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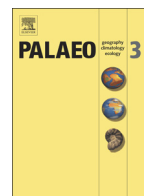
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Origin and palaeoenvironmental significance of *Lystrosaurus* bonebeds in the earliest Triassic Karoo Basin, South Africa



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ABSTRACT

Earth experienced its most devastating extinction event at the end of the Permian period 251 million years ago (Ma). Despite an estimated 75 to 90% loss of species globally in both marine and terrestrial realms across the Permian–Triassic Boundary (PTB), around 20% of the terrestrial tetrapod genera in southwestern Gondwana survived and were immediately joined by a number of immigrant taxa to occupy most of the vacant niches of the earliest Triassic. Preserved in the Karoo Basin of South Africa is an almost continuous stratigraphic record of terrestrial sedimentation through the PTB that hosts a fossil record of ecosystem collapse, survivorship and recovery. The adaptation of the mammal like reptiles (therapsids) of the *Lystrosaurus* Assemblage Zone to a highly seasonal, potentially drought prone semi-arid earliest Triassic Karoo Basin is associated with changes in modes of fossilisation. Isolated dicynodont skulls and postcranial elements are commonly found in the latest Permian. However, in the earliest Triassic the dicynodonts occur as articulated, curled-up skeletons and multi-individual monotaxic bonebeds. Lack of epiphyses and relatively small skull length confirm that the bonebeds comprise several subadult *Lystrosaurus declivis* (*L. declivis*) carcasses. No significant evidence for hydraulic bone concentration along with clusters of ribs in life position points to complete carcasses being present at the site of death, and suggests that animals behaviourally congregated before perishing together. The bonebeds are hosted by an 8 m thick horizon of floodplain mudrocks in the lower Katberg Formation named the *Lystrosaurus* abundant zone. The bonebed horizon is overlain by sand-filled mud cracks capped by coarse sediments indicative of rapid deposition during waning floods. Stable isotope analyses of pedogenic and early diagenetic calcite nodules in association with the bonebeds yield average $\delta^{13}\text{C}$ values ranging from -9.5 to -5% and $\delta^{18}\text{O}$ values of 13.5 to 16‰, respectively. These isotope values support a seasonally cold, semi-arid climate at high latitude ($\sim 55^\circ\text{S}$). The presence of vertebrate burrow casts on bonebed horizons and evidence of shelter sharing suggests that tetrapods were attempting to escape extreme climatic conditions. Aggregation behaviour of subadult *Lystrosaurus* during unusual cold snaps may best explain the origin of bonebed assemblages.

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1. Introduction

The South African Karoo Basin preserves one of the few relatively complete terrestrial Permian–Triassic successions in the World and as a result, is a rare window into what happened to terrestrial ecosystems during the greatest biological crisis to have affected life on Earth, 251 Ma. Globally this ‘mother of all mass extinctions’ (Erwin, 2006; pg. 9) is believed to have pushed 90% of marine life, 60% of land vertebrates, 30% of insects and 70% of land plants to extinction (Labandeira and Sepkoski, 1993; Stanley and Yang, 1994; Retallack, 1995; Benton and Twitchett, 2003; Wake and Vredenburg, 2008). There is some consensus that a number of factors came together to trigger rapid global

warming and the resultant end-Permian mass extinction event (Benton and Twitchett, 2003). Proposed causal factors include 1) global marine anoxia associated with global warming (Wignall and Hallam, 1992; Bottjer, 2012), 2) a combination of sea-level fall (from the formation of Pangea), volcanism, and anoxia (Erwin, 1993), 3) Siberian trap volcanism (Renne et al., 1995; Bowring et al., 1998), and 4) dissociation of methane gas hydrates from the seafloor (Heydari and Hassanzadeh, 2003). Deposits of the Karoo Basin indicate changes in fluvial style during the transition from Permian–Triassic and are believed to relate to vegetation die-off and onset of drier, highly seasonal conditions by the Early Triassic (Smith, 1995; Smith and Botha, 2005; Botha and Smith, 2006; Smith et al., 2011). Other terrestrial records across the PTB from Australia and Russia indicate similar changes in fluvial style (Michaelsen, 2002; Newell et al., 2010). In the Karoo Basin this change in fluvial style coincides with a stepped extinction of numerous therapsid genera as well as the entire glossopterid flora in the latest Permian, which gathered momentum across the PTB (Smith, 1995; Smith and Botha, 2005; Botha and Smith, 2006; Smith et al., 2011).

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Of the 48 tetrapod families living in the last three million years of the Late Permian, only 12 survived the extinction event (Benton, 1997). Although the disappearance of most therapsid groups was catastrophic, this account of destruction is also one of survival. The survivor's tale in the Karoo Basin begins just prior to the major pulse of extinction, with the appearance of a new dicynodont genus *Lystrosaurus* (Botha and Smith, 2007). *Lystrosaurus* was the more successful of the two surviving dicynodonts, the other being the very rare and diminutive *Myosaurus* (Cluver, 1971). *Lystrosaurus maccaigi* was the first *Lystrosaurus* species from the uppermost *Dicynodon* Assemblage Zone. Wet-floodplain adapted therapsid fauna of the *Dicynodon* Assemblage Zone begin to suffer extinction by the latest Permian and *L. maccaigi* is replaced by *Lystrosaurus curvatus* across the PTB. By the earliest Triassic, dry-floodplain adapted fauna from the *Lystrosaurus* Assemblage Zone appear and *L. curvatus* is replaced by *Lystrosaurus murrayi*, and *L. declivis* (Smith, 1995; Smith and Botha, 2005; Botha and Smith, 2006). It is speculated that with their downturned beaked jaws the genus *Lystrosaurus* was well adapted to forage on the drought tolerant horsetails that remained after the *Glossopteris* trees and shrubs had disappeared (Smith, 1995; Botha and Smith, 2007).

Although it was the cynodonts and not *Lystrosaurus* that went on to flourish and eventually evolve into mammals, the success of *Lystrosaurus* immediately after the extinction event may help us to understand the dynamics of mass extinction and recovery of faunal diversity in the Karoo Basin. *Lystrosaurus* fossils across the PTB provide insight into behavioural change, possibly linked to environmental changes because fossils of isolated skulls and postcranial material in the uppermost Permian are replaced by multi-individual, monotaxic bonebeds in the lowermost Triassic (Smith, 1995; Smith and Botha, 2005; Botha and Smith, 2006). The bonebeds of this study are considered monotaxic because they consist of the skeletal hard parts of terrestrial vertebrates preserved in a localised area, derived from more than one individual of a single species (Behrensmeyer, 2007). There are many different processes that can form skeletal concentrations, some more taphonomically intriguing than others (Eberth et al., 2007; Rogers and Kidwell, 2007) and monotaxic bonebeds rank amongst the most unusual and enigmatic features of the fossil record, conjuring up visions of ancient catastrophe and mass death (Rogers and Kidwell, 2007). Understanding the mode of accumulation and burial of monotaxic *Lystrosaurus* bonebeds and bone concentrations will help reconstruct the floodplain conditions and the behaviour of the inhabitants of this part of southern Gondwana as the ecosystems recovered from the end-Permian mass extinction event.

2. Lithostratigraphy and locality of study

The *Lystrosaurus* bonebed fossils in this study are preserved within semi-arid continental fluvial deposits of the Beaufort Group (Karoo Supergroup) in the Bethulie District of the southern Free State Province of South Africa on a privately owned farm (Fig. 1). The outcrop exposed here lies within the lowermost Triassic Katberg Formation, the lowest formation of the Tarkastad Subgroup. The farm is a well-known and productive fossil locality first discovered by James Kitching in 1977 (Abdala et al., 2006). The farm and its adjoining property occur in a large canyon where Smith (1995) first documented a fully preserved PTB sequence in the Karoo Basin and found vertebrate fossils that recorded the end-Permian mass extinction event. 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, terminating in a 9–15 m thick zone of maroon laminated mudstone at the top of the Balfour Formation, Beaufort Group (Adelaide Subgroup) (Smith and Botha, 2005; Botha and Smith, 2006). Evidence of Early Triassic faunal recovery is already apparent in the first 20 m above this event, and into the Katberg Formation (Botha and Smith, 2006). It was during the 2004 field season that the first large monotaxic bonebed was uncovered in the lower Katberg Formation. This bonebed consists of at least

nine *Lystrosaurus* individuals and was excavated in a single block, stabilised with a Plaster of Paris jacket, and then taken to the Iziko South African Museum where it was accessioned (SAM-PK-K8551) (Fig. 2). Subsequently, another five *Lystrosaurus* bonebeds were found, occurring in an approximately 8 m thick stratigraphic interval in the lower Katberg Formation, which was named the *Lystrosaurus* abundant zone (Botha and Smith, 2006). Due to the similar preservation style to SAM-PK-K8551, it was assumed that these five bonebeds contained the remains of more than one individual. As a result, they will be referred to as bonebeds until the Minimum Number of Individuals (MNI) is firmly established later in the study.

