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Changing palaeoenvironments and tetrapod populations in the *Daptocephalus* Assemblage Zone (Karoo Basin, South Africa) indicate early onset of the Permo-Triassic mass extinction

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ABSTRACT

Important palaeoenvironmental differences are identified during deposition of the latest Permian *Daptocephalus* Assemblage Zone (DaAZ) of the South African Beaufort Group (Karoo Supergoup), which is also divided into a Lower and Upper subzone. A lacustrine floodplain facies association showing evidence for higher water tables and subaqueous conditions on the floodplains is present in Lower DaAZ. The change to well-drained floodplain facies association in the Upper DaAZ is coincident with a faunal turnover as evidenced by the last appearance of the dicynodont *Dicynodon lacerticeps*, the therocephalian *Theriognathus microps*, the cynodont *Procynosuchus delaharpeae*, and first appearance of the dicynodont *Lystrosaurus maccaigi* within the Ripplemead member. Considering the well documented 3-phased extinction of Karoo tetrapods during the Permo-Triassic Mass Extinction (PTME), the facies transition between the Lower and Upper DaAZ represents earlier than previously documented palaeoenvironmental changes associated with the onset of this major global biotic crisis.

1. Introduction

The Permo-Triassic Beaufort Group, the oldest non-marine succession of the Karoo Supergroup, spans the Capitanian to Anisian epochs. It comprises repetitive sandstone and mudrock-rich intervals that vary in lateral and vertical distribution and thickness and were deposited by very large (>500 km) continental fluvial systems (Smith, 1993; Smith et al., 1993; Catuneanu et al., 1998; Catuneanu and Elango, 2001). Most geological research on the Beaufort Group has focussed on the sedimentology of strata-bound uranium occurrences (Kubler, 1977; Turner, 1985; Cole and Wipplinger, 2001) and its eight vertebrate biozones defined by the stratigraphic distribution of synapsid and other tetrapod fauna for which the Beaufort Group is world renowned (Keyser, 1979; Keyser and Smith, 1979; Rubidge et al., 1995; Day, 2013; Viglietti et al., 2016). Biozones have highlighted two significant faunal turnovers in the Beaufort Group co-incident with the end-Guadalupian (Day et al., 2015) and end- Permian extinction events (Smith, 1995; Botha and Smith, 2006; Smith et al., 2012; Botha-Brink et al., 2014; Smith and Botha-Brink, 2014; Gastaldo et al., 2015). This paper reports on facies associations documented through the latest Permian biostratigraphic zone in the main Karoo Basin, the newly proposed *Daptocephalus* Assemblage Zone (DaAZ), and how their stratigraphic distribution and abundance changed through time leading up to the PTME.

The (DaAZ) correlates to the upper parts of the Teekloof, Balfour, and Normandien formations (Beaufort Group), and it has recently undergone a major review (Viglietti et al., 2016, 2017b). This involved the revision of the stratigraphic ranges of the previous *Dicynodon* Assemblage Zone (DiAZ) index taxa (i.e. *Dicynodon lacerticeps*, *Theriognathus microps*, *Procynosuchus delaharpeae*) and the taxonomically revived dicynodontoid *Daptocephalus leoniceps* (Kammerer et al., 2011). The revival of *Daptocephalus* by Kammerer et al. (2011) and renaming of the DaAZ by Viglietti et al. (2016) was rejected by Lucas (2017) who follows the use of the genus "*Dicynodon*" in the sense of Cluver and Hotton (1981) (who synonymised *Daptocephalus* and *Dicynodon* using now obsolete taxonomy) for use in his land vertebrate faunachron (LVF) approach. Lucas (2017) argues that Kammerer et al. (2011) did not account for the variable

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morphological differences of "*Dicynodon*". This is contra to the large amount of morphometric data used in the Kammerer et al. (2011) study (i.e. for phylogenetic matrices as well as morphometric analyses). Lucas (2017) LVFs rely on long-ranging, globally distributed single species taxa, which has been criticised by several Triassic workers who demonstrate numerous shortcomings with this concept (Irmis, 2005; Parker, 2006; Rayfield et al., 2009; Butler, 2013). Similarly, in the Permo-Triassic Karoo Basin, if a single globally-distributed "*Dicynodon*" were to be imposed on Karoo Basin biostratigraphy, its resolution would at best span the entire Lopingian (i.e. *Tropidostoma, Cistecephalus, Daptocephalus* and *Lystrosaurus* assemblage zones) (Kammerer et al., 2011).

The revised DaAZ addresses the shortcomings of the previous DiAZ and they include 1) the co-occurrence of all old DiAZ index taxa in the *Cistecephalus* AZ, 2) the appearance of *Lystrosaurus maccaigi* in upper part of the zone below the *Lystrosaurus* AZ, and 3) positions of the new index taxa relative to the inferred 3-phased extinctions at the PTME in the Karoo Basin. It was found that the co-occurrence of *Daptocephalus leoniceps* and *Theriognathus microps* are the most suitable for this stratigraphic interval and thus the DiAZ was renamed the DaAZ, and includes an upper subzone defined by the appearance of the Permian *Lystrosaurus maccaigi*, and disappearance of *Dicynodon lacerticeps* along with other taxa (Viglietti et al., 2016). This faunal turnover occurs below the interval that contains the phased extinctions of Smith and Botha-Brink (2014), and below the radiometrically dated horizon of Gastaldo et al. (2015). The focus of this investigation is on the sedimentary facies associations of the DaAZ, and changes in their abundance through this stratigraphic interval, and whether these changes coincide with this newly documented faunal turnover.

2. Materials and methods

This study area in the south-central Karoo Basin includes large exposure of *Daptocephalus* Assemblage Zone strata (Fig. 1). Documenting the sedimentology included measuring vertical sections of natural outcrops with Jacob's staff and Abney level. Several different lithofacies were identified, traced out laterally, and grouped into distinct facies associations (Table 1, Figs. 2–5).

This study uses the lithofacies, facies association, and architectural element classification schemes modified from Miall (1996), Bordy and Catuneanu (2002), Colombera et al. (2013), and Wilson et al. (2014). Lithofacies are given a facies code which includes a capital letter to indicate the dominant grain size (G = gravel, S = sand, F = fines including very fine sand, silt, and mud) followed by a lower-case letter for the characteristic texture or structure of the lithofacies (e.g. p = planar cross–bedding, h = horizontal lamination). Facies associations are defined by assemblages of lithofacies that represent distinct depositional environments (Miall, 1996) (Table 2). Where possible, architectural element analysis of channel sandstone bodies was conducted to help with palaeoenvironmental interpretation. Finally, the data are synthesized by making comparisons of the stratigraphic distribution of facies associations with the ranges of index taxa for the DaAZ (Fig. 6).

