Historical Review

Charting the fossils of the Great Karoo: a history of tetrapod biostratigraphy in the Lower Beaufort Group, South Africa

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The interest in the fossil remains of the Beaufort Group and their stratigraphic significance goes back as far as the earliest geological studies in South Africa in the early 19th century. By the 1890s, the understanding of fossil distributions in the sedimentary rocks of the Karoo allowed the formulation of the first tetrapod biostratigraphic subdivisions. Since the beginning of the 20th century, the highest resolution subdivisions of the mostly undifferentiated fluvial sediments of the Beaufort Group have been biostratigraphic. More recent biostratigraphic studies in the Lower Beaufort Group have been crucial in understanding terrestrial ecological change in the Middle and Late Permian, and continue to be a leading area of research in South Africa palaeontology.

Keywords: Beaufort, biostratigraphy, history, Karoo.

INTRODUCTION

When Andrew Geddes Bain first comprehensively described the rock sequences of the southern Cape Colony, he used the presence of fossil reptiles as a defining character for the younger division of sedimentary rocks, which he named the 'Karoo or Reptiliferous Series' (Bain 1856). The fossil content of these rocks was soon recognized by subsequent geologists to vary between different strata. At first this was limited to simply the relative abundance of various fossils (Wyley 1859) but, as early as 1867, Ralph Tate and Thomas Rupert Jones produced a descriptive list of fossil forms attributed to the 'Beaufort Beds' and the overlying 'Stormberg Beds' (Tate 1867). Initially, invertebrate and plant fossils appear to have been of equal or greater interest than those of vertebrates; however, by the 1870s, when Richard Owen published his extensive description of the fossil reptiles from South Africa (Owen 1876), vertebrate fossils became sufficiently understood and sufficiently numerous to become useful stratigraphic tools.

EARLY TETRAPOD BIOSTRATIGRAPHY OF THE BEAUFORT GROUP

The first vertebrate palaeontologist to officially propose a stratigraphic division of faunas from what would become the Karoo Supergroup was Seeley (1892). Seeley divided the fossiliferous rocks of South Africa into five 'zones', the middle three of which are included in what now the Beaufort Group:

5. Zone of zanclodonts
4. Zone of highly specialized theriodonts
3. Zone of dicynodonts
2. Zone of pareiasaurians
1. Mesosaurian zone

The second zone was that of pareiasaurians, which he recorded to 'extend from south of Fraserburg Road Station [now Leeu-Gamka] to the foot of the Nieuwveldt [*sic*] Mountains, covering a breadth of about 50 miles of country, without evidence of a physical break at the bottom of the series' (Seeley 1892: 312). Such a description corresponds to the northern part of the Great Karoo region of the Western Cape Province, to the west of Beaufort West. As well as through his own collecting, the distribution of Seeley's 'zone of pareiasaurians' was influenced by the geological map drawn by Dunn (1887), whereby it corresponded to the lower part of Dunn's 'Upper Karoo Beds'.

This biostratigraphic organization of fossil occurrences was subsequently used by palaeontologists and geologists to supplement the lithostratigraphy. Rogers (1903) and Rogers & Schwartz (1903) grouped the middle three zones (i.e. pareiasaurians, dicynodonts and highly specialized theriodonts) into a division they called the 'Beaufort Series', also based upon Dunn's 'Upper Karoo Beds' (Dunn 1887). Du Toit (1905) further recognized that within these three zones, the upper 'zone of specialized theriodonts' corresponded to a lithologically distinct interval of red beds he called the 'Burghersdorps [*sic*] Beds'. This tripartite biostratigraphic division of the Beaufort Series was thus adopted by the two landmark textbooks on South African geology that were published that year (Hatch & Corstorphine 1905; Rogers 1905).

Shortly thereafter, a new subdivision of the Beaufort Series was introduced by Broom (1906a,b) that was based on his extensive collecting efforts in the Karoo. This proved innovative and still forms the basis of the biostratigraphic system used today. In Broom's view, there were six biozones in the Beaufort Series, which could be grouped into three broader divisions:

Upper Beaufort Beds
6. *Cynognathus* Beds
5. *Procolophon* Beds

Middle Beaufort Beds
4. *Lystrosaurus* Beds

Lower Beaufort Beds
3. *Kistecephalus* Beds
2. *Endothiodon* Beds
1. *Pareiasaurus* Beds

The youngest division, the 'Upper Beaufort Beds', were likely equivalent to the 'Burghersdorp Beds' of du Toit (1905). Below this the 'zone of dicynodonts' had been broken down into the '*Lystrosaurus* Beds', which comprised the middle subdivision, and the *Endothiodon* and *Kistecephalus* [*sic*] beds, which followed the '*Pareiasaurus* Beds' in the Lower Beaufort. The '*Pareiasaurus* Beds' themselves, however, were essentially unchanged from the designation of Seeley (1892).