3. Materials and methods

In order to understand the sedimentological and stratigraphic contexts of the *Lystrosaurus* bonebed occurrences, a 29 m thick vertical log was measured through the outcrop using a Jacob's staff with Abney level. Bed contacts were recorded to an accuracy of 5 cm and major bounding surfaces were traced approximately 50 m laterally to establish their rank. The log includes the lowermost strata exposed at the locality, which are stratigraphically 5 m above the base of the Katberg Formation. Lithology, texture, colour, sedimentary structures, bounding surfaces, scour marks, nodules, fossils, and ichnofossils (burrows and root traces) were recorded onto a graphic log at 1:10 scale (Fig. 3).

Carbonate nodules that occur in the *Lystrosaurus* bonebed-bearing horizons were collected for stable carbon and oxygen isotope analyses to investigate what they might reveal about the palaeoenvironment at the time of deposition or during burial diagenesis. Isotope analyses were performed at the stable isotope laboratory in the Department of Geological Sciences, University of Cape Town. Measured isotope samples were reported in per mil notation where the value was calculated by using the following model:

$$\delta^{13}\text{C}(\text{or}\delta^{18}\text{O}) = [\text{R}_{\text{sample}}/\text{R}_{\text{standard}} - 1] \times 1000.$$

$\text{R} = {}^{13}\text{C}/{}^{12}\text{C}$ and ${}^{18}\text{O}/{}^{16}\text{O}$ for carbon and oxygen, respectively. Drilled, powdered bulk samples from the centre to the rim of cut carbonate concretions were reacted offline with 100% phosphoric acid, following the method of McCrea (1950). Samples were then left for a minimum of 24 h in the reaction vessels and placed in a 25 °C water bath. CO was captured online and sealed in glass vials for isotope analysis. Samples were run on a MAT252 mass spectrometer and corrected using the CO calcite fractionation factor of 1.01025. The “in-house” standard Namaqualand Carbonate (pure calcite) was used in this study with values reported relative to the Pee Dee Belemnite (PDB; Craig, 1957) and Standard Meteoric Ocean Water (SMOW; Gonfiantini, 1984).

The taphonomic investigation conducted on the *Lystrosaurus* bonebeds followed genetic framework studies for vertebrate skeletal concentration defined by Rogers (1991) and Rogers and Kidwell (2007); and bonebed classification outlined by Behrensmeyer (2007) and Eberth et al. (2007). These authors generated their models from a database of thousands of documented bonebeds. This taphonomic study applied the methods of Behrensmeyer (1978, 1982) and Behrensmeyer and Chapman (1993) on the duration and rate of accumulation of modern bone assemblages to estimate duration of exposure prior to burial in the *Lystrosaurus* bonebeds. The results provide context for the *Lystrosaurus* bonebeds, and their position in the stratigraphy of the Beaufort Group deposits.

4. Sedimentary facies and palaeoenvironments

Five sedimentary facies, interpreted as having been deposited in different parts of the fluvial system, are recognised in the exposed section at the *Lystrosaurus* bonebed locality: 1) single-storey channel

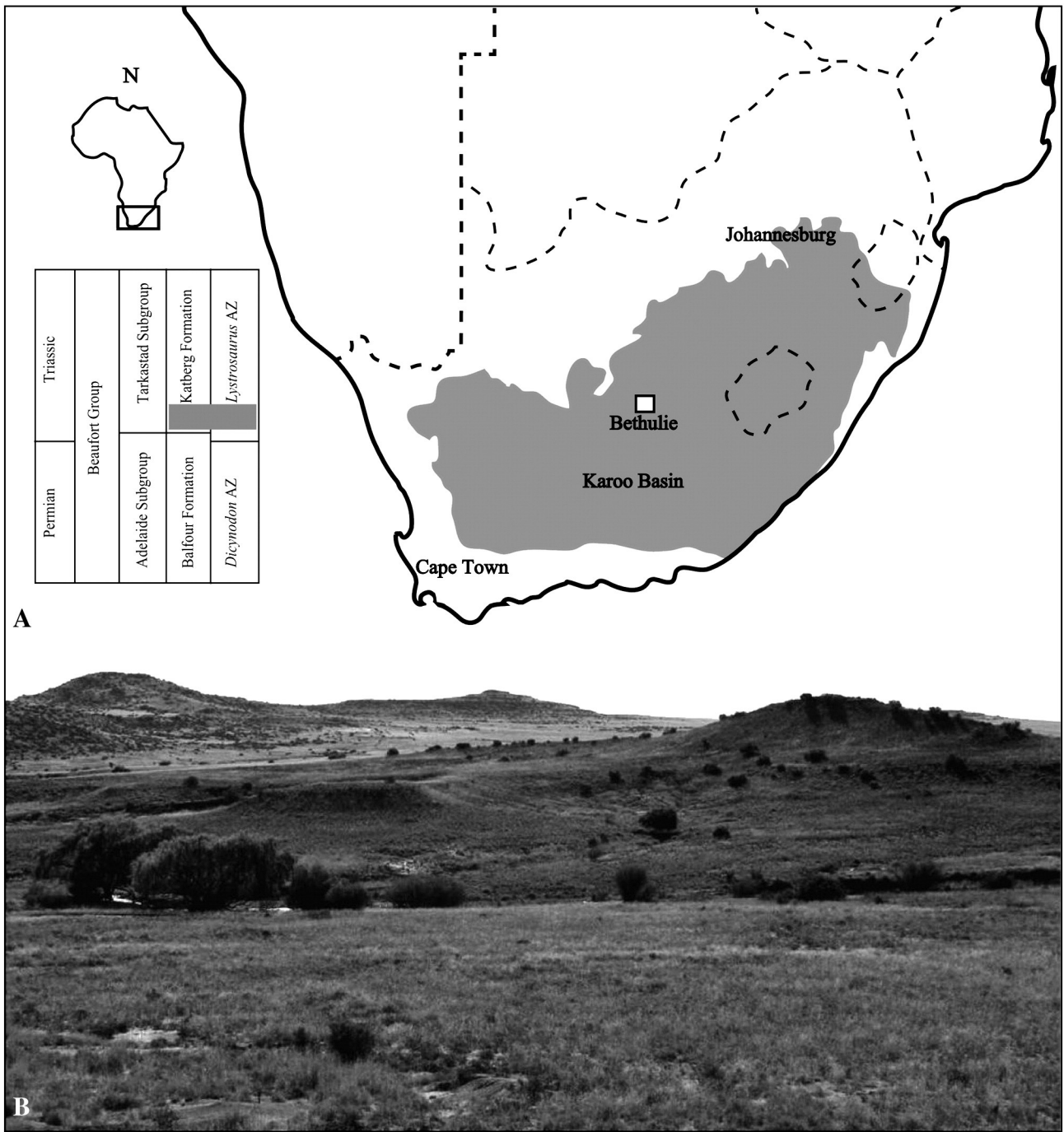


Fig. 1. (A) The town of Bethulie and the position of the study area (white square). The study area's position in the Beaufort Group stratigraphy is also shown (grey rectangle). (B) The study site where [Smith and Botha \(2005\)](#) first documented the *Lystrosaurus* bonebed occurrences.

sandstone, 2) multi-storey channel sandstone, 3) levee sandy siltstone and crevasse-splay sandstones, 4) floodplain siltstone, and 5) floodplain reworked nodule conglomerate ([Fig. 3](#)).

4.1. Facies 1 and 2: single and multi-storey channel sandstones

Facies 1 and 2 sandstone beds are olive-grey to light olive-grey (Munsell 5Y 5/2, 5Y 6/2) and vary from 0.5–1 m to 2–5 m thick, respectively. The texture of depositional units that comprise both single and multi-storeyed channel sandstone bodies fines upward from medium-grained (Wentworth 1/4–1/2 mm) at the base of the bed to fine-grained (Wentworth 1/8–1/4 mm) towards the top of the bed. Basal

contacts are sharp, undulatory and erosive with the multi-storey Facies 2 sandstones having more extensive and deeply scoured bases than single-storey Facies 1 sandstones. The scoured basal surfaces include elongate scour troughs that widen and narrow into gutters, or gullies from 0.3–1 m wide to 0.2–0.5 m thick. Sole markings, sand-filled mud cracks, and isolated pods of reworked intraformational pedogenic nodule conglomerate (Facies 5) commonly fill the scour troughs beneath the basal contact of sandstone beds. Massive and trough cross-bedded sandstone occurs immediately overlying the scoured base, followed by laminated sandstone that, in places, contains mud chip layers. The trough cross-bedding indicates north-northwest palaeoflow directions, which support palaeocurrent data from previous studies ([Hiller and](#)