3. Results

3.1. Facies descriptions

Over a total measured thickness of ~500 m for the Balfour Formation, twelve lithofacies were identified in the *Daptocephalus* Assemblage Zone which are grouped into 4 facies associations (Table 1). Refer to Figs. 2–4 for field examples of the various facies associations.

3.1.1. Facies association 1 (confined channelized deposits)

Multi- or single-storey units of cross-bedded or cross-laminated sandstone (Fig. 2C–H) dominated facies association 1 (F1), which are most common in the sandstone-rich members of the Balfour Formation (i.e. Oudeberg and Ripplemead members). Average thickness of F1 varies but normally outcrops reach ~25 m, with each storey being 5–10 m thick. Within the volumetrically dominantly argillaceous Balfour Formation, F1 occurs either as rare amalgamated units that are laterally continuous over tens of kilometres, or more commonly as laterally discontinuous single storey units that pinch out over hundreds of metres (Fig. 3). The lower contacts of F1 commonly undulate and are erosional, with locally abundant scour-fill lags (Gm1) and rip up clasts (Gm2) (Fig. 2A–B). Upper bounding surfaces are commonly flat, rarely concave-up with shallow undulations and ripple-marked surfaces, sharply contacting the overlying and underlying argillaceous deposits (Fig. 3A). Single-storey sandstone bodies have tabular lower and upper contacts and pinch out laterally over tens to hundreds of metres (Fig. 5E).

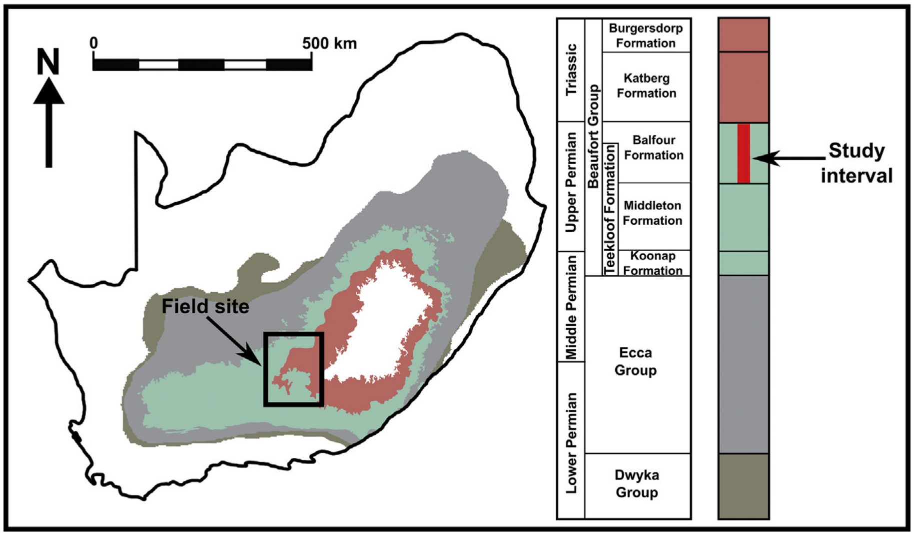

Fig. 1. A map of South Africa and the main Karoo Basin, showing the position of the field sites in the main Karoo Basin and local geology.

Table 1
Lithofacies classification and description.