Until this point, the lithostratigraphic subdivision of the Beaufort Series below the 'Burghersdorp Beds' of du Toit (1905) had been hampered by the homogeneity of the fluvial strata. Broom's fossil zones therefore became the predominant method of subdividing the Lower Beaufort strata, and as such were readily adopted in the second edition of Rogers' book on the geology of the Cape Colony (Rogers & du Toit 1909). Little alteration was made to Broom's scheme until the 1970s, but several important works appeared in the intervening years. The first came when D.M.S. Watson, who had visited the Karoo and found Broom's (1906a,b) biozone designations to be correct but inadequate in detail, published a thorough description of each division (Watson 1914a). In this he clarified the definition of the 'zones' (reverting to Seeley's terminology) through the suite of reptiles found in each, as well as the geographical extent of the exposures and the personalities involved in collecting each level. Watson's (1914a: 203) account of the '*Pareiasaurus* Zone' was remarkably accurate, stating that it contained:

> *…several species of pareiasaurs,…*[*which*] *have only a few small scutes round the neural spines of the dorsal region. Less common are the remains of Deinocephalia* [sic], *both Tapinocephaloids and Titanosuchia and many diverse forms of Therocephalia. Dicynodons* [sic] *occur in considerable numbers, but no large forms of Anomodont have ever been found, and the beds have been so thoroughly searched that their absence or excessive rarity is assured.*

Watson (1914a: 203) also mentioned the exposure of the *Pareiasaurus* zone in the 'great expanse of rolling country, the Gouph', to the south of Beaufort West and below the level of the town, which he describes as being situated on the *Endothiodon* zone. Furthermore, Watson was the first to depict the extent of the biozones on a map, which indicates that he was aware that the *Pareiasaurus* zone curled round the Nuweveld Mountains towards Victoria West (Fig. 1).

Another of the bountiful observations made by Watson concerned the validity of the name '*Pareiasaurus* zone'. He noticed that, while the presence of the type locality of *Pareiasaurus* at Blinkwater in the Eastern Cape Province would suggest the presence there of the eponymous zone, 'specimens in the British Museum which I have strong reasons for believing to belong to that type-specimen are of a type which would now be called *Propappus*, a typical *Cisticephalus* [*sic*] zone form' (Watson 1914a: 207). The observation that the most armoured species of pareiasaur, such as the type specimen of *Pareiasaurus*, were found only in the *Cistecephalus* zone therefore posed a problem. This was quickly developed and, after re-examining the British Museum's pareiasaur material, Watson (1914b) decided that the name '*Pareiasaurus* zone' was misleading, as that genus was indeed a '*Cistecephalus* zone' form; in any case, pareiasaurs were known from both zones. He therefore proposed the name '*Tapinocephalus* zone', as this genus was one of the more common variants of the Dinocephalia, which were unique to this stratigraphic interval.

Broom (1915), in an article detailing the type specimens acquired by the American Museum of Natural History from him, soon followed Watson's example and produced a map of his biozones. He did not, however, heed the recommendations of Watson (1914b) and continued to use the name '*Pareiasaurus* zone'. Perhaps more pertinent is that Broom considered the ornamented pareiasaur *Propappus* to occur in the '*Endothiodon* zone', which Watson (1914a), on the contrary, believed to be devoid of pareiasaurs. Broom (1915: 107) continued to describe two patterns of fossil distribution within the existing biozones: the first of these was within the '*Endothiodon* zone', where he stated that 'small species of *Dicynodon* are numerous and large anomodonts called *Endothiodon* are common in the lower part of the zone'; the second was within the '*Cistecephalus* zone', where he simply recorded that 'the lower beds are characterized by the presence of a peculiar small anomodont [*sic*] *Cistecephalus*.' Despite the seemingly restricted ranges for his original indicator taxa, he felt no need to rename his biozones. Broom (1915) also provided thicknesses for each biozone but these are, in several cases, quite unspecific and in the case of the upper zones appear to be gross overestimations. For the '*Pareiasaurus* zone' he gives a thickness of around 1000 feet and for the '*Endothiodon* zone' a thickness of around 1500 to 2000 feet.