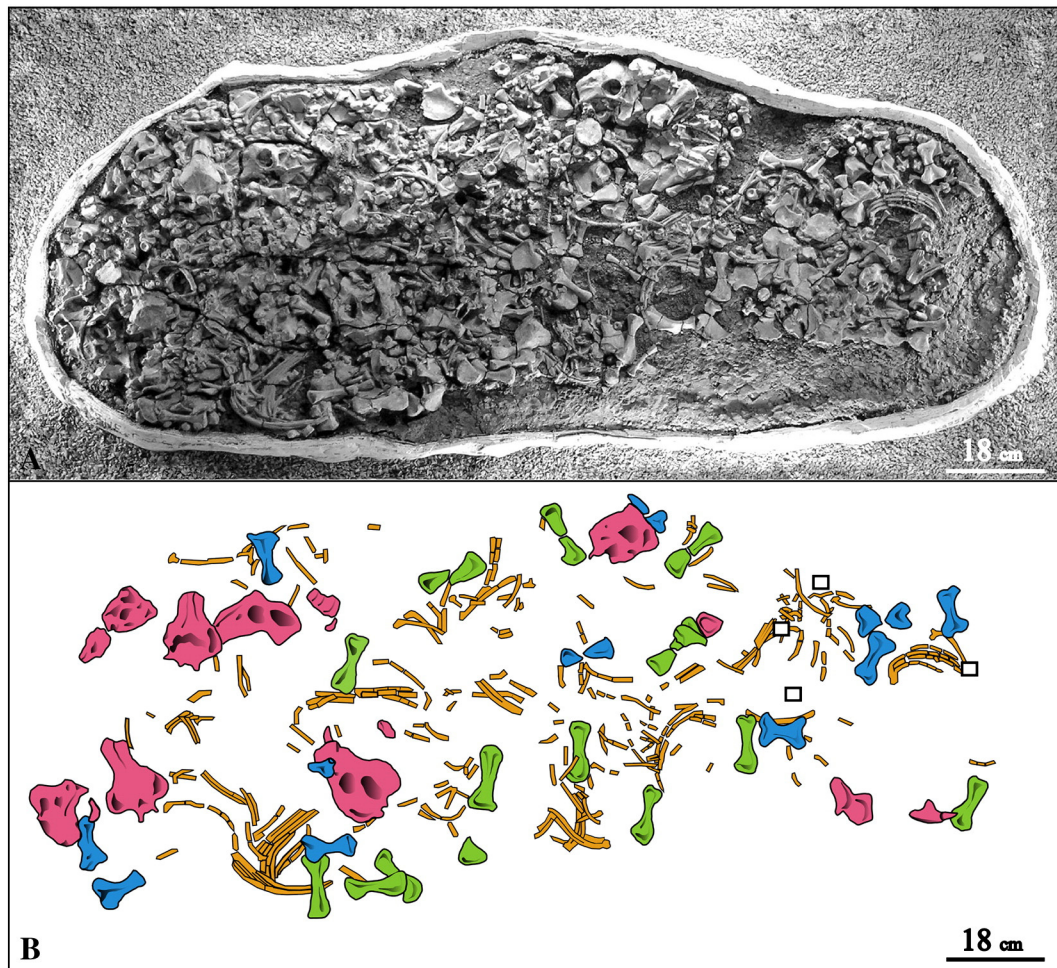


Fig. 2. (A) The SAM-PK-K8551 bonebed on display at the Iziko South African Museum in the Karoo Palaeontology exhibit. (B) A selection of different bone types that constitute ~50% of the assemblage (skulls, ribs, humeri, femurs) are shown in order to highlight their distribution and orientation. Note the unusual clumps of articulated ribs. White squares denote the position of four jaw fragments that belong to other taxa. Dimensions of the SAM-PK-K8551 plaster jacket are 180 × 72 cm. Source of (A): C. Payne (2007).

Stavrakis, 1984; Haycock et al., 1997; Pace et al., 2009). In contrast, the upper contacts of the channel sandstone facies are transitional and commonly interdigitate with the overlying units. Towards the top, sedimentary structures in the sandstone change to ripple cross-lamination, commonly climbing and terminating in ripple-topped surfaces preserved beneath thin siltstone drapes (see 6.8 m and 28.8 m in Fig. 3). Based on these observations of upward fining sand-dominated lithosomes deposited rapidly onto an eroded semi-consolidated floodplain surface, Facies 1 and 2 are interpreted to be in-channel deposits of northward flowing, wide, and shallow low-sinuosity rivers with fluctuating discharge that frequently avulsed and reworked the semi-arid floodplain alluvium (Smith, 1995; Smith and Botha, 2005).

4.2. Facies 3: levee sandy siltstone and crevasse-splay sandstones

Facies 3 light bluish-grey (Munsell 5Y 7/1) sandy siltstone beds are 0.3–1 m thick and interbedded with a few thin (<0.35 m), laterally continuous tabular fine sandstone beds. Facies 3 most commonly occurs immediately above Facies 1 and sandwiched between individual storeys of the multi-storey Facies 2 channel sandstone (Fig. 3). Facies 3 also occurs within the massive siltstone of Facies 4 as laterally restricted scour-fill deposits. The sandstone grain size is similar to the fine grained Facies 1 and 2 sandstones (~1/8–1/4 mm) and structured mainly with horizontal lamination. Blocky weathering makes it difficult to discern fine detail of structures in the sandy-siltstone. Based on the juxtaposition

to the channel belts, lack of channelised flow structures and generally silt-dominated grain size, Facies 3 is interpreted as levee and crevasse-splay deposits in the channel bank and proximal floodplain of a low sinuosity river system (Smith and Botha, 2005; Botha and Smith, 2006).

4.3. Facies 4: floodplain siltstone

Facies 4 siltstone beds vary from 0.5 to 1.5 cm thick and occur interbedded between Facies 1, 2, and 3 lithologies. Sedimentary structures within are commonly masked by a blocky weathering texture; however, in places, especially in the metamorphic zone flanking dolerite dykes, horizontal and ripple cross-laminations are discernible. The beds alternate between fine silt and clay (Wentworth 1/125–1/64 mm) and coarse silt (Wentworth 1/32–1/16 mm). The siltstones are either dull reddish-grey (Munsell 10R 3/1) or olive-grey (Munsell 5Y 5/2), and the colour boundaries are commonly gradational and irregular, suggesting a post-depositional pedogenic overprint. Small (2 cm diameter) sub-horizontal *Katbergia* burrow casts (Gastaldo and Rolerson, 2007) of possible crustaceans are common particularly where colour mottling is present. Medium sized burrow casts (10–15 cm diameter) attributed to cynodonts, and burrow casts (20–30 cm diameter), possibly constructed by *Lystrosaurus* (Smith and Botha, 2005), and are relatively common. Facies 4 is interpreted as a floodplain siltstone based on the above observations.

