

The *Daptocephalus* Assemblage Zone (Lopingian), South Africa: A proposed biostratigraphy based on a new compilation of stratigraphic ranges



Pia A. Viglietti^{a,*}, Roger M.H. Smith^{a,b}, Kenneth D. Angielczyk^{a,c},
Christian F. Kammerer^{a,d}, Jörg Fröbisch^{a,e}, Bruce S. Rubidge^a

^a Evolutionary Studies Institute, School for Geosciences, University of the Witwatersrand, Johannesburg, Private Bag 3 Wits 2050, South Africa

^b Iziko South African Museum, P.O. Box 61, Cape Town 8000, South Africa

^c Integrative Research Center, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA

^d Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Invalidenstraße 43, 10115 Berlin, Germany

^e Institut für Biologie, Humboldt-Universität zu Berlin, Invalidenstraße 110, 10115 Berlin, Germany

ARTICLE INFO

Article history:

Received 12 September 2015

Received in revised form

19 October 2015

Accepted 20 October 2015

Available online 26 October 2015

Keywords:

Dicynodon Assemblage Zone

Late Permian

Karoo biostratigraphy

ABSTRACT

The *Dicynodon* Assemblage Zone (DaAZ) of South Africa's Karoo Basin is one of the eight biostratigraphic zones of the Beaufort Group. It spans the uppermost Permian strata (Balfour, Teekloof, and Normandien formations) and traditionally has been considered to terminate with the disappearance of *Dicynodon lacerticeps* at the Permo-Triassic Boundary. We demonstrate that the three index fossils currently used to define the *Dicynodon* Assemblage Zone (*Dicynodon lacerticeps*, *Therapsidops microps*, and *Procyonosuchus delaharpeae*) have first appearance datums (FADs) below its traditionally recognized lower boundary and have ranges mostly restricted to the lower portion of the biozone, well below the Permo-Triassic Boundary. We propose re-establishing *Daptocephalus leoniceps* as an index fossil for this stratigraphic interval, and reinstating the name *Daptocephalus* Assemblage Zone (DaAZ) for this unit. Furthermore, the FAD of *Lystrosaurus maccaigi* in the uppermost reaches of the biozone calls for the establishment of a two-fold subdivision of the current *Dicynodon* Assemblage Zone. The biostratigraphic utility of *Da. leoniceps* and other South African dicynodontoids outside of the Karoo Basin is limited due to basinal endemism at the species level and varying temporal ranges of dicynodontoids globally. Therefore, we recommend their use only for correlation within the Karoo Basin at this time. Revision of the stratigraphic ranges of all late Permian tetrapods does not reveal a significant change in faunal diversity between the lower and upper DaAZ. However, the last appearance datums of the abundant taxa *Di. lacerticeps*, *T. microps*, *P. delaharpeae*, and *Diictodon feliceps* occur below the three extinction phases associated with the end-Permian mass extinction event. Due to northward attenuation of the strata, however, the stratigraphic position of the extinction phases may need to be reconsidered.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

The late Permian (Lopingian) is an important time in Earth's history. By this stage of the Permian, all the world's continents had coalesced into a single supercontinent (Pangea), which was surrounded by a global ocean (Panthalassa), and this had significant climatic implications (Erwin, 1990; Parrish, 1993; Stampfli et al., 2013). The extensive subpolar coal forests of the early to middle Permian had given way to drier continental climates (Cadle et al., 1993; Cairncross, 1989). This is believed to have been a major driver in the evolution and diversification of the amniotes (Sahney

* Corresponding author. Current address: Evolutionary Studies Institute, School for Geosciences, University of the Witwatersrand, Johannesburg, Private Bag 3 Wits 2050, South Africa.

E-mail addresses: pia.viglietti@gmail.com (P.A. Viglietti), rsmith@iziko.org.za (R.M.H. Smith), kangielczyk@fieldmuseum.org (K.D. Angielczyk), christian.kammerer@mfn-berlin.de (C.F. Kammerer), joerg.froebisch@mfn-berlin.de (J. Fröbisch), bruce.rubidge@wits.ac.za (B.S. Rubidge).

et al., 2010). The Permian is best known for its radiation of non-mammalian synapsids (including the therapsids, the synapsid subclade containing mammals as their extant representatives). The Lopingian represents the golden age of the therapsids, which by this time were at the peak of their ecological domination, occupying almost every available niche, although they began to relinquish this position during the end-Permian mass extinction (Benton and Twitchett, 2003; Benton and Newell, 2014; Erwin, 2006; Fröbisch, 2013; Smith and Botha-Brink, 2014). Events immediately prior to this great extinction and its aftermath in the terrestrial realm have received deserved attention from varied scientific disciplines including sedimentology and taphonomy (Botha and Smith, 2006; Smith, 1995; Smith and Ward, 2001; Smith and Botha, 2005; Viglietti et al., 2013; Ward et al., 2005); global climate and ocean modelling (Bottjer, 2012; Sun et al., 2012; Wignall and Twitchett, 1996); and disparity, ecology, and ecosystem modelling (Benton et al., 2004; Roopnarine et al., 2007; Ruta et al., 2013; Sahney and Benton, 2008).

South Africa's Beaufort Group (part of the Karoo Supergroup) is unique because it preserves, with little tectonic disturbance, a near continuous sequence of non-marine deposits documenting this radiation, ranging from the late Guadalupian (Capitanian) to the middle Triassic (Anisian). The abundant fossil tetrapods from the Beaufort Group have been divided into six Permian (*Eodicynodon*, *Tapinocephalus*, *Priesterognathus*, *Tropidostoma*, *Cistecephalus*, *Dicynodon*) and two Triassic (*Lystrosaurus*, *Cynognathus*) assemblage zones (AZs), biostratigraphic units based on therapsid index fossils. Apart from its record of the Permo-Triassic extinction, a new set of radiometric dates (Rubidge et al., 2013) has recently made possible the identification of a mid-Permian (end-Guadalupian) extinction event in the terrestrial realm at 260 Ma (upper *Tapinocephalus* Assemblage Zone, Abrahamskraal Formation (Day et al., 2015)). However, for many of the other assemblage zones the available stratigraphic range data are not up to date and need to be re-evaluated before an accurate picture of faunal composition and turnover patterns can be discerned.

The *Dicynodon* Assemblage Zone (DiAZ) is the terminal Permian biostratigraphic assemblage zone of the Beaufort Group and is one of the thickest of the Beaufort Group's biozones (~500 m). During the time represented by this zone, the Karoo retroarc foreland system was in an overfilled phase and non-marine (molasse) environments occupied the entirety of the Karoo Basin for the first time in its history (Catuneanu et al., 1998; Smith et al., 2012). Recent radiometric dates suggest that the DiAZ spans approximately three million years (Rubidge et al., 2013). It is currently defined by the first appearance datum (FAD) of the therapsids *Dicynodon lacerticeps* (Dicynodontia), *Theriongnathus microps* (Therocephalia), and *Procynosuchus delaharpeae* (Cynodontia) (Rubidge et al., 1995), and is considered to terminate with the LAD of *Di. lacerticeps*, associated with three extinction phases in a 70 m thick interval spanning the Permo-Triassic Boundary (Smith and Botha-Brink, 2014) (Fig. 1). It roughly coincides with the lithologically defined Balfour Formation in the east, Teekloof Formation in the west, and Normandien Formation in the north of the basin.

Based on its use as an index fossil in the Karoo Basin, *Dicynodon* sensu lato has been used in the past to correlate various Karoo-aged basins within the Platbergian land vertebrate faunachron (LVF), a global biostratigraphic unit that covers the ages of the uppermost *Cistecephalus* Assemblage Zone (CAZ) and the entire DiAZ. The other Late Permian LVFs are the Hoedemakeraan (defined by the first appearance of *Tropidostoma*) and the Steilkransian (defined by the first appearance of *Cistecephalus*) (Lucas, 2006). As a result, *Dicynodon* sensu lato has a long history of being used to make biostratigraphic correlations between the Karoo Basin and other areas such as Tanzania and Zambia (Anderson and Cruickshank,

1978; Angielczyk et al., 2014a, 2014b; King, 1992; Lucas, 1997, 1998a,b, 2001, 2002, 2005, 2006; Rubidge, 2005; Smith et al., 2012). However few definitive DiAZ strata have been found outside of the main Karoo Basin, as many of these Karoo-aged basins are now believed to correlate with the CAZ (Angielczyk et al., 2014a, 2014b). Nonetheless, a few places globally do have strata that correlate with the DiAZ, such as the Guodikeng Formation in northwestern China (Metcalfe et al., 2001) and the Sokolki fauna near Vyazniki and Gorokhovets on the Russian Platform (Newell et al., 2010). It has also been recognized for some time that the paraphyly of the traditionally-recognized genus *Dicynodon* and taxonomic confusion at the species level made it a poor index fossil (Angielczyk and Kurkin, 2003a,b). Therefore *Dicynodon* sensu lato in various Karoo-aged basins do not represent the same taxon and as a result give no guarantee they had similar temporal ranges (Kammerer et al., 2011).

Recently, Kammerer et al. (2011) undertook a comprehensive taxonomic revision of *Dicynodon*, reducing the 168 nominal species to 15 species in 14 genera globally and underscoring the polyphyly of *Dicynodon* sensu lato. In the Karoo Basin, Kammerer et al. (2011) recognized five valid species of basal (non-lystrosaurid, non-kannemeyeriiform) dicynodontoids: *Basilodon woodwardi*, *Daptocephalus leoniceps*, *Dicynodon lacerticeps*, *Dinanomodon gilli*, and *Sintocephalus alticeps*. Additionally, they erected new genera (*Keyseria* and *Euptychognathus*) for the Karoo-occurring former "*Dicynodon*" species "*D.*" *benjamini* and "*D.*" *bathyrhynchus*, which they recovered as a basal cryptodont and lystrosaurid, respectively. However, they expressed uncertainty about the stratigraphic ranges of some of these species, noted that *Da. leoniceps* might be a more appropriate index fossil for the *Dicynodon* Assemblage Zone than *Di. lacerticeps*, and suggested that additional scrutiny was needed to fully understand the biostratigraphic utility of *Dicynodon* and its closest relatives. Indeed, the change in nomenclature from the older *Daptocephalus* Zone (Kitching, 1977) to the current *Dicynodon* Assemblage Zone (Rubidge et al., 1995) was driven entirely by obsolete taxonomy, which viewed *Daptocephalus* as a junior synonym of *Dicynodon* and expressed uncertainty as to whether *Da. leoniceps* was a junior synonym of *Di. lacerticeps* (Cluver and Hotton, 1981; Cluver and King, 1983; King, 1988).

Beyond the uncertainty surrounding the stratigraphic occurrences of *Dicynodon* and its close relatives, the current definition of the DiAZ is also problematic because all three index species (*Di. lacerticeps*, *T. microps*, and *P. delaharpeae*) are reported to have FADs that predate the traditionally-recognized base of the DiAZ. Therefore the use of *Dicynodon* sensu lato in the LVF biostratigraphic scheme is problematic in the Karoo Basin because it is considered to be concurrent with *Cistecephalus microrhinus* and therefore would overlap the Steilkransian LVF (Kammerer et al., 2011). *Theriongnathus microps* is also known to be present in the upper CAZ (Huttenlocker, 2014) and *P. delaharpeae* has an even earlier FAD in the Hoedemakeraan LVF (*Tropidostoma* Assemblage Zone) (Botha-Brink and Abdala, 2008). Given these ranges, the first co-occurrence of these species would be in rocks traditionally assigned to the CAZ, requiring a redefinition of the zone such that it is based on a suite of taxa that do not also co-occur in other assemblage zones. A similar problem occurs at the top of the zone, where *Lystrosaurus maccaigi* first appears in late Permian rocks that are below the traditional lower bound of the *Lystrosaurus* Assemblage Zone (LAZ) just after the Permo-Triassic boundary (PTB) (Botha and Smith, 2007).

