), who examined a number of skulls that ranged 30–50 mm in length. Judging from the dimensions of the subtemporal opening, we estimate that UFRGS PV 0494 T would have a total skull length, from the anteriormost tip of the snout to the posterior margin of the supratemporals, of just under 60 mm (Fig. 2). Accordingly, UFRGS PV 0494 T is slightly smaller than BP/1/4284 and CGP 1-87, undescribed skulls of *P. trigoniceps* from the Katberg Formation of South Africa that exceed 60 mm in total length.

The most conspicuous morphological feature of UFRGS PV 0494 T is the presence of a large, globular boss on the quadratojugal, whereas single or multiple spines are present on the quadratojugal in several genera of procolophonids (e.g., a single process in both *Procolophon* and *Teratophon*, and multiple processes in *Leptopleuron* and *Hypsognathus*). No boss of this shape has been described in a procolophonid heretofore, but the specimen described by Kemp (1974, fig. 2) exhibits a quadratojugal process that, when examined in ventral view, is greater than 10 mm in thickness at its greatest point. Similarly, BP/1/4284 and CGP 1-84 feature similarly thickened quadratojugal processes, which indicates that the quadratojugal process of *Procolophon* (Broili and Schröder 1936; Carroll and Lindsay 1985) changes in shape and relative size during ontogeny. Given such a small sample size, it is unclear if this is a sexually dimorphic feature. The globular construction of the quadratojugal process of UFRGS PV 0494 T is probably a manifestation of individual variation in the genus *Procolophon*. The specimen illustrations of skulls of the Late Triassic leptopleuronine *Hypsognathus fenneri* in Colbert (1946) and Sues et al. (2000) reveal that the quadratojugal processes of this procolophonid vary in size and orientation, and thus it is not unreasonable to infer a similar range of variation in size and shape for the single quadratojugal process of *Procolophon*.

Fig. 2
near
here

Most of the bones that are preserved in UFRGS PV 0494 T are virtually indistinguishable from those of *Procolophon* described and illustrated by previous workers (Broili and Schröder 1936; Kemp 1974; Carroll and Lindsay 1985; Hamley and Thulborn 1993). The posteriormost three marginal teeth positions are preserved in UFRGS PV 0494 T. The alveolus of the anteriormost position is a shallow pit, which is consonant with the observations for protothecodont tooth implantation in procolophonids (Small 1997). The remaining teeth are well preserved and are indistinguishable from the teeth of *Procolophon trigoniceps* (Gow 1977). Close to the posterior ends of the vomers, and over their sutural contact, there is a rounded and shallow fossa (a vomerine midline pit), which we have not observed in any species of *Procolophon* (Fig. 2B). What is preserved of the palatal dentition indicates that the row on the pterygoid, bordering the interpterygoid vacuity, and the pterygopalatine row are present, and that both appear to exhibit individual variation in the number of teeth when compared to described specimens of *Procolophon* (Carroll and Lindsay 1985, fig. 9; Cisneros and Schultz 2002, fig. 1).

Fig. 3
near
here

Vertebrae

The vertebrae are presumably presacrals because of the remarkable lateral expansion of the neural arches. The posterior zygapophyses are heavily buttressed, a condition that has been described as “swollen” in earlier literature (Sumida and Modesto 2001). The neural arches are approximately twice as broad as they are long (Figs. 3D, 3H, 3L). The articular facets of the prezygapophyses of UFRGS PV 0252 T are oriented horizontally, whereas those MCN/PUCRS 3790 and UFRGS PV 0498 T are angled slightly. According to deBraga (2003), the angulation of the articular facets changes from a slight incline in anterior presacrals to a horizontal orientation in posterior presacral vertebrae, and this suggests that UFRGS PV 0252 T would occupy a more posterior position compared to MCN/PUCRS 3790 and UFRGS PV 0498 T. The neural spine, preserved only in UFRGS PV 0498 T, is a stout quadrangular pillar with a flat tip. The transverse process does not project far from the lateral surface of the vertebra. The facet for the rib has an elongate, reniform outline in lateral view, and extends from just below the zygapophyseal plane to the midpoint of the centrum. The pleurocentrum is strongly amphicoelous in UFRGS PV 0252 T and MCN/PUCRS 3790; that of UFRGS PV 0498 T is too damaged to confirm that amphicoely was present. A pair of deep excavations are present ventrally, and a double ridge separates the excavations along the midline. The presence of a double midline ridge was listed as a procolophonid synapomorphy by Laurin and Reisz (1995), although it has been illustrated only for *Procolophon trigoniceps* (deBraga 2003).