Facies Names and Code	Grain size	Description	Geometry	Occurrence	Interpretation
Gm1 Scour-fill lag	Very coarse sand to granule sized clasts.	Mudstone or quartz, rare lithic, feldspar clasts, bone, carbonate nodule and plant fragments. Forms poorly sorted, clast-supported pods or lenses. Mudstone clasts are well-rounded, and quartz, feldspar clasts and bone, angular to subrounded. May be weakly normally graded and weathers recessively (i.e. faster than overlying sandstone).	Discontinuous beds, forming lenses or pods within erosional scours. Thickness varies but never greater than 2 m.	Occurs in the basal parts of sand bodies, and sometimes within erosional boundaries between sandstone storeys. Most frequently as filling scours into underlying mudstones.	Lag deposit from rapidly waning flow close to position of the thalweg. Rounded mudstone clasts and angular lithic fragments indicate relatively short transport in pulsatory rapid-flows. Calcareous nodules and fossil material are evidence for erosion of floodplain deposits.
Gm2 Sandstone matrix with rip-up mudstone clasts	Fine to coarse-grained sand with mudrock clasts 0.5-10 cm in diameter.	Colour ranges from greyish brown (5YR 3/2) to pale olive (10Y 6/2). Contains matrix supported mudrock fragments that can be well-rounded to subrounded (friable). They are normally dark greenish grey (5GY 4/1) but also moderate brown (5YR 3/4) are found. Broken up plants fragments on the millimetre and centimetre scale are often associated and stem and leaf impressions that are reasonably intact.	Heterolithic units below other sandstone facies or as isolated pods or lenses. Average thickness is ~ 25 cm but it can occur as deposits less than 10 cm and greater than 1 m.	This facies is laterally restricted, occurring in close proximity to Gm1 as pods (1-2 m long, 20-50 cm thick) or small isolated (<1 m) lenses.	Chaotic fabric indicates deposition during rapidly waning flow in the channel or in a point sourced splay on the proximal floodplain and adjacent to broken levees.
Sp Planar cross–bedded sandstone	Fine to coarse sand.	Weathers yellowish-grey (5Y 7/2) but otherwise pale olive (10Y 6/2) and sometimes greenish-grey (5GY 6/1). Cross-bedding angle normally 20-30 degrees, cross-bed foresets are often silt draped and sometimes fine upwards. Rare in comparison to St.	Small tabular or wedge shaped beds less than 1 m thick with small foresets greater than 1 cm. Can be classed as planar cross-laminae in some instances.	Rare but observed in the middle to lower portions of sandstone bodies. In some cases is associated with Sr.	Small dunes with linear or slightly sinuous crests formed in deeper/faster flowing parts of the channel. Rarely preserved as 3D bedforms as part of unconfined deposition on proximal floodplain.
Sl Low angle cross–bedded sandstone	Fine to coarse sand.	Low angle cross-beds or laminae similar to Sp except for the low angle of deposition occurring on the foresets (5-10 degrees). Normally pale olive (10Y 6/2) but sometimes greenish-grey (5GY 6/1).	Ribbon or wedge shaped layers up to 1 m thick and a few metres across. Truncated on lower and upper bounding surfaces by St and often changes laterally into St.	More common than Sp. In some cases likely mistaken for truncated St. Found in the middle to lower portions of the sandstone bodies in association with St.	Represents deposition in low relief downstream migrating large wavelengths/low amplitude sand waves.
Sh Horizontally laminated sandstone	Fine to medium sand.	Thinly-laminated (< 1 cm) and thinly-bedded (> 1 cm) fine-grained pale olive (10Y 6/2) sand. Often fines upward between laminae. Lower bounding surfaces commonly sharp.	Tabular sheets 1-3 m thick. Over a few metres often changes into Sl (vertically or laterally).	Common. Parting lineation and obstacle marks, such as currents crescents are observed on the upper bounding surfaces where exposed.	Upper flow regime conditions in any part of the fluvial channel where stable bedforms are unable to form.
St Trough cross–bedded sandstone	Fine to coarse sand.	Cross-bedded greenish-grey (5GY 6/1) units in which one or both bounding surfaces are curved. Often this is in the form of truncating another facies. Sometimes silt draping is visible between foresets. The most common facies encountered in the sandstone bodies during this study.	Lateral and vertical size variation. Minimum thickness of between 9 and 15 cm in the axis pinching out laterally. Maximum size ~ 50 to 85 cm. The lower and upper contacts are erosional, creating the pinching and swelling shapes.	Occur in the lower to middle portions of sandstones. Laterally the larger St can become large ribbons where multiple beds truncate one another. The bases of these ribbons are St whereas the upper bed is Sh or comprises Sl.	Three dimensional sinuous crested dunes which form in the deeper and/or faster flowing sections of the channel. The troughs are scoured into the sand bed during peak flood and then filled by migrating dunes during waning flow.
Sm Massive/weakly graded sandstone	Fine to coarse sand.	Massive, apparently structure-less medium to fine-grained pale olive (10Y 6/2) or greenish grey (5GY 6/1) sandstone. Sometimes mud drapes or mud chip layers are present. Bioturbation features have been observed in some cases on upper bounding surfaces. Lower bounding surfaces often erosional but can be flat or sharp. Weathering of the rock surface obscures faint sedimentary features.	Forms tabular beds or sheets within channel sandstone storeys and smaller (< 2 m) overbank sandstone bodies. Can be several metres in thickness and width.	Occurs in the channel fill deposits and common in the floodplain facies associations.	Deposited in proximal parts of unconfined point sourced splays or debris flows in fluvial channels. Bioturbation by plant roots and invertebrates can also cause the lack of structure.
Sr Ripple cross laminated sandstone	Coarse silt to fine sand.	Greenish grey (5GY 6/1) but also dusky yellow green (5GY 5/2) or brownish grey (5YR 4/1). Frequent asymmetrical rippled surfaces with siltstone drapes present throughout	Occurs in two forms: 1) Laterally and vertically extensive tabular to wedge shaped beds for tens of metres. 2) Sheet-like ~ 1 m	Common in Facies association 1. Symmetrical and planed off ripples frequent in the Facies association 3.	Indicative of sustained unidirectional flow in waning energy or water depth conditions. In the case of climbing ripples,

Table 1 (*continued*)

Facies Names and Code	Grain size	Description	Geometry	Occurrence	Interpretation
		sandstone bodies. Occasionally changes vertically into trough cross lamination (Rib and furrow) and laterally into climbing ripples.	thick laterally restrictive beds beds. Can be preserved by silt draping on upper bounding surfaces.		rapid deposition of inclined bar forms. Ripples in Facies association 3 can mean wind action in shallow ponds or lakes.
Sdef Soft sediment deformed sandstone	Fine to medium sand.	Medium to fine-grained sandstone with slump structures, boundins, sandstone pillows, flames, and hummocks.	Not common but when present can be laterally continuous over tens of metres.	Common at the type locality of Tordiffe's (1978) Barberskrans Member where it is laterally extensive within the Oudeberg Member sandstone (> 50 m).	Represents physical disturbance of sediment before consolidation. It is locally caused by storm discharge but where it is more extensive seismic activity and subsequent dewatering may be the cause.
Fm Massive coarse siltstone	Medium to coarse silt.	Mostly greenish grey (5GY 6/1) but sometimes dusky yellow green (5GY 5/2) or brownish grey (5YR 4/1). Mud chips, invertebrate burrows, rootlets, carbonate nodules, fossils are encountered in this facies. Sometimes is locally sandy (flaser bedding) or locally muddy (lenticular bedding).	Laterally extensive on the scale of hundreds of metres as tabular, lense, or sheet shaped bodies ranging from 1-10 m thick.	Occurs most commonly in the floodplain facies association, but also close to the bases of the channel facies.	Fm represents floodplain with high water table. Waterlogged or marshy conditions, such as vegetated wetland environments of the floodplain.
Fl Finely laminated siltstone	Fine silt to coarse silt.	Frequently alternating beds of greenish grey and dusky yellow green (5GY 6/1, 5GY 5/2), or brownish grey (5YR 4/1) siltstone. Colours often indicate slightly differing grain sizes, brownish grey normally being fine-grained and fissile. Mottling and disturbance of the laminations often associated with worm trails, burrows, rootlet horizons, carbonate nodules, and fossil remains.	Laterally extensive on the scale of hundreds of metres as tabular or sheet shaped bodies ranging from 1-10 m thick.	Occurs in close association with Fm.	Suspension settling in ephemeral floodplain ponds where the water table seasonally intersects the surface. Can also be deposited under subaqueous or lacustrine conditions if associated with rhythmites (i.e. Facies association 4).
N Carbonate nodules		This code documents carbonate nodule types observed in Facies association 2 during this study.	Irregular in shape and size. Pedogenic nodules often only a few centimetres across but the larger diagenetic ones can range in size from ~20 cm in length all the way to >10 m across. Most commonly they range in size from 0.2 m to 1 m.	Found throughout the Balfour Formation, normally associated with palaeosol horizons.	Diagenetic and pedogenic origin to the carbonate nodules. Pedogenic nodules associated with palaeosols are precipitated in the soil horizon during seasonal rise and fall of the water table.

The common sequence of sedimentary structures upward from the base include scour-fill lag (Gm1), trough cross-bedding (St), massive bedding (Sm), low angle cross-bedding (Sl), horizontal lamination (Sh), ripple cross-lamination (Sr) which generally reflect waning energy and fining upward textures.