The aim of this investigation is to address the shortcomings of the current manifestation of the *Dicynodon* Assemblage Zone. First, we reassess the stratigraphic ranges of *Di. lacerticeps*, other basal dicynodontoids, and additional DiAZ-occurring taxa in the Karoo Basin and test their utility as index fossils. Second, we redefine the assemblage zone by replacing the DiAZ with the *Daptocephalus*

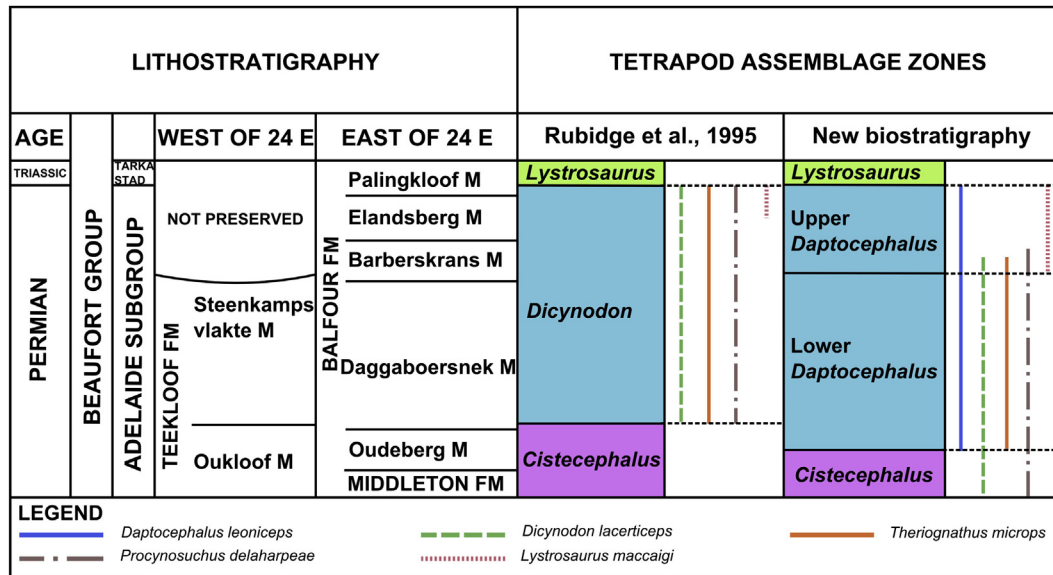


Fig. 1. The current *Dicynodon* Assemblage Zone (sensu Rubidge et al., 1995) and our proposed *Daptocephalus* Assemblage Zone biostratigraphic schemes with lithostratigraphic subdivisions. Note the new range data for *Dicynodon lacerticeps*, *Theriognathus microps*, and *Procynosuchus delaharpeae*. In this new framework, the base of the lower *Daptocephalus* Assemblage Zone will be defined by the FAD of *Daptocephalus leoniceps* and *Theriognathus microps* and the base of the upper *Daptocephalus* Assemblage Zone will be defined by the FAD of *Lystrosaurus maccaigi*. The LAD of *Daptocephalus leoniceps* and *Lystrosaurus maccaigi* (and the upper boundary of the *Daptocephalus* Assemblage Zone) is within Smith and Botha-Brink's (2014) phase 2 extinction approximately at their stratigraphically defined Permo-Triassic Boundary.

Assemblage Zone (DaAZ), using a group of taxa that only occur within rocks assigned to this zone and re-establishing *Da. leoniceps* as the index fossil for this stratigraphic interval (Fig. 1). Third, we resolve the biostratigraphic problem of the late Permian FAD of *L. maccaigi* by informally dividing the DaAZ into a lower and upper subzone. Fourth, we investigate the lower and upper DaAZ for differences in faunal diversity. Finally, we provide an updated faunal list and set of stratigraphic ranges for the vertebrates of the new *Daptocephalus* Assemblage Zone biostratigraphic scheme (Fig. 2), and identify how their LADs relate to Smith and Botha-Brink's (2014) three extinction phases associated with the end-Permian mass extinction event.

2. Materials and methods

2.1. Lithostratigraphy and study locations

The DaAZ coincides with three formations in the main Karoo Basin: the Teekloof Formation west of 24°E, the Balfour Formation east of 24°E, and the Normandien Formation in the northern Free State and Kwa-Zulu Natal provinces. The uppermost Steenkampsvlakte Member of the Teekloof Formation is assigned to the lower DaAZ and has been inferred as a lateral equivalent to the lower Balfour Formation (Cole and Wipplinger, 2001). Poor exposure and uncertain correlation with southern Karoo Basin stratigraphy are reasons that the Normandien Formation is poorly constrained temporally. However, based on sequence stratigraphy, Catuneanu et al. (2005) suggest that it is representative of only the latest Permian (see also Catuneanu et al., 1998).

The Balfour Formation, occurring in the eastern part of the basin, includes the most thoroughly studied DaAZ exposures and therefore was the main focus of this investigation. It is currently divided into the Oudeberg, Daggaboersnek, Barberskrans, Elandsberg, and Palingkloof members (Fig. 1). For ease of correlation and for the purpose of describing stratigraphic ranges within this study, the DaAZ has been split into “lower” and “upper” zones. The lower DaAZ is defined by the FADs of *Daptocephalus leoniceps* and

Theriognathus microps and correlates to the upper Oudeberg Member of the Balfour Formation, and the Teekloof Formation's upper Oukloof and Steenkampsvlakte members. The upper DaAZ correlates approximately with the base of the Barberskrans Member and terminates at the PTB in the lowermost Palingkloof Member. The upper DaAZ here is defined by the FAD of *Lystrosaurus maccaigi*, which is a maximum of ~150 m below the PTB (170 m below the Katberg Formation). Study sites were selected where strata of the DaAZ were exposed along with the underlying CAZ, the overlying *Lystrosaurus* Assemblage Zone (LAZ), or both. At the chosen field sites, vertical sections were measured and logged with a Jacob's staff and Abney level. Locations of the study sites are shown in Fig. 3 and farm names are listed below:

- 1). Krugerskraal, Ripplemead, and Doornplaats, Graaff-Reinet District, Eastern Cape Province.
- 2). Hales Owen and Lower Clifton, Cradock District, Eastern Cape Province.
- 3). Inhoek, Schalkwykskraal, and Van Wyksfontein, Gariep Dam area, Eastern Cape Province.
- 4). Oukloof Pass in the Beaufort West District, Western Cape Province.

Additional stratigraphic information was retrieved from the literature for the following locations: Bethulie, Free State and Lootsberg Pass, Eastern Cape (Botha-Brink et al., 2014; Botha and Smith, 2006; Smith and Botha-Brink, 2014). The combined lithostratigraphic information allowed for the creation of composite sections and for lateral correlation between different field sites (Fig. 5). There is a significant attenuation of the strata northwards, which was observed by Kitching (1977) in the Gariep Dam area, by Groenewald (1984) in the northern Free State Province (Normandien Formation), and is also confirmed in this study.

2.2. Determining stratigraphic positions of fossils used in this study

Prior to 1976, only farm names and elevations were used by

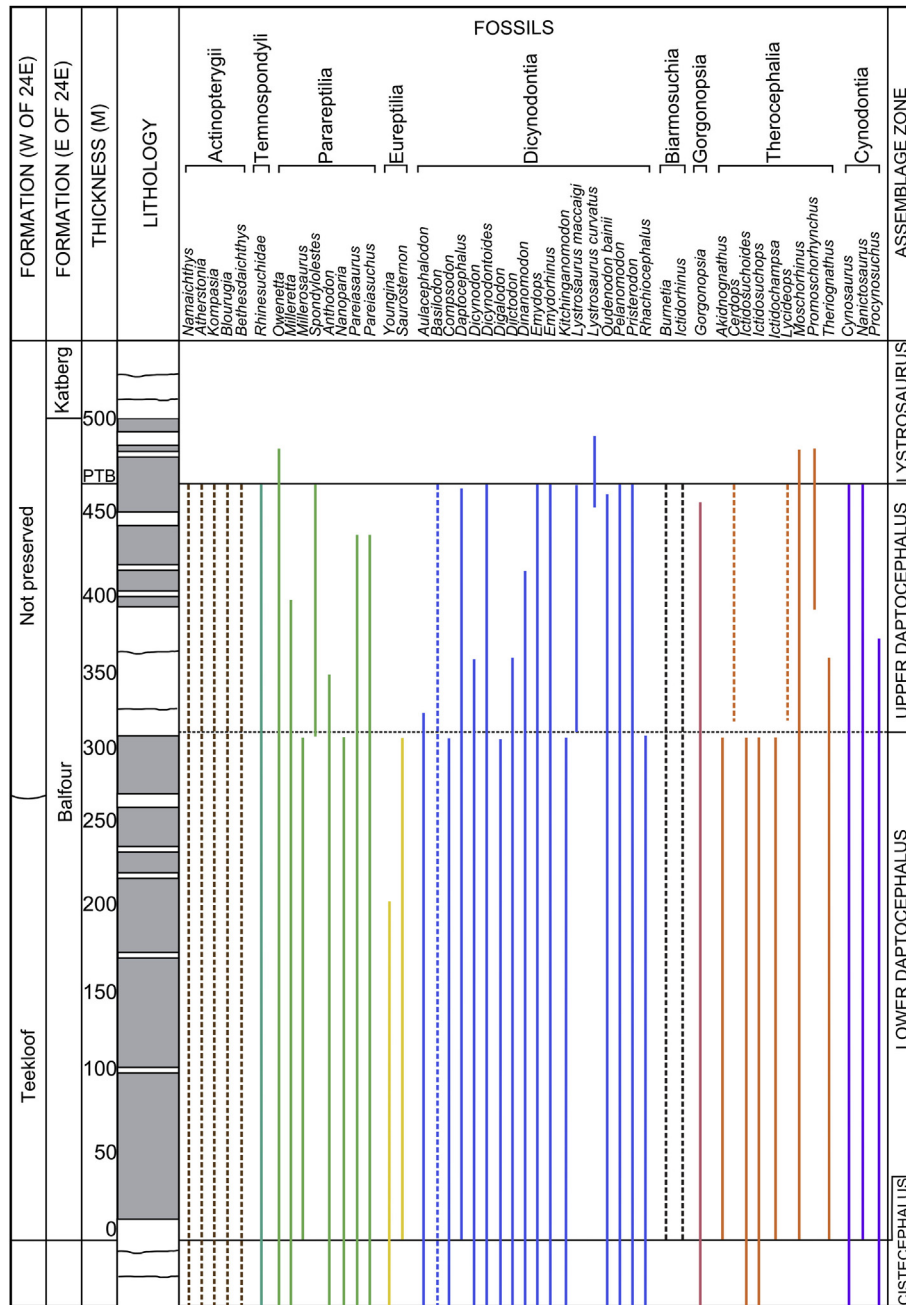


Fig. 2. Updated stratigraphic ranges of vertebrate fauna of the newly proposed *Daptocephalus* Assemblage Zone. Note temnospondyls and gorgonopsia are represented by a single higher taxon due to taxonomic confusion and current lack of stratigraphic data available for them. Ranges of taxa at genus or species level that were not able to be verified in this study have dotted lines.