Discussion

In most respects UFRGS PV 0494 T is virtually indistinguishable from skulls referred to *Procolophon trigoniceps*; the exceptions are the presence of the vomerine midline pit and the globular morphology of the quadratojugal process. The function, if any, of the vomerine midline pit is uncertain, and we do not believe that its presence is attributable to anything other than individual variation. The conspicuously large, globular process of the quadratojugal is remarkable, but not unexpected in a large *Procolophon* skull; the distinctive roundness of the process may be attributable to individual or regional variation in species of *Procolophon*. We have a very limited appreciation of the range of morphologies of the quadratojugal process of very large specimens of *Procolophon*, even in materials from South Africa where most collections of this procolophonid have been made. The size of the skull is not unusual, although most researchers are probably familiar mostly with the smaller skulls of medium-sized individuals (small adults?) of *Procolophon* from publications such as Broili and Schröder (1936) and Carroll and Lindsay (1985).

The fragmentary preservation of UFRGS PV 0494 T does not allow us to make an assignment to a known species. Cisneros and Schultz (2002) distinguished *Procolophon trigoniceps*, *P. pricei*, and *P. brasiliensis* on the basis of palatal tooth patterns. The palatal dentition of UFRGS PV 0494 T, however, is not complete enough for comparative purposes. Furthermore, a review of the genus *Procolophon* suggests that palatal dentition might not be a reliable indicator of specific identity (J. Cisneros, personal communication, 2005).

The taxonomic identity of the vertebrae is much less certain. We identify them as procolophonid based on the observation that procolophonids are the only continental tetrapods of Early Mesozoic age that are known to exhibit "swollen" neural arches and columnar neural spines. Furthermore, the centra feature the double midline ridges that have been described in *Procolophon* (deBraga 2003). MCN/PUCRS 3790, UFRGS PV 0525 T, and UFRGS PV 0498 T are clearly from a much larger individual than those skeletons of *Procolophon* that are documented in the literature (e.g., Broili and Schröder 1936; deBraga 2003). The Sanga do Cabral vertebrae, however, are of the size that would be expected for the individual represented by the skull fragment UFRGS PV 0494 T. Finally, taking into consideration that the cranial materials of procolophonids that have been collected from the Sanga do Cabral Formation are referred to the genus *Procolophon* (Lavina 1983; Cisneros and Schultz 2002; this study), we feel confident in assigning the vertebrae to this genus.

The dimensions of the neural arches, with a transverse breadth approximately twice their length, are unusual because they have never been described in a procolophonoid. These neural arch dimensions are similar to those of pareiasaurs, diadectomorphs, or seymouriamorphs (e.g., Sumida and Modesto 2001, figs. 3, 4) rather than those usually seen in procolophonoids, where the breadth of the neural arch is usually equal to its length (e.g., Colbert 1946, pl. 27, figs. 5, 6; deBraga 2003, fig. 4). The presence of midline double ridges on the pleurocentra, however, clearly identify the vertebrae as procolophonid. The great transverse breadth of the neural arches, therefore, suggests that the vertebrae of *Procolophon* became more like those of pareiasaurs as members of this genus achieved maximum body size. Unfortunately, the largest known *Procolophon* skeletons from South Africa are those of medium-sized individuals, which we regard as those of small adults (Broili and Schröder 1936; deBraga 2003); the largest known skulls, such as BP/1/4284 and CGP 1-27, were not associated with postcrania beyond elements of the atlas-axis complex.

