

Rapid vertebrate recuperation in the Karoo Basin of South Africa following the End-Permian extinction

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Abstract

The mass extinction that occurred at the end of the Permian Period approximately 251 Mya is widely accepted as the most devastating extinction event in Earth's history. An estimated 75–90% of global diversity from both marine and terrestrial realms disappeared synchronously within at most one million and perhaps as little as 100,000 years. To date, most research has focused on the marine record and it is only recently that a few fully preserved terrestrial Permo-Triassic boundary sequences have been discovered. The main Karoo Basin of South Africa hosts several well-preserved non-marine Permo-Triassic boundary sequences that have been the focus of intensive research into the nature of the extinction and its possible causes. This study uses sedimentological and biostratigraphic data from boundary sequences near Bethulie in the southern Karoo Basin to make assumptions about the rates and timing of recovery of the terrestrial fauna in this portion of southern Gondwana after the extinction event. The biostratigraphic data gathered from 277 *in situ* vertebrate fossils allows us to define more accurately the temporal ranges of several taxa. These data also confirm a more precise extinction rate in this part of the basin of 54% of latest Permian vertebrate taxa, followed by the onset of a relatively rapid recovery, within an estimated 40–50 thousand years (based on the calculation of floodplain aggradation rates and compaction ratios) that included the origination of at least 12 new vertebrate taxa from amongst the survivors.

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1. Introduction

The magnitude of the End-Permian mass extinction event, estimated to have occurred around 251.4 Mya (Bowring et al., 1998), has been well researched and is currently considered to be the most catastrophic mass extinction event in Earth's history (Erwin, 1994; Retallack, 1995; Benton, 2003; Benton and Twitchett, 2003; Erwin et al., 2002; Erwin, 2003). Over a relatively short time-span, certainly less than one million years and possibly as little as 100,000 years (Smith and Ward, 2001), most of the dominant marine groups of the Palaeozoic disappeared including the tabulate and rugose corals, articulate

brachiopods, stenolaemate bryozoans and stalked echinoderms (Erwin, 1994). On land, several groups of terrestrial vertebrates either became extinct (e.g. gorgonopsians) or were drastically reduced in number and diversity (e.g. dicynodonts) (Rubidge, 1995; Smith and Ward, 2001) in an apparently synchronous event. Various causes of the End-Permian extinction event have been proposed, including bolide impact (Becker et al., 2001, 2004), atmospheric pollution from basaltic flooding (Renne et al., 1995; Sephton et al., 2005), oceanic anoxia (Wignall and Twitchett, 1996; Isozaki, 1997; Hotinski et al., 2001), oceanic overturn (Knoll et al., 1996), excessive methane release (Krull et al., 2000; Sheldon and Retallack, 2002), rapid global warming and terrestrial aridification (Ward et al., 2000, 2005; Smith and Ward, 2001), food-web collapse (Wang et al., 1994), and a combined “tangled web of destruction”

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caused by the temporary breakdown of the Earth's natural recycling mechanisms (Erwin, 1994).

Most End-Permian extinction studies have focused on marine strata on the assumption that the most complete Permo-Triassic boundary (PTB) sequences are found in marine sediments (e.g. Clark et al., 1986; Gruszczynski et al., 1989; Wignall and Hallam, 1992; Wignall and Twitchett, 1996; Isozaki, 1997; Bowring et al., 1998; Jin et al., 2000; Mundil et al., 2001; Sephton et al., 2005). Recently, however, several transitional PTB sequences occurring in non-marine strata have been described from Australia (Retallack, 1995, 1998; Retallack and Krull, 1999; Sheldon and Retallack, 2002), Antarctica (Retallack et al., 1998; Sheldon and Retallack, 2002), South Africa (Ward et al., 2000; Macleod et al., 2000; Smith and Ward, 2001; Retallack et al., 2003), China (Shu and Norris, 1999; Metcalfe et al., 2001; Wang et al., 2002) and Russia (Newell et al., 1999; Tverdokhlebov et al., 2003; Benton, 2003; Benton et al., 2004).

The studies conducted on the terrestrial transitional PTB sections in the South African Karoo succession have included palaeomagnetic and stable isotope analyses, sedimentological and pedological facies analysis and the documentation of the faunal and floral changes both in species composition and taphonomic style (Retallack, 1995; Ward et al., 2000; Smith and Ward, 2001; Sheldon and Retallack, 2002; Retallack et al., 2003; Gastaldo et al., 2005). More recent work on the terrestrial PTB sequences in the Bethulie and Graaff-Reinet Districts in the southern and central Karoo Basin has provided palaeoenvironmental and biostratigraphical information allowing the patterns of disappearance of various vertebrate taxa across the Permo-Triassic boundary to be documented in greater detail (Ward et al., 2005; Smith and Botha, 2005). However, there is still little understanding of the recovery of diversity among the terrestrial vertebrates immediately after the extinction event and the strategies that these "post-apocalyptic" Early Triassic vertebrate communities used to survive and radiate in what appears to have been a much harsher environment than before the event. By 'recovery' we mean the process of restoring the numbers of vertebrate genera in a range of trophic levels similar to what was present before the extinction event in the Karoo Basin. Our aim here is to study the progressive increase in diversity immediately following the extinction rather than a detailed comparison of long before with long after the event.

The current study includes new data collected from the Early Triassic *Lystrosaurus* Assemblage Zone in the Bethulie District, which has allowed us to complete several ranges of Early Triassic vertebrate taxa and to provide updated information regarding the onset of recovery of the Karoo Basin ecosystem immediately after the End-Permian extinction event in South Africa.

2. Field techniques

Detailed sedimentological logs were measured to an accuracy of 10 cm from the PTB to some 240 stratigraphic

metres into the earliest Triassic strata exposed on the farms Fairydale, Heldemoed and Bethel in the Bethulie District of the southern Free State (Figs. 1 and 2). The stratigraphic positions of all 277 *in situ* vertebrate fossils found during the course of fieldwork were accurately plotted on these logs in order to complete the biostratigraphic ranges of as many taxa as possible and to determine the changes in vertebrate communities during the Early Triassic.