collectors to record fossil localities in the Karoo Basin. As a result the majority of South African fossils in collections today have poor provenance data. Historical specimens from these collections were utilized in this study only if the stratigraphy was well known in the area in which the fossils were found. For such specimens rough locality and stratigraphic positions were assigned using the farm centroids derived from Google Earth (van der Walt et al., 2011). However, much more accurate locality and biostratigraphic information was generated through systematic collecting of tetrapod fossils in the outcrops where detailed stratigraphic sections were logged by PAV (PV) and RMHS (RS). More recently discovered fossils have accurate GPS coordinates and have also been positioned on

measured vertical sections, which allows for some species to be assigned a reliable FAD or LAD. A total of 1212 fossils reliably provenanced to the upper CAZ or DaAZ were investigated. They are stored at the following institutions: Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg (BP), Iziko South African Museum, Cape Town (SAM-PK), Rubidge Collection, Wellwood, Graaff-Reinet (RC), Albany Museum, Grahamstown (AM), Ditsong (Transvaal Museum), Pretoria (TM), National Museum, Bloemfontein (NM), Council for Geoscience (Geological Survey), Pretoria (CGS), Bremner Collection (SAM satellite collection, Graaff-Reinet Museum) (B), RMHS field specimens, not accessioned (RS), specimens collected during doctoral work for PAV (PV), American

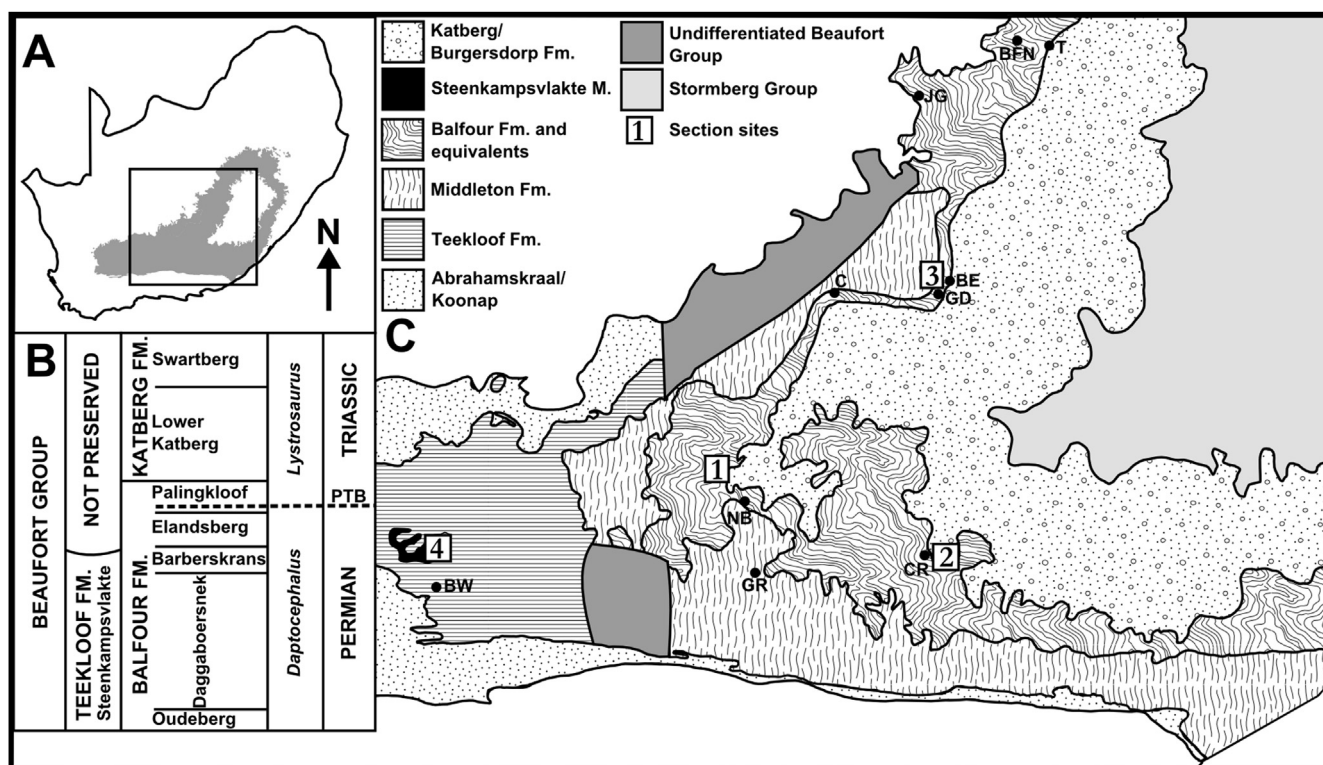


Fig. 3. A) South Africa and the position of the Karoo Basin. B) Formal lithostratigraphic subdivisions of strata correlated to the *Daptocephalus* and *Lystrosaurus* assemblage zones. C) Map of the main Karoo Basin of South Africa showing the distribution of strata of the Beaufort and Stormberg groups. Numbered field sites where stratigraphic sections were measured are: 1) Krugerskraal, Ripplemead, and Doornplaats farms, Graaff-Reinet, Eastern Cape Province; 2) Hales Owen and Lower Clifton farms, Cradock, Eastern Cape Province; 3) Inhoek, Schalkwykskraal, and Van Wyksfontein farms, Gariet Dam, Eastern Cape Province; 4) Oukloof Pass, Beaufort West, Western Cape Province. Abbreviations for town names are: Thaba Nchu (T), Bloemfontein (BFN), Bethulie (BE), Gariet Dam (GD), Colesburg (C), Cradock (CR), Nieu Bethesda (NB), Graaff-Reinet (GR), Beaufort West (BW).

Museum of Natural History, New York, USA (AMNH), Natural History Museum, London, UK (NHMUK), University of California Museum of Paleontology, Berkeley, USA (UCMP), University Museum of Zoology, Cambridge, UK, (UMZC), and the National Museum of Natural History, Washington, DC, USA (USNM). A list of the specimens used in this study can be found in the supplementary datasheet.

2.3. Biostratigraphy

Since the last biostratigraphic review of the Beaufort Group (Rubidge et al., 1995), the taxonomy of many DaAZ occurring tetrapods has been revised. Dicynodont genera have been the subject to particularly thorough taxonomic revision, whereas some other vertebrate groups are still in a state of flux, including Actinopterygii (Bender, 2001), Temnospondyli (Damiani and Rubidge, 2003; Latimer et al., 2002; Marsicano et al., 2015), Parareptilia, (Cisneros et al., 2008; Gow and Rubidge, 1997; Jalil and Janvier, 2005; Lee, 1997), Therocephalia (Huttenlocker et al., 2011), and Gorgonopsia (Gebauer, 2007; Kammerer, 2015; Norton, 2012). Stratigraphic reassessment of the currently-recognized fauna in the DaAZ shows that this biozone contains 46 other taxa from nine different major vertebrate clades (Fig. 2).

To review the stratigraphic range of a fossil taxon three conditions need to be met (Day, 2013): 1) thorough understanding of the lithostratigraphy throughout the basin; 2) robust taxonomic framework; and 3) re-identification of all relevant specimens in collections based on the most recent taxonomic framework. The first criterion has mostly been met through fieldwork and literature studies, although some fossils found in the Normandien Formation were excluded from consideration because its temporal correlation

remains poorly understood. Thus, all DaAZ taxa within temporally constrained strata from the basin were investigated, and the stratigraphic ranges updated from this data pool (Fig. 2). Lingering taxonomic confusion associated with some DaAZ species meant that for two groups (Temnospondyli and Gorgonopsia) only the higher-level taxon was considered. Genus or species-level ranges could not be updated for these groups, pending revision. Additionally, difficulty in identifying parareptile specimens to species meant that we measured abundances in this group at higher taxonomic levels (Pareiasauria and Millerettidae). Six hundred and twenty-eight specimens from the DaAZ (477 lower DaAZ, 151 upper DaAZ) met the three criteria and were arranged according to rough stratigraphic position, new higher taxon name or species where appropriate, and also as fossil taxa abundance pie charts for lower and upper DaAZ (Fig. 4).

Additionally, the following taxa were investigated in further detail to assess their potential utility as DaAZ index fossils: the dicynodonts *Dicynodon lacerticeps*, *Da. leoniceps*, and *L. maccaigi* and the therocephalian *T. microps*, and the cynodont *P. delaharpeae*. Where possible, the FADs and LADs were determined for each species by the lowest and highest occurring specimen in the database with reliable stratigraphic information (Table 1). Because the taxonomic revision of *Dicynodon* is recent (Kammerer et al., 2011), many museum collections databases have not yet been updated and only specimens of *Di. lacerticeps* and *Da. leoniceps* that were directly re-examined by CFK, JF, and KDA were used. The hyper-abundant dicynodont *Diictodon feliceps*, and the PTB-crossing therocephalian *Moschorhinus kitchingi* were also investigated in further detail and their updated FADs and LADs were compared to those of the index fossils and also the phased extinctions outlined by Smith and Botha-Brink (2014). The phased

