Problems of correlation of South African and South American tetrapod faunas across the Permian–Triassic boundary

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ABSTRACT

The best record of continental tetrapod faunas crossing the Permo–Triassic boundary (PTB) is found in the Karoo Basin of South Africa. Similar records are not known elsewhere among the former Gondwanan land masses, but it was recently proposed on the basis of palaeontological evidence that the Buena Vista Formation of Uruguay preserves a South American record of continental PTB tetrapods. The Buena Vista Formation was previously correlated to the Lower Triassic (Olenekian) Sanga do Cabral Formation of Brazil on the basis of lithostratigraphic evidence, but recent collecting in the former unit has produced a tetrapod fauna that is distinct to that documented for the latter. The unequivocal tetrapod fossils that have been described thus far from the Buena Vista Formation include indeterminate mastodonsaurid temnospondyls, a plagiosauroid temnospondyl, and a procolophonid reptile. The temnospondyls belong to Triassic groups, whereas the procolophonid is allied most closely with Early Triassic taxa from the Karoo Basin. We conclude that there is no compelling palaeontological evidence for placing any part of the Buena Vista Formation in the Permian. A precise placement of the Buena Vista Formation in the Triassic on the basis of its tetrapod fauna is not possible at this time. Accordingly, the Karoo Basin of South Africa remains the only Gondwanan basin that records a PTB tetrapod fauna.

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1. Introduction

Studies of the severity of the Permo–Triassic extinction event on terrestrial vertebrates have been advanced by recent palaeontological and geological field work in the Karoo Basin of South Africa (Ward et al., 2000, 2005; Smith and Ward, 2001; Smith and Botha, 2005; Botha and Smith, 2006) and the South Urals Basin of Russia (Tverdokhlebov et al., 2002, 2005; Benton et al., 2004). In the Karoo Basin, Botha and Smith (2006) identified a PTB tetrapod fauna, which they subdivided into three categories: (1) an extinction fauna, composed entirely of Permian taxa; (2) a survivor fauna, composed of three species whose ranges demonstrably cross the Permian–Triassic boundary (PTB); and (3) a recovery fauna, which is entirely Triassic (Fig. 1). Apart from the Karoo Basin, there are no unequivocal records of tetrapod faunas that cross the PTB in basins of the former Gondwanan land masses of India, Antarctica, Australia, and South America.

India, Australia, and Antarctica each preserve rich Early Triassic tetrapod faunas. Those of India and Antarctica appear most similar to the Early Triassic *Lystrosaurus* Assemblage Zone (AZ) of South Africa in that these three areas share several species of the therapsid genus *Lystrosaurus* (Colbert, 1974; Lucas, 1998, 2006). Antarctica demonstrates the strongest faunal connection with the Karoo Basin, with the amniote species *Procolophon trigoniceps* and *Thrinaxodon liorhinus* shared with the *Lystrosaurus* AZ in addition to three species of *Lystrosaurus* (Collinson et al., 2006; Collinson and Hammer, 2007). The Early Triassic tetrapod fauna of Australia is interesting in that it is dominated by stereospondyls, and amniotes are much less common than in coeval African, Indian, and Antarctic faunas (e.g. *Lystrosaurus* is identified from a few fragments only), and the one species shared with the *Lystrosaurus* AZ is the lydekkerinid temnospondyl *Lydekkerina huxleyi* (Warren et al., 2006). Whereas the formations preserving these Early Triassic tetrapod faunas are conformably underlain by Permian strata in India, Australia, and Antarctica, none of these Permian formations preserves tetrapods. The Kundaram Formation of India, which preserves a rich Late Permian fauna dominated by dicynodonts and shares many species in common with correlative strata in South Africa (Ray, 1999; Ray and Bandyopadhyay, 2003), is conformably overlain by the Permo–Triassic Kamthi Formation, which does not preserve Early Triassic tetrapods (Bandyopadhyay et al., 2002). Antarctica has not produced Permian tetrapod fossils useful for correlation (Collinson and Hammer, 2007).