The new measured sections were also correlated with previous sections published by Smith and Botha (2005) and Neveling (2004). The former included a compilation of sedimentological logs and the stratigraphic positioning of all *in situ* vertebrate fossils recovered from several PTB sections in the Bethulie and Graaff-Reinet Districts. Most of these logs extend from approximately 50 m below to 50 m above the PTB, which lies a few metres above the base of the Palingkloof Member of the Balfour Formation. Neveling (2004) measured lithostratigraphic logs and conducted intensive fossil collecting from the upper *Lystrosaurus* Assemblage Zone into the lowermost overlying *Cynognathus* Assemblage Zone. He also identified a basin-wide, arenaceous marker horizon, informally called the "Swartberg member" (not yet approved by the South African Committee for Stratigraphy), within the middle portion of the Katberg Formation. The stratigraphic interval covered by this present study provides a much-needed link between the data previously collected by Smith and Botha (2005) and that of Neveling (2004) and fills a gap in the documentation of the Early Triassic stratigraphic and palaeontological record of the Karoo Basin.

3. Palaeoenvironment of the early Triassic Karoo Basin

3.1. Sedimentology and taphonomy of the PTB sequence

The biostratigraphic evidence for the main faunal extinction in the Karoo Basin at the end of the Permian occurs over approximately 40 m of strata at both the Bethulie and Graaff-Reinet localities. Lithostratigraphically, the extinction event ends at the top of a maroon laminate bed some 9–15 m above the first occurrence of red mudrock that marks the base of the Palingkloof Member at the top of the Balfour Formation (Fig. 1).

Detailed sedimentological logs compiled from several sections at both the Bethulie and Graaff-Reinet study areas show that the facies sequences in the boundary beds are remarkably similar. The overall lithological transitions are from drab greenish grey and blue-grey thickly-bedded and pedogenically modified massive siltstone beds with interbedded, laterally-accreted fine-grained sandstone bodies grading upwards into progressively more maroon coloured siltstone beds interbedded with vertically accreted tabular sandstones with distinctive erosional gullies at the base and includes a regionally extensive interval of maroon

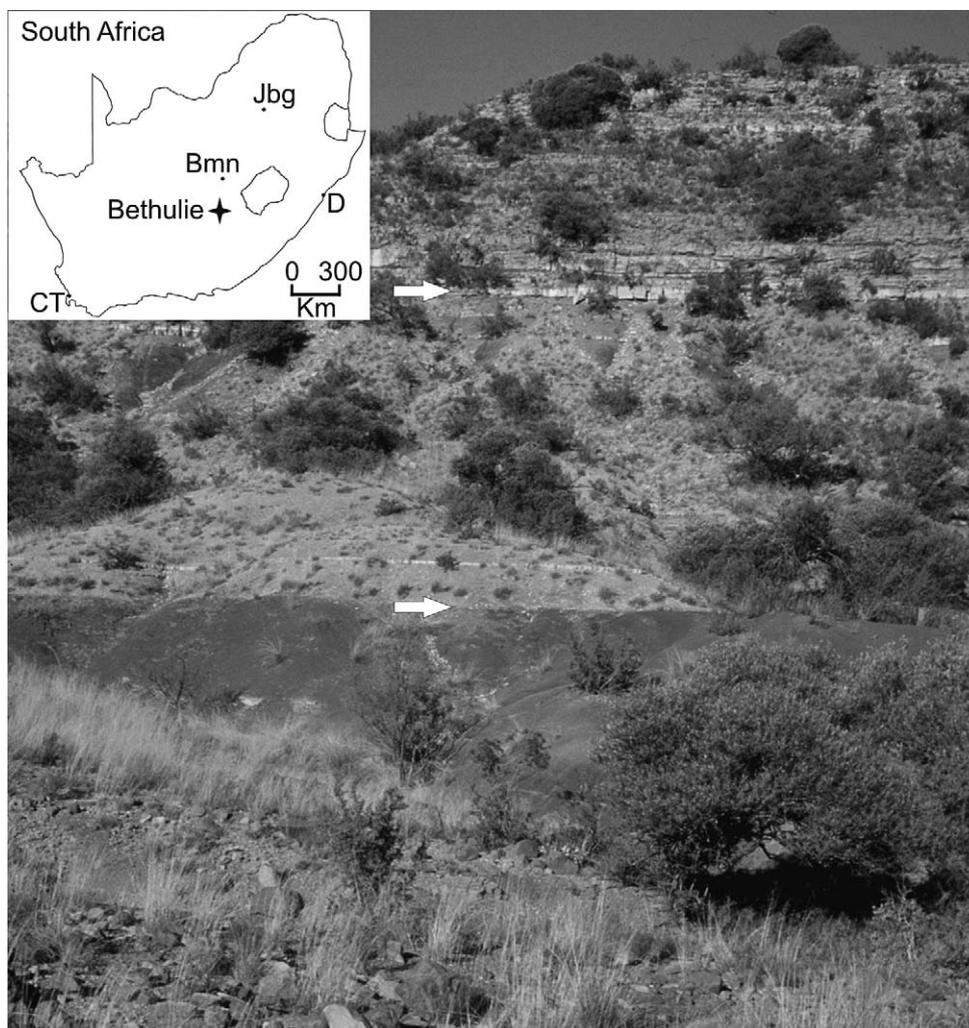


Fig. 1. The Permo-Triassic boundary sequence exposed on the farm Bethel 763 in the Bethulie District of South Africa. The PTB is positioned at the top of a basin-wide “event bed” of maroon-coloured laminated mudrocks (bottom arrow). Most of the Early Triassic recovery takes place in the overlying 20 m of floodplain dominated sediments below the base of the arenaceous Katberg Formation (top arrow). Abbreviations: Bmn = Bloemfontein, CT = Cape Town, D = Durban, Jbg = Johannesburg.

coloured thinly bedded laminites. The PTB sequence is capped by a succession dominated by thick conglomeratic sandstone bodies—the Katberg Formation of the Lower Triassic (Figs. 1 and 2).