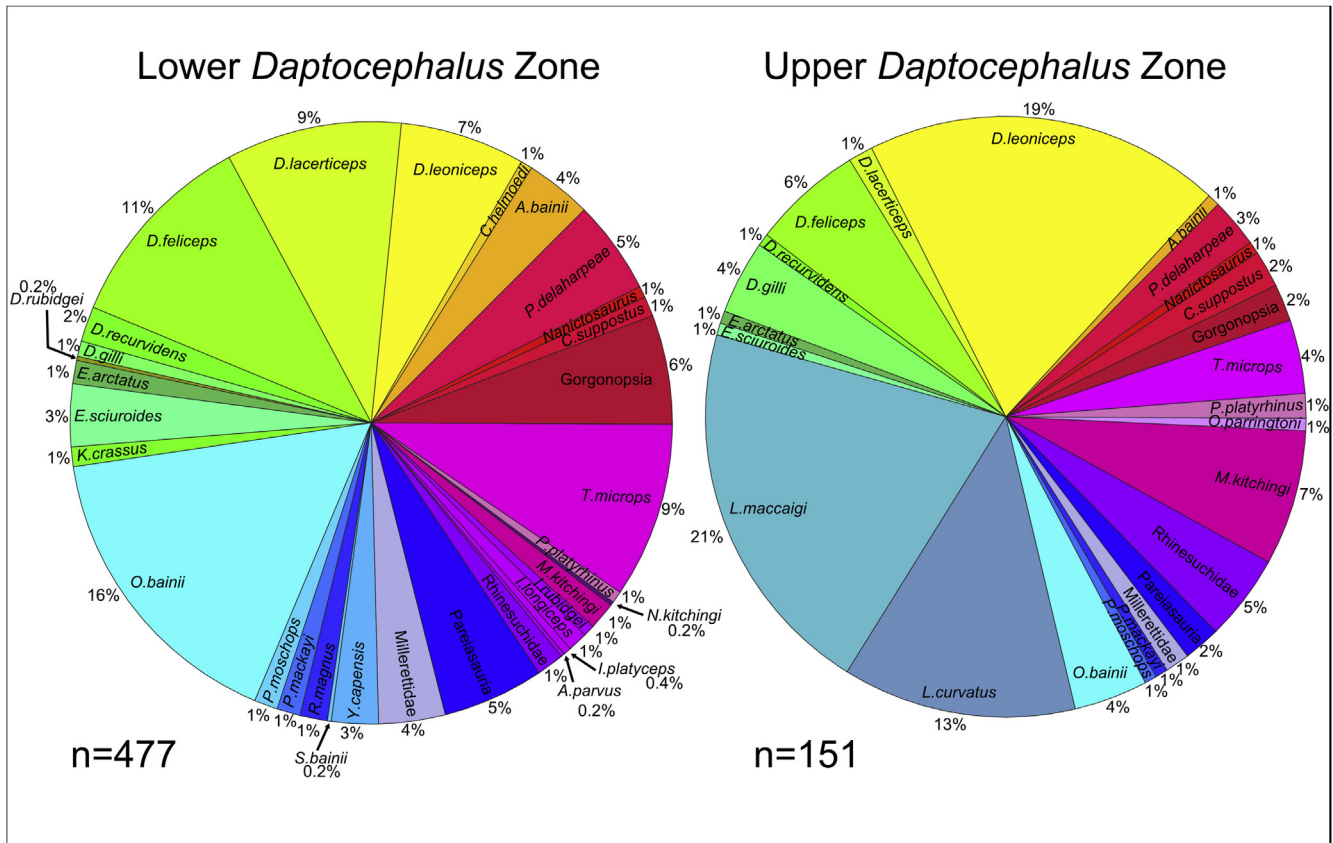


Fig. 4. Pie charts representing percentages of different tetrapod taxa occurring in the lower and upper *Daptocephalus* Assemblage Zone. Note the changes in relative abundance in some species (i.e., *Dicynodon lacerticeps*) and also the number of fossil specimens in the lower (477) and upper (151) *Daptocephalus* Assemblage Zone for this study.

extinctions occur between 45 and 30 m below the PTB (phase 1), 20–0 m below the PTB (phase 2), and 30–45 m above the PTB (phase 3). The ranges of the five potential index taxa were also plotted relative to the local stratigraphy at the four main study areas and compared to positions of the inferred phased extinctions (Fig. 5).

2.4. Rarefaction analysis

An individual rarefaction analysis was conducted to ascertain whether or not the lower species richness of the upper DaAZ in comparison to the lower DaAZ reflects a real decrease in diversity, or a simple sampling bias (see Fig. 4). Rarefaction is a common statistical tool used to assess species richness in modern and ancient communities (Croft, 2013; Erwin, 1990; Guinot, 2013; Irmis et al., 2013; Lindsey and Seymour, 2015; Oreska et al., 2013; Tarailo and Fastovsky, 2012; Vila et al., 2015; Wilson et al., 2014). The analysis uses counts of individuals present in each taxon for two or more samples/localities/faunal horizons. In the present case, faunal horizons (i.e., upper and lower DaAZ) were used, so the analysis asks given the observed numbers of individuals and taxa in each horizon, what would the species richness of the larger sample (lower DaAZ) be if it was represented by the same number of specimens as are available for the smaller sample (upper DaAZ)?

This provides insight into whether the reduced species richness of the upper DaAZ is likely to be real or an artefact of sampling. Specimens and taxa are included for each subzone in the supplementary datasheet. For the data used in the test, only specimens and taxa that definitely were in the lower or upper DaAZ (i.e., only specimens that had lower or upper as their stratigraphic level)

were considered. Indeterminate specimens were not included in the analysis, other than Rhinesuchidae indet. Altogether, 477 specimens in the lower DaAZ and 151 in the upper DaAZ were included. There are a total of 48 taxa in the dataset (45 in the lower DaAZ and 28 in the upper, although there is considerable overlap between the subzones). A rarefaction curve with 95% confidence intervals was plotted for the lower and upper DaAZ datasets for comparison (Fig. 6). The rarefaction analysis was carried out in PAST 2.17c (Hammer et al., 2001), which uses the algorithm of Krebs (1989) for individual rarefaction analyses.

3. Results

3.1. Significance of the revised biostratigraphic ranges

The new stratigraphic ranges of potential index fossils for the DaAZ (*Dicynodon lacerticeps*, *Daptocephalus leoniceps*, *Lystronotus maccaigi*, *Therapsid microlops*, and *Procyonotus delaharpeae*) along with other co-occurring species and higher taxa (*Aulacephalodon bainii*, *Diictodon feliceps*, *Oudenodon bainii*, *Cynosauros suppostus*, *Nanictodops kitchingi*, *Nanictosaurus kitchingi*, *Moschorhinus kitchingi*, *Gorgonopsia*, *Parareptilia*, *Eureptilia*, and *Rhinesuchidae*) are discussed in Table 1. These results are then also compared to the traditional range of the DaAZ (see Figs. 1 and 2) and also with reference to Smith and Botha-Brink's (2014) phased extinctions hypothesis (Fig. 5). Note that for many taxa the metres above lower datum could not be determined due to poor provenance data available from the database.

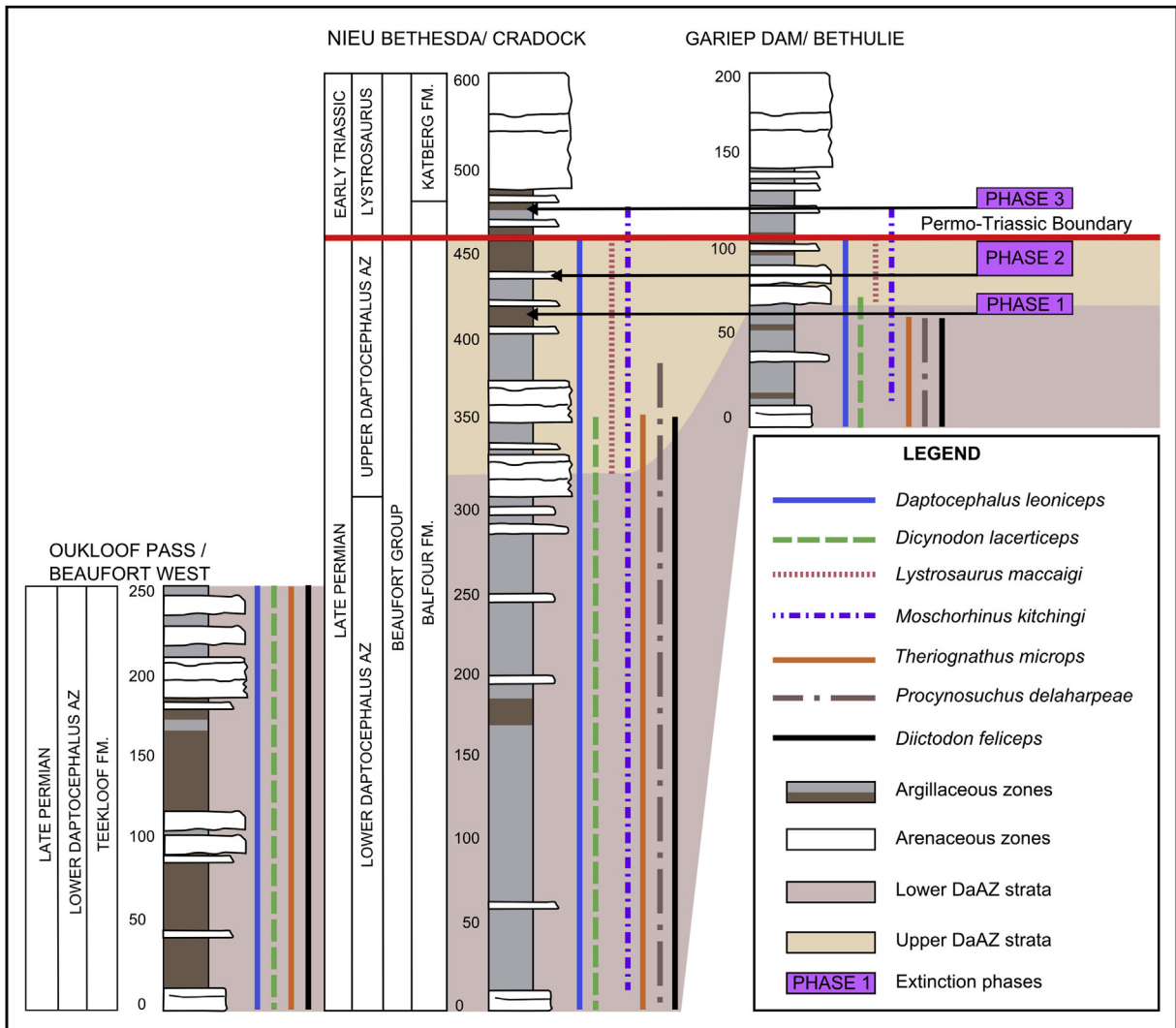


Fig. 5. Composite sections showing the stratigraphic succession exposed near Beaufort West, Nieu Bethesda/Cradock, and Gariep Dam/Bethulie. Fossil specimens from the database were assigned a stratigraphic range using GPS positions or from stratigraphic collecting of fossils from Smith and Botha-Brink (2014), and from the current study. This allowed for a relatively accurate range determinates for *Daptocephalus leoniceps*, *Dicynodon lacerticeps*, *Lystrosaurus maccaigi*, *Moschorhinus kitchingi*, *Theriognathus microps*, *Procynosuchus delaharpeae*, and *Diictodon feliceps*. Strata assigned to lower and upper *Daptocephalus* Assemblage Zone have been highlighted with the current position of Smith and Botha-Brink's (2014) extinction phases on their Bethulie section. Note the attenuation of the stratigraphic units northwards (i.e. towards Gariep Dam/Bethulie) and the LADs of *Di. lacerticeps*, *T. microps*, *P. delaharpeae*, and *D. feliceps*.

3.1.1. *Dicynodontia*

Many of the dicynodont species in the DaAZ have long stratigraphic ranges and therefore were not considered useful as index fossils (see Fig. 2). Nevertheless there were some surprises in this group. Database information shows that *Dicynodon lacerticeps* occurs in the CAZ and is assumed to range throughout the biozone until a reliable FAD is determined (Table 1). Additionally *Di. lacerticeps* does not range through the entire DaAZ because the LAD specimen is from 25 m below the PTB. This means it is only 5 m into the upper DaAZ due to the attenuation of the strata at the site of its collection, which is Bethel Canyon in the Free State Province (see Fig. 5).

The FAD of *Daptocephalus leoniceps* is RC 602, a specimen that was located in the current upper CAZ. Therefore the lower boundary of the DaAZ had to be lowered. Since this specimen had poor stratigraphic data, at this stage the lower boundary is defined by the FAD of a reliably sourced *T. microps* specimen from Ofontein, Graaff-Reinet (See Table 1). *Da. leoniceps* is consistently present throughout the DaAZ and its LAD in the database is a

stratigraphically well-defined specimen from Carlton Heights in the Eastern Cape Province. This specimen was collected 10 m below the PTB, which fits with Smith and Botha-Brink's (2014) observation that *Da. leoniceps* is involved in their phase 2 extinction.