In a slightly later review of the Karoo, Von Huene (1925) was the first author to adopt Watson's (1914b) redesignation of the '*Tapinocephalus* zone'. Other than this there was little deviation from the existing scheme, although he does provide another map. Thereafter, little work was undertaken until 1942, when Watson (1942) wrote a summary of Permian and Triassic tetrapods. While retaining the existing biozones, he recognized several patterns regarding the distribution of fossil taxa within them and proposed subdivisions thereof. About half of these built upon the brief observations of Broom (1915). Firstly, Watson regarded the *Endothiodon* zone as being distinguishable into an A and B zone, with the A zone conforming to the usual definition in containing abundant large endothiodonts

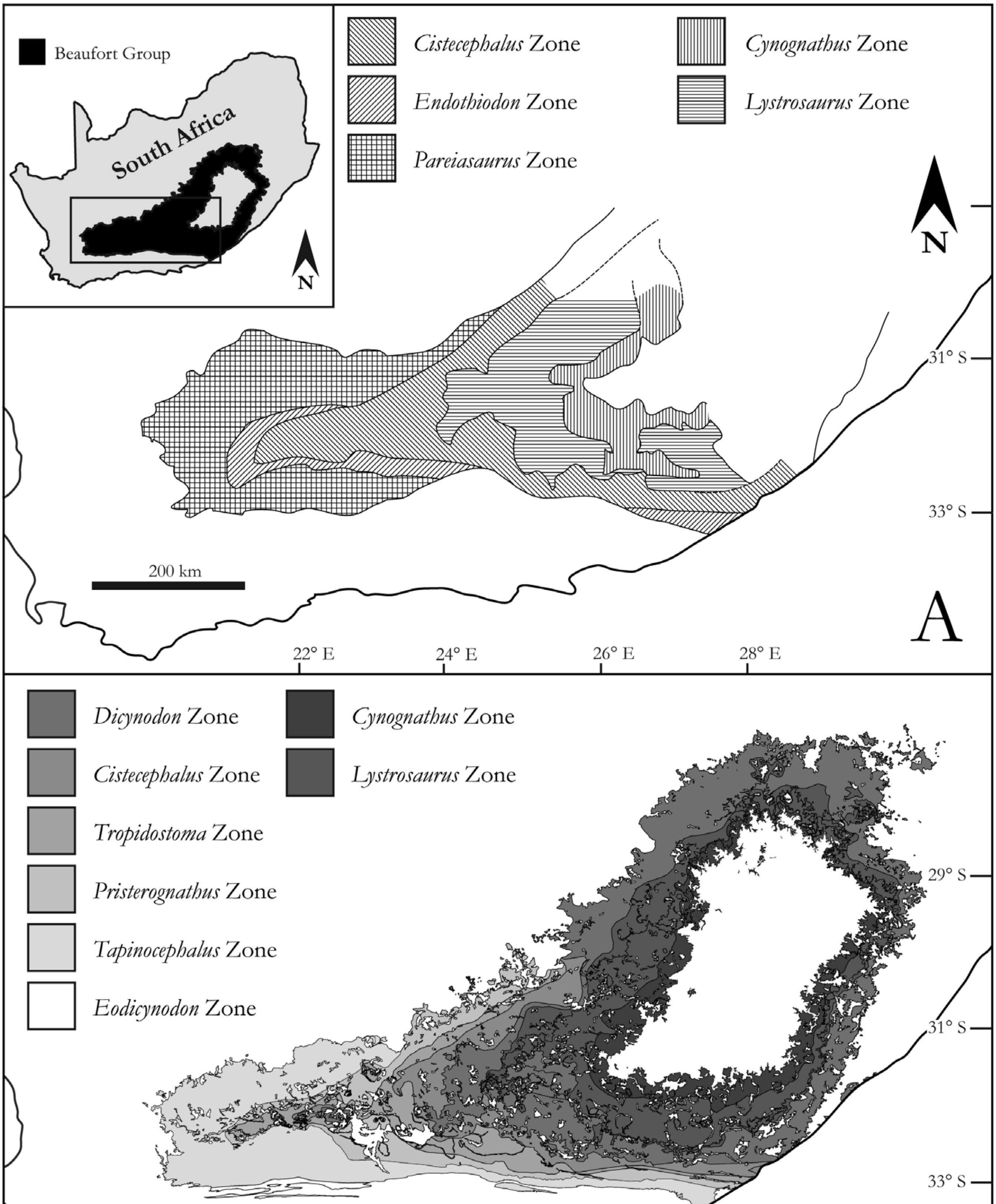

Figure 1. Changes in the perceived distribution of Beaufort Group tetrapod biozones. **A,** The first Beaufort Group biozone map produced by Watson (1914a) showing the distribution of Broom's (1906a,b) biozones. This was produced shortly before Watson (1914b) suggested the name '*Tapinocephalus* Zone' in lieu of '*Pareiasaurus* Zone'. **B**, The most recent Beaufort Group biozone map, taken from Van der Walt *et al.* (2010). Several biozones have been added throughout the 20th century but most of the older biozones are still used.