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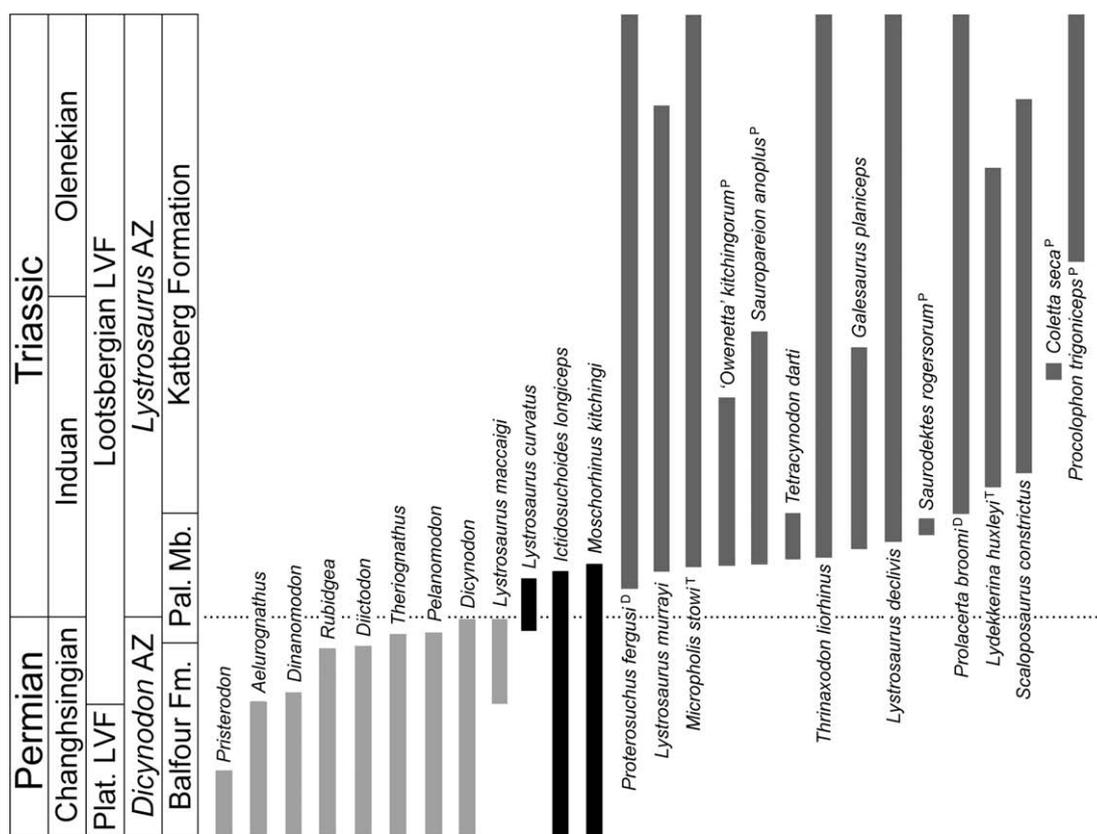 E-mail address: sean_modesto@cbu.ca (S.P. Modesto).

Fig. 1. Stratigraphic ranges of PTB tetrapod fauna from the Beaufort Group of South Africa. The extinction, survivor, and recovery faunas of Botha and Smith (2006) are indicated by light grey, black, and dark grey bars, respectively. The PTB is indicated by the dotted line. Land vertebrate faunachrons modified from Lucas (1998, 2006) and Lucas et al. (2007). Ranges from Botha and Smith (2006) and Botha et al. (2007), with additional information from Kitching (1977), Damiani et al. (2004), and Neveling (2004). Non-synapsid taxa are identified with superscripted abbreviations: D, Diapsida; P, Procolophonoidea; T, Temnospondyli. Abbreviations: AZ, assemblage zone; Fm., Formation; LVF, land vertebrate faunachron; Mb., Member; Pal., Palingkloof; Plat., Platbergian.

A possible continental Permo–Triassic sequence may be represented in South America by the Sanga do Cabral Supersequence, which is composed of the Sanga do Cabral Formation in Brazil and Buena Vista Formation in Uruguay. These formations have been regarded as time and facies equivalent units on lithostratigraphic evidence (Andreis et al., 1980; Zerfass et al., 2003, 2004). Because they contain no datable minerals or rocks, the age of these formations has been based on their fossil tetrapod assemblages. Whereas tetrapod fossils collected from the South African, Russian, Indian, and Antarctic basins come predominantly from argillaceous rocks, which have produced specimens ranging in completeness from partial bones to complete skeletons, fossils from the Sanga do Cabral and Buena Vista formations have been collected from intraformational conglomerates, which so far have yielded only partial skulls and disarticulated postcranial elements (Piñeiro et al., 2003, 2007; Dias-da-Silva et al., 2007).