3.1.1. –50 to –5 m interval below the PTB—green and grey massive mudrocks with laterally accreted sandstone bodies (upper Balfour Formation)

In the drab coloured dark grey (5Y 4/1) and olive grey (5Y5/2) mudrocks below the PTB, large dark brown weathering calcareous nodules and claystone lined-root channels as well as *Planolites* and *Taenidium* burrows are evidence for several extended periods of stasis and soil formation in the floodplain. Vertebrate fossils are relatively rare in these strata, but can be assigned to elements of the Late Permian *Dicynodon* Assemblage Zone fauna. They comprise disarticulated post-cranial bones of medium and large dicynodonts, lower jaws and isolated skulls. This interval has an unusually high incidence of skull fragments,

especially isolated caniniform processes of tusked dicynodonts. Approaching the PTB, thin beds of dark red (10R3/6) mudrock appear in the succession, becoming thicker and more reddish brown in colour until this facies dominates the succession.

3.1.2. –5 to 0 m interval immediately below the PTB—rhythmically laminated rubified mudrocks (lower Palingkloof Member)

At both localities, and possibly throughout the southern Karoo Basin, the last occurrence of *Dicynodon* (marking the biostratigraphic PTB) coincides with an interval of rhythmically-bedded laminated mudrock containing a single horizon of large brown weathering calcareous nodules (Figs. 1 and 2). This facies comprises a distinctive succession of thinly bedded dark reddish-brown (2.5YR3/4) and olive-grey (5Y5/2) siltstone/mudstone couplets. As with all the mudrock colours, they are very sensitive to contact metamorphism such that close to dolerite intrusions,

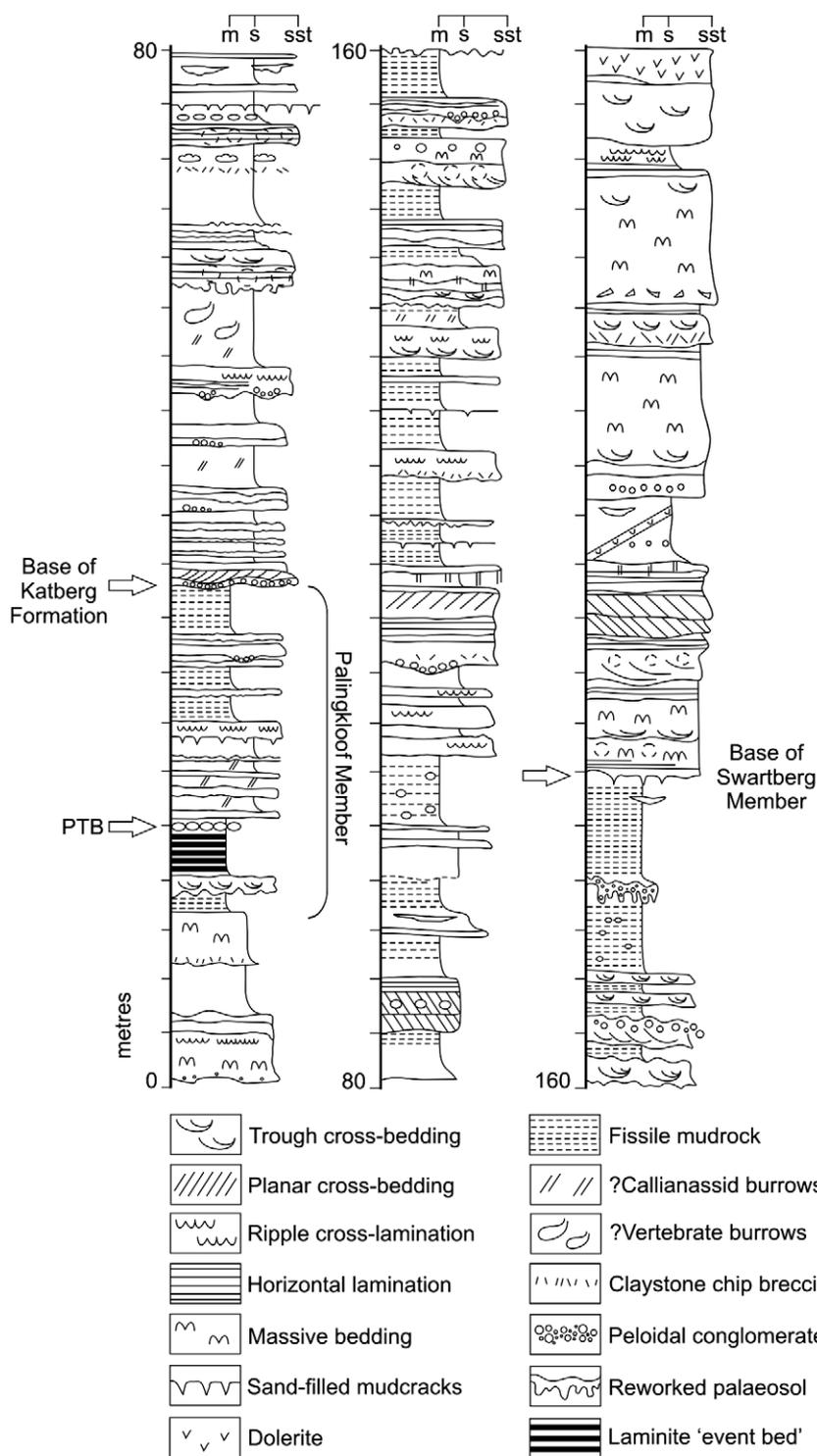


Fig. 2. Sedimentological log of Late Permian and Early Triassic strata on the farms Bethel 763, Heldemoed 677 and Donald 207, Bethulie District. Vertical scale tick marks represent 4 m. Abbreviations: m = mudstone; s = siltstone; sst = sandstone, PTB = Permo-Triassic Boundary.

the maroon colour of the laminites is converted to light grey. Upper surfaces of the centimetre-thick siltstone beds commonly display small oscillation ripples and some pustular textures that resemble the impressions of algal mats. This facies has very little evidence for pedogenesis, however, Retallack et al. (2003) report distinctive long cylindrical

cal unbranched callianassid-like burrow casts with possible scratch marks on the outer surface. At the Bethulie locality very rare partial skulls of *Lystrosaurus maccaigi* and *Moschorhinus* have been recovered from this interval confirming a Permian relict fauna rather than a new Triassic radiation.