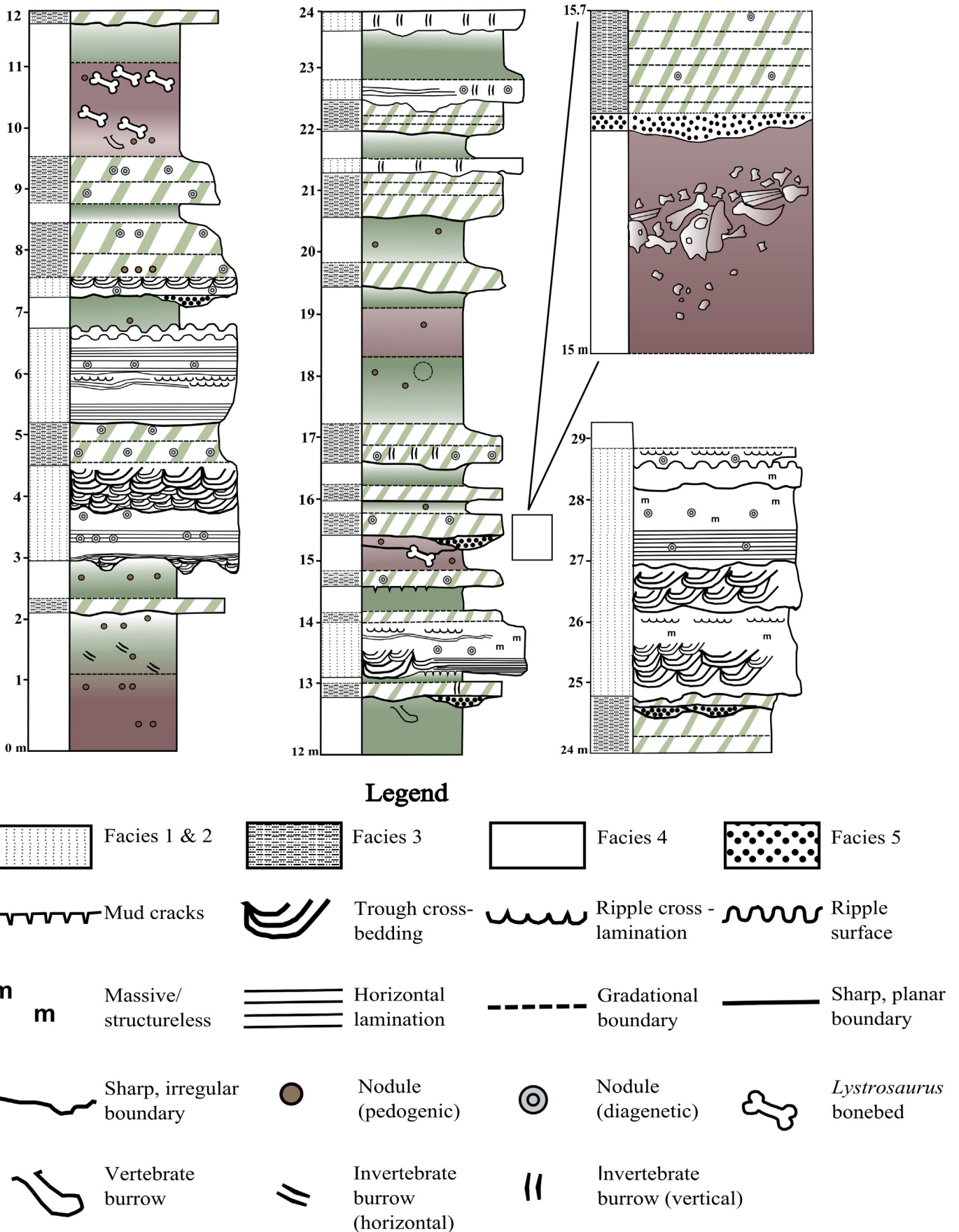


Fig. 3. Sedimentological log of the study site near Bethulie including a detail of the SAM-PK-K8551 *L. declivis* bonebed as logged by Smith and Botha (2005) during excavation. A white square indicates where Smith and Botha's (2005) detailed log originates on this study's section.

4.4. Facies 5: floodplain reworked nodule conglomerate

Facies 5 is a nodule-rich conglomerate. In situ examples are commonly weathered, with nodule clasts preferentially eroded out, leaving voids. Large blocks of Facies 5 conglomerate that are unweathered show minor elephant skin weathering texture, which indicates cementation by calcium carbonate. The Facies 5 conglomerate consists of pedogenic calcareous nodules of mostly medium to pebble size (Wentworth 1/4 mm–4 cm). Most of the nodule intraclasts are spherical to oblate and have septarian shrinkage cracks, suggesting that they are pedogenic or early diagenetic nodules reworked from Facies 3 to 4 (Smith, 1995; Smith and Botha, 2005). Amongst the nodule clasts are isolated and abraded bones as well as unidentifiable lithic and small mudrock fragments. Some fossil bone occurs as rounded pebbles that display a polished surface indicating that the bone had been buried and partially mineralised before being reworked. Facies 5 is not laterally extensive and occurs as scour fills at the bases of the thickest Facies 1 and 2 sandstone beds as well as isolated lenses in scour troughs within the Facies 3 and 4 over bank deposits. Facies 5 is interpreted as the result of high-energy, shallow sheet floods indicative of the onset of flood events in the depositional basin rather than a long-term base-level change (Smith, 1995; Smith and Botha, 2005).

4.5. Palaeoenvironmental interpretation

Deposition of the lower Katberg Formation in the study area is interpreted as similar to that of modern sandy braided rivers (Ashworth et al., 2007; Sambrook Smith et al., 2009; Horn et al., 2012). Observations from the study area also fit fluvial style changes observed across the PTB by Smith (1995), Smith and Botha (2005) and Botha and Smith (2006) for the upper Balfour and lower Katberg formations. Facies 1 and 2 sandstones at the locality show architectural and morphological features of fine sand deposited in braided river channels. The sandstones contain sedimentary structures that indicate vertical accretion in the waning flow, likely following a flood event (Smith, 1995; Smith and Botha, 2005; Ashworth et al., 2007; Sambrook Smith et al., 2010; Horn et al., 2012). Due to the erosive action of floodwaters under high velocity flow regimes, little preservation occurs during the immediate flooding conditions of braided rivers and often previous waning flood deposits are partially or completely eroded away. Therefore erosional boundaries between sandstone packages of the multi-storey sandstone facies most likely indicate successive erosion and waning flood cycle deposits in an active channel. The association of Facies 5 nodule conglomerate and irregular sandstone bases where they contact floodplain sediments (Facies 4) points to evidence of floodplain erosion during flood events (Smith, 1995; Smith and Botha, 2005). Braided sandstone morphology and flood dominated deposition alone is not enough to prove the presence of a semi-arid climate, but it does suggest seasonal extremes in rainfall. Tooth (2000) noted the importance of large floods and variable flow regimes in dryland river morphology, particularly in modern Australian and southern African arid zones. The result of the non-uniform nature of flow and sediment due to lack of bank stabilising vegetation and seasonal flooding causes the functioning of dryland systems to be discontinuous. This is why these rivers are sometimes characterised by lack of equilibrium between process and form, which could explain waning flood deposits observed in this study. However, dryland systems are not generalised to this rule due to the fact that arid environments occur in a wide spectrum of settings (Tooth, 2000).

Another factor argued previously as evidence for aridity in the Katberg Formation is reddening of Facies 4 floodplain sediments (Smith and Ward, 2001; Botha and Smith, 2006). A case study by Sheldon (2005) on the origin of upper Permian red beds from north western Sardinia suggests that their red colour merely represents well-drained conditions and provides no information on palaeoclimatic conditions at the time of their formation. Retallack (1991) has also

contested rock colour models and refers to many examples of diagenetic reddening of non-desert palaeosols by dehydration of iron oxides. Nevertheless, in conjunction with sedimentological evidence, there is some evidence of seasonal aridity in the lower Katberg Formation braided system, but the degree of aridity is difficult to quantify.

The presence of horizons of in-situ carbonate nodules in the lower Katberg Formation floodplain facies does provide compelling support for their pedogenic origin in a terrestrial environment subject to a highly seasonal rainfall regime (Smith, 1995; Smith and Botha, 2005). Calcretes and other carbonate precipitates are important components of modern and ancient semi-arid depositional systems and characteristic of regions experiencing a mean annual rainfall of around 500 mm forming during seasonal wetting and drying cycles at the sediment water interface in the soil profile (Khadkikar et al., 1998). Droughts are more difficult to recognise than seasonal aridity in the rock record because droughts are short-lived events primarily caused by loss of vegetation leading to collapse of the food chain (Rogers, 1991). Also, due to the fact that the precipitation of nodules is predominantly controlled by groundwater level fluctuations, nodules do not necessarily indicate high mean annual temperatures. Smith and Botha (2005) interpreted the lower Katberg Formation as a low-sinuosity fluvial network prograding from the south and subjected to discharge fluctuations in a hot semi-arid dryland setting that was prone to severe droughts. This study uses palaeoclimatic interpretations based on nodule stable isotope data to test the validity of the Smith and Botha (2005) scenario.

4.6. Stable isotope data interpretation

Carbonate nodules in the study section are divided into pedogenic and diagenetic based on their shape (roundness), size, internal structure (micritic or radial calcite) and host facies (Smith, 1990, 1995; Tabor et al., 2007). Pedogenic carbonate nodules occur only in Facies 4 floodplain deposits and are considered to be the most useful in palaeoenvironment reconstruction of the earliest Triassic due to their preservation within palaeosol horizons (Smith, 1995; Smith and Botha, 2005). Early diagenetic nodules were found in Facies 1, 2, and 3 deposits and are generally less useful as their isotope geochemistry often reflects groundwater composition only. Facies 4 pedogenic nodules, and some early diagenetic carbonate nodules from Facies 3, were sampled where they occurred interbedded between Facies 4 deposits in association with the *Lystrosaurus* bonebed horizons. The stable isotope analysis

Table 1

Stable isotope data collected from carbonate nodules in association with *Lystrosaurus* bonebed fossils. Numbers (3, 4) refer to the facies from which the nodules were collected. NM95 (Namaqua Marble) is the internal standard by the stable isotope laboratory, University of Cape Town.

Sample	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
NM95	−0.02	23.82
NM95	0.13	23.36
3i	−12.74	13.97
3ii	−8.54	16.15
3iii	−6.28	16.60
3iv	−7.06	16.38
3v	−13.36	13.86
3vi	−8.55	15.33
3vii	−10.33	15.91
3viii	−8.05	16.53
4i	−15.77	11.94
4ii	−6.93	14.58
4iii	−7.69	15.25
4iv	−8.35	14.39
4v	−6.61	14.86
4vi	−7.56	13.47
4vii	−7.58	16.98
4viii	−7.80	15.25
4ix	−7.14	14.46

yielded $\delta^{13}\text{C}$ values ranging on average from -9.5 to -5% and $\delta^{18}\text{O}$ values of 13.5 to 16% , although there were outliers (Table 1).