Although not a biozone index fossil, *A. bainii* is a species which is ubiquitous in the CAZ and lower DaAZ, but is essentially absent from the upper DaAZ. The highest specimen with reliable stratigraphic data comes from Bethel Canyon and ~16 m into the upper DaAZ, although in this part of the basin attenuation must be taken into account (See Fig. 5). *Diictodon feliceps* is frequently encountered in the lower biozones, but does not range far into the upper DaAZ (Figs. 2 and 5), particularly in the Nieu Bethesda area. The LAD specimen is only 45 m into the upper DaAZ (~105 m from the PTB). This is 60 m below the beginning of Smith and Botha's (2014) extinction phase 1 (see Fig. 5).

The FAD of *Lystrosaurus maccaigi* marks the beginning of the upper DaAZ. The FAD of *L. maccaigi* was previously documented as ~30 m below the PTB (Botha and Smith, 2007) from specimens collected close to or within the Bethulie section (RS 37, RS 40, RS 41,

Table 1
FAD and LAD specimens for taxa investigated for stratigraphic utility in the *Daptocephalus* Assemblage Zone. Note that for many taxa poor stratigraphic data does not allow for calculation of range in metres above lower datum.

Table 1	FAD specimen	FAD position	LAD specimen	LAD position	Above lower datum (m)	Distance from PTB (m)
Dicynodontia						
<i>Aulacephalodon bainii</i>	PV/GD6	Cistecephalus AZ	RS 52	Upper DaAZ	131	-20
<i>Daptocephalus leoniceps</i>	RC 602	Lower DaAZ	SAM-PK-K10093	Upper DaAZ	Unknown	-10
<i>Dicynodon lacerticeps</i>	CGS WB 222 (CGP/1/479)	Cistecephalus AZ	SAM-PK-K9949	Upper DaAZ	Unknown	-25
<i>Diictodon feliceps</i>	Below DaAZ	<i>Tapinocephalus</i> AZ	RS 94	Upper DaAZ	Unknown	-105
<i>Lystrosaurus curvatus</i>	RS 92	Upper DaAZ	SAM-PK-K11045	<i>Lystrosaurus</i> AZ	64	+25
<i>Lystrosaurus maccaigi</i>	SAM-PK-10920	Upper DaAZ	SAM-PK-K10376	Upper DaAZ	148	-2
<i>Oudenodon bainii</i>	PV/GD5	Cistecephalus AZ	PV/GD19	Upper DaAZ	40	-3
Terocephalia						
<i>Moschorhinus kitchingi</i>	BP/1/2205	Lower DaAZ	SAM-PK-K10698	<i>Lystrosaurus</i> AZ	Unknown	+29
<i>Theriongnathus microps</i>	SAM-PK-10981	Lower DaAZ	SAM-PK-K10505	Upper DaAZ	224	-96
Gorgonopsia						
Gorgonopsia	Below DaAZ	<i>Tapinocephalus</i> AZ	RS 19	Upper DaAZ	Unknown	-27
Cynodontia						
<i>Cynosaurus suppostus</i>	SAM-PK-05211	Cistecephalus AZ	BPI/1/5741	Upper DaAZ	Unknown	Unknown
<i>Nanictosaurus kitchingi</i>	RC 48	Lower DaAZ	TM 279	Upper DaAZ	Unknown	Unknown
<i>Procynosuchus delaharpeae</i>	SAM-PK-10138	<i>Tropidostoma</i> AZ	SAM-PK-K8142	Upper DaAZ	Unknown	-86
Parareptilia						
Parareptilia	SAM-PK-004020	<i>Tropidostoma</i> AZ	RS 12	Upper DaAZ	Unknown	-24
Eureptilia						
<i>Youngina capensis</i>	SAM-PK-K7710	<i>Tropidostoma</i> AZ	SAM-PK-K11289	Lower DaAZ	Unknown	-279
Temnospondyli						
Rhinesuchidae	Below DaAZ	<i>Tapinocephalus</i> AZ	SAM-PK-10506	Upper DaAZ	Unknown	-6

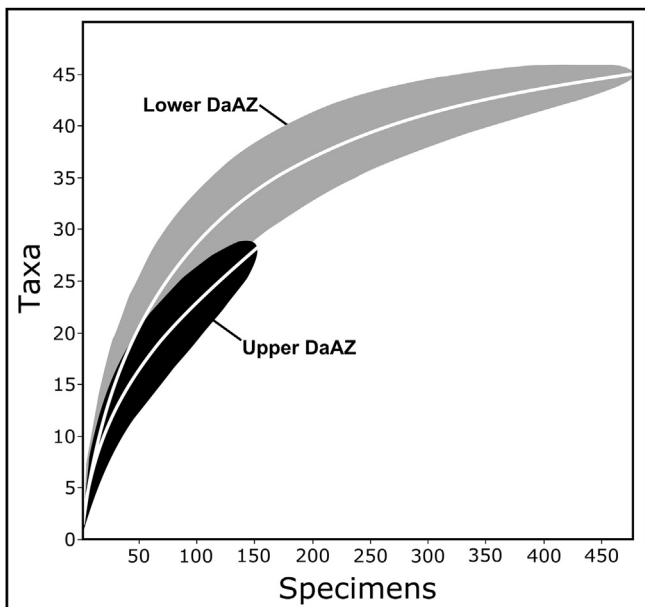


Fig. 6. Individual rarefaction curves, with 95% confidence intervals for the lower and upper *Daptocephalus* Assemblage Zone. See text for more information.

RS 48, RS 49, and SAM-PK-K9958 in database). More recently Botha-Brink et al. (2014) recorded their stratigraphically lowest *L. maccaigi* specimen (NMQR 3706) at 33 m below the PTB on Nooitgedacht 68 farm near the Bethulie section. However the FAD within the Graaff-Reinet area is ~150 m from the PTB (See Table 1). The stratigraphically highest *L. maccaigi* specimen in the current dataset is SAM-PK-K10376 which is recorded as 2 m below the PTB. Similarly Botha-Brink et al.'s. (2014) LAD of *L. maccaigi* is ~1.5 m below the PTB. This study has revealed significant attenuation of the strata in this area so the stratigraphic positions of these specimens may require reinvestigation. *Lystrosaurus curvatus* has been documented previously as occurring between 8 m below and 30 m

above the PTB (Botha and Smith, 2007; Smith and Botha-Brink, 2014), and our study is consistent with this result. At this stage *Lystrosaurus curvatus* is the only *Lystrosaurus* species in the Karoo Basin that is present in both the Permian and Triassic (Botha and Smith, 2007), although *Lystrosaurus maccaigi* is also known from the earliest Triassic strata in Antarctica (Collinson et al., 2006; Cosgriff et al., 1982).

3.1.2. Terocephalia

Theriongnathus microps is currently a DiAZ biozone indicator fossil but this study has identified that it also occurs also in strata currently assigned to the upper CAZ. The FAD specimen is from Ofontein farm, Graaff-Reinet (Table 1) and therefore the base of the new DaAZ is defined by the FAD of *T. microps* in co-occurrence with *Da. leoniceps* (see Figs. 1 and 2). The LAD specimen with reliable stratigraphic data is from 96 m below the PTB. This suggests that *T. microps* goes extinct below the extinction phase 1, which lies between 45 and 30 m below the PTB in the Gariiep Dam/Bethulie area (Smith and Botha-Brink, 2014) (Fig. 5).

Moschorhinus kitchingi has potential to serve as a useful index fossil in association with *Da. leoniceps*. However none of the lower DaAZ specimens have reliable stratigraphic data which means the species distribution through the entire DaAZ cannot be proven at this stage. According to Smith and Botha's (2014) observations, this species' LAD is within their phase 3 extinction event. The only reliable specimen from the Triassic is SAM-PK-K10698 and this specimen was located at ~29 m above the PTB, corroborating this observation.

3.1.3. Gorgonopsia

The Gorgonopsia comprise a large component of the latest Permian faunal assemblages (Smith et al., 2012), but their current taxonomy is highly confused. Therefore we did not attempt to reconstruct their ranges at the genus or species level. Smith and Botha-Brink (2014) recognized that all gorgonopsians go extinct within their extinction phases 1 and 2, but given the unreliability of the available identifications, any attempt to infer the extinction horizon of a particular gorgonopsian species would be speculative

at this time. The LAD gorgonopsian in the database was located from Old Lootsberg Pass near Graaff-Reinet and 27 m below the PTB, therefore corroborating Smith and Botha-Brink's (2014) results (see Table 1).

3.1.4. Cynodontia

Three cynodont species are present in the DaAZ (Fig. 2) but few specimens and little stratigraphic data means their ranges are not well constrained (Table 1). *Procynosuchus delaharpeae* is the only cynodont from the DaAZ to satisfy most of our criteria as there are 33 specimens available in the consulted collections. Huttenlocker et al. (2011) reported the presence of *P. delaharpeae* in the upper CAZ, and this is supported by work conducted by Botha-Brink and Abdala (2008) who described SAM-PK-10138, a single specimen from the *Tropidostoma* Assemblage Zone (TAZ), Beaufort West. Accordingly *P. delaharpeae* is no longer regarded as a useful index fossil for the DaAZ. The LAD specimen was located 86 m below the PTB, below the phased extinction range of Smith and Botha-Brink (2014) (Table 1).

3.1.5. Parareptilia

The majority of the parareptiles are not unique to the DaAZ with many species first appearing as early as the TAZ (*Pareiasuchus peringueyi*, *Pareiasuchus nasicornis*, *Pareiasaurus serridens*, *Anthodon* sp., *Milleretta rubidgei*, *Millerosaurus nuffieldi*) and CAZ (*Nanoparia pricei*, *Owenetta rubidgei*). Only one procolophonoid (*Spondylolestes rubidgei*) and three pareiasaur specimens are known from the upper DaAZ. The uppermost pareiasaur specimen occurs 24 m below the PTB which fits with the extinction of pareiasaurs in Smith and Botha's (2014) extinction phase 2 (Table 1). The specimen is currently identified as *P. serridens* in the database, likely due to its size, but it consists of only a femur. This element is not diagnostic to the species level, so the femur could also represent *P. nasicornis*, *P. peringueyi*, or *Anthodon* sp. The uppermost *Anthodon* sp. in the database is SAM-PK-7841, which is approximately 109 m from the PTB from Zuurplaats farm near Nieu Bethesda in the Eastern Cape. *Nanoparia pricei* has one specimen in the database with a reliable stratigraphic position (SAM-PK-K10498), but this specimen comes from Beaufort West where only the lower DaAZ is known to be present. Therefore the LAD of this species is regarded as the uppermost lower DaAZ until further information can be gathered.

3.1.6. Eureptilia

Youngina capensis is not unique to the DaAZ and has also been found in the *Tropidostoma* and *Cistecephalus* assemblage zones (Smith and Evans, 1996). The apparent LAD of this species in the lower DaAZ is SAM-PK-K11289, a juvenile aggregation in a nodule from 279 m below the PTB (~129 m from upper DaAZ), found at Osfontein farm near Graaff-Reinet in the Eastern Cape.