The most common tetrapod specimens collected from the Sanga do Cabral Formation are the remains of rhytidosteid temnospondyls (Lavina and Barberena, 1985; Dias-da-Silva et al., 2006). Unequivocal rhytidosteids are known only from Triassic strata; although Marsicano and Warren (1998) described a Late Permian form from Australia that may represent an early rhytidosteid, its identity is not certain (Yates and Warren, 2000). The most common amniote in the Sanga do Cabral Formation is the pararreptile *P. trigoniceps* (Lavina, 1983; Cisneros and Schultz, 2002; see Cisneros, 2008a for systematic revision of the genus *Procolophon*); the presence of the genus *Procolophon* prompted Andreis et al. (1980) to assign an Early Triassic age to the formation. Because *Procolophon* is not present in the lower part of the Katberg Formation of South

Africa (Botha and Smith, 2006; Botha et al., 2007), the Sanga do Cabral Formation appears to be no older than Olenekian, and there is a consensus that the PTB is not present in Brazil (Zerfass et al., 2003, 2004; Dias-da-Silva et al., 2007).

The Buena Vista Formation has been investigated by palaeontologists only during the last decade, and much less tetrapod material has been collected from this unit than from its putative correlative in Brazil. The first informative specimen was a partial temnospondyl skull described by Marsicano et al. (2000), who assigned it to the Permo–Triassic group Dvinosauria and thus had no reason to question the Early Triassic age assignment for the formation. Recent collecting efforts by Piñeiro and colleagues, however, demonstrate the existence of a limited fauna (Fig. 2) that is distinct from the tetrapod assemblage of the Sanga do Cabral Formation. Rhytidosteid temnospondyls and *Procolophon* appear to be absent from the Buena Vista Formation, and instead other temnospondyls and procolophonoids are present. Most significantly, vertebrae that Piñeiro et al. (2003) have ascribed to the basal synapsid clade Varanopidae led those authors to reassign the fossiliferous conglomerates of the Buena Vista Formation to the Permian.

Piñeiro et al.'s (2003) taxonomic assignment of the Buena Vista vertebrae to Varanopidae has become problematic (Lucas, 2006). Dias-da-Silva et al. (2007) recently reviewed the problems surrounding a varanopid assignment of these vertebrae. They argued that because varanopids cannot be diagnosed from vertebral features alone (Reisz and Dilkes, 2003), and because several varanopid taxa have been misidentified as diapsids in the past (e.g., Reisz and Modesto, 2007), it is possible that the vertebrae described by Piñeiro et al. (2003) may instead belong to a diapsid reptile. Although

the particular composition of the tetrapod fauna of the Buena Vista Formation does appear to support Piñeiro et al.'s (2003) contention that the formation is not time equivalent to the Sanga do Cabral Formation, they have not applied a precise age of to the former rock unit: Piñeiro et al. (2003, 2004) initially regarded the fossiliferous conglomerates of the formation as Upper Permian, but more recently (Piñeiro et al., 2007a,b,c) have advocated a "Permo–Triassic" age for these levels. Piñeiro and colleagues, however, do not mark the PTB in sections detailing the productive levels of the Buena Vista Formation (cf. Piñeiro et al., 2007a, Fig. 1; 2007b, Fig. 1; 2007c, Fig. 2) (Fig. 2), an omission that complicates using the taxic occurrences in the formation for PTB survivorship analysis.

We reassess the palaeontological evidence assembled by Piñeiro et al. (2003, 2004, 2007a,b,c) as to whether the Buena Vista Formation can be regarded as Permo–Triassic in age on the basis of its faunal content. If the Buena Vista Formation indeed records the PTB in South America, this is an important development in studies of the Permo–Triassic extinction event, because the Buena Vista Formation would represent only the third continental system with the potential to produce extinction and survivor PTB tetrapod faunas (sensu Botha and Smith, 2006). It is critical to studies of PTB tetrapod survivorship to establish whether the Buena Vista Formation preserves the PTB in South America, because a Permian age assignment for the fossiliferous levels of the formation has the potential to alter the calibration of the first appearances for Mesozoic tetrapods such as mastodonsaurids and plagiosauroids, and thus to
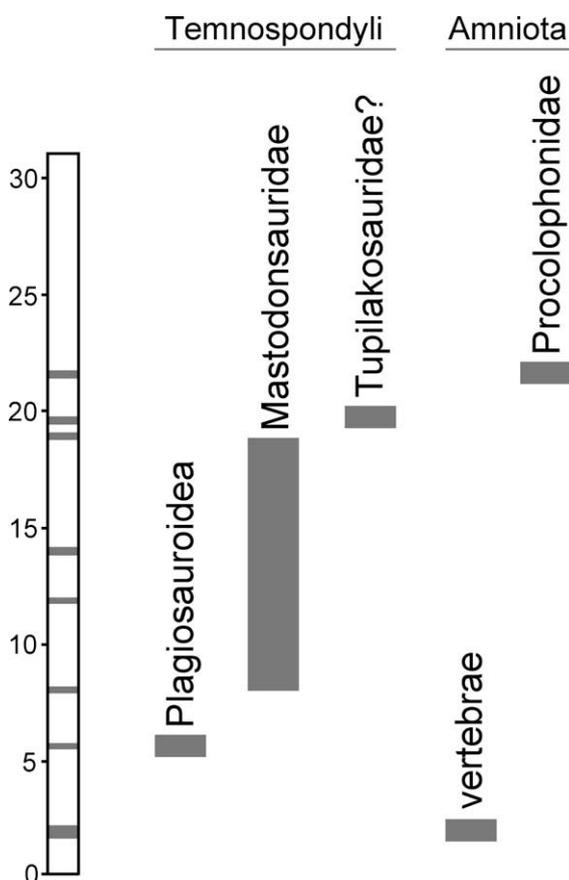