The pedogenic and diagenetic carbonate nodule stable isotope data are compared to modern and ancient global terrestrial calcrete and carbonate nodule values from the literature to infer the possible palaeoclimate at the time of their formation (Andrews et al., 1998; MacLeod et al., 2000; Rowe and Maher, 2000; Srivastava, 2001; Neymark et al., 2005; Schmid et al., 2006; Herbert and Compton, 2007; Tabor et al., 2007; Ringrose et al., 2009) (Fig. 4). The $\delta^{13}\text{C}$ values obtained by MacLeod et al. (2000) and Tabor et al. (2007) on Early Triassic carbonate nodules from the Bethulie and Carlton Heights area are similar to values of this study. The $\delta^{13}\text{C}$ values are consistent, but the $\delta^{18}\text{O}$ values are low for the carbonate nodules in comparison to the range of values reported for Quaternary carbonates in warm, arid climates (Andrews et al., 1998; Srivastava, 2001; Schmid et al., 2006; Ringrose et al., 2009). The low $\delta^{18}\text{O}$ values imply cold temperatures, having the closest overlap in $\delta^{18}\text{O}$ values with Pleistocene carbonates formed under seasonally cold and semi-arid conditions (Rowe and Maher, 2000; Neymark et al., 2005). Ringrose et al. (2009) interpreted anomalous low $\delta^{18}\text{O}$ values as drier and cooler periods than usual for the Makgadikgadi Pans (Botswana) region about 80–90,000 years ago. Due to the inferred latitude of 55°S for Late Permian southern Africa (Smith et al., 1981), it is likely the Karoo Basin climate included seasonally cold weather as well, alternating between cold-wet and warm-dry periods.

$\delta^{13}\text{C}$ values of soil CO_2 are predominantly controlled by biogenic sources such as the respiration of plants and decay of organic matter (Cerling and Harris, 1999). CO_2 can also be sourced from rainwater (atmosphere) and from chemical weathering of rocks, but organic matter CO_2 in most soils will dominate $\delta^{13}\text{C}$ values. Thus factors that influence $\delta^{13}\text{C}$ values in pedogenic or diagenetic carbonate nodules are the abundance and species composition of plant communities which generally operate either under the C3 or C4 photosynthetic pathways (Schmid et al., 2006). C3 land plants have average $\delta^{13}\text{C}$ values of -27% and C4 plants -13% , and carbonate nodules and calcretes forming under a C3 or C4 dominated plant community will have $\delta^{13}\text{C}$ values of -12% and $+2\%$, respectively (Cerling and Harris, 1999). C4 plants had not yet appeared in the Triassic, thus soil CO_2 in the Triassic was most likely more enriched in ^{12}C than modern soils. Schmid et al. (2006) argue that $\delta^{13}\text{C}$ values in Holocene calcretes from Broken Hill Australia reflect variation in moisture availability due to changes

in precipitation and evaporation. Reduced moisture availability and reduced plant cover increase the importance of atmospheric CO_2 in the subsurface (Schmid et al., 2006). Carbonate nodules with $\delta^{13}\text{C}$ values between -10 and -15% may represent wetter periods when the water table was high relative to the soil profile and there was plenty of C3 plant cover, and thus less atmospheric CO_2 influence on the subsurface. Tabor et al. (2007) suggest that pedogenic carbonate nodules in the Karoo Basin having $\delta^{13}\text{C}$ values more negative than -10.6% reflect calcite precipitation under poorly drained swampy areas in the palaeolandscape (Fig. 4). The range in $\delta^{13}\text{C}$ values for this study (Table 1) suggests that the amount of vegetation and moisture was variable or seasonal in the palaeolandscape, but the preservation of the *Lystrosaurus* bonebed interval in the earliest Triassic generally occurred when the water table was low relative to the soil profile, allowing more influence from atmospheric CO_2 .

The relatively low $\delta^{18}\text{O}$ values of nodules in this study may represent differences in groundwater $\delta^{18}\text{O}$ values, which are also a function of latitude and elevation (Smith et al., 1981) as observed in a study on the Grootegeluk Formation (Waterberg Basin), South Africa (Faure et al., 1995). Using $\delta^{18}\text{O}$ values for meteoric water of -13% derived from the δD value of carbonate lenses in coal-bearing deposits and the calcite-H₂O fractionation factor of O'Neil et al. (1969), the crystallisation temperature was estimated to be between 15°C and 20°C for upper Permian carbonate lenses from the Grootegeluk Formation (Faure et al., 1995). If it is assumed that the $\delta^{18}\text{O}$ value of meteoric water of -13% for the upper Permian Grootegeluk Formation was similar to the earliest Triassic Katberg Formation, and southern Africa did not change significantly from its inferred latitudinal position (55°S) during the Permian–Triassic transition, then a similar temperature range can be used for the carbonate nodules of this study. The meteoric water $\delta^{18}\text{O}$ value at the time of formation is unknown, but the consistently lower $\delta^{18}\text{O}$ values of carbonate nodules from this and other Karoo studies (MacLeod et al., 2000; Tabor et al., 2007) in comparison to other studies suggest a semi-arid and seasonally cold climate for the Karoo Basin in the earliest Triassic. Although values are not as low as Dwyka tillite carbonate nodules formed during the Early Permian ice age (Herbert and Compton, 2007), the claim by Haycock et al. (1997) that snow cover may have existed on the highest peaks of the Gondwanide Mountains during the Early Triassic appears plausible.

5. Vertebrate taphonomy

Although the taphonomic work conducted in this study mainly focuses on the taphonomy of monotaxic *Lystrosaurus* bonebeds, the taphonomy of other vertebrate fossils encountered is used in palaeo-environment reconstruction. The massive red siltstone beds of Facies 4 are host to the bulk of the vertebrate remains found in the lower Katberg Formation (Botha and Smith, 2006). Vertebrate remains are present as isolated fragments, complete skeletons or, in the case of some *Lystrosaurus declivis* remains, bonebeds. Nearly 90% of fossils at the locality consist of *Lystrosaurus* (*L. declivis* and *L. murrayi*), with the other 10% consisting of cynodonts *Thrinaxodon* and *Galesaurus* and theropod *Regisaurus* and *Scalposaurus*. Other vertebrate taxa include amphibians (mainly *Micropholis*), archosauromorphs (*Prolacerta*, *Proterosuchus*), and the very rare parareptile *Colletta*.

A total number of six *Lystrosaurus declivis* bonebeds were recovered in the study area in two Facies 4 red siltstone beds at approximately 10 m and 15 m on the logged vertical section. Quantitative analysis of each bonebed occurrence was done to determine: (1) Minimum Number of skeletal Elements (MNE) and (2) Minimum Number of Individuals present (MNI) (Table 2). Bone fragments were counted if they could be assigned to the skeletal element in question otherwise they were assigned the name “other” in Table 2.

Quantitative analysis reveals that bonebeds 1–3 comprise disarticulated but associated bones of single individuals and are, therefore, not bonebeds according to the definition of Behrensmeier (2007). This

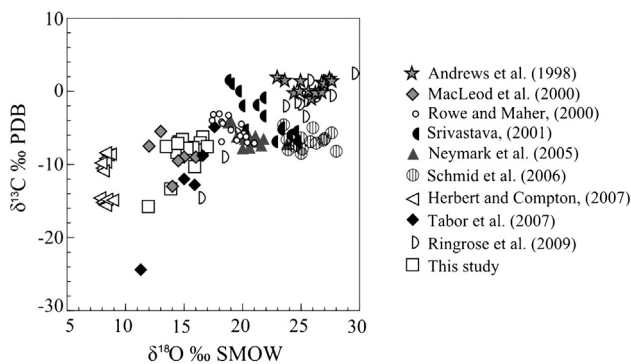


Fig. 4. Stable isotope data from early diagenetic and pedogenic carbonate nodules collected during this study (white squares) in comparison to other studies. Fields shown are from the Thar Desert arid calcretes (NW India) (Andrews et al., 1998); Pleistocene carbonates from the Chinese Loess Plateau (Rowe and Maher, 2000); Early Triassic pedogenic carbonate nodules from Bethulie, South Africa (MacLeod et al., 2000); Holocene Gangetic Plains arid calcretes (Srivastava, 2001); Pleistocene and Holocene Crater Flat calcretes Nevada, U.S.A (Neymark et al., 2005); Early Quaternary Broken Hill arid calcretes, Australia (Schmid et al., 2006); Late Carboniferous Dwyka group early diagenetic carbonate nodules (Herbert and Compton, 2007); Early Triassic pedogenic carbonate nodules from Carlton Heights, South Africa (Tabor et al., 2007); and Quaternary Makgadikgadi Pans duricrusts and calcretes (Botswana) (Ringrose et al., 2009).

Table 2
Minimum Number of individuals (MNI) counted in the six fossils studied. “Other” refers mainly to broken bone pieces that were unidentifiable as well as other bone types that were not used in the quantitative analyses (i.e. phalanges, ulnas, radii, tibiae, and fibulae). Note that SAM-PK-K8551 is now the only bonebed as its MNI came to more than one individual present. The other five fossils are now referred to as bone accumulations.