3.1.7. Temnospondyli

Two species of temnospondyl amphibians (*Rhinesuchus muchos* and *Laccocephalus insperatus*) were known from the DaAZ at the time of the revision of the Karoo biostratigraphy by Rubidge et al. (1995). Subsequent taxonomic revisions (Damiani and Rubidge, 2003; Latimer et al., 2002; Marsicano et al., 2015) have revealed an updated list of DaAZ temnospondyls (including *Laccocephalus watsoni*, *Rhinesuchus capensis*, *Rhinesuchus waitsi*, and *Uranocentron senekalensis*) but the collections database has not yet been updated to reflect these changes. Therefore, the higher taxon Rhinesuchidae was used to represent all late Permian temnospondyls in this study (Fig. 2, Table 1). The uppermost DaAZ specimen from the database is from 6 m below the PTB and was found on Pienaarsbaken farm near Graaff-Reinet (SAM-PK-10506). Smith and Botha-Brink (2014) indicate from their study that *Rhinesuchus*

sp. went extinct in extinction phase 2. Additionally Smith and Botha-Brink (2014) indicate *U. senekalensis* disappears in extinction phase 1, but with only one informally identified *U. senekalensis* specimen in the database (SAM-PK-10574), this is difficult to corroborate in our study. Furthermore, rhinesuchids are not restricted to the DaAZ because the clade is first known in the middle Permian in the Karoo Basin, and one taxon (*Broomistega putterilli*) occurs in the early Triassic LAZ (Shishkin and Rubidge, 2000). Revised identifications of the rhinesuchid specimens in collections will be necessary before we can comment on their ranges and potential roles in the Permo-Triassic extinction phases.

3.2. Lower versus upper Dicynodon Assemblage Zone trophic structure

This investigation using 628 stratigraphically provenanced tetrapod fossil specimens revealed a distinct change in number of fossil specimens found in the lower (477 specimens) and upper (151 specimens) DaAZ (Fig. 4). However, the disparity in numbers of specimens between lower and upper DaAZ does not seem to reflect a fundamental change in community structure leading up to the PTB. This means that the decrease in diversity as a result of the end-Permian mass extinction event was over a very short time interval, which is what has been outlined by previous workers (Smith and Botha-Brink, 2014).

The rarefaction analysis calculated an estimated richness for the lower DaAZ at around 33.8 for 150 specimens, with a 95% confidence interval that spans 29.3–38.3. The upper DaAZ richness is estimated to be 27.9 species with a confidence interval of 27.3–28.5. Although the confidence intervals fail to overlap by a small amount at this sample size, these results still suggest that the upper DaAZ is not significantly less diverse than we would expect if its observed richness was simply an artefact of sampling. The rarefaction curves bear this out as well (see Fig. 6); the upper DaAZ does not level off much and the confidence intervals for the two faunas mostly overlap for nearly all of their ranges. Based on these results, we cannot strongly reject the hypothesis that the lower richness of the upper DaAZ is based on the smaller sample size available for this portion of the assemblage zone. Therefore caution must be taken in how much the apparent lower diversity in upper DaAZ as a whole is interpreted.

4. Discussion

The index fossils whose concurrent ranges are presently used to define the base of the DiAZ, *Dicynodon lacerticeps*, *Theriongnathus microps* and *Procynosuchus delaharpeae* (Rubidge et al., 1995), are considered to be present in strata currently within the CAZ due to their co-occurrence with *Cistecephalus microrhinus* in the Oudeberg Member. In addition *P. delaharpeae* is now confirmed to occur within the TAZ (Botha-Brink and Abdala, 2008). Together, these observations indicate that the current definition of the DiAZ is problematic. Therefore we propose redefining the base of the biozone and assign *Daptocephalus leoniceps* (Kammerer et al., 2011) as the index fossil. Kitching (1977) used *Da. leoniceps* as the index fossil for the original manifestation of the biozone (called the *Daptocephalus* Zone in that paper), which was only renamed *Dicynodon* Assemblage Zone by Keyser and Smith (1979) because of the assumed synonymy of *Daptocephalus* with *Dicynodon* (Cluver and Hotton, 1981). Now that *Daptocephalus* has been resurrected, the original name of this unit should be restored. Furthermore, this taxon ranges well into the proposed DaAZ, unlike *Dicynodon lacerticeps*. We also recognize the subdivision of the DaAZ into lower and upper subzones, with the upper subzone being defined by the FAD of *Lystrosaurus maccaigi*. In this framework the base of the

lower DaAZ would be defined by the FAD of *Daptocephalus leoniceps* and *T. microps* and the base of the upper DaAZ be defined by the FAD of *L. maccaigi*. The LAD of *Da. leoniceps* and *L. maccaigi* (and the boundary of the DaAZ) is within Smith and Botha-Brink's (2014) phase 2 extinction approximately at their stratigraphically defined PTB (Fig. 1).

4.1. Implications for biostratigraphic correlation

Previously, interbasinal biostratigraphic correlations have been made using poorly provenanced specimens and poorly defined taxa. Taxonomic revision often reveals that the best index fossils have limited geographic distributions, which calls into question many previous correlations (e.g., Angielczyk and Kurkin, 2003a; Angielczyk et al., 2014a). Kammerer et al. (2011) indicated that *Dicynodon sensu lato* should no longer be considered a useful correlation tool because even though most of the species previously assigned to this genus are closely related, most of them represent basinal endemics and may vary significantly in their temporal ranges. Therefore even if they are useful index fossils in the Karoo, they are not useful for biostratigraphic correlation beyond this basin. One exception is the dicynodontoid *Euptychognathus bathyrhynchus* (Kammerer et al., 2011), but this species is known from very few specimens and this extreme rarity does not make it an ideal biostratigraphic tool for correlation. Similar faunal compositions have also been described from the Guodikeng Formation in China where the dicynodontoid *Jimusaria sinkianensis* co-occurs with *Lystrosaurus* much like in the upper DaAZ (Cao et al., 2008; Metcalfe et al., 2001). Additionally the Russian Sokolki fauna may be another coeval deposit outside of the Karoo Basin, but again the temporal distribution of Russian dicynodontoids (*Delectosaurus areffeji*, *Peramodon amalitzkii*, and *Vivaxosaurus trautscholdi*) may not be the same as *Dicynodon lacerticeps* or *Daptocephalus leoniceps*. *Lystrosaurus maccaigi* has been described in Antarctica (Cosgriff et al., 1982). However, the only known specimen from Shenk Peak in Antarctica (AMNH FARB 9509) is from the earliest Triassic lower Fremouw Formation (Collinson et al., 2006; Cosgriff et al., 1982), suggesting the taxon may have persisted longer than previously thought.

4.2. Faunal turnovers in the latest Permian Karoo Basin

The base of the DaAZ has been dated close to 255.22 ± 0.16 Ma (Rubidge et al., 2013). Bearing in mind that dates from the Global Stratotype Section at Meishan China define an end-Permian extinction interval of 251.941 ± 0.037 and 251.880 ± 0.031 Ma (60–48 ky) (Burgess et al., 2014), this means the temporal range of the DaAZ encompasses ~3 Ma. This is a significant amount of time for climatic and other environmental changes to occur, and concomitant changes in the populations of terrestrial tetrapods would be an expected outcome. Smith and Botha-Brink's (2014) phased extinctions span a 70 m stratigraphic interval, which they suggested represent about 120,000 y. If this estimate is correct then the most significant faunal and environmental changes appear to have occurred only in the uppermost DaAZ and perhaps just prior to the onset of the global end-Permian mass extinction event.

Recently the first high precision age of 253.48 ± 0.15 Ma (early Changhsingian) has been retrieved from strata close to the inferred PTB in South Africa from zircons in a silicified ash layer on Old Lootsberg Pass (Gastaldo et al., 2015). The authors also report on an apparently Permian dicynodontoid skull preserved in strata defined as earliest Triassic due to its presence in an intraformational conglomerate lag. The authors suggest this is evidence for the PTB and *Daptocephalus-Lystrosaurus* Assemblage Zone boundary being stratigraphically higher than is currently reported by the

disappearance of taxa in the phased extinctions of Smith and Botha-Brink (2014). However, ash layers in the Beaufort Group often show evidence for significant reworking (McKay et al., 2015; Rubidge et al., 2013), and intraformational conglomerates are common in the upper DaAZ strata (Smith, 1995). Therefore the placement of the PTB by Gastaldo et al. (2015) is potentially questionable. Furthermore, the specimen in question is poorly preserved and due to its preservation within a conglomeric lag this is not surprising. This is because these deposits formed by the reworking of floodplain sediments (Smith, 1995; Viglietti et al., 2013; Smith and Botha-Brink, 2014). The specimen's poor preservation means any diagnostic affinity with *Di. lacerticeps*, *Da. leoniceps*, or *L. maccaigi* is speculative. The preserved features of the specimen could also identify the specimen as the two Triassic *Lystrosaurus* species (*Lystrosaurus declivis* and *Lystrosaurus murrayi*), or *Lystrosaurus curvatus* which is known from latest Permian and earliest Triassic strata. Additionally it is now evident that *Lystrosaurus maccaigi* survives the end-Permian mass extinction event in Antarctica (Cosgriff et al., 1982; Collinson et al., 2006) which means there is the possibility that *L. maccaigi* may have survived in the Karoo Basin as well. Consequently these data does not necessitate moving the current position of the PTB at this stage, or the boundary of the *Daptocephalus* and *Lystrosaurus* Assemblage Zones in the main Karoo Basin.

Our study has identified that the stratigraphic placement of Smith and Botha-Brink's (2014) phased extinctions mostly fits with the LADs of taxa in the DaAZ. However the stratigraphic succession in the south (Nieu Bethesda/Cradock sector), is much thicker than in the north (Gariiep Dam/Bethulie sector), indicating great attenuation of the strata north of the Orange River. This is corroborated by the LADs of *Di. lacerticeps*, *T. microps*, *P. delaharpeae*, and *D. feliceps* occurring apparently lower than the extinction phases. This evidence suggests that the placement of the extinction phases may need to be reconsidered in the south where the late Permian lithostratigraphy has not been so greatly affected by attenuation. This does not mean that the time represented by the extinction phases will need to be reconsidered because thinning in the north has likely been due to increased hiatuses.

5. Conclusions

This study updates the stratigraphic ranges of late Permian tetrapod fauna from the Karoo Basin, proposes a new biostratigraphic scheme (*Daptocephalus* Assemblage Zone), and provides the following conclusions.

The current manifestation of the *Dicynodon* Assemblage Zone (DiAZ) is problematic because the three index fossils currently used to define the DiAZ, *Dicynodon lacerticeps*, *Theriongnathus Microps*, and *Procynosuchus delaharpeae*, have FADs below the traditionally recognized lower boundary. Therefore we redefine the assemblage zone by replacing the DiAZ with the *Daptocephalus* Assemblage Zone (DaAZ) where *Daptocephalus leoniceps* is reinstated as the index taxon for the DaAZ in co-occurrence with *T. microps*. We use the FAD of *Da. leoniceps* and *T. microps* to define the base of the DaAZ which incorporates strata previously defined as the uppermost *Cistecephalus* Assemblage Zone. A two-fold lower and upper DaAZ subdivision is also recognized to reflect the appearance of *Lystrosaurus maccaigi* in the upper part of the zone only.

Dicynodon sensu lato has been used in the past to correlate various Karoo-aged basins within the Platbergian land vertebrate faunachron (LVF) yet it is now apparent it is unable to define a time unit finer than the Lopingian. This means *Dicynodon sensu lato* and the other South African dicynodontoids have little biostratigraphic utility outside of the Karoo Basin at this stage because at this time they are not known to be present in other basins, are known from

very few specimens (*Euptychognathus bathyrhynchus*), and vary significantly in their temporal ranges. *Daptocephalus leoniceps* in co-occurrence with *L. maccaigi* may provide correlation with late Permian deposits in China (Guodikeng Formation) and the Sokolki fauna of Russia but further investigation is required. *Lystrosaurus maccaigi* on its own is not a useful correlation tool due to its survival into the early Triassic in Antarctica.