Fig. 2. Stratigraphic ranges of tetrapods from the Buena Vista Formation of Uruguay. Grey bars in chart indicate fossiliferous intraformational conglomerates. More inclusive tetrapod taxa are indicated at top of figure. Numerals indicate thickness of formation in metres. Plagiosauroidea = *Uruyiella liminea*, Procolophonidae = *Pintosaurus magnidentis*, Tupilakosauridae? = FC-DVP 285, and "vertebrae" = specimens assigned to Varanopidae by Piñeiro et al. (2003). Modified from Piñeiro et al. (2007c).

increase estimates of PTB survivorship for these groups and for tetrapods as a whole.

2. Biostratigraphic review of the Buena Vista Formation

Marsicano et al. (2000) described the first tetrapod material from the formation, a partial skull (FC-DVP 285), which they assigned to Dvinosauria (sensu Yates and Warren, 2000). Because this temnospondyl clade ranges from the Early Permian to the Early Triassic (Shishkin, 1973; Warren, 1999; Milner and Sequeira, 2004), Marsicano et al. (2000) found no reason to question the Early Triassic age assignment of the Buena Vista Formation. Piñeiro et al. (2004) concluded that this specimen was not biostratigraphically useful because its fragmentary preservation did not permit a precise placement within Dvinosauria, but in a recent review of the temnospondyl material from the formation, Piñeiro et al. (2007c) posited that the specimen represented a dvinosaur that was most similar to the Russian genus *Dvinosaurus*. Because *Dvinosaurus* is restricted to Permian rocks in Russia, Piñeiro et al. (2007c) argued that FC-DVP 285 supported a Permian age for the Buena Vista conglomerates. See the succeeding section for a tentative, alternative taxonomic assignment for this specimen.

The next material collected from the formation comprised disarticulated amniote vertebrae described by Piñeiro et al. (2003) and attributed by those authors to the basal synapsid clade Varanopidae. Dias-da-Silva et al. (2007) have reviewed the evidence for a varanopid identity and concluded that the vertebrae described by Piñeiro et al. (2003) could just as well be diapsid, and that they have no or little biostratigraphic value. We refer readers to Dias-da-Silva et al. (2007) and do not consider these specimens further.

Piñeiro et al. (2004) described the partial skull of a procolophonoid reptile, for which they erected the new genus and species *Pintosaurus magnidentis*. Their phylogenetic analysis of procolophonoids suggested that *P. magnidentis* was either the sister species of *Coletta seca*, which is known from a single specimen from the Lower Triassic of South Africa, or that *P. magnidentis* is the sister taxon of a procolophonoid clade that included *C. seca* as its most basal member. Dias-da-Silva et al. (2007) pointed out that the former phylogenetic scenario would be suggestive of an Lower Early Triassic age for the Buena Vista Formation, whereas the latter would suggest that *P. magnidentis* is of no biostratigraphic use for dating the formation because Procolophonidae (sensu Modesto and Damiani, 2007) is known from the Upper Permian through to the Upper Triassic. Pursuant to this idea, the Permian records for this group have been reduced to two taxa, both of which are represented by single specimens (Cisneros, 2008b), whereas procolophonids are relatively common members of Early Triassic tetrapod communities.