3.1.3. 0–20 m interval above the PTB—rubified mudrocks with discontinuous thin tabular sandstone beds (upper Palingkloof Member)

Above the laminated beds at both localities, the section comprises massively bedded red (2.5YR4/6) and olive-grey siltstone interbedded with minor thin gullied sandstone sheets and horizons of sand-filled mudcracks. Large dark reddish brown weathering calcareous nodules occur isolated and along horizons within the red siltstone beds. Lenses of reworked pedogenic glaebules fill the gullies on the basal surfaces of some of the sandstones. Articulated *Lystrosaurus* skeletons become relatively more abundant in this interval and are commonly thickly enveloped in calcareous nodular material. The callianassid-type cylindrical burrows are also present in this interval.

3.1.4. 20–160 m interval above the PTB—rubified mudrocks with vertically accreted tabular channel sandstone bodies (lower Katberg Formation)

At both localities, the massive red siltstone facies grades rapidly into a much more sandstone-rich succession composed of stacked tabular light olive grey (5Y6/2) fine-grained sandstone bodies separated by olive and dark reddish brown mudrocks (Figs. 1 and 2). These Lower Katberg Formation sandstones contain numerous scoured disconformities lined with lenses and stringers of intraformational mud pebble and distinctive pedogenic glaebule conglomerate.

The thick (6.5 m) fine- to medium-grained tabular sandstone body that occurs at 62 m on the Bethulie log has a distinctively “gullied” basal contact filled with lenses of reworked pedogenic carbonate peloids and mudrock clasts. This grades upwards into horizontal lamination, medium scale trough cross-bedding and ripple cross-stratified sandstone. The uppermost ripple cross-laminated sandstone stringers form an undulating surface of sandstone ridges and siltstone swales. These swale fill siltstones are host to numerous medium to large *Lystrosaurus* skeletons that occur within brown weathering oblate calcareous nodules in such numbers that this interval has been informally dubbed the “*Lystrosaurus* abundant zone” (Smith and Ward, 2001) (Fig. 3). They comprise articulated and partially articulated curled-up skeletons as well as completely disarticulated, but associated individual skeletons.

A diagnostic feature of these Katberg sandstone bodies is the ubiquitous occurrence of spherical to ovoid brown-weathering calcareous concretions with concentric structure and septarian shrinkage cracks in the core. The alteration haloes and regular shape of these nodules suggests that they are of late diagenetic origin precipitated from groundwater flowing through the more porous zones of the buried, yet still not fully cemented, sand bodies (Johnson, 1976).

The thick intervening mudrock dominated intervals are composed of dark reddish-brown (2.5YR 3/6) and olive (5Y5/6) siltstone with numerous thin (<1.5 m) pale olive (5YR 6/3) sandstone lenses (Fig. 2). Fossils in these



Fig. 3. Articulated specimen of *Lystrosaurus declivis* within the lower Katberg strata on Heldemoed some 68 m above the PTB with middle Katberg Swartberg member (see Fig. 2) forming the vertical cliffs at the top of the Swartberg mountain in the background. The prepared skeleton was returned to its locality for this staged photograph.

rubified mudrock intervals are mostly encrusted with calcareous nodular material with a coating of haematite. The taphonomic signature of these mudrock intervals is a combination of articulated small cynodonts, some of which were probably preserved within underground burrows (Kitching, 1977, Fig. 4) along with partly articulated, but associated sub-adult *Lystrosaurus* as well as distinctive “bonebeds” of several disarticulated, but otherwise undamaged *Lystrosaurus* skeletons in a chaotic melange.

Higher than 116 m above the PTB, the fragmented jaws of *Procolophon* are within the intraformational conglomerates (Fig. 5). The increased relative abundance and the unique taphonomic style of the fossils in this interval has been interpreted as the result of drought accumulations in an arid floodplain setting (Smith and Botha, 2005).

3.1.5. 160–220 m interval above the PTB—thick amalgamated tabular channel sandstones (Swartberg member of Neveling, 2004)

This facies is a prominent cliff forming sandstone that caps many of the mesas in the Bethulie District (Figs. 1 and 2). It comprises three thick (>50 m) amalgamated sandstone bodies with minor interbedded mudrock stringers. Each sandstone body is composed of medium grained



Fig. 4. Fully-articulated skeleton of the cynodont *Galesaurus planiceps* collected from 48 m above the PTB on Donald 207. Scale bar = 5 cm.



Fig. 5. An *in situ* *Procolophon trigoniceps* maxilla in peloidal conglomerate at the base of a lower Katberg channel sandstone indicating the First Appearance Datum of this taxon 116 m above the PTB. This specimen was positively identified as *P. trigoniceps* based on the low number of teeth (compared to owenettids or *Coletta seca*), the tooth wear and transverse expansion (J. Cisneros, pers. comm., 2005). Scale bar = 1 cm.

massive and trough cross-bedded sandstone with numerous internal scour surfaces commonly lined with mudstone “biscuit”-shaped clasts and reworked pedogenic nodules. Isolated large (up to 50 cm in diameter) oblate, brown weathering, smooth-surfaced concretions occur in a horizon midway up the lowermost sandstone.