3.1.2. *Facies association 2 (floodplain deposits)*

Facies association 2 (F2) is the most commonly encountered facies association of the Balfour Formation and DaAZ, and is most common in the Daggaboersnek, Elandsberg, and Palingkloof members of the Balfour Formation. F2 comprises finely-laminated siltstone or mudstone (Fl), and massive siltstone or mudstone (Fm) (Fig. 2J–P) in association with carbonate nodules (Fig. 2N,O), rooted horizons (Fig. 2J,P), and palaeosols (Fig. 2M). Rare volcanic ash layers have been documented (Gastaldo et al., 2015; McKay et al., 2015) but none were encountered in this study. F2 deposits commonly have sheet like geometry and are laterally continuous over hundreds of metres and tens of meters vertically (Fig. 3C). Slickensides, blocky to fissile weathering features (Fig. 2M–O), desiccation cracks (Fig. 2O), and vertebrate fossils are also locally common in F2. Additionally, many of the fine-grained lithologies (Fl, Fm) grade laterally into coarser siltstone or Sm which are thin and discontinuous.

3.1.3. *Facies association 3 (unconfined proximal overbank deposits)*

F3 is rare but mostly occurs in the Elandsberg and Palingkloof members of the Balfour Formation. F3 occurs as thin deposits (between 0.5 and 3 m) of Sm, Sp, Sh, Sr (Fig. 2C,E,H). These occur as lens or pod-shaped bodies laterally extending over tens to hundreds of metres (Fig. 4A–C). Basal contacts with other facies associations are sharp and sometimes gullied (Fig. 4A), whereas upper bounding surfaces can be either sharp or gradational (Fig. 4B). In places, undulatory upper contacts are present if erosion occurred prior to burial (Fig. 4B), or fine upwards into ripple surfaces (Fig. 4C). Based upon the lack of sedimentary structures that indicate channelized flow (i.e. Gm1, Gm2, St, Sl), and absence of sedimentary structures which indicate slow aggradation and pedogenesis (i.e. palaeosols, rooted horizons, slickenslides), F3 is therefore a facies association distinct from F1 and F2.

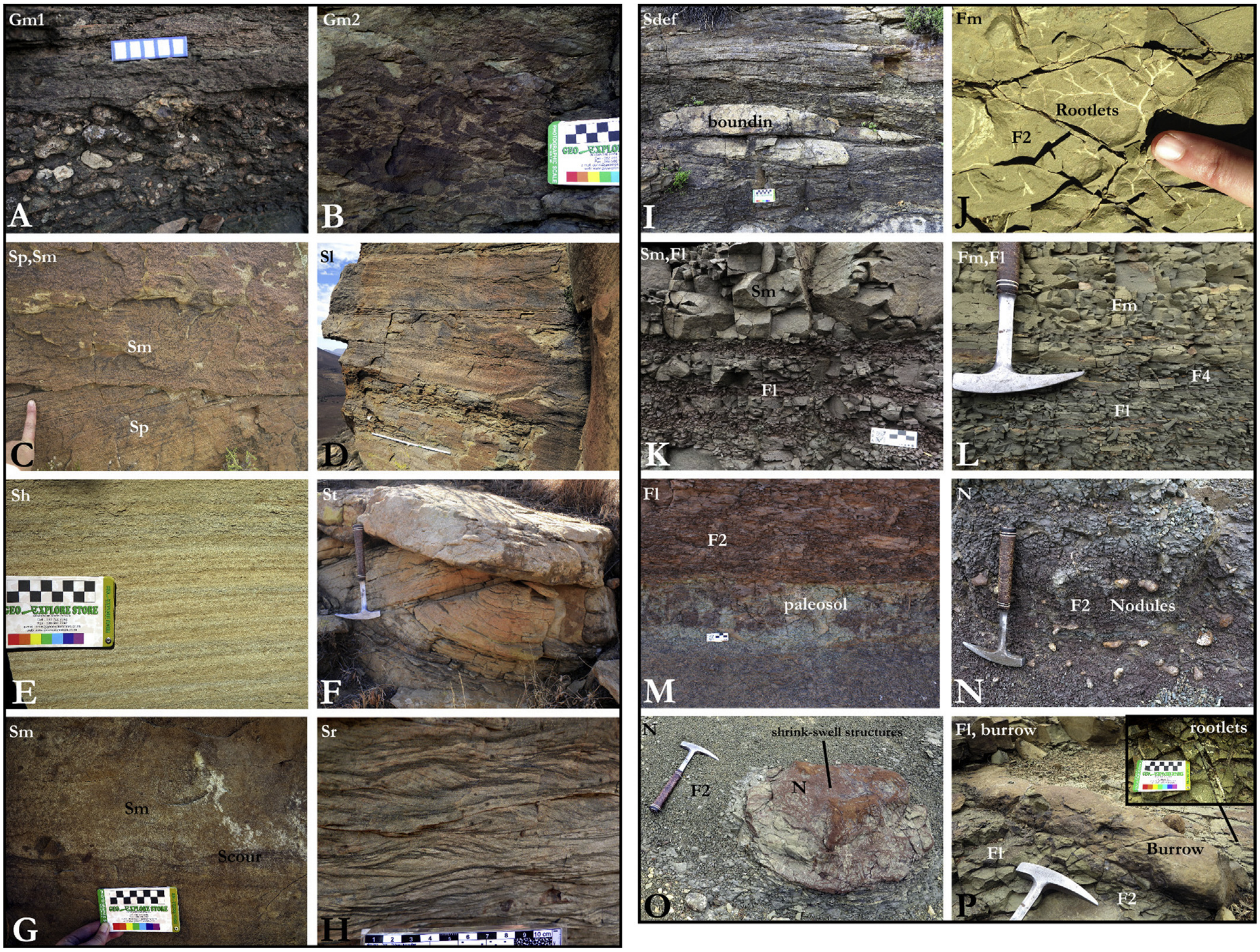

Fig. 2. Examples of lithofacies (Gm1, Gm2, Sp, Sl, Sh, St, Sm, Sr, Sdef, Fm, Fl, and N), and also features of Facies association 2 (F2) identified in the *Daptocephalus* Assemblage Zone (DaAZ). See Table 1 for more detailed descriptions of each lithofacies.