and only small toothless dicynodonts. The B zone in his view 'probably contain[s] only small endothiodonts of different genera and yield[s] also Dicynodons of medium size' (Watson 1942: 111). He also found a similar pattern in the *Cistecephalus* zone, describing a lower A zone that contained *Cistecephalus* itself and a B zone which was dominated by 'large Dicynodons … and advanced Gorgonopsids.' He even postulated the existence of a C zone containing diverse therocephalians, but did not include this on his diagram (Watson 1942: 115). The '*Tapinocephalus* zone' again remained unchanged, with the apparent disappearance in pareiasaurs and dinocephalians apparently providing a very natural boundary.

EARLY SUBDIVISION OF THE *TAPINOCEPHALUS* ZONE

The first observed differences in the ranges of fossil tetrapod taxa within the '*Tapinocephalus* Zone' were only made a decade later, during the production of a geological map of the Merweville area (Rossouw & de Villiers 1953). This map covered the area cited by all previous authors as the primary outcrop area for the *Tapinocephalus* Zone and Rossouw & de Villiers made extensive lists of the fossil specimens found in the region. They then used their understanding of the regional stratigraphy and the distribution of fossil taxa therein, supported by the presence of 'chert' bands, to suggest a three-fold biostratigraphic subdivision of the Lower Beaufort rocks around Merweville.

The lower zone was situated below and immediately above what they termed the 'Droëfontein 'chert'', while the upper zone surrounded the 'Green 'chert' and Poortjie sandstone' (Rossouw & de Villiers 1953: 59). Between these two they loosely designated an intermediate zone. It is astonishing that, from the relative abundance of fossil taxa within each of these zones, these authors then drew several enduring conclusions about faunal change through the *Tapinocephalus* Zone. Firstly, they describe a decrease in pareiasaurs up to the vicinity of the green 'chert' and Poortjie sandstone, as well as a similar if less dramatic decrease in dinocephalians. They also record a 'phenomenal' increase in dicynodont abundance from the lower to upper zones. Rossouw & de Villiers' (1953) zonation, with a brief description based on their original numbers, is as follows:

3. Zone of the green 'chert' and Poortjie sandstone
   Dicynodonts dominant and pareiasaurs rare.
2. Intermediate zone
   Dicynodonts and dinocephalians dominant and subequal in abundance, pareiasaurs half as common.
1. Zone of the Droëfontein 'chert'
   Pareiasaurs and dinocephalians dominant and subequal in abundance, dicynodonts moderately abundant.

Such a division was expanded, if not directly acknowledged, by Boonstra (1969), who had worked on the *Tapinocephalus* Zone since the late 1920s. Boonstra did not question the name of the zone itself but he did record in this publication some opinions on its integrity. Like Rossouw & de Villiers (1953), Boonstra determined there to be three subdivisions within the *Tapinocephalus* Zone but did not make mention of lithological constraints. In Boonstra's breakdown, the lower division contained the greatest abundance of dinocephalians, pareiasaurs, endothiodont dicynodonts and pristerognathid therocephalians. All these taxa decreased distinctly in abundance into his middle division, with only dicynodonts becoming more common. In contrast to Rossouw & de Villiers (1953), Boonstra (1969) considered pristerognathid therocephalians to decline in abundance into the middle division.

Most radically, Boonstra's upper division is characterized by the disappearance of most families and the severely reduced abundance of those that remained. The only groups he records within this division are dicynodonts, hipposaurids, galesuchids, pristerognathid therocephalians and the parareptile *Eunotosaurus*, representing a 63% loss of families. Boonstra's work therefore provided the first comprehensive account of the loss of dinocephalian therapsids at the family level.