Piñeiro et al. (2007a) also described a new temnospondyl, *Uruyiella liminea*, on the basis of a partial skull. This species formed a sister-group relationship with *Laidleria gracilis*, from the *Cynognathus* Assemblage Zone (AZ) of South Africa (Warren, 1998), in Piñeiro et al.'s (2007a) cladistic analysis. The latest Early or Middle Triassic age of *L. gracilis* (the exact level of the type locality in the *Cynognathus* AZ is not known: Damiani and Rubidge, 2004) appears to have tempered the Permian age assignment of the fossiliferous conglomerates asserted previously by Piñeiro et al. (2003, 2004), because Piñeiro et al. (2007a, Fig. 5) position *U. liminea* directly on the PTB.

Most recently, Piñeiro et al. (2007b) described partial temnospondyl mandibles from the Buena Vista Formation and assigned them to the Triassic family Mastodonsauridae. One of the mandibular fragments exhibits a double row of teeth on the middle and posterior coronoids, which is a primitive feature among stereospondylous temnospondyls that had not been documented pre-

viously for mastodonsaurid temnospondyls. The earliest mastondonsaurids are the Early Triassic genera *Benthosuchus* and *Wetlugosaurus* from Russia and the genus *Watsonisuchus* from South Africa (Damiani, 2001). Like the mastodonsaurid material from the Buena Vista Formation, the *Watsonisuchus* record from the *Lystrosaurus* AZ of South Africa is based on a mandibular fragment, but its stratigraphic provenance is unknown (it is either Induan or early Olenekian; Damiani et al., 2001). The Russian mastodonsauroids are known from nearly complete skulls (Ivakhnenko et al., 1997).

Finally, Piñeiro et al. (2007b, p. 695) mention the presence of "probable prolacertiform archosauromorphs" in the Buena Vista Formation, but these materials have yet to be described and illustrated. "Prolacertiformes" is a polyphyletic group of basal archosauromorphs (Dilkes, 1998; Modesto and Sues, 2004), ranging from the Late Permian (*Protorosaurus speneri*) to the Late Triassic (drepanosaurids, tanystropheids) (Dilkes, 1998, Fig. 30). These reptiles are morphologically diverse, with distinctive vertebral apomorphies (particularly of the cervical vertebrae), and so the basal archosauromorph materials from the Buena Vista Formation can be expected to be informative for biochronological purposes.

3. Comments on the taxonomic identity of FC-DVP 285

Whereas Marsicano et al. (2000) were unable to resolve the taxonomic placement of this specimen beyond a general placement within a dvinosaur clade that included *Dvinosaurus* and tupilakosaurids, Piñeiro et al. (2007c) reexamined the specimen and concluded that the cranial sutural pattern of FC-DVP 285 is "consistent with that described for the Permian *Dvinosaurus*" (Piñeiro et al., 2007c, p. 174).

We disagree that the published evidence is sufficient enough to support the hypothesis that FC-DVP 285 represents a *Dvinosaurus*-like dvinosaur. The photographs in Piñeiro et al. (2007c, Fig. 5) show that FC-DVP 285 is a small fragment that preserves only the left circumorbital region of a skull. The exposed bone appears to be well abraded, such that only a short length of the supraorbital sensory sulcus is preserved (Piñeiro et al., 2007c, Fig. 6). Thus, this specimen preserves only one (character 2, state 1) of the 11 synapomorphies listed in the diagnosis of the *Dvinosaurus*-tupilakosauroid clade identified previously by Piñeiro et al. (2007a, Fig. 4). Centres of growth for the preserved elements can be seen in Piñeiro et al.'s (2007c) Fig. 5; these features are represented by the radiating lines in Fig. 6 of those authors (Fig. 3a). Piñeiro et al. (2007c,

Fig. 6) identified a suture running posterolaterally from the posterolateral corner of the orbit, which they interpret as the contact between the jugal and the postorbital. Following from this, Piñeiro et al. (2007c) identified the large bone forming the posterodorsal corner of the orbit as the postfrontal, and arrived at a sutural configuration that is reminiscent of that seen in *Dvinosaurus* (Shishkin et al., 2000, Fig. 3.12).