The more precisely determined stratigraphic ranges of all later Permian tetrapods do not reveal a significant change in faunal abundance between the lower and upper DaAZ which implies diversity drops attributed to the end-Permian mass extinction event were rapid and only occurring within the uppermost DaAZ. However the stratigraphic succession in the south (Nieu Bethesda/Cradock sector), is much thicker than in the north (Gariiep Dam/Bethulie sector), indicating great attenuation of the strata north of the Orange River. This is corroborated by the LADs of *Di. lacerticeps*, *T. microps*, *P. delaharpeae*, and *D. feliceps* occurring apparently lower than the extinction phases. Therefore it is further proposed that the position of the extinction phases be reconsidered in the south where the late Permian lithostratigraphy has not been affected by attenuation to fit with the disappearances of, *Di. lacerticeps*, *T. microps*, *P. delaharpeae*, and *D. feliceps* in this interval.

Acknowledgements

This work was made possible by financial support to PAV and BSR from the Palaeontological Scientific Trust (PAST) and its Scaterlings of Africa programmes, as well as the National Research Foundation (NRF) ((AAGR/JUID=826103). The support of the DST/NRF Centre of Excellence in Palaeosciences (CoE in Palaeosciences) towards this research is hereby acknowledged. CFK acknowledges the support of the Deutsche Forschungsgemeinschaft (Eigene Stelle KA 4133/1-1) and he and JF also acknowledge support from the Alexander von Humboldt Foundation (Sofja Kovalevskaja Award to JF). We thank Fernando Abdala, Luke Norton, and Adam Huttenlocker for invaluable discussions on the taxonomy and distribution of late Permian Cynodontia, Gorgonopsia, and Theroccephalia. Fossil finds by Jennifer Botha-Brink, Michael Day, Marc Van Den Brandt, Mike Strong, Derik Wolvaardt, and Ian Woods during fieldtrips contributed information to this study. We are grateful to Patrick Eriksson, Jennifer Botha-Brink, and Christian Sidor for valuable comments on the original manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jafrearsci.2015.10.011>.

References

- Anderson, J.M., Cruickshank, A.R.I., 1978. The biostratigraphy of the Permian and Triassic Part 5. A review of the classification and distribution of the Permian–Triassic tetrapods. *Palaeontol. Afr.* 21, 15–44.
- Angielczyk, K.D., Kurkin, A.A., 2003a. Has the utility of *Dicynodon* for late Permian terrestrial biostratigraphy been overstated? *Geology* 31, 363–366.
- Angielczyk, K.D., Kurkin, A.A., 2003b. Phylogenetic analysis of Russian Permian dicynodonts (Therapsida: Anomodontia): implications for Permian biostratigraphy and Pangaeon biogeography. *Zool. J. Linn. Soc.* 139, 157–212.
- Angielczyk, K.D., Huertas, S., Smith, R.M.H., Tabor, N.J., Sidor, C.A., Steyer, J.-S., Tsuji, L.A., Gostling, N.J., 2014a. New dicynodonts (Therapsida, Anomodontia) and updated tetrapod stratigraphy of the Permian Ruhuhu Formation (Songea Group, Ruhuhu Basin) of southern Tanzania. *J. Vertebr. Paleontol.* 34, 1408–1426.
- Angielczyk, K.D., Steyer, S., Sidor, C.A., Smith, R.M.H., Whatley, R.L., Tolan, S., 2014b. Permian and triassic dicynodont (Therapsida: Anomodontia) faunas of the Luangwa Basin, Zambia: taxonomic update and implications for dicynodont biogeography and biostratigraphy. In: Kammerer, C.F., Angielczyk, K.D., Fröbisch, J. (Eds.), *Early Evolutionary History of the Synapsida*. Springer, Netherlands, pp. 93–138.
- Bender, P., 2001. A new actinopterygian fish species from the late Permian Beaufort Goup, South Africa. *Palaeontol. Afr.* 37, 25–40.
- Benton, M.J., Twitchett, R.J., 2003. How to kill (almost) all life: the end-Permian extinction event. *Trends Ecol. Evol.* 18, 358–365.
- Benton, M.J., Tverdokhlebov, V.P., Surkov, M., 2004. Ecosystem remodelling among vertebrates at the Permian–Triassic boundary in Russia. *Nature* 432, 97–100.
- Benton, M.J., Newell, A.J., 2014. Impacts of global warming on Permian–Triassic terrestrial ecosystems. *Gondwana Res.* 25, 1308–1337.
- Botha-Brink, J., Abdala, F., 2008. A new cynodont record from the *Tropidostoma* Assemblage Zone of the Beaufort Group: implications for the early evolution of cynodonts in South Africa. *Palaeontol. Afr.* 43, 1–6.
- Botha-Brink, J., Huttenlocker, A.K., Modesto, S.P., 2014. Vertebrate paleontology of nooitgedacht 68: a *Lystrosaurus maccaigi*-rich Permian–Triassic boundary locality in South Africa. In: Kammerer, C.F., Angielczyk, K.D., Fröbisch, J. (Eds.), *Early Evolutionary History of the Synapsida*. Springer, Netherlands, pp. 289–304.
- Botha, J., Smith, R.M.H., 2006. Rapid vertebrate recuperation in the Karoo Basin of South Africa following the End-Permian extinction. *J. Afr. Earth Sci.* 45, 502–514.
- Botha, J., Smith, R.M.H., 2007. *Lystrosaurus* species composition across the Permian–Triassic boundary in the Karoo Basin of South Africa. *Lethaia* 40, 125–137.
- Bottjer, D.J., 2012. Life in the early triassic ocean. *Science* 338, 336–337.
- Burgess, S.D., Bowring, S., Shen, S., 2014. High-precision timeline for Earth's most severe extinction. *Proc. Natl. Acad. Sci.* 111, 3316–3321.
- Cadle, A.B., Cairncross, B., Christie, A.D.M., Roberts, D.L., 1993. The Karoo Basin of South Africa: type basin for the coal-bearing deposits of southern Africa. *Int. J. Coal Geol.* 23, 117–157.
- Cairncross, B., 1989. Paleodepositional environments and tectonosedimentary controls of the postglacial Permian coals, Karoo Basin, South Africa. *Int. J. Coal Geol.* 12, 365–380.
- Cao, C., Wang, W., Liu, L., Shen, S., Summons, R.E., 2008. Two episodes of 13 C-depletion in organic carbon in the latest Permian: evidence from the terrestrial sequences in northern Xinjiang, China. *Earth Planet. Sci. Lett.* 270, 251–257.
- Catuneanu, O., Hancox, J.P., Rubidge, B.S., 1998. Reciprocal flexural behaviour and contrasting stratigraphies: a new basin development model for the Karoo retroarc foreland system, South Africa. *Basin Res.* 10, 417–439.
- Catuneanu, O., Wopfner, H., Eriksson, P.G., Cairncross, B., Rubidge, B.S., Smith, R.M.H., Hancox, J.P., 2005. The Karoo basins of south-central Africa. *J. Afr. Earth Sci.* 43, 211–253.
- Cisneros, J.C., Rubidge, B.S., Manson, R., Dube, C., 2008. Analysis of millerettid parareptile relationships in the light of new material of *Broomia perplexa* Watson, 1914, from the Permian of South Africa. *J. Syst. Palaeontol.* 6, 453–462.
- Cluver, M.A., Hotton, N., 1981. The genera *Dicynodon* and *Diictodon* and their bearing on the classification of the Dicynodontia (Reptilia, Therapsida). *Ann. South Afr. Mus.* 83, 99–146.
- Cluver, M.A., King, G.M., 1983. A reassessment of the relationships of Permian Dicynodontia (Reptilia, Therapsida) and a new classification for dicynodonts. *Ann. S. Afr. Mus.* 91, 195–273.
- Cole, D.I., Wipplinger, P., 2001. Sedimentology and Molybdenum Potential of the Beaufort Group in the Main Karoo Basin, South Africa. *Memoir- Geological Survey, Pretoria*.
- Collinson, J.W., Hammer, W.R., Askin, R.A., Elliot, D.H., 2006. Permian-triassic boundary in the central Transantarctic Mountains, Antarctica. *Geol. Soc. Am. Bull.* 118, 747–763.
- Cosgriff, J.W., Hammer, W.R., Ryan, W.J., 1982. The Pangaeon reptile, *Lystrosaurus maccaigi*, in the lower Triassic of Antarctica. *J. Paleontol.* 56, 371–385.
- Croft, D.A., 2013. What constitutes a fossil mammal community in the early Miocene Santa Cruz Formation? *J. Vertebr. Paleontol.* 33, 401–409.
- Damiani, R.J., Rubidge, B.S., 2003. Temnospondyls from the Beaufort Group (Karoo Basin) of South Africa and their biostratigraphy. *Gondwana Res.* 7, 165–173.
- Day, M.O., 2013. Middle Permian Continental Biodiversity Changes as Reflected in the Beaufort Group of South Africa: a Bio- and Lithostratigraphic Review of the *Eodicynodon*, *Tapinocephalus*, and *Pristerognathus* Assemblage Zones. University of the Witwatersrand, p. 394. Ph.D thesis.
- Day, M.O., Ramezani, J., Bowring, S.A., Sadler, P.M., Erwin, D.H., Abdala, F., Rubidge, B.S., 2015. When and how did the terrestrial mid-Permian mass extinction occur? Evidence from the tetrapod record of the Karoo Basin, South Africa. *Proc. R. Soc.* 282, 1–8.
- Erwin, D.H., 1990. The End-Permian mass extinction. *Annu. Rev. Ecol. Syst.* 69–91.
- Erwin, D.H., 2006. *Extinction: How Life on Earth Nearly Ended 250 Million Years Ago*. Princeton University Press, New Jersey.
- Fröbisch, J., 2013. Vertebrate diversity across the End-Permian mass extinction — Separating biological and geological signals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 372, 50–61.
- Gastaldo, R.A., Kamo, S.L., Neveling, J., Geissman, J.W., Bamford, M., Looy, C.V., 2015. Is the vertebrate-defined Permian–Triassic boundary in the Karoo Basin, South Africa, the terrestrial expression of the End-Permian marine event? *Geology* 43 (10), 1–5.
- Gebauer, E.V.L., 2007. Phylogeny and Evolution of the Gorgonopsia with a Special Reference to the Skull and Skeleton of GPIT/RE/7113 (*Aelurognathus parringtoni*). Universität Tübingen, p. 328. Ph.D thesis.
- Gow, C.E., Rubidge, B.S., 1997. The oldest known procolophonid (Amniota: Parareptilis) — new discovery from the lower Beaufort Group of South Africa. *Palaeontol. Afr.* 34, 49–53.
- Groenewald, G.H., 1984. Stratigrafie en Sedimentologie van die Groep Beaufort in die Noordoos Vrystaat. Rand Afrikaans University, p. 250 (Ph.D thesis).