3.1.4. *Facies association 4 (lacustrine deposits)*

F4 comprises ~20 m thick sheet like bodies of Fl (Fig. 5A). In many cases, thin Sr (<10 cm) and Fm are also present (Fig. 2H,L; 5B). Plant fossils, leaf and stem impressions, fossil fish bones, and rare bivalves have been identified from this facies association (Fig. 5C,D,G). F4 is only found in the Daggaboersnek Member of the Balfour Formation (Lower *Daptocephalus* Assemblage Zone) where it is a laterally continuous and ubiquitous facies association. The lack of nodules, and presence of laterally extensive thickly-laminated mudstone or siltstone couplets, and sandstone channel deposits (F1) with load structures and soft-sediment deformation preserved at their bases (from rapid deposition on top of unconsolidated water saturated sediment), are indicators of lacustrine conditions on the floodplains (Reading, 1978; Boggs, 2006) (Fig. 5A,B,E). The presence of rare and localised bivalve fossils also points to a subaqueous environment for this facies association (Fig. 5C and D).

4. Discussion

4.1. *Facies interpretations*

Based on the observations of each identified facies association, the following palaeoenvironmental interpretations are made. For facies association 1 (F1), upward-fining sandstone-dominated lithosomes are interpreted as being deposited in confined channelized systems with a fluctuating discharge regime that was likely influenced by a seasonal rainfall (Stear, 1983, 1985; Haycock et al., 1997; Viglietti et al., 2013; Smith and Botha-Brink, 2014). The architectural elements identified in F1 are mainly downstream accretion (DA), lateral accretion (LA), downstream and laterally accreting (DLA) barforms, and sandy bedforms (SB) (Fig. 3). Fluvial style was variable throughout the *Daptocephalus* Assemblage Zone, although lower sinuosity units tend to coincide with the appearance of subaerial unconformities that are likely linked to tectonic activity (Viglietti et al., 2017a).

Facies association 2 (F2) normally has sharp lower and upper bounding contacts with the other facies associations which is interpreted as deposition by unconfined, waning overbank floods where incremental aggradation of fines on the floodplain is the norm (Walker, 1984). Additionally, if floodplain accretion occurred over long periods of time, plants could take hold and soil forming processes could begin. Evidence of this in the study area include locally common palaeosol horizons (Fig. 2M), which are common as horizons containing carbonate nodules (Fig. 2N,O), slickensides, and colour mottling(Fig. 2M)(Smith, 1995, Smith and Botha, 2005).

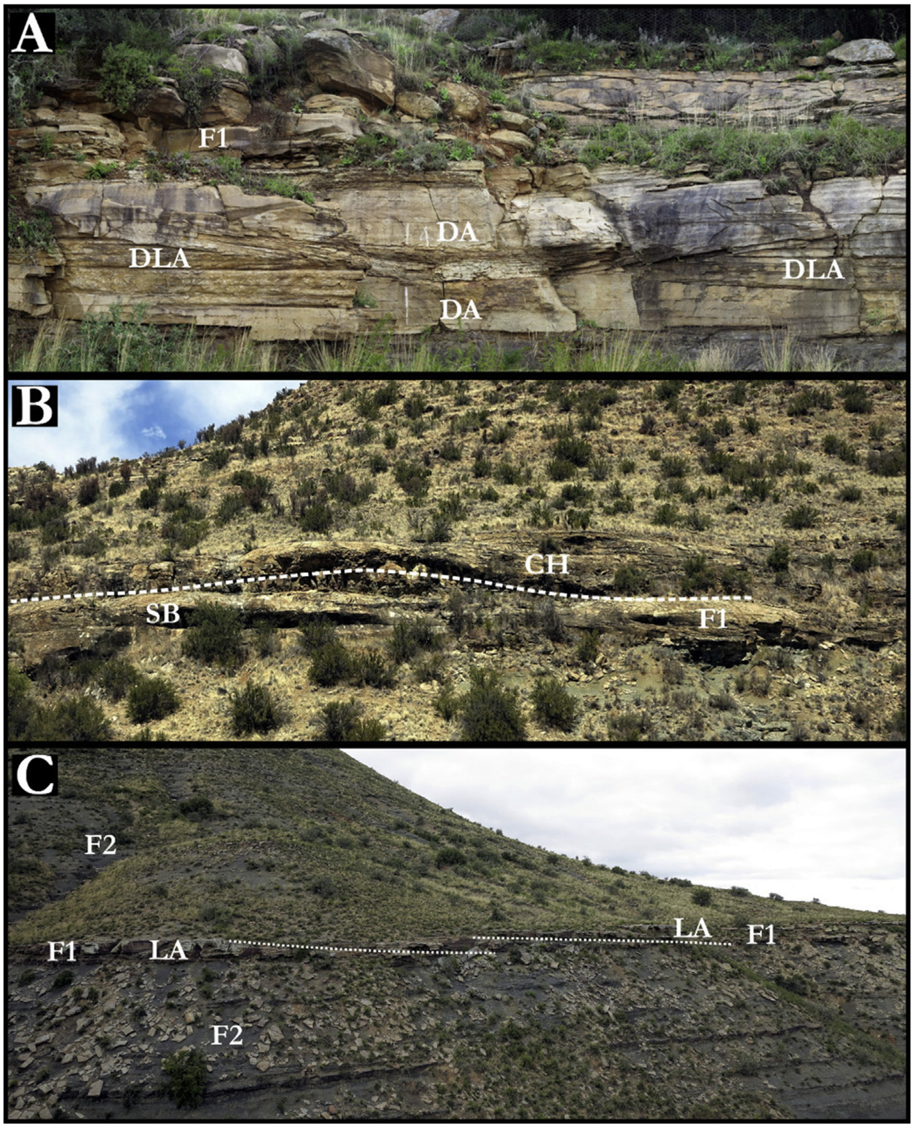

Fig. 3. Examples of: A) downstream accretion (DA), downstream and lateral accretion (DLA), B) sandy bedform (SB), channel form (CH) C) and lateral accretion (LA) architechtural elements observed in facies association 1 (F1) of the *Daptocephalus* Assemblage Zone.

Commonly these floodplain deposits are eroded by an overlying F1 or facies association 3 (F3) (Figs. 3A and 4C) deposit into the immediate area following a flood, as is evidenced by the interruption of F2 deposition by F1 or F3 deposition (Viglietti et al., 2013).

Facies Association3 (F3) is considered to have resulted from unconfined overbank deposition where sediment was dumped rapidly ontooverbank environments. F3 may be part of a crevasse splay complex as they bear similarities with decimetre thick sheet sandstones from the Oligocene Guadalop-Matarranya System (northern Spain) described by Mohrig et al. (2000) and overbank sheet floods described by Graf and Lecce (1988), and Long (2006). F3 thus represents the deposits of unconfined shallow sheet floods, likely attributed to crevasse splays, on the proximal overbank environments but comprises coarser grained bedload rather than suspended load.

