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

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The fluvio-lacustrine rocks of the Beaufort Group, South Africa have long been known for their tetrapod fossil record, which is the richest and most complete Middle Permian to Middle Triassic record for any terrestrial sequence in the world. The abundance of fossil material has enabled the Beaufort Group to be biostratigraphically subdivided into between 8 and 10 tetrapod assemblage zones, of which the lowest three (*Eodicynodon*, *Tapinocephalus* and *Pristerognathus*) are attributed to the Middle Permian. These lower assemblage zones record the earliest therapsid-dominated faunas and, because they were recorded during a largely uninterrupted period of deposition, make the Beaufort Group the only place in the world where biodiversity change through the terrestrial Middle Permian can be effectively studied.

In the last two decades, much interest has focused on an extinction of marine invertebrates at or close to the end of the Middle Permian (Guadalupian epoch), but the existence of a concurrent extinction in the terrestrial realm is contentious. The Beaufort Group is already well known to record the Permo-Triassic Mass Extinction but it also records an earlier extinction at the top of the *Tapinocephalus* Assemblage Zone (AZ). This extinction is very poorly understood but recent radiometric dates for many Permian assemblage zones of the Beaufort Group have confirmed a Middle Permian age for *Eodicynodon*, *Tapinocephalus* and *Pristerognathus* assemblage zones and

suggest that the end-*Tapinocephalus* AZ extinction may coincide with the marine extinctions.

A recently produced GIS database that accommodates all Beaufort Group fossil material curated in South Africa formed the basis on which the stratigraphic range of individual specimens was calculated. To put the fossil localities in a stratigraphic context, lithostratigraphic information was retrieved from the literature and extensive fieldwork was conducted, which measured stratigraphic sections in key areas and traced the surface outcrop of lithostratigraphic units. In order to compensate for lateral variations in lithostratigraphy, the basin was split into sectors, each represented by a stratigraphic section. The stratigraphic ranges of fossil specimens and, subsequently, of genera and families could then be calculated and a workable biostratigraphic subdivision of the Middle Permian Beaufort Group proposed.

The Abrahamskraal Formation, which forms the majority of the Middle Permian Beaufort sequence, can be divided into six lithostratigraphic members based on the occurrence of sandstone 'packages'. These members were traced laterally across the Basin and their correspondence with fining-upwards cycles was refined and correlated with the newly defined biostratigraphic units. This refined two-pronged stratigraphic subdivision allowed the recognition of a waning period of subsidence in the proximal sector of the Karoo Basin during the Middle Permian.

Stratigraphic ranges of individual genera were found to be far more heterogeneous than previously recognised. Dicynodont genera are useful biostratigraphic indicators due to their relative abundance and well-defined stratigraphic ranges, while dinocephalians and pareiasaurs are clustered in the upper part of the Abrahamskraal Formation. The stratigraphic range of *Eodicynodon* extends further up in the Abrahamskraal Formation than was previously recognised. The *Tapinocephalus* AZ is restricted to approximately the upper fifth of the Abrahamskraal Formation and is characterised by advanced tapinocephalid dinocephalians and the pareiasaur *Bradysaurus*. Between these two biozones is a stratigraphic interval dubbed the mid-Abrahamskraal Formation Transition Zone, where both *Eodicynodon* and advanced tapinocephalids coexisted.

A 75 % loss of generic diversity occurred between the upper *Tapinocephalus* AZ and the base of the *Pristerognathus* AZ, which corresponds to a stratigraphic interval between the mid-Karelskraal Member of the Abrahamskraal Formation and the mid-Poortjie Member of the Teekloof Formation. Several taxa that survive the end-*Tapinocephalus* AZ extinction, and are relatively common in the overlying *Pristerognathus* AZ (scylacosaurid therocephalians, the dicynodont genus *Eosimops* and the parareptile *Eunotosaurus*), all became extinct in the upper Poortjie Member at a time when generic originations are increasing. This suggests a second wave of extinctions in a similar fashion to that recorded at the Permo-Triassic boundary.