LOWER BEAUFORT GROUP BIOSTRATIGRAPHY AFTER 1970

After collecting throughout the Beaufort Group for 25 years, Kitching (1970) became the first palaeontologist to challenge the Broomian paradigm. The biozone nomenclature was in the most part retained but the extent of several zones was modified and both the *Endothiodon* and *Procolophon* zones were discarded. The former became absorbed into the '*Cistecephalus* zone' on the basis that, despite the thickness of 1500 to 2000 feet suggested for the zone by Broom (1915), the appearance of *Cistecephalus* occurred only a couple of hundred feet above the '*Endothiodon* beds' at Beaufort West; in addition, the two genera were known to occur in close association in several places.

Above this, the upper boundary of the '*Cistecephalus* zone' was lowered to a level just above the horizon in which this genus reached its maximum abundance, and above which no specimens of it had been found. This understanding that *Cistecephalus* was rare or absent in the upper portion of its eponymous biozone had, of course, been made three decades earlier by Watson (1942). However, while Watson was conservative, Kitching (1970: 310) proposed the name *Daptocephalus* or *Whaitsia* zone for the vacant space between the *Cistecephalus* acme horizon and the base of the *Lystrosaurus* zone, reasoning that within this interval '[*Daptocephalus*] is fairly evenly distributed and completely confined to these beds.'

Kitching referred matters of the *Tapinocephalus* zone to Boonstra (1969) and did not implement any further subdivision of that biozone. In terms of its geographic distribution, Kitching (1970) now confined the *Tapinocephalus* zone to the very southwest of the basin, not considering it to extend any further north than Fraserburg. He therefore situated Victoria West well within his *Cistecephalus* Zone, contrary to the earlier work of Watson (1914a). Kitching's (1970) subdivision of the Lower Beaufort was as follows:

5. *Cynognathus* zone
4. *Lystrosaurus* zone

3. *Daptocephalus/Whaitsia* zone
2. *Cistecephalus* zone
1. *Tapinocephalus* zone

Kitching (1972, 1977) described these zones in further detail, and included extensive lists of all the fossil localities he had collected. Each also included a map of these localities which were represented symbolically by biozone.

Soon after Kitching's (1977) publication, Keyser & Smith (1977) published another biostratigraphic subdivision of the Beaufort Group, which for the first time was closely integrated with their proposed lithostratigraphic units. This was primarily aimed at the southwest of the Karoo basin but earlier mapping in the east by Keyser (1973) had already revealed a link between the lowest appearance of *Cistecephalus* and a unit called the Oudeberg sandstone in the region of Graaff-Reinet. In the Lower Beaufort, this scheme differed from that of Kitching (1977) in several important areas, especially in nomenclature. The '*Daptocephalus* Zone', while maintaining its integrity, was renamed the *Dicynodon* Assemblage Zone (AZ) because the former genus was in the process of being synonymized with the latter (Cluver & Hotton 1981). The name '*Cistecephalus* Zone' was discarded due to its confusing history of use, as well as its uneven occurrence; instead, Keyser & Smith (1977) considered *Aulacephalodon baini* to be a far superior index fossil and so adopted the name without much change in the stratigraphic extent of the biozone.

They also resurrected the former '*Endothiodon* zone' but dropped that genus as an index fossil in favour of the dicynodont *Tropidostoma*; this was justified on the basis that *Endothiodon* was relatively rare and its stratigraphic range was not exclusive of other index taxa. Conversely, *Tropidostoma* had a short range and was restricted to this new biozone. They also supported this designation with lithological characteristics.

Keyser & Smith (1977) also formally subdivided the *Tapinocephalus* AZ for the first time, based partly on the work of Rossouw & de Villiers (1953) and of Boonstra (1969). The upper division of Boonstra (1969) was now considered separate and renamed the *Pristerognathus/Diictodon* Assemblage Zone, defined by the abundance of these genera there in the absence of dinocephalians.

Keyser & Smith (1977: 17) noted that, while a disparity between the lower and middle divisions of the *Tapinocephalus* AZ may be genuine, 'these subdivisions were not created as a workable biostratigraphy … [and so] it is proposed that the lower and middle divisions of the *Tapinocephalus* Zone be grouped to form the Dinocephalian Assemblage Zone, based on the total stratigraphic range of the dinocephalian group of mammal-like reptiles.' When considering the abundance of fossil taxa through the Dinocephalian Assemblage Zone, Keyser & Smith (1977: 18) only acknowledged some change for *Embrithosaurus,* which was noticed to become less abundant in its upper division. Keyser & Smith's (1977) biozone designations for the Beaufort Group were as follows:

7. *Kannemeyeria* Assemblage Zone
6. *Lystrosaurus* Assemblage Zone
5. *Dicynodon lacerticeps* Assemblage Zone
4. *Aulacephalodon baini* Assemblage Zone
3. *Tropidostoma microtrema* Assemblage Zone
2. *Pristerognathus/Diictodon* Assemblage Zone
1. Dinocephalian Assemblage Zone

SACS (1980) largely accepted this scheme but adopted the modifications of Keyser (1979) in using two genera to define each zone. This alteration was made in order to conform to the International Subcommission on Stratigraphic Classification (ISSC 1976) regulations on biostratigraphic nomenclature. The Dinocephalian Zone remained unchanged as it had a family-based definition and thus the biozonation of the Beaufort Group became:

7. *Kannemeyeria-Diademodon* Assemblage Zone
6. *Lystrosaurus-Thrinaxodon* Assemblage Zone
5. *Dicynodon lacerticeps-Whaitsia* Assemblage Zone
4. *Aulacephalodon-Cistecephalus* Assemblage Zone
3. *Tropidostoma-Endothiodon* Assemblage Zone
2. *Pristerognathus-Diictodon* Assemblage Zone
1. Dinocephalian Assemblage Zone

Working on the lower contact of the Beaufort Group in the southwest Karoo basin, Rubidge (1984, 1987, 1988) and Rubidge *et al.* (1983) then extended the Beaufort Group down to encompass strata that had previously been assigned to the marine Ecca Group, to a stratigraphic horizon that they identified as the palaeoshoreline. It was in these rocks, now part of Beaufort Group, that fossils of the basal dicynodont *Eodicynodon* had first been recovered (Barry 1970, 1974). Rubidge therefore recognized an entirely new biozone comprising a therapsid fauna dominated by *Eodicynodon* and the basal tapinocephalid dinocephalian, *Tapinocaninus* (Rubidge 1987, 1988, 1990a).

The addition of the *Eodicynodon* Assemblage Zone was accepted in the most recent biostratigraphic review of the Beaufort Group (ed. Rubidge 1995). This publication resurrected the name '*Cistecephalus*' Assemblage Zone and '*Tapinocephalus*' Assemblage Zone and provided more information for each biozone, including the first diagram illustrating the ranges of individual genera throughout the Beaufort Group. It also included a biozone map of the entire Beaufort Group, rather than just the southwest of the basin. This publication reverted to the use of a single genus in the names of the zones, in accordance with the new ISSC (1994) recommendations:

8. *Cynognathus* Assemblage Zone
7. *Lystrosaurus* Assemblage Zone
6. *Dicynodon* Assemblage Zone
5. *Cistecephalus* Assemblage Zone
4. *Tropidostoma* Assemblage Zone
3. *Pristerognathus* Assemblage Zone
2. *Tapinocephalus* Assemblage Zone
1. *Eodicynodon* Assemblage Zone

RECENT SUBDIVISION OF THE *TAPINOCEPHALUS* ASSEMBLAGE ZONE

Loock *et al.* (1994) were the first to link proposed lithostratigraphic members to the stratigraphic ranges of fossil taxa within the *Tapinocephalus* AZ, thereby creating the first union of litho- and biostratigraphy within the *Tapinocephalus* AZ. These authors found strong support for the idea of Rossouw & de Villiers (1953) and Boonstra (1969) that dinocephalians were more common lower in the stratigraphy, while dicynodonts became more common in the upper part of the zone. Loock *et al.* (1994) also observed decreases in abundance within other taxa. Unlike Rossouw & de Villiers (1953), Boonstra (1969) or Keyser & Smith (1977), they found pareiasaurs to be equally common in the upper and lower divisions of their field area.

This change in abundance coincided with the boundary of the Koornplaats and Wilgerbos members of the Abrahamskraal Formation. Unfortunately, these authors did not collect thoroughly in the uppermost part of the *Tapinocephalus* AZ in their field area, north of Laingsburg, which limits the significance of their results. The primary merit of the study lies in its association of lithostratigraphy with fossil occurrence and in that it has remained unique for the *Tapinocephalus* AZ.