3.2. Interpreted palaeoenvironmental changes across the PTB

The facies sequence through the PTB is interpreted as a relatively rapid change in fluvial landscape from an alluvial plain traversed by a few large, highly meandering rivers with expansive lowland floodplains (*massive dark grey mudrock*) through a transitional stage when the rivers straightened and branched into a distributary channel

network that scoured the now abandoned floodplains (*massive red siltstone*) (Smith, 1995). The field evidence of more flashy discharge in the Triassic is the appearance of distinctive gullies at the base of the channel sandstones filled with reworked pedogenic nodules and large mudrock rip up clasts. The rapid switching of the thalweg within a wide, low sinuosity channel is indicated by the numerous vertically-stacked sheet sandstones with glaebule conglomerate-lined disconformities. It has been proposed that this switch in fluvial style was triggered primarily by the die-off of bank strengthening vegetation (Ward et al., 2000). As the run-off charged sediment load increased, these channels widened and in-channel bars eventually separated the flow into a braided pattern of interconnected sand-dominated ephemeral channels (*conglomeratic sandstone*). Gastaldo et al. (2005) investigated the plant remains in this interval at both the Bethulie and Graaff-Reinet localities and found that a distinctive change in taphonomic style had occurred some 10–15 m below the PTB. This change from parautochthonous assemblages of complete *Glossopteris* and *Phyllothea* leaves to allochthonous accumulations of reworked plant trash in scour fill structures is interpreted as an indication of the change from high groundwater tables in essentially wet floodplain conditions to fluctuating groundwater with more erratic flood events over seasonally dry floodplains.

During deposition of the massive red siltstone facies there was an apparently synchronous depositional event that immediately followed the extinction of *Dicynodon*—the last of the Permian dicynodonts to disappear from the Karoo Basin. This resulted in the accumulation of up to 5 m of finely laminated mudrocks (*maroon laminites*) that show evidence of shallow standing water with periodic sub-aerial exposure and desiccation. Thin sections of the laminae show light/dark alternations that may be interpreted as varves and suggest accumulation within a

thermally stratified standing water body, which in this climatic setting would be termed a playa lake. Periodic flooding deposited sand/mud couplets show little post-depositional colonization by either animal or plant life except burrows of a possible crustacean. The conclusion drawn from this evidence is that for a short period following the disappearance of *Dicynodon*, the central Karoo Basin floodplains were almost devoid of vegetation and were seasonally occupied by widespread playa lakes. Using the average floodplain accretion of 1.5 mm calculated by Retallack et al. (2003) from the weak palaeosol development in the laminites, applying a 60% compaction ratio (Baldwin and Butler, 1985) and adding two short periods of pedogenesis, gives an estimated time interval for the 5 m thick laminites of approximately 10,000 years.

Above the laminites, the floodplain accretion rates decrease and pedogenic overprinting is again evident, except the palaeosol character has changed. The massive red siltstone beds are interpreted as having been initially deposited by overbank flood events, but subsequently re-worked by wind action as loess (Smith, 1995). The palaeosols, although distinctively red in colour, have a slightly greater depth to calcic horizon than those of the latest Permian. Retallack et al. (2003) interpret this as a modest increase in seasonal precipitation from an estimated 346 mm to 732 mm across the boundary, combined with an increase in mean annual temperature and a change in vegetation type from a *Glossopteris* dominated flora to an equisetalian flora. Perhaps a more plausible interpretation of the observed changes in fluvial style and pedogenesis is that they were brought about by an increase in mean annual temperature combined with the onset of a monsoonal rainfall regime (Retallack et al., 2003). Within a completely continental setting such as the Karoo Basin, this resulted in more highly seasonal rainfall and increased storm intensity, but with lower reliability.

The taphonomic style of vertebrate remains, especially the appearance of monospecific bonebed occurrences in these reddened mudrocks, reflects periods of extended drought and a more erratic rainfall regime. Gradually, through time, the low sinuosity channels became wider and straighter and more bedload-dominated until they all but eliminated the intervening floodplains. These now truly braided channels were sourced in the Gondwanide mountains to the south and they eventually amalgamated to form a braidplain that covered much of the southern Karoo Basin (the “Swartberg member” of Neveling (2004)).

3.3. Vertebrate biostratigraphy and relative abundance

The biostratigraphic data obtained during this study allows us to better define the ranges of several vertebrate taxa that were previously poorly constrained (Fig. 6). Shishkin et al. (1996) suggested that the range of the small amphibian *Lydekkerina huxleyi* was restricted to the middle and upper portion of the *Lystrosaurus* Assemblage Zone. However, our results show that *L. huxleyi* only

occurs in the lower Katberg Formation (approx. 45–147 m above PTB). Neveling (2004) also confirms its absence from the upper Katberg Formation.

The archosauriform *Proterosuchus* is the first taxon to appear above the PTB (Smith and Botha, 2005) and, as suggested by Kitching (1977), we can now confirm that it too is restricted to the lowermost *Lystrosaurus* Assemblage Zone (lithostratigraphically confined to the upper Palingkloof Member and lowermost Katberg Formation).

The first appearance datum (FAD) of the procolophonid *Procolophon trigoniceps* was originally placed at 60 m above the PTB (Smith and Botha, 2005). However, this specimen, which consists only of a series of articulated vertebrae (RS152), was recently re-examined and found not to be *P. trigoniceps*. From the current study, we have found that the first positively identified *in situ* specimen of *P. trigoniceps* (Fig. 5) is located at 116 m above the PTB in the lower Katberg Formation. To date, *P. trigoniceps* has not been found in the underlying Palingkloof Member below the Katberg Formation. The number of *P. trigoniceps* specimens recovered increases significantly just below the Swartberg member at about 160 m above the PTB. These specimens include several *in situ* fragmentary skulls or jaws and numerous loose, easily identifiable jaws of *P. trigoniceps*. Although Broom's (1906) proposal for a separate *Procolophon* Zone between the *Lystrosaurus* and *Cynognathus* assemblage zones was not accepted (Watson, 1914; Haughton, 1919) and was instead incorporated into the *Lystrosaurus* Assemblage Zone, Neveling (2004) has suggested that a “*Procolophon* abundant zone” may still be recognized in the upper portion of the *Lystrosaurus* Assemblage Zone. He places the “*Procolophon* abundant zone” in the uppermost Katberg Formation, above the Swartberg member.

