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

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ABSTRACT

The *Dicynodon* Assemblage Zone (DiAZ) 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*, *Theriognathus microps*, and *Procynosuchus 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.

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

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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*, *Pristerognathus*, *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), *Theriognathus 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 Hoedemakeran (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). *Theriognathus microps* is also known to be present in the upper CAZ (Huttenlocker, 2014) and *P. delaharpeae* has an even earlier FAD in the Hoedemakeran 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*