Most recently, the *Tapinocephalus* AZ has been subject to scrutiny in reference to its constituent dicynodonts. The description of several new genera (e.g. Angielczyk & Rubidge 2010; Modesto *et al*. 2002; Modesto *et al*. 2003) as well as the morphological and stratigraphic review of existing ones (e.g. Angielczyk & Rubidge 2009, 2012) has contributed to a subdivision of the *Tapinocephalus* AZ based on the appearance of small dicynodonts (Angielczyk & Rubidge, 2012; Rubidge & Angielczyk 2009). Rubidge & Angielczyk (2009) suggested that *Eodicynodon* occurs up to 1100 m above the base of the Beaufort Group, while *Diictodon* only appears at 1900 m. In between, they suggested that *Robertia* first appears above the range of *Eodicynodon* but below that of *Diictodon*. The genus *Colobodectes* was also recognized to only occur north of the Great Escarpment, thereby indicating provincialism in dicynodonts. Angielczyk & Rubidge (2010) provided a stratigraphic ordering for the first appearances of the small dicynodonts within the *Eodicynodon* and *Tapinocephalus* assemblage zones:

4. *Diictodon* and *Pristerodon*
3. *Lanthanostegus*, *Robertia*, *Prosictodon*
2. *Colobodectes*
1. *Eodicynodon*

These ranges have so far not been linked to lithostratigraphic units within the Abrahamskraal Formation, which incorporates the vast majority of the *Tapinocephalus* AZ, but a disparity in the appearances of the different genera is evident.

CONCLUSION

The biostratigraphy of the Lower Beaufort Group today forms one of the most dynamic areas of research in the South African Karoo. Intensive collecting efforts in a lithostratigraphic context, combined with the taxonomic reassessment of most constituent tetrapod groups, are revealing patterns of occurrence that greatly improve the scientific understanding of terrestrial ecosystem change in the later Permian and early Triassic. The discovery of new taxa and the refinement of the stratigraphic ranges of more common genera are allowing the further subdivision of the Lower Beaufort Group and the quantification of extinction events. The following decade is likely to see many more changes to the existing biostratigraphic scheme.

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REFERENCES

ANGIELCZYK, K.D. & RUBIDGE, B.S. 2009. The Permian dicynodont *Colobodectes cluveri* (Therapsida, Anomodontia), with notes on its ontogeny and stratigraphic range in the Karoo Basin, South Africa. *Journal of Vertebrate Paleontology* **29**, 1162–1173.

ANGIELCZYK, K.D. & RUBIDGE, B.S. 2010. A new pylaecephalid dicynodont (Therapsida, Anomodontia) from the *Tapinocephalus* Assemblage Zone, Karoo Basin, Middle Permian of South Africa. *Journal of Vertebrate Paleontology* **30**, 1396–1409.

ANGIELCZYK, K.D. & RUBIDGE, B.S. 2013. Skeletal morphology, phylogenetic relationships and stratigraphic range of *Eosimops newtoni* Broom, 1921, a pylaecephalid dicynodont (Therapsida, Anomodontia) from the Middle Permian of South Africa. *Journal of Systematic Palaeontology* **11**, 191–231.

BAIN, A. 1856. On the geology of southern Africa. *Transactions of the Geological Society of London* **7**, 175–192.

BARRY, T.H. 1970. Terrestrial vertebrate fossils in Ecca-defined beds in South Africa. **In**: Haughton, S.H. (ed.), *Proceedings of the 2nd Symposium of Gondwana Geology and Palaeontology,* 653–659. Cape Town and Johannesburg. Pretoria, C.S.I.R.

BARRY, T. H. 1974. A new dicynodont ancestor from The Upper Ecca. *Annals of the South Africa Museum* **64**, 117–136.

BOONSTRA, L.D. 1969. The fauna of the *Tapinocephalus* zone (Beaufort beds of the Karoo). *Annals of the South Africa Museum* **56**, 1–73.

BROOM, R. 1906a. On the Permian and triassic faunas of South Africa. *Geological Magazine* **5**, 29–30.

BROOM, R. 1906b. The classification of the Karoo Beds of South Africa. *Geological Magazine* **5**, 36.

BROOM, R. 1915. Catalogue of types and figured specimens of fossil vertebrates in the American Museum of Natural History: II Permian, Triassic and Jurassic reptiles of South Africa. *Bulletin of the American Museum of Natural History* **25**, 105–164.

CLUVER, M.A. & HOTTON, N. 1981. The genera *Dicynodon* and *Diictodon* and their bearing on the classification of the Dicynodontia (Reptilia, Therapsida). *Annals of the South African Museum* **83**, 99–146.

DU TOIT, A.L. 1905. Geological Survey of the divisions of Aliwal North, Herschel, Barkly east, and a part of Wodehouse. *Annual Report of the Geological Commission 1904, Cape of Good Hope.*

DUNN, E.J. 1887. *Geological sketch map of South Africa; I inch = 33 miles*. Melbourne, Sands and McDougal.