The extent of the “*Lystrosaurus* abundant zone”, first identified by Smith and Ward (2001) in the Bethulie sections, has now been constrained to between 48 and 56 m above the PTB, in the lower Katberg Formation (Fig. 7). This abundant zone contains a significantly higher proportion of *Lystrosaurus declivis* specimens (Fig. 3) compared to elsewhere in the stratigraphy and includes individual skulls, complete articulated skeletons and bonebed accumulations of several disarticulated skeletons (commonly as many as 8–10 skulls in one occurrence). Taphonomic analysis suggests that the large numbers of *Lystrosaurus* fossils reflects a period of time when drought accumulations were more common, rather than reflecting any increase in the living populations of these taxa (Smith and Botha, 2005).

The therocephalian *Scaloposaurus constrictus* is restricted to the lower Katberg Formation (FAD approx. 42 m above PTB) with its Last Appearance Datum (LAD) occurring at 164 m above the PTB, just below the Swartberg member. The cynodont, *Galesaurus planiceps*, is restricted to the very upper portion of the Palingkloof Member (FAD approx. 22 m above PTB) and the lowermost Katberg Formation (LAD approx. 85 m above PTB).

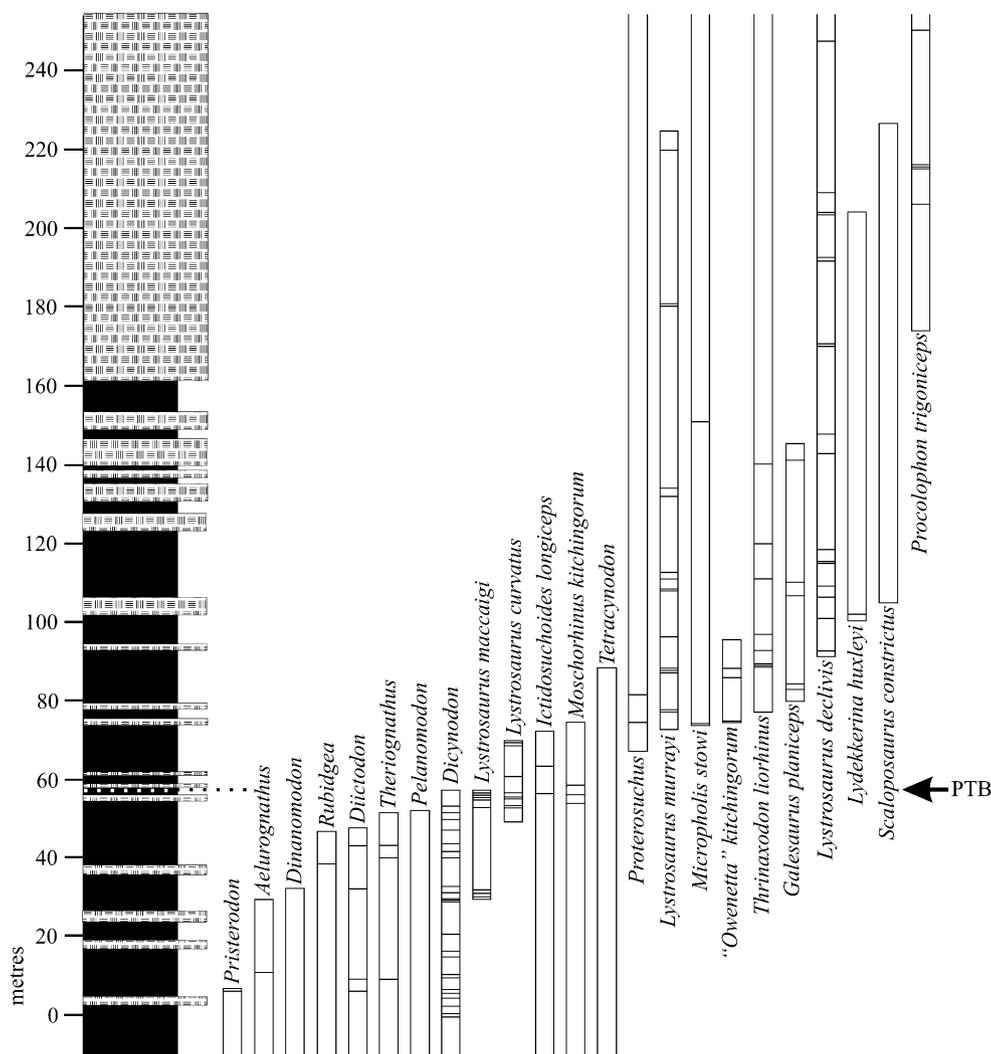


Fig. 6. Range chart of *in situ* vertebrate fossils found in the PTB sequences of the southern and central Karoo Basin of South Africa (modified and updated from Smith and Botha, 2005). Note that the tick marks only indicate the presence of *in situ* fossils in each 1 m interval, they do not represent the number of specimens. The informally named *Lystrosaurus* "abundant zone" occurs between 48 and 56 m above the PTB. In this interval, one tick mark represents the accumulation of 10 disarticulated *Lystrosaurus declivis* skeletons figured in Smith and Botha (2005). *Ex situ* specimens, of which there are many, are not indicated.

4. Discussion

4.1. Faunal ranges

The extensive and rigorous collecting efforts made by numerous researchers (e.g. Neveling, 1998a,b, 2004; Neveling et al., 2000; Hancox and Rubidge, 2001; Hancox et al., 2002; Smith and Ward, 2001; Damiani and Rubidge, 2003; Damiani et al., 2003; Retallack et al., 2003) in the Karoo Basin over the last decade has yielded a vast number of fossils, including several new taxa. This data has facilitated an update of the ranges of vertebrate taxa in the *Lystrosaurus* Assemblage Zone that was originally compiled by Rubidge (1995) (Fig. 7).