Facies association 4 (F4) is interpreted as representing subaqueous or lacustrine palaeoenvironmental conditions. Johnson (1976) interpreted parts of the lower Balfour Formation as representing lacustrine environments based on the thin tabular sandstones and moderately developed varved rhythmites of fine sandstone and dark green shales. He noted the presence of dark green shales with locally abundant leaf impressions which he attributed to deposition in either coastal marshes or swamps adjacent to a standing water body large enough to produce the wind generated wave ripples along the margins. These observations bear much similarity to those identified during this study (Fig. 5), including the rippled surfaces which in this study have been observed containing trace fossils made by aquatic organisms such as fish and invertebrates (Fig. 5H). This evidence all supports the interpretation that F4 units represent deposits of large perennial waterbodies.

4.2. *Distribution of facies and palaeoenvironmental changes across the Daptocephalus Assemblage Zone*

Fig. 6 shows the stratigraphic distribution of the four different facies associations alongside the stratigraphic ranges for all tetrapod taxa of the *Daptocephalus* Assemblage Zone. Except for facies association 4 (F4), which is restricted to the lower Balfour Formation (Lower *Daptocephalus* Assemblage Zone), all the other

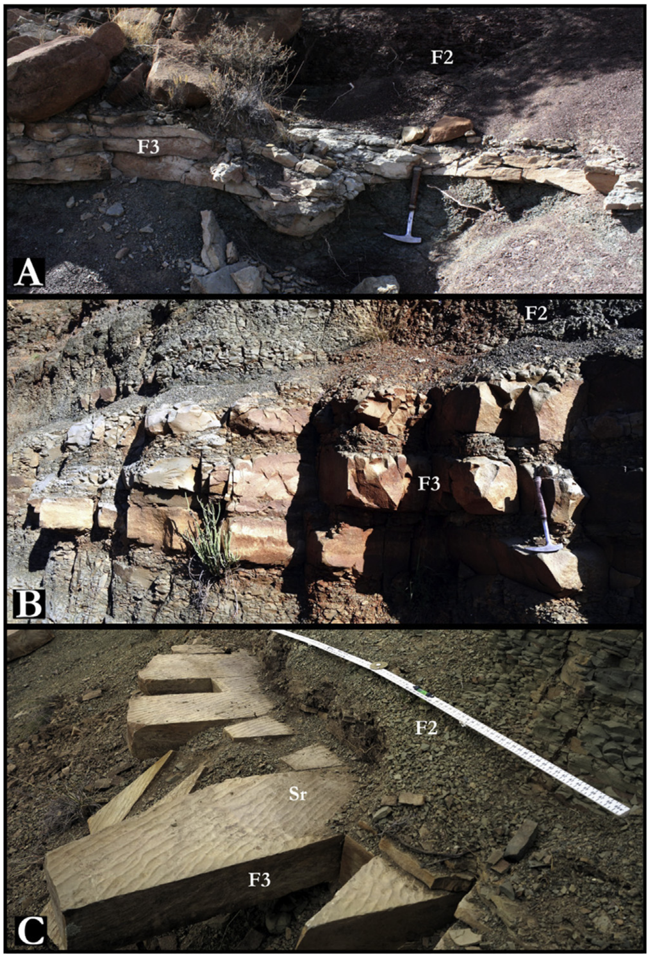

Fig. 4. Examples of facies association 3 (F3) observed during this study showing A) gullying at the base of sandstone bodies, B) fining-upward upper contacts, and C) ripple-topped sandstone surfaces.

facies associations occur with the same frequency throughout the Balfour Formation.

The geographic and stratigraphic distribution of F4 in the Balfour Formation (*Daptocephalus* Assemblage Zone) is considered evidence for significant lacustrine and subaqueous conditions in the flood basins and generally higher groundwater levels on the floodplains adjacent to the channelized river systems, in the Lower DaAZ. New geochemical data for the DaAZ rocks show this interval comprised periodically waterlogged floodplains with high water tables (Li et al., 2017). This study provides increased detail by documenting the presence of large lacustrine systems in the Lower DaAZ. Facies association 4 is not encountered in the Upper DaAZ which suggests the loss of these large standing water bodies in the uppermost DaAZ. Coinciding with the loss of F4 up section is the appearance of mature palaeosols (Fig. 2M), the appearance of large brown weathering carbonate nodules with preserved shrink-swell structures (Fig. 2O), and the disappearance and reduced abundance of Lopingian tetrapod fauna (Viglietti et al., 2016). It is tempting to link these change to observations made in the uppermost DaAZ by previous workers (Smith et al., 2012; Smith and Botha-Brink, 2014) who interpret an increase in maturity of palaeo-pedogenic carbonate horizons, xeromorphic taproot structures, and changes in the taphonomic signature of tetrapod fossils as drop mean annual rainfall and increased aridity.

Contra to Li et al. (2017) the colouration of sediments has not been used as an indicator of palaeoenvironmental change or aridity in this investigation, but rather to identify lithological units in the field. This paleoenvironment model provides evidence that environmental changes leading to the loss of F4 lacustrine conditions were occurring at the boundary of the Lower and Upper DaAZ and coincide with a newly recognised faunal turnover (Fig. 6). This faunal turnover is lower than the extinction phases of Smith and Botha-Brink (2014), and below the dated horizon of Gastaldo et al. (2015) (Fig. 6). We propose that the loss of lacustrine facies indicates the onset of more arid conditions in the Karoo Basin that eventually led to the loss of ground-cover vegetation and the Phase 1 faunal extinction of Smith and Botha-Brink (2014). This aridity has been challenged (Li et al., 2017), however recent isotopic studies (MacLeod et al., 2017; Rey et al., 2017) point to significant climatic changes and increased aridity occurring in the Upper DaAZ, such that changes identified down section in this study could therefore be a precursor to large scale palaeoenvironmental changes relating to aridification encountered higher up section.

4.3. Implications for timing of the onset of the Permo-Triassic mass extinction

The Lower to Upper *Daptocephalus* Assemblage Zone transition is defined by the first appearance datum (FAD) of *Lystrosaurus maccaigi* and roughly coincides with the disappearance of the dicynodont *Dicynodon lacerticeps*, the therocephalian *Theriognathus microps*, and the cynodont *Procynosuchus delarharpeae* along with several Lopingian tetrapod taxa (Viglietti et al., 2016a) (Fig. 6). These disappearances occur low in the Upper DaAZ, and rarefaction analysis conducted by Viglietti et al. (2016) reflect this. While extinctions were minor at the boundary of the Lower and Upper DaAZ in comparison to those observed up section, the data indicate significant relative abundance changes occurring among Lopingian tetrapod taxa at this interval. These changes in abundance of taxa are believed to be associated with the climatic changes documented between the Lower and Upper DaAZ as they coincide with the loss of the lacustrine facies (facies association 4) from the floodplain deposits (Fig. 6).