<i>Lystronotus</i> bone count	SAM-PK-K8551 bonebed	Bone concentration 1	Bone concentration 2	Bone concentration 3	Bone concentration 4	Bone concentration 5
Skulls	9	1	1	1	2	1
Lower jaws	6	0	0	0	1	2
Humeri	12	1	1	1	2	3
Femurs	14	2	0	0	1	0
Ribs	117	4	20	7	8	6
Vertebrae	129	14	5	10	9	13
Other	20	38	13	15	13	45
MNI	9	1	1	1	2	2

result reveals the uncertainty of using the MNI analysis, with the possibility that more than one individual may be present, but not enough bones are preserved or observed to prove it. A complete *Lystronotus* skeleton had 2 humeri, 2 femurs, 54 ribs, and 41 vertebrae (Watson, 1913), so not nearly enough bones were counted to constitute one complete skeleton in any of the bonebeds, except SAM-PK-K8551. Over half

of the rib (369) and vertebrae bones (240) are missing, however most of the limb bones for the nine individuals (deduced by number of skulls) in the bonebed SAM-PK-K8551 can be accounted for. Given the above uncertainties, only the fully prepared SAM-PK-K8551 bonebed is discussed further, and the other five *Lystronotus* fossils defined as bone concentrations rather than bonebeds.

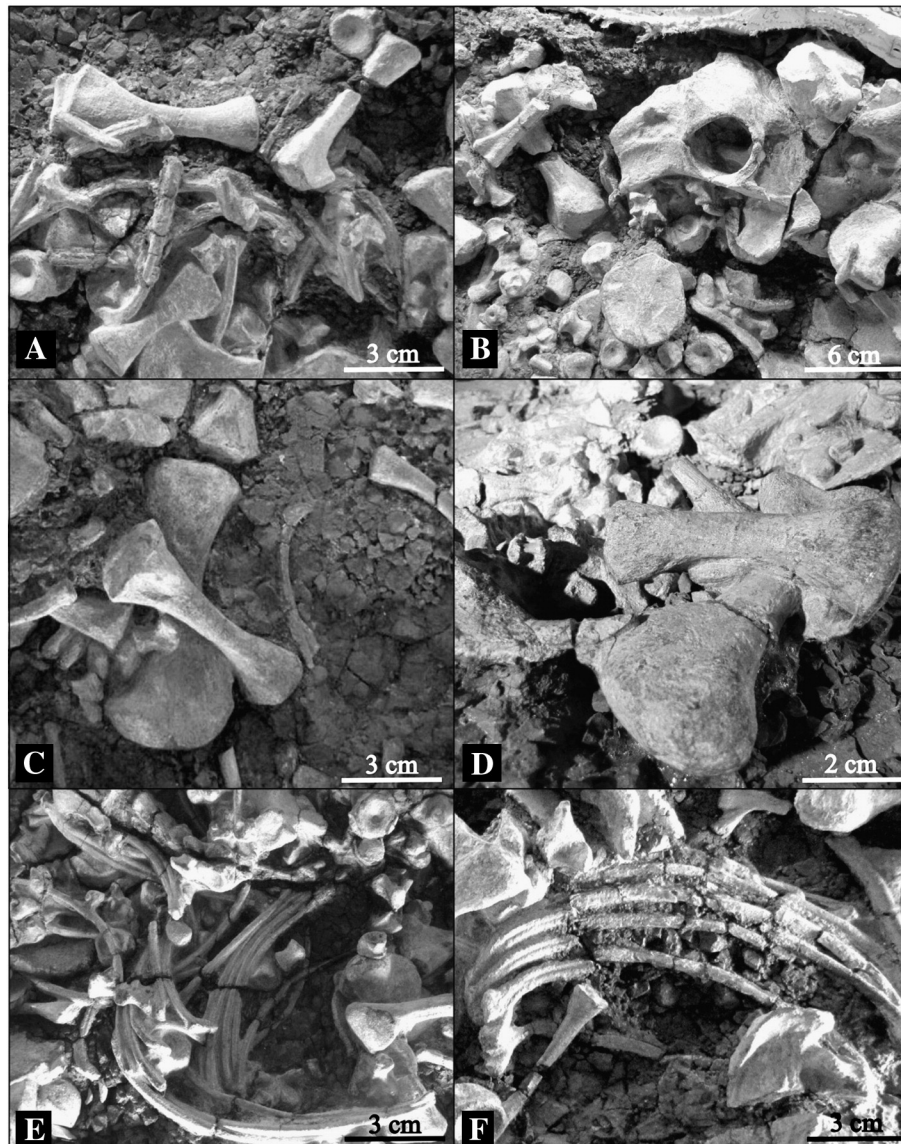


Fig. 5. Details of the SAM-PK-K8551 bonebed showing (A) missing epiphyses on limb bones (B) skulls of *Lystronotus* individuals (C, D) disarticulated limb bones and (E, F) articulated rib clusters that occur in several parts of the bonebed.

5.1. Taphonomy of the SAM-PK-K8551 *Lystrosaurus* bonebed

The SAM-PK-K8551 *Lystrosaurus* bonebed consists mainly of disarticulated elements, but many postcranial elements such as vertebrae and limb bones lie immediately adjacent to one another, indicating that the bones likely have not been disturbed since disarticulation (Fig. 5). Some rib bones have remained articulated in their life positions despite being disarticulated from the vertebrae and sternal plate, whereas disarticulated rib bones are mostly missing from the bonebed (Fig. 5E, F). The bones are generally well preserved with no fragmented or broken bones except for those broken during burial diagenesis. The lack of longitudinal cracks or fissures, and generally pristine bone surfaces indicates weathering stage 0 or 1 as defined by Behrensmeyer (1978) or 0–1 year that the *Lystrosaurus* skeletons lay on the proximal floodplain surface before burial.

Lystrosaurus declivis and *L. murrayi* co-existed in the Early Triassic Karoo and *L. murrayi* fossils are common in the study area as articulated skeletons. However, the long, ridged premaxilla (snout) indicates that the SAM-PK-K8551 bonebed is monotoxic with all nine individuals belonging to *L. declivis* (Botha and Smith, 2007). Although dominated by *L. declivis* individuals, the SAM-PK-K8551 bonebed yielded four small jaw fragments from other vertebrate taxa (Fig. 6). The backwardly recurved teeth in two of the fragments suggest that they belong to an archosauromorph, possibly *Prolacerta broomi*. Although badly damaged, the peg-like tooth morphology and size of the other two fragments suggests that they may belong to indeterminate parareptiles (Smith pers. comm., 2012).

Dimensions of the *Lystrosaurus declivis* skulls in the SAM-PK-K8551 bonebed are compared to *L. declivis* specimens housed in collections at Iziko South African Museum, and the Bernard Price Institute (now the Evolutionary Sciences Institute), University of Witwatersrand to estimate their stage of ontogenetic growth at death (Fig. 7). For each specimen the skull dimensions included total skull length (tip of premaxilla to occipital condyle), snout length (length of maxilla and premaxilla), and orbital diameter. Although all the nine individual skulls, which range in length from 125 to 181 mm, fall within the adult range of skull lengths compiled by Botha and Smith (2007), none are the maximum size of their species as observed from measurements taken from specimens from Iziko and the BPI. This indicates that these animals were subadult at their time of death; however, different skull lengths indicate they are not all the same age and, therefore, the bonebed does not

represent a single brood. A subadult age is supported by the absence of epiphyseal bone (Fig. 5A). In juvenile and subadult animals the epiphysis is cartilaginous while in adult animals the bone epiphysis is hard and fused to the main bone shaft and thus more likely to fossilise.

6. Discussion of the origin of *Lystrosaurus declivis* bonebed

The disarticulated but associated taphonomic style that is prevalent in the *Lystrosaurus declivis* SAM-PK-K8551 bonebed suggests minimal, if any, transportation after disarticulation, yet the preferential loss of ribs and vertebrae is difficult to explain. The question remains, however, as to how the nine carcasses of subadult *L. declivis* were preserved in such a dense accumulation. Behavioural aggregation (grouping) during an unusual cold snap or hydraulic concentrations of drought-stricken carcasses are two possible hypotheses that appear to fit well with the evidence. It is important to try and distinguish between these two possibilities, because the former has implications on how *Lystrosaurus* and possibly its ancestors and related species may have survived periods of stress including the end-Permian mass extinction event.