New taxa including the amphibians *Thabanchuia oomie*, *Eolydekkerina magna* and *Broomistega putterilli* (Damiani and Rubidge, 2003), the procolophonoids 'Owenetta'

kitchingorum (Modesto et al., 2003; soon to be placed in another genus, Modesto pers. comm., 2005), *Saurodekteles rogersorum*, *Sauropareion anoplus* and *Coletta seca* (Modesto et al., 2001, 2002, 2003), the therocephalian *Ictidosuchoides longiceps* (Smith and Botha, 2005) and the cynodont *Progalesaurus lootsbergensis* (Sidor and Smith, 2004) have been added to the *Lystrosaurus* Assemblage Zone vertebrate range chart. The dicynodont *Lystrosaurus* has also been re-evaluated and the range of this genus is now divided into its respective Triassic species (i.e. *Lystrosaurus curvatus*, *Lystrosaurus murrayi*, *L. declivis*; Botha and Smith, in press). The ranges of the amphibians *Micropholis stowi* and *L. huxleyi*, the procolophonid *P. trigoniceps*, the eosuchians *Prolacerta broomi* and *Proterosuchus*, the therocephalians *Moschorhinus kitchingi*, *Olivierosuchus parringtoni* (previously *Olivieria*, Kammerer and Sidor, 2002), *S. constrictus*, *Tetracynodon* and *Erciolacerta parva*,

are now considered to be junior synonyms of *L. huxleyi* (Damiani and Rubidge, 2003) and *Uranocentrodon senekalensis* is now restricted to the Permian (Smith, 1995; Hancox et al., 2002; Latimer et al., 2002), resulting in the absence of this genus from the *Lystrosaurus* Assemblage Zone. The range of *Kestrosaurus dreyeri* appears to be mostly constrained to the *Cynognathus* Assemblage Zone (Damiani and Rubidge, 2003; Neveling, 2004), although two fragmentary specimens recently recovered from the uppermost Katberg Formation by Neveling (2004) and tentatively assigned to *K. dreyeri*, may in future place the FAD of this genus in the *Lystrosaurus* Assemblage Zone (Neveling, 2004).

4.2. Survivorship of the End-Permian mass extinction

Of the 29 taxa so far collected from strata representing the onset of the post-extinction recovery phase, 12 of these taxa (43%) have a confirmed first appearance in the Palingkloof Member (0–20 m above the PTB) and a further eight taxa have a probable FAD in the Palingkloof Member. The ranges of these eight taxa, which include amphibians and eosuchians (Fig. 7), need to be confirmed, however, as properly embedded *in situ* specimens have not yet been recovered from the Palingkloof Member.

The 12 taxa with a confirmed record in the Palingkloof Member may have had ghost lineages that crossed the PTB, and if added to the confirmed four survivor taxa (*L. curvatus*, *Moschorhinus kitchingi*, *Tetracynodon*, *I. longiceps*), this indicates that 16 out of the 35 *Lystrosaurus* Assemblage Zone taxa survived the extinction. This reflects a 46% survival rate, which translates into a 54% extinction rate; that is if every taxon in the Palingkloof Member crossed the PTB. However, it should be noted that there may have been some rapid speciation within the earliest Early Triassic, resulting in fewer ghost lineages crossing the PTB.

The four taxa, namely, *L. curvatus*, *Tetracynodon*, *M. kitchingi* and *I. longiceps* that survived the extinction event remained marginal and disappeared rapidly after the extinction. Surviving a mass extinction does not guarantee success during a post-extinction recovery phase (Jablonski, 2002), because there are several factors (such as climate change, inter-specific competition, predation-resistance, etc.) that affect survival rates. Jablonski (2002) refers to these survivor taxa that disappear soon after an extinction event as “Dead Clade Walking” or DCWs. It is possible that the conditions that were favourable for the originating Early Triassic taxa were not favourable for the taxa that survived the extinction causing these four survivor taxa to become DCWs.

Although the various species of *Lystrosaurus* have different biostratigraphic ranges (Botha and Smith, in press) and the species *L. curvatus* disappeared soon after the extinction event, the FAD of the genus occurs in the latest Permian *Dicynodon* Assemblage Zone (*L. maccaigi*) and extends far into the Early Triassic *Lystrosaurus* Assemblage Zone

(*L. murrayi*, *L. declivis*). To date, *Lystrosaurus* is the only dicynodont taxon known to have survived the End-Permian extinction and appears to be not only the most extinction-resistant taxon amongst the dicynodonts, but amongst all synapsids as well. Furthermore, originating taxa often have wide geographical distributions (Sepkoski, 1998) and thus, the wide geographical distribution of the Triassic species of *Lystrosaurus* (South Africa, Antarctica, India, Russia, China) may have been a contributing factor to its survival and success during the Early Triassic.

4.3. Onset and duration of recovery

The appearance of 43% of the Early Triassic faunal diversity within 20 stratigraphic metres of the PTB is indicative of a relatively rapid onset of recovery and radiation in the Karoo Basin. The speed of the onset may be roughly estimated by calculating the aggradation rates of the ancient fluvial systems that deposited this interval. Holocene deposits in the arid continental basin of south central Australia are considered to be a good modern analogue for the sediments of this part of the Karoo sequence. Studies of the modern Cooper Creek system have calculated normal floodplain aggradation rates of 2–2.5 mm (Knighton and Nanson, 2000; Pickup, 1991). Applying this to ancient Karoo systems, assuming no major hiatuses and applying a compaction correction of 5 (Baldwin and Butler, 1985) it would have taken approximately 40–50,000 years to accumulate the 20 m of floodplain strata during which time the Early Triassic recovery began to take place.