Examination of the photographs in Piñeiro et al.'s (2007c) Fig. 5 shows that the suture between the jugal and the postorbital cuts tangentally across a centre of ossification, which appears egregious with respect to the other sutures and centres of ossification that Piñeiro et al. (2007c) have identified. In light of the damage to the bone in the area forming the posterolateral corner of the orbit in FC-DVP 285 (c.f. Piñeiro et al., 2007c, Fig. 5), we regard the 'jugal-postorbital suture' of Piñeiro et al. (2007c) as an artefact of preservation. An alternative interpretation is that the areas identified as "jugal" and "postorbital" by Piñeiro et al. (2007c) are regions of a single bone that forms the posterolateral corner of the orbit, a bone that can be identified as the jugal; the element dorsomedial to it is the postorbital, and the postfrontal is a small element positioned between the frontal and the orbit (this last area was interpreted as a posterior process of the prefrontal by Piñeiro et al., 2007c). The resultant configuration (Fig. 3b) of the circumorbital elements is more characteristic of a tupilakosaurid (Fig. 3c) than of *Dvinosaurus*. If we are correct in this alternative interpretation, FC-DVP 285 has little biostratigraphic utility because tupilakosaurids range from the Early Permian to the Early Triassic (Warren, 1999; Milner and Sequeira, 2004) (Fig. 4). Careful additional preparation of the specimen to expose the ventral surface of the skull roof may help to establish the exact sutural patterns of the circumorbital elements. FC-DVP 285 may be a tupilakosaurid dvinosaur, but pending a personal examination of this specimen and its further preparation, we conservatively regard FC-DVP 285 as an indeterminate limnarchian temnospondyl (sensu Yates and Warren, 2000).

4. Discussion

The unequivocal tetrapods of the Buena Vista Formation, the indeterminate mastodonsaurids, the plagiosauroid *U. liminea*, and the procolophonid reptile *P. magnidentis*, are suggestive of a Triassic age for the Buena Vista Formation. Mastodonsaurids span nearly the entire Triassic (Damiani, 2001, Fig. 39) (Fig. 4), so the
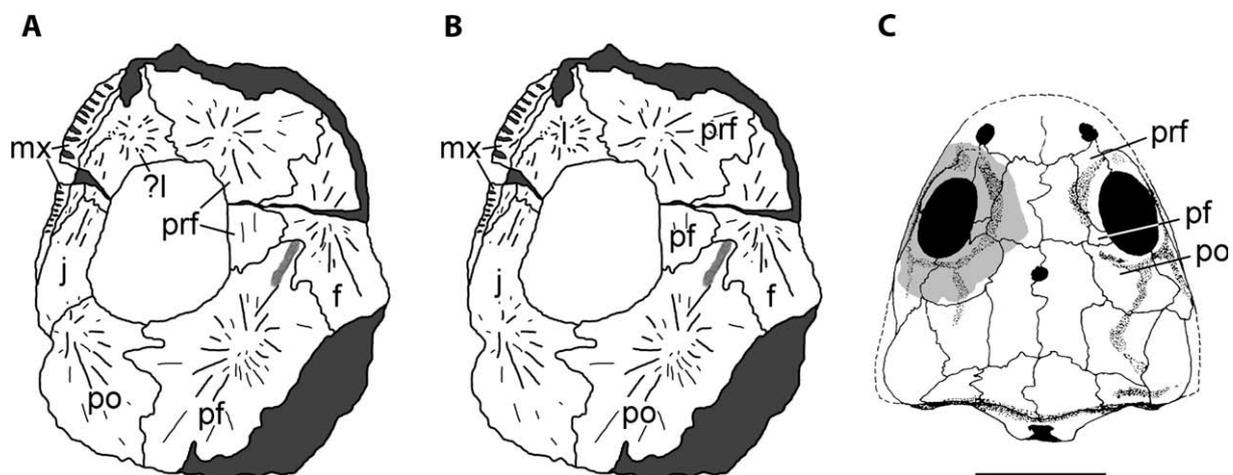