Finally, the appearance of *Lystrosaurus maccaigi* coeval with this faunal turnover also supports the proposed palaeoenvironmental changes. The first appearance datum of *Lystrosaurus maccaigi*, taken from the supplementary database of Smith and Botha-Brink (2014). SAM-PK-K10920 from Krugerskraal near Nieu Bethesda (Eastern Cape), is the lowest stratigraphic occurrence of this taxon recorded to date from the upper part of the Ripplemead member. Further north in the Bethulie area *L. maccaigi* has also been recovered from near the top of the Ripplemead member (SAM-PK-K10685), but in this part of the basin the same lithostratigraphic unit is ~30 m below the PTB as the strata are significantly attenuated in this part of the basin with more pedogenic horizons indicating longer periods of non-deposition (Viglietti et al., 2017a,b).

Lystrosaurus is demonstrated to have anatomical adaptions advantageous to vegetation changes during the latest Permian (King et al., 1989; King and Cluver, 1990; Jasinoski et al., 2010) and earliest Triassic Karoo Basin (Smith and Botha, 2005; Botha and Smith, 2007). Moreover, the oldest *Lystrosaurus* species, *L. maccaigi*, is now accepted as having survived Phase 2 of the PTME in Antarctica (Collinson et al., 2006) and South Africa (Botha-Brink, pers, comm. 2017). We therefore propose that the first appearance of *Lystrosaurus* could be used and as an indicator genus for the beginning of the biotic crisis that culminated in the Permo-Triassic mass extinction in Gondwana, and possibly Pangea.

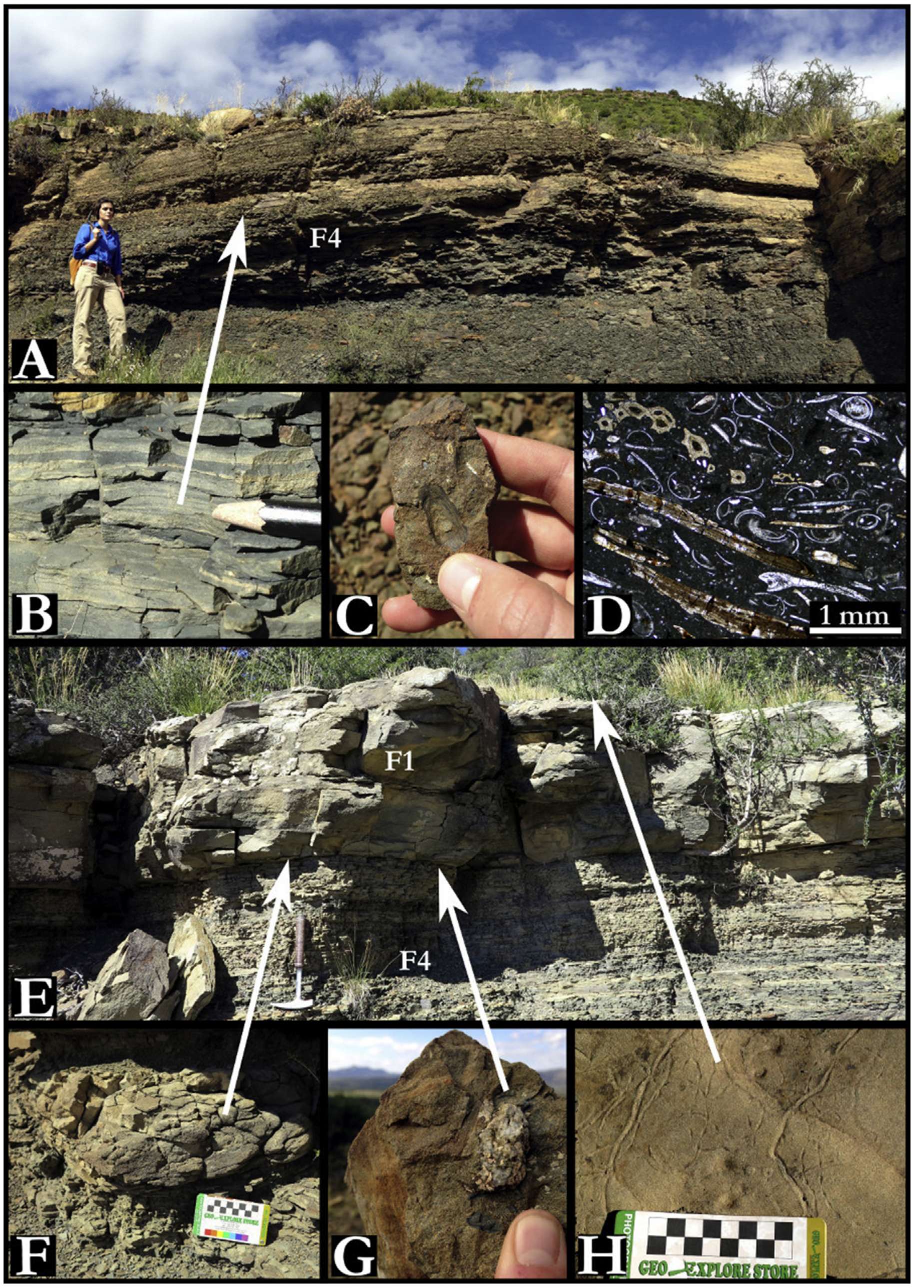

Fig. 5. Examples of the sedimentological features that make up facies association 4 (F4). They include (A,B,E) finely laminated "rhythmite" like deposits of siltstone and fine sandstone, (C,D), bivalve and fish fossils (F,G), load structures at the bases of facies association 1 deposits that indicate high energy deposition over water saturated sediment and tranquil subaqueous settings.

Table 2
Facies associations and their distinct lithofacies assemblages.