These results are in contrast to previous reports that suggest that there was a 5 million year delay before the onset of recovery during the Early Triassic (Erwin, 2001). Most studies of post-extinction recovery phases have focused on marine ecosystems, because data is usually more readily available for such studies (e.g. Sepkoski, 1984, 1998; Erwin, 1994; Jablonski, 1998; Rampino and Adler, 1998; Racki, 1999; Jablonski, 2002). It is possible that the 5 million year lag between the End-Permian extinction and the onset of the post-extinction recovery (Erwin, 2001) may only be applicable to marine ecosystems.

There are a number of possible reasons for the apparent onset of such a rapid recovery in the Karoo Basin, including preservational bias, different recovery rates between marine and terrestrial environments, the rapid infilling of vacant niches, climatically induced endemism, monsoonal conditions, drought tolerance leading to diversity “hot-spots”, as well as competitive ability or predation-resistance (Jablonski, 2002). Preservational bias is an unlikely explanation as there is no evidence for hiatuses at the study sites and the preferential preservation of particular taxa is also unlikely as all sizes of animal are preserved in both channel and floodplain environments.

The duration of a post-extinction recovery phase can be defined as the period between the peak in extinction rates and the peak in origination rates following the extinction (Kirchner and Weil, 2000; Erwin, 2000). Using

this definition, Kirchner and Weil (2000) suggest that recovery phases in general persist for approximately 10 million years, regardless of the severity of the extinction. If this is the case, the duration of the recovery period in the Karoo Basin would have lasted until about the mid-Anisian (early middle Triassic, approximately 240 Mya; *Cynognathus* Assemblage Zone), when a peak in origination rates should have been reached. However, the fossils record a higher biodiversity in the *Lystrorhynchus* Assemblage Zone than the overlying *Cynognathus* Assemblage Zone. To date, 35 taxa have been noted in the *Lystrorhynchus* Assemblage Zone (Fig. 7) compared to 29 in the *Cynognathus* Assemblage Zone (Rubidge, 1995), which suggests that origination rates peaked in the *Lystrorhynchus* Assemblage Zone, rather than the *Cynognathus* Assemblage Zone and thus, took less than 10 million years to do so. However, it should be noted that the biodiversity of both zones are under revision.

4.4. Adaptation vs. migration

Several authors have previously proposed migration as a reason for the appearance of the post-extinction Early Triassic Karoo fauna (Kitching, 1977; King and Jenkins, 1997; Reisz et al., 2000). Pfefferkorn (1999) noted that there are often no new species in a given region after an extinction that would be capable of filling recently vacated niches, and thus, new species would have to evolve and then migrate into the area. Pfefferkorn (1999) also suggests that if a large amount of genetic diversity has been removed from the system, as with the End-Permian extinction, a complete replacement of taxa would require a long period of time. However, as our results indicate a relatively quick appearance of originating taxa (within 20 m of the PTB) it would suggest that migration into the basin was remarkably rapid and a return to high diversity levels took less than 5 million years.

Regionally restricted environmental changes can also account for different recovery rates in different regions (Jablonski, 2002) and can lead to climatically induced endemism as well. Thus, it is possible that the onset of monsoonal climatic conditions in southern Gondwana (Smith and Botha, 2005) favoured a more rapid recovery in the Karoo Basin of South Africa compared to the South Urals Basin in Russia (Benton et al., 2004), where the onset of recovery appears to have taken longer.

Another possible factor influencing the origination of new taxa in the earliest Triassic Karoo Basin is the environmental selection for drought tolerance. Many of these new taxa are archosauromorphs and parareptiles, which may have been pre-adapted to an arid environment. Extant reptiles are highly efficient at conserving water: they rarely drink water (water from food and metabolic water gains are usually sufficient), they have tough, water-resistant integuments, low ventilation rates, solute-linked water reabsorption mechanisms and they excrete relatively dry faecal pellets (Withers, 1992; Pough et al., 1996). Although extant mammals also have efficient mechanisms for con-

serving water, they lose water more easily as they drink more, have less water-resistant integuments and higher ventilation rates compared to reptiles (Withers, 1992; Pough et al., 1996). The Early Triassic parareptiles and archosauromorphs (which underwent significant radiation to become highly diverse and successful during the Triassic; Reisz et al., 2000) were probably adept at conserving water and well adapted to aridity and drought.

Many of the Early Triassic taxa probably used burrowing as a survival strategy as well (Smith and Botha, 2005). There is sedimentological and taphonomic evidence to suggest that animals such as *Procolophon*, *Lystrorhynchus*, *Galesaurus* and *Thrinaxodon* (Groenewald, 1991; Miller et al., 2001; Damiani et al., 2003; Retallack et al., 2003; Neveling, pers. comm., 2004) were fossorial, which would have allowed them to ameliorate the fluctuations in temperature and humidity that characterise monsoonal-type climates.

5. Conclusions

(1) New biostratigraphic data (using species level taxonomy) have better defined the ranges of several vertebrate taxa in the Early Triassic *Lystrorhynchus* Assemblage Zone that were previously poorly constrained.

(2) The climatic changes that occurred during the End-Permian extinction may have exceeded the adaptive limitations of the survivor taxa, but the post-extinction recovery phase appears to have begun during the survival phase and thus, the appearance of the originating taxa may also have had an adverse affect on the survivor taxa, causing them to become extinct shortly after the extinction event.

(3) Although fossils of only four survivor taxa have actually been recovered from either side of the PTB, several of the 12 taxa that first appear in the earliest Triassic Palingkloof Member may have had ghost lineages that crossed the boundary. Taking these ghost lineages into account, our results suggest an extinction rate of 54% in the Karoo Basin.

(4) *Lystrorhynchus* appears to have been the most extinction-resistant taxon during the End-Permian; taking refuge in burrows may have allowed this genus to persist at low diversity (only two species) for such a long period.

(5) Although the vertebrate extinction in the Karoo Basin was rapid ($\pm 100,000$ years), the Early Triassic recovery phase was possibly even shorter than the extinction. Calculating the aggradation rates of the ancient fluvial system, we estimate that the Karoo Basin vertebrate diversity recovered to close to pre-extinction levels within approximately 40–50,000 years.

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