- Guinot, G., 2013. Late Cretaceous elasmobranch palaeoecology in NW Europe. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 388, 23–41.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. Palaeontological statistics software package for education and data analysis. *Palaeontol. Electron.* 4, 1–9.
- Huttenlocker, A.K., Sidor, C.A., Smith, R.M.H., 2011. A new specimen of *Promoschorynchus* (Therapsids: Therocephalia: Akidnognathidae) from the Lower Triassic of South Africa and its implications for theriodont survivorship across the Permo-Triassic boundary. *J. Vertebr. Paleontol.* 31, 405–421.
- Huttenlocker, A.K., 2014. Body size reductions in nonmammalian eutheriodont therapsids (Synapsida) during the End-Permian mass extinction. *PLoS One* 9, e87553.
- Irmis, R.B., Whiteside, J.H., Kammerer, C.F., 2013. Non-biotic controls of observed diversity in the paleontological record: an example from the Permo-Triassic Karoo Basin of South Africa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 372, 62–77.
- Jalil, N.E., Janvier, P., 2005. Les pareiasaures (Amniota, Parareptilia) du Permien supérieur du Bassin d'Argana, Maroc. *Geodiversitas* 27, 35–132.
- Kammerer, C.F., Angielczyk, K.D., Fröbisch, J., 2011. A comprehensive taxonomic revision of *Dicynodon* (Therapsida, Anomodontia) and its implications for dicynodont phylogeny, biogeography, and biostratigraphy. *Society of Vertebrate Paleontology Memoir* 11 31, 1–158.
- Kammerer, C.F., 2015. Cranial osteology of *Arctognathus curvimola*, a short-snouted gorgonopsian from the late Permian of South Africa. *Pap. Palaeontol.* 1, 41–58.
- Keyser, A.W., Smith, R.M.H., 1979. Vertebrate biozonation of the Beaufort Group with special reference to the western Karoo Basin. *Annu. Geol. Surv. S. Afr.* 12, 1–36.
- King, G.M., 1988. Anomodontia, vol. 17C. *Handbuch der Paläoherpetologie*.
- King, G.M., 1992. The palaeobiogeography of Permian anomodonts. *Terra Nova* 4, 633–640.
- Kitching, J.W., 1977. The Distribution of the Karoo Vertebrate Fauna. Bernard Price Institute for Palaeontological Research Memoir 1, pp. 1–131.
- Krebs, C.J., 1989. *Ecological Methodology*. Harper and Row, New York, p. 624.
- Latimer, E.M., Hancox, P.J., Rubidge, B.S., Shishkin, M.A., Kitching, J.W., 2002. The temnospondyl amphibian *Uranocentron*, another victim of the End-Permian extinction event: research letter South African. *J. Sci.* 98, 191–193.
- Lee, M.S.Y., 1997. A taxonomic revision of pareiasaurian reptiles: implications for Permian terrestrial Palaeoecology. *Mod. Geol.* 21, 231–298.
- Lindsey, E.L., Seymour, K.L., 2015. “Tar pits” of the western neotropics: paleoecology, taphonomy, and mammalian biogeography. In: Harris, J.M. (Ed.), *La Brea and Beyond: the Paleontology of Asphalt-preserved Biotas*. Natural History Museum of Los Angeles County. Science Series, 42, pp. 111–123.
- Lucas, S.G., 1997. *Dicynodon* and late Permian Pangaea. In: Wang, N.R.J. (Ed.), *Proceedings of the 30 International Geological Congress*. VSP, Utrecht.
- Lucas, S.G., 1998a. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 143, 347–384.
- Lucas, S.G., 1998b. Toward a tetrapod biochronology of the Permian. *New Mexico Museum of Natural History and Science Bulletin*. 71–92.
- Lucas, S.G., 2001. Chinese Fossil Vertebrates. Columbia University Press, New York.
- Lucas, S.G., 2002. Tetrapods and the subdivision of Permian time. In: Hills, L.V., Henderson, C.M.E.W.B. (Eds.), *Memoir – Canadian Society of Petroleum Geologists*, 19, pp. 479–491.
- Lucas, S.G., 2005. Permian tetrapod faunachrons. In: Lucas, S.G., Zeigler, K.E. (Eds.), *New Mexico Museum of Natural History and Science Bulletin*, 30, pp. 197–201.
- Lucas, S.G., 2006. Global Permian tetrapod biostratigraphy and biochronology. In: Lucas, S.G., Cassinis, G., Schneider, J.W. (Eds.), *Non-Marine Permian Biostratigraphy and Biochronology*, 265. The Geological Society of London, London, pp. 65–93.
- Marsicano, C.A., Latimer, E.M., Rubidge, B.S., Smith, R.M.H., 2015. The Rhinesuchidae and Early History of the Stereospondyli (Amphibia, Temnospondyli) at the End of the Palaeozoic. Unpublished.
- McKay, M.P., Weislogel, A.L., Fildani, A., Brunt, R.L., Hodgson, D.M., Flint, S.S., 2015. U-Pb zircon tuff geochronology from the Karoo Basin, South Africa: implications of zircon recycling on stratigraphic age controls. *Int. Geol. Rev.* 57, 393–410.
- Metcalfe, I., Nicoll, R.S., Mundil, R., Foster, C., Glen, J., Lyons, J., Xiaofeng, W., Chengyuan, W., Renne, P.R., Black, L., 2001. The Permian-Triassic boundary & mass extinction in China. *Episodes* 24, 239–244.
- Newell, A.J., Sennikov, A.G., Benton, M.J., Molostovskaya, I.I., Golubev, V.K., Minikh, A.V., Minikh, M.G., 2010. Disruption of playa-lacustrine depositional systems at the Permo-Triassic boundary: evidence from Vyazniki and Gorkhovets on the Russian Platform. *J. Geol. Soc.* 167, 695–716.
- Norton, L.A., 2012. Relative Growth and Morphological Variation in the Skull of *Aelurognathus* (Therapside: Gorgonopsia). University of the Witwatersrand, p. 185. MSc thesis.
- Oreska, M.P.J., Carrano, M.T., Dzikiewicz, K.M., 2013. Vertebrate paleontology of the Cloverly Formation (Lower Cretaceous), I: faunal composition, biogeographic relationships, and sampling. *J. Vertebr. Paleontol.* 33, 264–292.
- Parrish, J.T., 1993. Climate of the supercontinent Pangea. *J. Geol.* 215–233.
- Roopnarine, P.D., Angielczyk, K.D., Wang, S.C., Hertog, R., 2007. Trophic Network Models Explain Instability of Early Triassic Terrestrial Communities. *Proceedings of the Royal Society Series B*, 274, pp. 2077–2086.
- Rubidge, B.S., Johnson, M.R., Kitching, J.W., Smith, R.M.H., Keyser, A.W., Groenewald, G.H., 1995. Biostratigraphy of the Beaufort group (Karoo supergroup). In: *Biostratigraphic Series 1*, South African Committee for Stratigraphy.
- Rubidge, B.S., 2005. 27th Du Toit Memorial Lecture: re-uniting lost continents – fossil reptiles from the ancient Karoo and their wanderlust. *S. Afr. J. Geol.* 108, 135–172.
- Rubidge, B.S., Erwin, D.H., Ramezani, J., Bowring, S.A., de Klerk, W.J., 2013. High-precision temporal calibration of Late Permian vertebrate biostratigraphy: U-Pb zircon constraints from the Karoo Supergroup, South Africa. *Geology* 10, 1–4.
- Ruta, M., Angielczyk, K.D., Fröbisch, J., Benton, M.J., 2013. Decoupling of morphological disparity and taxic diversity during the adaptive radiation of anomodont therapsids. *Proc. R. Soc. Lond. B Biol. Sci.* 280, 1071–2013.
- Sahney, S., Benton, M.J., 2008. Recovery from the most profound mass extinction of all time. *Proc. R. Soc. Lond. B Biol. Sci.* 275, 759–765.
- Sahney, S., Benton, M.J., Falcon-Lang, H.J., 2010. Rainforest collapse triggered Carboniferous tetrapod diversification in Euramerica. *Geology* 38, 1079–1082.
- Shishkin, M.A., Rubidge, B.S., 2000. A relict rhinesuchid (Amphibia: temnospondyli) from the lower triassic of South Africa. *Palaeontology* 43, 653–670.
- Smith, R.M.H., 1995. Changing fluvial environments across the Permian-Triassic boundary in the Karoo Basin, South Africa and possible causes of tetrapod extinctions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 117, 81–104.
- Smith, R.M.H., Evans, S.E., 1996. New material of *Youngina*: evidence of juvenile aggregation in Permian diapsid reptiles. *Palaeontology* 39, 289–303.
- Smith, R.M.H., Ward, P.D., 2001. Pattern of vertebrate extinctions across an event bed at the Permian-Triassic boundary in the Karoo Basin of South Africa. *Geology* 29, 1147–1150.
- Smith, R.M.H., Botha, J., 2005. The recovery of terrestrial vertebrate diversity in the South African Karoo Basin after the End-Permian extinction. *Comptes Rendus Palevol* 4, 623–636.
- Smith, R.M.H., Rubidge, B.S., Van der Walt, M., 2012. Therapsid biodiversity patterns and Palaeoenvironments of the Karoo Basin, South Africa. In: Chinsamy-Turan, A. (Ed.), *Forerunners of Mammals*. Indiana University Press, Bloomington, pp. 31–62.
- Smith, R.M.H., Botha-Brink, J., 2014. Anatomy of a mass extinction: sedimentological and taphonomic evidence for drought-induced die-offs at the Permo-Triassic boundary in the main Karoo Basin, South Africa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 396, 99–118.
- Stampfli, G.M., Hochard, C., Vèrard, C., Wilhem, C., 2013. The formation of Pangea. *Tectonophysics* 593, 1–19.
- Sun, Y., Joachimski, M.M., Wignall, P.B., Yan, C., Chen, Y., Jiang, H., Wang, L., Lai, X., 2012. Lethally hot temperatures during the early triassic greenhouse. *Science* 338, 366–370.
- Tarailo, D.A., Fastovsky, D.E., 2012. Post-Permo-Triassic terrestrial vertebrate recovery: southwestern United States. *Paleobiology* 38, 644–663.
- van der Walt, M., Day, M.O., Rubidge, B.S., Cooper, A.K., Netterberg, I., 2011. A new GIS-based biozone map of the Beaufort Group (Karoo Supergroup), South Africa. *Palaeontol. Afr.* 45, 1–5.
- Viglietti, P.A., Smith, R.M.H., Compton, J., 2013. Origin and palaeoenvironmental significance of *Lystrosaurus* bonebeds in the earliest Triassic Karoo Basin, South Africa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 392, 9–21.
- Vila, B., Sellés, A.G., Brusatte, S.L., 2015. Diversity and Faunal Changes in the Latest Cretaceous Dinosaur Communities of Southwestern Europe. *Cretaceous Research*. <http://dx.doi.org/10.1016/j.cretres.2015.07.003>.
- Ward, P.D., Botha, J., Buick, R., de Kock, M.O., Erwin, D.O., Garrison, G.H., Kirschwick, J.L., Smith, R.M.H., 2005. Abrupt and gradual extinctions among Late Permian land vertebrates in the Karoo Basin, South Africa. *Science* 309, 709–714.
- Wignall, P.B., Twitchett, R.J., 1996. Oceanic anoxia and the End Permian mass extinction. *Science* 272, 1155–1158.
- Wilson, G.P., DeMar, D.G., Carter, G., 2014. Extinction and survival of salamander and salamander-like amphibians across the Cretaceous-Paleogene boundary in northeastern Montana, USA. *Geol. Soc. Am. Spec. Pap.* 503, 271–297.