Correlates of the Sanga do Cabral Formation

In their comparison of Early Triassic depositional environments of southern Africa and eastern South America, Souto-Ribeiro and Holz (1998) proposed a “taphocorrelation” between the Sanga do Cabral Formation of Brazil and the Katberg Formation of South Africa, claiming that they were deposited in similar environmental conditions. In both formations, sandstones are the dominant facies, and interbedded laminated mudstone lenses are present and have been related to deposition in small ponds and playa lakes (see Scherer et al. 2000; Zerfass et al. 2003; Smith and Botha 2005). Thus, sedimentologic evidence in Triassic strata from both the Karoo Basin and Paraná Basin shows that both depositional environments were quite similar. Ward et al. (2000) interpreted the Katberg sandstones as being deposited in braided river systems that scoured the floodplains characteristic of the underlying Balfour Formation, comprised predominantly of silt- and mudstones that are thought to have been laid down by fewer, highly meandering, Mississippi or Ganges-like rivers. The Sanga do Cabral sandstones are presumably the result of the same processes that formed the Katberg Formation; the lowermost Triassic is not represented in Brazil and it cannot be determined if the Paraná Basin underwent the same change from an environment characterized by few, large, meandering rivers that dominated the Permian, to one with more numerous, braided rivers that formed the massive sandstones of the Sanga do Cabral and Katberg formations.

Faunal diversity of the Sanga do Cabral Formation is low compared to that of the Katberg Formation (Groenewald and Kitching 1995), prompting Cisneros and Schultz (2002) to suggest that the former formation can be correlated with, or very close stratigraphically to the uppermost part of the latter, which forms the lower part of the “impoverished zone” of the upper Beaufort Group described by Neveling et al. (1999). Interestingly, the tetrapod material from the Sanga do Cabral Formation is from intraformational conglomerates rather than from mudstones. The concentration of collecting efforts on the conglomerates of the Sanga do Cabral Formation may account for reports that the synapsid genus *Lystrosaurus* is not known from South America, although it is known unequivocally from Africa, Europe, Asia, and Antarctica (King 1988).

In strong contrast to the recovery of Early Triassic tetrapods from the Sanga do Cabral conglomerates in Brazil, Early Triassic tetrapods from South Africa are collected predominantly from the mudstones of the *Lystrosaurus* Assemblage Zone (Groenewald and Kitching 1995; SPM, pers. obs.). The mudstones of the lower part of the Katberg Formation are highly fossiliferous and recent collecting efforts have been concentrated on this facies. Those of the “impoverished zone” of the upper part of the Katberg Formation and lower part of the Burgersdorp Formation, however, are so poorly fossiliferous that prospecting of intraformational conglomerates is an attractive alternative (J. Neveling, personal communication, 2005). Identifiable fragments of temnospondyls and cranial materials of both *Procolophon* and *Lystrosaurus* from scour-fill sandstone were discovered by Neveling (2004) in his investigation of the nature of the contact between the Katberg and Burgersdorp formations. Neveling (2004) does not remark on the relative abundance of diagnostic specimens from conglomerates, but the second author recently collected a *Lystrosaurus* mandible from conglomerate on the farm De Rust (Middelburg District, Eastern Cape Province), in the course of field work with J. Botha in the lower part of the Katberg Formation in February 2006. No *Lystrosaurus* materials were discovered in conglomerate on the five other farms that were prospected, which suggests that this genus is rarely preserved in conglomerate, even in that part of the formation in which it is most abundant (Neveling, 2004; Smith and Botha, 2005). The rarity of *Lystrosaurus* in Katberg conglomerate suggests that the Sanga do Cabral Formation may not be a correlate of only the "impoverished zone" portion of the Katberg Formation, but may be more broadly correlative with any part of the Katberg; as a consequence, the Sanga do Cabral Formation might not be assignable to an age more specific than Early Triassic. We conclude that further field work is needed in the Katberg Formation, with greater attention to its intraformational conglomerates below the "impoverished zone", to facilitate and to refine comparisons with the Lower Triassic of South America. Further field work is needed also in the Sanga do Cabral Formation, in order to expand upon the known faunal diversity.