Facies Association	Major Facies	Interpretation
F1	Gm1, Gm2 Sm, Sh, St, Sl, Sr, N	Confined channelized deposits
F2	Fl, Fm, N	Floodplain deposits
F3	Sm, Sh, Sr, Fl, Fm	Unconfined proximal overbank deposits
F4	Fl, Fm, Sr	Suspension dominated lacustrine deposits

5. Conclusions

Four facies associations recognized in the Lopingian Balfour Formation (*Daptocephalus* Assembalge Zone) of the Beaufort Group have enabled the recognition of palaeoenvironmental change in the main Karoo Basin towards the end of the Permian. Three of the facies associations occur with similar frequencies throughout the stratigraphic interval, but facies association 4 (lacustrine/subaqueous system) is present only in the Lower DaAZ. This demonstrates that local palaeoenvironmental changes were occurring low in the Upper DaAZ, and below the phased extinctions of Smith and Botha-Brink (2014).

Coinciding with the palaeoenvironmental changes between the

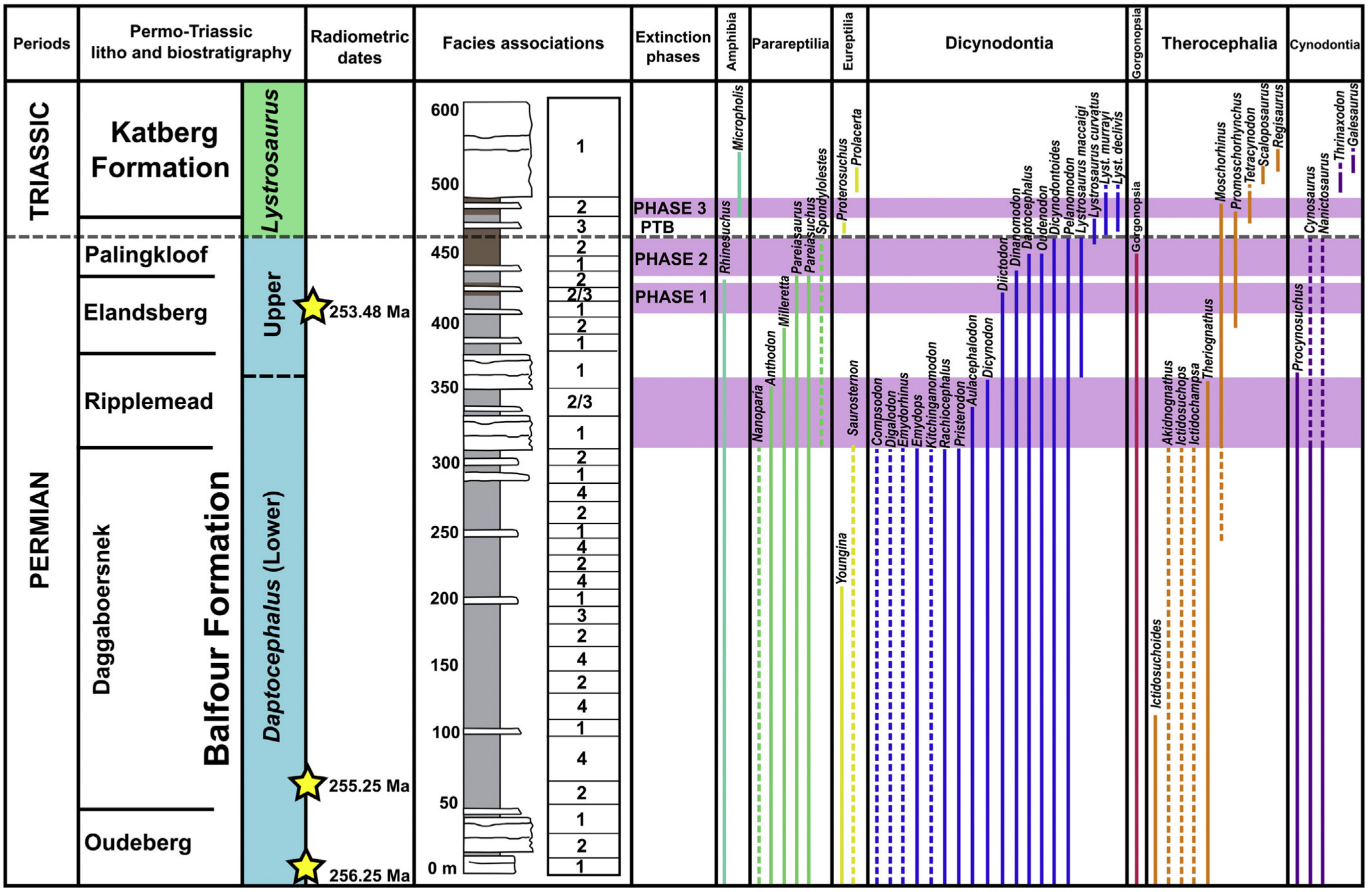

Fig. 6. The diagram shows the stratigraphic position of published absolute dates (i.e. Rubidge et al., 2013; Gastaldo et al., 2015), a composite section for the *Daptocephalus* Assemblage Zone (Balfour Formation), the facies associations (1–4), position of the extinction phases of Smith and Botha-Brink (2014) and Viglietti et al. (2016), and the stratigraphic distribution of all *Daptocephalus* Assemblage Zone tetrapods alongside some *Lystrosaurus* Assemblage Zone tetrapods. The total thickness of the Balfour Formation in metres is variable depending on the position in the basin (i.e. in the south it is ~500 m and in the north it is ~100 m) but is here represented by its maximum thickness. The facies associations column represents the most common facies association encountered at the stratigraphic position in question, and not the total thickness of the facies association. Note the coeval faunal turnover identified below the phased extinctions of Smith and Botha-Brink (2014) marked by the first appearance of *Lystrosaurus maccaigi*, and the disappearance of previous index taxa for the former *Dicynodon* Assemblage Zone (i.e. *Dicynodon lacerticep*s, *Theriognathus microps*, and *Procynosuchus delaharpeae*. Also note the significant drop in diversity of the Dicynodontia and Therocephalia in this interval. Taxa with reliable first and last appearance datums have solid lines whereas those without are stippled.

Lower and Upper DaAZ are significant changes in the relative abundance and disappearance of tetrapod populations including the first appearance of *Lystrosaurus maccaigi* and the extinction of *Dicynodon lacerticeps*, *Theriognathus microps*, and *Procynosuchus delaharpeae*, which all occurs well below the radiometrically dated horizon of Gastaldo et al. (2015). We propose that the first appearance of *L. maccaigi*, coupled with extinction of other long ranging Permian tetrapod taxa along with facies abundance changes, are indicators of early climatic drying, pre-empting the biotic crisis at the end of the Permian period.

Contributions

P.A.V, B.S.R, R.M.H wrote the article. P.A.V conducted the investigation, fieldwork, and created all figures and took all photographs.

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