Fig. 3. Temnospondyl skulls in dorsal view. (A) "*Dvinosaurus*-like" interpretation of FC-DVP 285 of Piñeiro et al. (2007c). (B) Tupilakosaurid interpretation of FC-DVP 285 in this paper. (C) The tupilakosaurid *Thabanchuia* from Milner and Sequeira (2004) for comparison. Dark grey in A and B indicates broken bone surface and/or matrix. Light grey field on left side of skull in C represents region of skull preserved in FC-DVP 285. See text for discussion. Images in A and B redrawn from Piñeiro et al. (2007c). Image in C reproduced by permission of Andrew R. Milner. Abbreviations: f, frontal; j, jugal; l, lacrimal; mx, maxilla; pf, postfrontal; po, postorbital; prf, prefrontal. Scale bar = 1 cm.
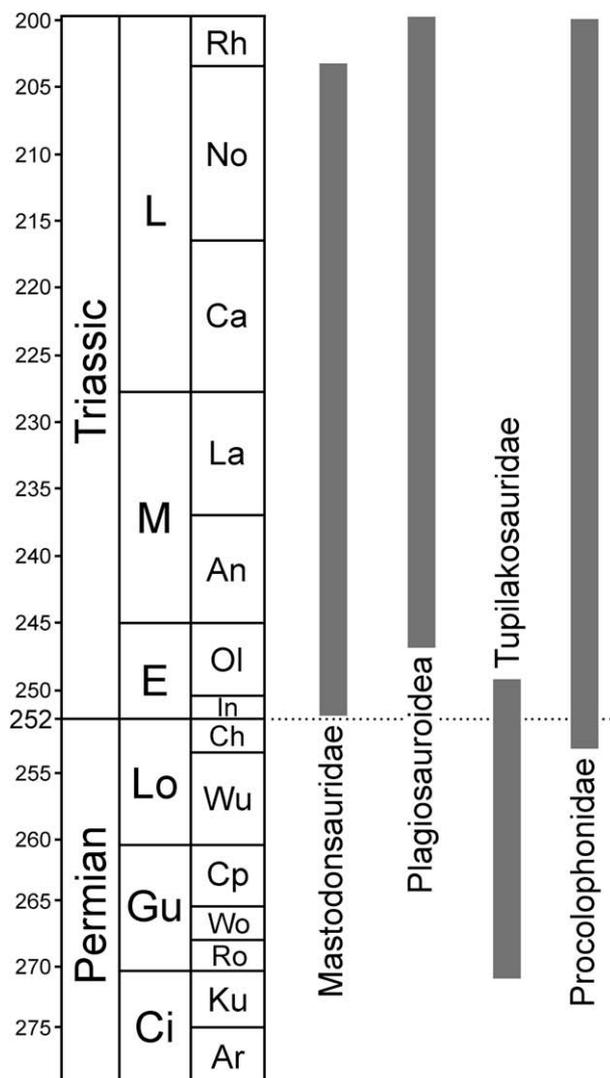
Fig. 4. Stratigraphic ranges of the temnospondyl groups Mastodonsauridae, Plagiosauroidea, and Tupilakosauridae, and the reptile group Procolophonidae. The PTB is indicated by the dotted line. Ranges from Cisneros (2008b), Damiani (2001), Milner and Sequeira (2004), and Yates and Warren (2000). Timescale (in Ma) from Gradstein and Ogg (2004) with age of PTB updated from Mundil et al. (2004). Note that the two earliest Permian stages (Asselian, Sakmarian) are omitted to save space. Abbreviations: An, Anisian; Ar, Artinskian; Ca, Carnian; Ch, Changhsingian; Ci, Cisuralian; Cp, Capitanian; E, Early; Gu, Guadalupian; In, Induan; Ku, Kungurian; L, Late; La, Ladinian; Lo, Lopingian; M, Middle; No, Norian; Ol, Olenekian; Rh, Rhaetian; Ro, Roadian; Wo, Wordian; Wu, Wuchiapingian.

mastodonsaurid mandibular fragments described by Piñeiro et al. (2007b) alone do not permit a precise placement of the formation within this period. The temnospondyl group Plagiosauroidea (sensu Yates and Warren, 2000), to which *U. liminea* belongs ("clade D" of Piñeiro et al., 2007a), also spans most of the Triassic (Fig. 4). However, the identification of *U. liminea* as the sister taxon of *L. gracilis* (Piñeiro et al., 2007a) is of biochronological interest because the latter species is the only other plagiosauroid known from Gondwana, and it is from Lower or Middle Triassic (Olenekian or Anisian) strata of the *Cynognathus* AZ of South Africa (Warren, 1999). Thus, *U. liminea* is suggestive of an Olenekian or Anisian age for the Buena Vista Formation.

The age assignments suggested by the known mastodonsaurid and plagiosauroid records are, however, not in total agreement with an age assignment drawn from the procolophonid reptile *Pintosaurus*. This genus was determined by Piñeiro et al. (2004) to be either the sister taxon of the Early Triassic *Coletta* from the *Lystrosaurus* AZ of the Karoo Basin, or to a procolophonid clade that included *Coletta* as its most basal member. Modesto and Damiani (2007) reran the Piñeiro et al. (2004) data matrix and discovered three optimal trees, the consensus of which places *Pintosaurus* in a trichotomy with *Coletta* and a clade consisting of all other procolophonids. This lack of precise phylogenetic placement complicates a biostratigraphic assessment of the former genus. However, because Lower Triassic rocks of Induan age in both South Africa and Russia preserve small assemblages of basal procolophonids (Ivakhnenko et al., 1997; Botha et al., 2007), and because they are not known from the Middle Triassic and only two singletons are known from the Upper Permian (Cisneros, 2008b), we infer that *Pintosaurus* is suggestive of an Induan (earliest Triassic) age for the Buena Vista Formation. This age is compatible with that suggested by the mastodonsaurid materials, but it contrasts with the Olenekian/Anisian age for the formation suggested by the plagiosauroid *Uruyiella*.