A recent development in the Triassic biostratigraphy of eastern South America is the Late Permian age assignment of Piñeiro et al. (2003) to the Buena Vista Formation of Uruguay. Previous workers (e.g., Andreis et al. 1980) correlated this formation with the Sanga do Cabral Formation. Crucial to Piñeiro et al.'s (2003) Late Permian age assignment of the Buena Vista

Formation is their referral of several disarticulated vertebrae to the Permian synapsid clade Varanopidae. There is a contextual problem with Piñeiro et al.'s (2003) Late Permian age assignment to their fossil localities, because they drew upon studies (Reisz et al. 1998; Modesto et al. 2001; Reisz and Berman 2001) that used the previous temporal concept that divided the Permian into Early and Late units. The Permian, however, is now divided formally into Early, Middle, and Late units (Jin et al. 1997). Piñeiro et al. (2003) were working in the context that the youngest varanopids were Late Permian in age, but following the designation of a Middle Permian time unit, the youngest unequivocal varanopid materials, known from the *Tapinocephalus* Assemblage Zone of the Beaufort Group in South Africa (Dilkes and Reisz 1996; Reisz et al. 1998; Modesto et al. 2001) and the Mezen assemblage of localities of cis-Uralian Russia, are now recognized as Middle Permian in age (Lucas 2002). Unless the Buena Vista vertebrae have been reworked, Piñeiro et al.'s (2003) assignment of these specimens to Varanopidae suggests that the Buena Vista Formation is Middle Permian. The specimens, however, exhibit the same preservation as other materials from the same levels (S.P. Modesto, personal observation), which, together with the observation that the vertebrae were collected from the same locality (a road cut), suggests to us that it is unlikely that they were reworked from older strata. The other possibility is that the Buena Vista vertebrae are indeed Late Permian, and so represent a varanopid that is much younger than the South African and Russian varanopids (and, in turn, the youngest known "pelycosaur").

We believe the idea that the vertebrae described by Piñeiro et al. (2003) are varanopid (and its corallary that the age of the Buena Vista Formation is Late Permian) is unwarranted. Two varanopid species are known to have been misidentified as diapsid reptiles, and this suggests the possibility that the Buena Vista vertebrae may have been misidentified in converse fashion. The oldest known varanopid *Archaeovenator hamiltonensis* (Reisz and Dilkes, 2003) was identified originally as an early diapsid (Reisz 1989). *Mesenosaurus romeri*, described originally as a varanopid, was identified later as a diapsid by Ivachnenko and Kurzanov (1979) only to have its varanopid identity reaffirmed by Reisz and Berman (2001). The Early Permian amniote *Apsisaurus witteri*, described by Laurin (1991) as an eosuchian diapsid, is undergoing redescription because it is suspected to be a varanopid (R. Reisz, personal communication, 2005). In the cases of *Archaeovenator* and *Mesenosaurus*, both taxa were reidentified as varanopids mainly on the basis of cranial characters; only two of the eleven varanopid synapomorphies listed by Reisz and Dilkes (2003, p. 676) are postcranial characters, and neither concerns vertebral morphology. The two postcranial characters do not work for disarticulated materials such as those preserved in the Buena Vista conglomerates because the first (No. 10 of Reisz and Dilkes 2003: femur long and slender) is a derived characteristic found also in many diapsids (Laurin 1991), and the second (No. 11 of Reisz and Dilkes, 2003: two subequal sacral ribs are present) requires complete, articulated sacrals for determination. Accordingly, we are forced to conclude that the presence of varanopids in the Buena Vista Formation can be made confidently only on the basis of cranial materials. We note that no such materials have been reported from the fossiliferous conglomerates of the Buena Vista Formation.