6.1. Hydraulic concentration of drought stricken carcasses

The SAM-PK-K8551 bonebed was interpreted by Smith and Botha (2005) to be a drought accumulation of *Lystrosaurus declivis* individuals washed into and collected within a floodplain scour surrounded by mudrock chips. During droughts, animals die intermittently throughout the drought event, and one would expect animals at different degrees of articulation decay, and weathering stage to be present on the floodplain at the end of drought. The articulated elements in the SAM-PK-K8551 bonebed such as a front foot, ribs and some vertebrae may have been held together by dry skin, mummified by the hot and dry climate prior to the focussing of carcasses during the flood event and final burial (Hill and Behrensmeyer, 1984; Weigelt, 1989). Many fossils of *Lystrosaurus* and other taxa have been found as complete skeletons on or near the same horizon as the SAM-PK-K8551 bonebed, and mummification could be an explanation for the preserved articulation (Smith pers. comm., 2012). Drought is a significant and recurring killing agent in modern ecosystems (Rogers and Kidwell, 2007). Results from the database referred to by Behrensmeyer (2007) and Eberth et al. (2007) reveal the most common kinds of bonebed origins are caused by either floods, or droughts, both of which are interpreted to have been strong

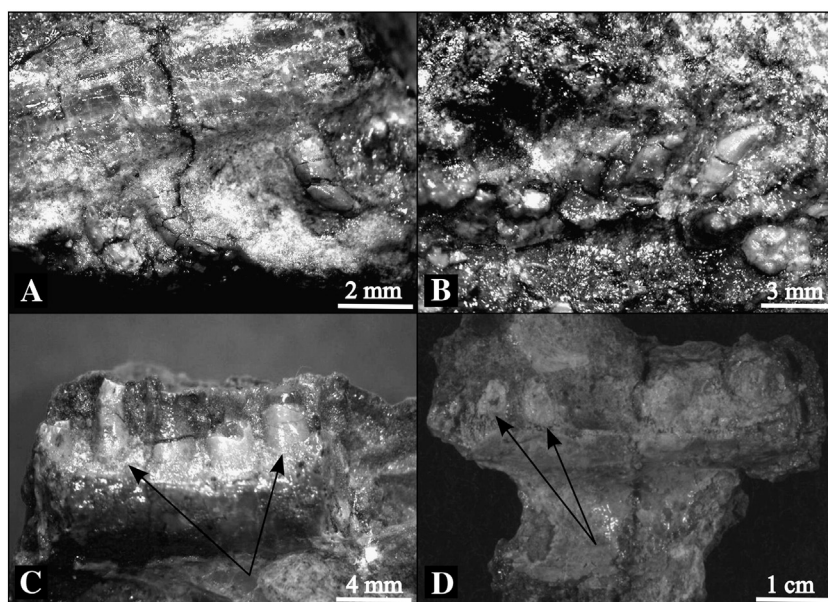


Fig. 6. Small jaw fragments identified as belonging to infant individuals of the archosauromorph *Prolacerta broomi* (A, B) and juvenile parareptiles (C, D). Arrows point to teeth in C and D as they are badly damaged.

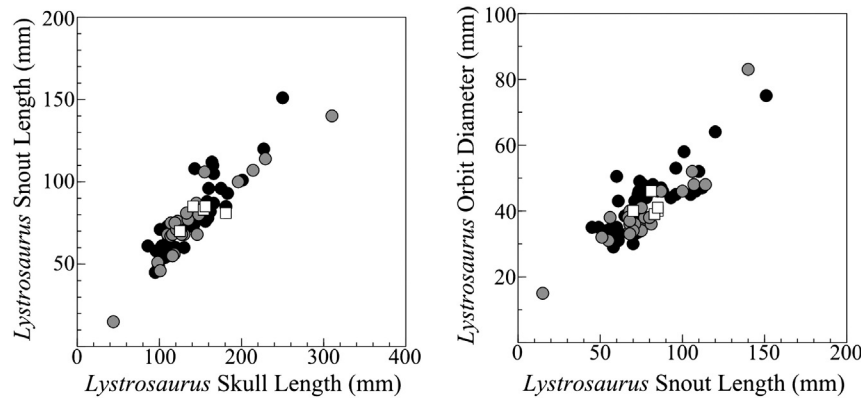


Fig. 7. Skull measurements of *Lystrosaurus declivis* specimens in collections housed at Iziko South African Museum in Cape Town (black circles), and at the Bernard Price Institute at the University of Witwatersrand, Johannesburg (grey circles) and from the SAM-PK-K8551 bonebed individuals are also shown (white squares). Skull lengths within the 109–258 mm range are considered subadult for *Lystrosaurus declivis* (Botha and Smith, 2007). Note that most *L. declivis* specimens in collections are subadult in size.

controls on the environment in the Karoo Basin during the earliest Triassic. Mass killings by flood events are common for herding and grouping animals. For example, [Turnbull and Martill \(1988\)](#) interpreted fossil remains of the extinct titanothere *Mesatirhinus* at many stages of growth within high energy fluvial deposits as a herd overwhelmed by a flood. Nevertheless, it is unlikely that the SAM-PK-K8551 bonebed individuals died in a flood because death by flood kills all in its path and cannot selectively kill a single age group of a specific species ([Turnbull and Martill, 1988](#)). The floodplain sediments that buried the SAM-PK-K8551 bonebed are mudstones and would not have been deposited by fast flowing channel water.

Droughts often force species to congregate together along remaining water and food sources regardless of their normal habitat preferences or behaviour, forming unnatural congregations ([Shipman, 1975](#)). If drought conditions persist and resources are depleted, then animals (particularly juveniles) begin to weaken and succumb, often from starvation rather than thirst ([Shipman, 1975](#); [Rogers and Kidwell, 2007](#)). Accounts of age and species specific deaths due to drought are common, as noted by [Behrensmeyer \(2011\)](#) from work conducted on animal carcasses in the Amboseli National Park Kenya. Once extreme drought set in there were almost no juvenile animals in the population as they had died in the earlier drought phases. [Behrensmeyer's \(2011\)](#) work supports drought event sequences laid out previously by [Shipman \(1975\)](#), where juvenile and subadult animals are greatly reduced in the population profile in the latest phase of drought (phase 3). Therefore, drought death assemblages appear to selectively focus on juveniles or subadults of a single species.

[Rogers \(1991\)](#) identified monotaxic *Hadrosaur* and *Ceratopsian* bonebeds from the Two Medicine Formation of northwestern Montana as drought-related assemblages based on the abundance of juveniles. The Late Triassic *Coelophysis* bonebed at Ghost Ranch, New Mexico preserves thousands of semi-articulated skeletons belonging to juveniles ([Schwartz and Gillette, 1994](#)). Evidence for seasonal aridity suggests that this assemblage represents several groups of individuals that died over time due to droughts ([Schwartz and Gillette, 1994](#)). Such a scenario could explain the selective mass killing of only subadult *Lystrosaurus declivis*. The presence of the small jaw fragments of other species might indicate some later hydraulic influence as the *Lystrosaurus* bonebed could have become a hydraulic trap for these small fragments during sheet flooding.

6.2. Behavioural grouping of subadults during unusual cold snap

A previously under-researched aspect of the palaeoenvironment of the earliest Triassic is diurnal and seasonal temperature fluctuations. Continental climate in the aftermath of the end-Permian mass extinction was warmer, drier, and in general more extreme ([Sun et al.,](#)

[2012](#)). These more extreme conditions likely included temperature fluctuations. Cold climate has not been cited as a cause of the end-Permian mass extinction event; however, given the land-locked position of the earliest Triassic Karoo in southern Gondwana at a high palaeolatitude of ~55°S ([Faure et al., 1995](#); [Smith, 1995](#)), it is possible that animals had to cope with not only seasonal cessation of rainfall, but also seasonal drops in temperature. Therapsids were clearly adapted for living in strongly seasonal, high latitude biomes but their physiology was not that of a fully endothermic animal ([Kemp, 2011](#)). The possibility of cold temperatures, as suggested by the carbonate nodule isotope results of this study, provides an alternative explanation for the origin of the *Lystrosaurus declivis* bonebed.

Grouping behaviour is an important factor in the formation of bonebed deposits ([Brinkman et al., 2007](#); [Rogers and Kidwell, 2007](#)), especially when combined with unusual weather phenomenon. Death by unusual weather has been recorded in extant and extinct herding animals, often in juveniles or subadults less experienced in coping with sudden turns in the weather ([Weigelt, 1989](#)). Modern semi-arid environments typically have large diurnal temperature changes ([Kinlaw, 1999](#)) and many modern desert reptiles have evolved to cope well with these temperature fluctuations by either burrowing or shelter sharing ([Bridgeman Cowles and Mitchill Bogert, 2006](#)). Although there is evidence that *Lystrosaurus* occupied underground burrows, it is unclear if they dug the burrows they occupied ([Groenewald, 1991](#)). The diameters of known burrows are too small to allow for nine individuals to group underground and suggest that aggregation of the SAM-PK-K8551 bonebed individuals occurred in an open surface depression rather than a burrow.

Grouping in modern, as well as ancient, reptiles has thermoregulatory significance ([Brattstrom, 1974](#); [Aleksiuk, 1977](#)). Many reptiles display cold-induced or winter aggregation behaviour such as garter snakes ([Aleksiuk, 1977](#)), marine iguanas ([White, 1973](#)), geckos ([Cooper et al., 1985](#)), lizards ([Graves and Duvall, 1995](#)) and tree lizards ([Ernst et al., 1999](#)). Aggregation behaviour reduces the rate of cooling ([Aleksiuk, 1977](#)), gives protection from the elements, and aggregation at night during winter months allows for natural foraging and feeding when daytime temperatures are high enough ([Ernst et al., 1999](#)). Due to their smaller size and larger surface-to-volume ratio compared to adults, subadult *Lystrosaurus declivis* may have found it more difficult to up-keep their body temperature efficiently when temperatures dropped below a critical temperature. It is possible when seasonal drops in temperature occurred, certain species with limited ability to thermoregulate may have adapted other means to keep warm and to retain metabolic activity.