Regardless of a lack of precision in placing the Buena Vista Formation in the Triassic, the unequivocal tetrapod fauna of the Buena Vista Formation does not support a Permian age assignment for this rock unit: the mastodonsaurid material, the plagiosauroid *Uruyiella*, and the procolophonid *Pintosaurus* broadly suggest a Triassic age. The slight disagreements in the possible Triassic ages for the Buena Vista Formation that are suggested by *Uruyiella* on one hand (Olenekian/Anisian) and *Pintosaurus* on the other (Induan) might not be as intractable as it would seem. The phylogeny of Yates and Warren (2000, Fig. 12) suggests that Plagiosauroidea has a ghost lineage (a phylogenetically-inferred, downward range extension: Norell, 1992) that extends down to the PTB. Piñeiro et al. (2007a) identified a different sister group for plagiosauroids (an unnamed clade consisting of *Dvinosaurus* and tupilakosaurids), and their tree topology (excluding *Uruyiella* from consideration as a plagiosauroid for the purpose of argument) suggests that Plagiosauroidea has a ghost lineage that extends into the Late Permian. Considering that the ghost lineage for Plagiosauroidea extends at least to the PTB, it is not unreasonable to expect to discover Lower Triassic plagiosauroid specimens. Thus, from a phylogenetic perspective, the identification of *Uruyiella* as a plagiosauroid does not preclude an Early Triassic age assignment for the Buena Vista Formation, because the available temnospondyl phylogenies intimate that we can expect to find plagiosauroids in lowermost Triassic rocks.

A precise placement for the Buena Vista Formation in the Lower Triassic is not possible with the known, limited tetrapod fauna. Accordingly, the hypothesis that this formation is homotaxial to the Sanga do Cabral Formation of Brazil and the Katberg Formation of South Africa cannot be refuted at the present time. Piñeiro et al. (2003, 2004, 2007a) argued that the Buena Vista Formation could not be a lateral equivalent of the Sanga do Cabral Formation because materials of *Procolophon* and thrinaxodontid synapsids are totally unknown in the Buena Vista Formation. While this rationale lends circumstantial support to Piñeiro et al.'s (2003, 2004, 2007a) argument, it is the weakest form of biostratigraphical reasoning because it is based on negative evidence. Pursuant to this idea is the realization that the taxa used to correlate the Sanga do Cabral Formation to the Katberg Formation are not particularly abundant: only three skulls of *Procolophon* and several disarticulated vertebrae tentatively assigned to the genus have been described from the Sanga do Cabral Formation (Lavina, 1983; Cisneros and Schultz, 2002; Dias-da-Silva et al., 2007), and only five specimens (femoral fragments) comprise the thrinaxodontid material from the same formation described by Abdala et al. (2002). Considering that the Sanga do Cabral Formation has been examined by vertebrate palaeontologists for more than 30 years and the Buena Vista Formation for only the past decade, the absence of both *Procolophon* and thri-

naxodontids could be attributed to lack of systematic collecting in the latter formation.

5. Conclusions

Reconsideration of the limited tetrapod fauna of the Buena Vista Formation reveals that there is no unequivocal evidence of Late Permian taxa in this rock unit, and the evidence from unequivocally assigned taxa instead supports a Triassic age assignment. Based on *Pintosaurus* and the ghost-lineage reconstruction for Plagiosauroidea that *Uruyiella* partly serves to fill in (for this predominantly late Olenekian to Rhaetian temnospondyl group), we suspect that the Buena Vista Formation is Lower Triassic. We anticipate that the description of the "probable prolacertiform" archosauromorph material from the formation will help to test this idea. Ideally, we would like to see carbon-isotope and palaeomagnetic analyses on the Buena Vista Formation in order to test the biochronological signature of the tetrapod fauna. Both marine and continental PTB localities are characterized by a major negative shift in ^{13}C that coincides with a period of normal magnetism at PTB localities in China and South Africa (Ward et al., 2005; Erwin, 2006), which are equated to the ^{13}C anomalies recorded close to the PTB at Antarctic localities (but where paleomagnetic studies are confounded by Jurassic igneous intrusions: Collinson et al., 2006).

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