The misidentifications of *Archaeovenator* and *Mesenosaurus* as diapsids leads us to suggest that the vertebrae described by Piñeiro et al. (2003) may be attributable to diapsids. Indeed, the Buena Vista vertebrae resemble very closely (S.P. Modesto, personal observation) those of *Prolacerta broomi* (Gow 1975), a relatively common archosauromorph diapsid in Early Triassic faunas of South Africa (Modesto and Sues 2004). Accordingly, the vertebrae described by Piñeiro et al. (2003) may belong to a basal archosauromorph or to another kind of diapsid. If so, the vertebrae do not allow a confident age assessment of the Buena Vista Formation: diapsids appear first in the Late Carboniferous (Reisz 1977) and archosauromorphs make their appearance in the Late Permian. In this contex it is noteworthy that diapsids become relatively common elements of herpetofaunas only during the Early Triassic (Reisz et al. 2000).

Finally, Piñeiro et al. (2004) recently published a description of a partial procolophonoid skull from the Buena Vista conglomerates, for which they erected the new genus and species *Pintosaurus magnidentis*. According to their phylogenetic analysis, Piñeiro et al. (2004) identified *P. magnidentis* either as the sister taxon of *Coletta seca*, an Early Triassic procolophonoid from South Africa (Gow 2000; Modesto et al. 2002), or as the sister taxon of a procolophonoid clade that includes *C. seca* as its most basal member. In our opinion, the former scenario is more suggestive of a Triassic age than a Permian one for the Uruguayan procolophonoid. The latter phylogenetic scenario would be compatible equally with a Permian or a Triassic age for *P. magnidentis*, considering that Owenettidae (the sister taxon of the clade containing *C. seca* and Procolophonidae in most recent analyses, e.g., Modesto et al. 2002) has a range extending from Late Permian to Middle Triassic (Cisneros et al. 2004). We conclude that the Uruguayan procolophonoid does not provide compelling support for the Late Permian age attributed to the Buena Vista Formation by Piñeiro et al. (2003).

Conclusion

New procolophonoid materials from the Lower Triassic Sanga do Cabral Formation of Brazil are referred to the genus *Procolophon*. No assignment to species is possible because the regions that have been used to distinguish the species of *Procolophon* are not preserved. Both the partial skull and the vertebrae attest to the presence of large *Procolophon* in western Gondwana (what is now eastern South America) during the Early Triassic.

The manner of preservation of tetrapod material from the Sanga do Cabral Formation is compared with that of tetrapods from the Katberg Formation of South Africa. The predominance of fossils collected from the conglomerates of the former formation contrasts with the predominance of mudstone preservation in the latter, and may explain the apparent absence of the index taxon *Lystrosaurus* in South America. The Sanga do Cabral Formation is very similar lithologically to the Buena Vista Formation of Uruguay, and the two have been regarded as lateral equivalents. Although *Procolophon* has not yet been described from the Buena Vista Formation, it is argued that the available evidence from the tetrapods does not contradict the Triassic age that was attributed previously to the formation and based on lithostratigraphic work, in contrast to recent paleontological work that advocates an earlier age. The Permian age assignment for the Buena Vista Formation appears to be based on misidentification of poorly diagnostic vertebrae as belonging to synapsids of the Permo-Carboniferous clade Varanopidae. We suggest that these vertebrae may be attributable to diapsid reptiles, and thus are of questionable use for determining the age of the Buena Vista Formation.

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Figure Captions

Fig. 1. Photographs of partial skull UFRGS PV 0494 T in (A) lateral and (B) palatal views. Scale bar represents 10 mm.

Fig. 2. Interpretive drawings of partial skull UFRGS PV 0494 T in (A) lateral and (B) palatal views. Scale bar represents 10 mm. ect, ectopterygoid; in, internal naris; iv, interpterygoid vacuity; j, jugal; mx, maxilla; p, parietal; pl, palatine; po, postorbital; pt, pterygoid; q, quadrate; qj, quadratojugal; qr, quadrate ramus of the pterygoid; sf, subtemporal fenestra; sq, squamosal; st, supratemporal; v, vomer; vmp, vomerine midline pit; vt, vomerian teeth.