The presence of only subadult *Lystrosaurus declivis* in the SAM-PK-K8551 bonebed suggests a grouping of individuals of similar age in a cohort. This behaviour has been proposed for a Late Permian dicynodont

assemblage consisting of 17 juvenile *Diictodon* from northern Zambia (Gale, 1988). Due to their identical stage of ontogenetic growth and preserved articulation, it was proposed that they were a brood killed by a flood while occupying a nesting site. Similar explanations are proposed by Sun (1978) for a group of juvenile Triassic dicynodonts (*Parakanmeyeria*) from China, whereas a group of 10 juvenile *Dinodontosaurus* from Triassic deposits in southern Brazil were interpreted as being killed during collapse of a burrow or protected spot where they were grouping (Bueno et al., 2011). Data from these bonebeds suggests that some form of grouping behaviour was normal in juvenile dicynodonts (Brinkman et al., 2007).

Weigelt (1989) studied many death assemblages of modern animals (mainly domestic livestock) resulting from strong seasonal fluctuations in temperature and rainfall. In the years 1925–26, winter storms were observed by Weigelt (1989) in the vicinity of Houston Texas, USA, following prolonged droughts that weakened animals in the summer. In extreme cases temperatures dropped by as much as 20 °C within a few hours following icy northerly winds (northers), killing thousands of heads of livestock huddled on southern fence boundaries (Weigelt, 1989). Behrensmeyer and Miller (2012) refer to an extract from Charles Darwin's *Voyage of the Beagle* (1860) where Darwin describes mass mortalities of guanacos (related to the llama and alpaca) which he believed were overwhelmed by sudden snow storms. Many of the animals had crawled, before dying, beneath and amongst bushes. Darwin's (1989) and Weigelt's (1989) observations combined with results from this study reveal the possibility of the nine juvenile *Lystrosaurus declivis* being exposed to severe conditions, and perhaps dying en masse after seeking refuge huddled together in a protected area as part of their normal behavioural response to mitigate against unusually cold temperatures.

6.3. Death by drought or cold?

Both the drought and cold snap scenarios for the SAM-PK-K8551 bonebed origin outlined above have their merits, but the behavioural grouping of subadult *Lystrosaurus declivis* during an unusual cold snap is the hypothesis argued to better explain the origin of the SAM-PK-K8551 bonebed. Species and age specific bonebeds signify drought according to the literature; nevertheless, there is no single defining feature in the deposit or in the carbonate nodule isotope data that could temporally resolve a major drought associated with the SAM-PK-K8551 bonebed horizon. Red floodplain sediments, flood dominated deposition, and carbonate nodules are circumstantial evidence of droughts in semi-arid environments (Retallack, 1991; Sheldon, 2005). Fossils of other species may indicate the presence of mummified carcasses in the environment (Smith pers. comm., 2012); however this is not unexpected given the semi-arid climate models for the Early Triassic Karoo. This leaves open the probability of other unusual phenomena, such as a cold snap combined with grouping behaviour of subadult *Lystrosaurus* forming a bonebed assemblage.

The death by drought hypothesis does not explain why all the bones in the SAM-PK-8551 bonebed are at an equal weathering stage. If the animals died one by one at different stages of the drought, or over multi-year droughts some carcasses may have lain exposed to the sun for up to several years longer than other carcasses before burial. This would have caused variation in degree of articulation and decay, which would have affected the condition of the preserved bone. It could be argued that the drought was severe enough to kill many animals in one event, but then one would expect to find adult animals incorporated into the bonebed as they too would have succumbed according to the phases of drought outlined by Shipman (1975). Therefore, the bones gathered together by flood waters would be expected to be more heterogeneous in their extent of weathering than is observed in the SAM-PK-K8551 bonebed.

Trampling is a common feature in drought-related bonebeds (Rogers, 1991), yet the only broken bones found in the SAM-PK-K8551 bonebed are two skulls. Cracks and breaks are present in some

of the limb bones, but these were caused by breakage during burial diagenesis and lithification. Behrensmeyer (2011) noted the importance of vegetation in disarticulating bone elements that preferentially grew around the carcasses of drought stricken animals after the first rains following a drought in Amboseli National Park. This could be one explanation for the associated disarticulation and preferential loss of ribs and vertebrae in the *Lystrosaurus declivis* SAM-PK-8551 bonebed. Vegetation growing around carcasses may have limited weathering, and if the subadult *Lystrosaurus* congregated around shrinking water sources before their death this could explain the same weathering stage of the bones. This scenario however does not explain the dense and spatially distinct concentration of bones without evidence for hydraulic focussing, and associated disarticulation of many of the skeletal elements suggests little if any influence by water. Trampling should have also been a greater influence as other animals would have continued to use the water source, causing the scattering and breaking of bones.

The behavioural grouping of subadults provides some answers to the problems posed by the accumulation of nine drought-stricken carcasses. If the animals grouped together while living and then perished, all the skeletal elements would be brought together in one place and explain their identical weathering stage, taphonomic style, and why only one species is present in the bonebed. The exception are the four jaw fragments which were most likely added later by minor sheet flooding as they are broken rounded fragments that appear to have undergone a greater degree of weathering than the *Lystrosaurus* bones in the SAM-PK-K8551 specimen. Many ribs and vertebrae are missing which may reflect transportation before burial or, alternatively, post depositional processes such as plant growth and invertebrate burrowing preferentially destroying less dense bones (Behrensmeyer pers. comm., 2012). Mudrock chips are just as likely to have been transported to the scour depression later by a contemporaneous flood event. A pre-existing dry floodplain scour depression could have been selected as an aggregation site for protection from the elements, especially if vegetated. Global climate models paint a picture of an Early Triassic hot house Earth (Benton and Twitchett, 2003; Ward, 2007; Sun et al., 2012), but for local climates and environments the situation was likely more complex, especially at 55°S. Stable isotope work on the Beaufort Group from this and previous studies (MacLeod et al., 2000; Tabor et al., 2007) provides important data on possible palaeoclimate and environmental extremes to which therapsids and other reptiles had to adapt.

In extant and extinct reptiles, grouping is mainly for reasons related to mating, egg laying, or thermoregulation (Brattstrom, 1974). Since the nine *Lystrosaurus declivis* in the SAM-PK-K8551 bonebed are subadults and likely not sexually mature, it is more probable they were grouping to thermoregulate. Many of the Late Permian and Early Triassic tetrapods that lived in the Karoo Basin show evidence for aggregation behaviour and shelter sharing in burrows (Smith, 1987; Smith and Evans, 1996; Abdala et al., 2006; Fernandez et al., 2013). These adaptations were likely useful for environmental extremes such as drought, cold, and heat. Although the *L. declivis* bonebed is unlikely to be a burrow deposit due to the size of the accumulation, grouping behaviour above or below ground was one way animals could adapt and potentially survive extreme conditions.

7. Conclusions

The taphonomy of the SAM-PK-K8551 *Lystrosaurus declivis* bonebed combined with sedimentological and palaeoenvironmental evidence from carbonate nodules provides the following conclusions as to how *Lystrosaurus* as a genus survived and thrived in the “post apocalyptic” Karoo Basin

- 1) Facies interpretations of earliest Triassic rocks at the study site suggest the onset of conditions drier than in the Late Permian, with

sediments mainly deposited during waning flood events on a large low angle braidplain. Climate was highly seasonal and semi-arid as indicated by the presence of pedogenic carbonate nodules, flash flood sedimentary structures and desiccation features. However, it is not possible to identify short-term drought events in the sedimentological record.

- 2) These changes coincide with taphonomic style changes across the PTB. In the earliest Triassic, *Lystrosaurus* fossils occur as articulated, curled-up skeletons and multi-individual monotaxic bonebeds or bone accumulations. Their presence combined with other evidence has formulated two hypotheses on their origin, the hydraulic concentration of drought stricken carcasses or a behavioural grouping of subadults during an unusual cold snap.
- 3) Stable isotope data from pedogenic and early diagenetic carbonate nodules suggest seasonally dry and cold conditions with maximum mean temperatures estimated between 15 °C and 20 °C. Large temperature fluctuations may have been a feature of the highly seasonal palaeoclimate of southern Africa at 55°S palaeolatitude during the earliest Triassic.
- 4) Behavioural grouping of subadult *Lystrosaurus declivis* during an unusual cold snap is the preferred mechanism to explain the SAM-PK-K8551 bonebed horizon. This is due to circumstantial evidence for drought in the associated rocks, insignificant hydraulic concentration to explain close proximity of nine individuals, little trampling, or weathering of skeletal elements; evidence for grouping behaviour in other juvenile and subadult dicynodont species, and shelter sharing by other Early Triassic Karoo vertebrate taxa above or below ground.
- 5) Grouping behaviour may have enhanced the survival of *Lystrosaurus* and been the reason dicynodonts, and other survivor taxa of the end-Permian mass extinction event continued their success in the Triassic. Therefore, aggregation above or below ground could have been a survival adaptation for fauna in the unpredictable climate of the earliest Triassic Karoo Basin.

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