Fig. 3. Vertebrae in (A, E, I) anterior, (B, F, J) posterior, (C, G, K) right lateral, and (D, H, L) ventral views. (A–D) MCT/PUCRS 3790, (E–H) UFRGS PV 0252 T, and (I–L) UFRGS PV 0498 T. Scale bar represents 10 mm.

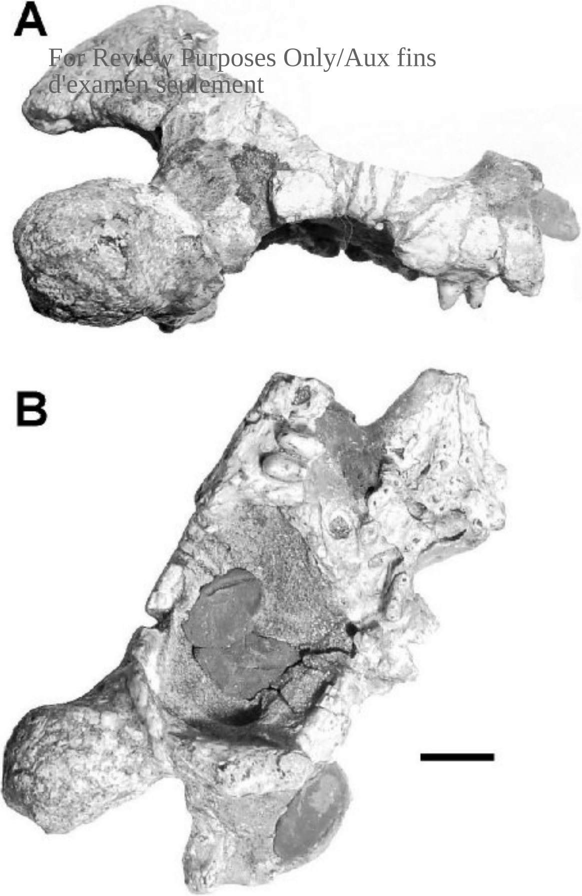

Figure 1

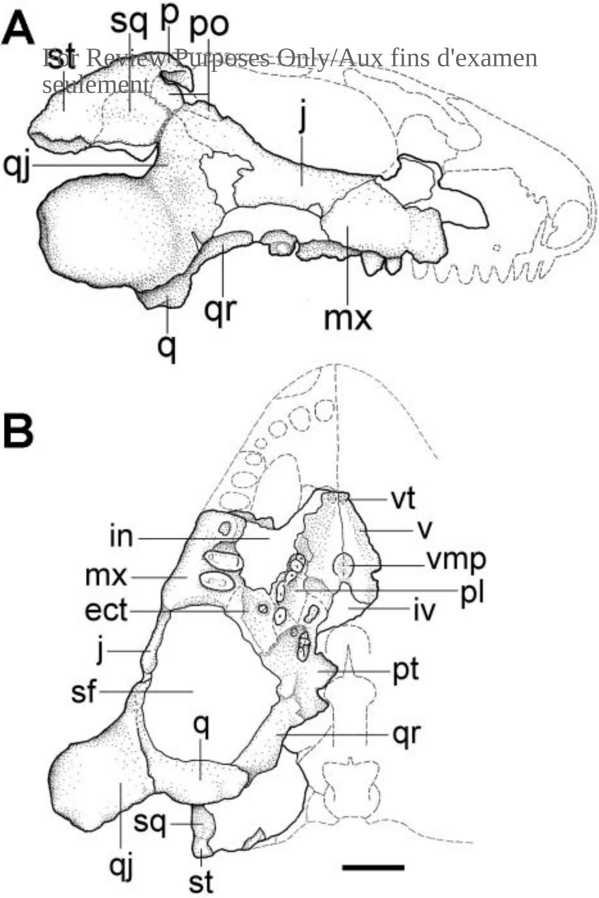

Figure 2

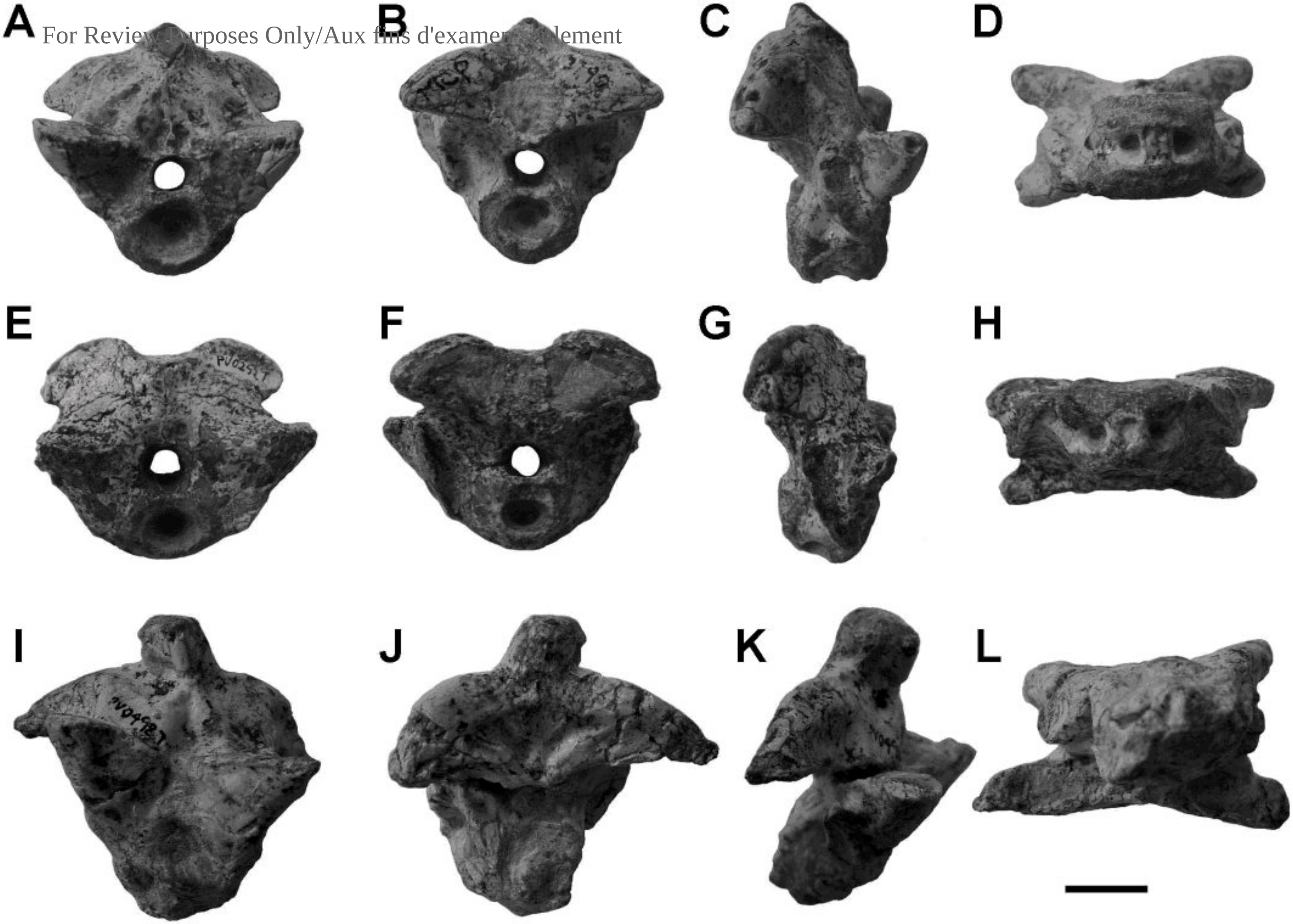

Figure 3