HATCH, F.H. & CORSTORPHINE, G.S. 1905. *The Geology of South Africa* (1st edn). London, Macmillan.

ISSC 1976. *International Stratigraphic Guide* (1st edn). New York, John Wiley and Sons.

ISSC 1994. *International Stratigraphic Guide* (2nd edn). Boulder, Geological Society of America.

KEYSER, A.W. 1973. A preliminary study of the type area of the *Cisticephalus* zone of the Beaufort series and a revision of the anomodont family Cisticephalidae. *Memoirs of the Geological Survey of South Africa* **62**, 1–71.

KEYSER, A.W. 1979. A review of the biostratigraphy of the Beaufort Group in the Karoo Basin of South Africa. *Geocongress Abstracts II.* Johannesburg, Geological Society of South Africa.

KEYSER, A.W. & SMITH, R.H.M. 1977. Vertebrate biozonation of the Beaufort Group with special reference to the Western Karoo Basin. *Annals of the Geological Survey, Republic of South Africa* **12**, 1–36.

KITCHING, J.W. 1970. A short review of the Beaufort zoning in South Africa. **In**: Haughton, S.H. (ed.), *Proceedings of the 2nd Symposium of Gondwana Geology and Palaeontology,* Cape Town and Johannesburg. Pretoria, C.S.I.R.

KITCHING, J.W. 1972. *On the distribution of the karroo vertebrate fauna: with special reference to certain genera and the bearing of this distribution on the zoning of the Beaufort Beds.* Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.

KITCHING, J.W. 1977. The distribution of the Karroo vertebrate fauna. *Memoirs of the Bernard Price Institute for Palaeontological Research, Memoir*

No. 1. Johannesburg, Bernard Price Institute for Palaeontological research, University of the Witwatersrand.

LOOCK, J.C., BRYNARD, H.J., HEARD, R.G., KITCHING, J.W. & RUBIDGE, B.S. 1994. The stratigraphy of the Lower Beaufort Group in an area north of Laingsburg, South Africa. *Journal of African Earth Sciences* **18**, 185–195.

MODESTO, S., RUBIDGE, B., VISSER, I. & WELMAN, J. 2003. A new basal dicynodont from the Upper Permian of South Africa. *Palaeontology* **46**, 211–223.

MODESTO, S.P., RUBIDGE, B.S. & WELMAN, J. 2002. A new dicynodont therapsid from the lowermost Beaufort Group, Upper Permian of South Africa. *Canadian Journal of Earth Science* **39**, 1755–1765.

OWEN, R. 1876. *Descriptive Illustrated Catalogue of the Fossil Reptilia of South African the Collections of the British Museum*. London, British Museum.

ROGERS, A.W. 1903. Report of the Acting Geologist for the year 1902. *Annual Report of the Geological Commission 1902, Cape of Good Hope*, 3–10.

ROGERS, A.W. 1905. *An Introduction to the Geology of the Cape Colony* (1st edn). London, Longmans Green and Co.

ROGERS, A.W. & DU TOIT, A.L. 1909. *An Introduction to the Geology of the Cape Colony* (2nd edn). New York, Longmans Green and Co.

ROGERS, A.W. & SCHWARTZ, E.H.L. 1903. Report on a survey of parts of the Beaufort West, Prince Albert and Sutherland divisions. *Annual Report of the Geological Commission 1902, Cape of Good Hope*, 97–128.

ROSSOUW, P.J. & DE VILLIERS, J. 1953. The geology of the Merweville area, Cape Province: an explanation of sheet 198 (Merweville). Pretoria, Geological Survey of South Africa.

RUBIDGE, B.S. 1984. The cranial morphology and palaeoenvironment of *Eodicynodon* Barry (Therapsida: dicynodontia). *Annals of the National Museum, Bloemfontein* **4**, 325–402.

RUBIDGE, B.S. 1987. South Africa's oldest land-living reptiles from the Ecca-Beaufort transition in the southern karoo. *South African Journal of Science* **83**, 165–166.

RUBIDGE, B.S. 1988. *A palaeontological and palaeoenvironmental synthesis of the Permian Ecca-Beaufort contact in the southern Karoo between Prince Albert and Rietbron, Cape Province, South Africa.* Unpublished Ph.D. thesis, University of Port Elizabeth, Port Elizabeth.

RUBIDGE, B.S. 1990a. A new vertebrate biozone at the base of the Beaufort Group. *Palaeontologia africana* **27**, 17–20.

RUBIDGE, B.S. (ed.) 1995. *Biostratigraphy of the Beaufort Group (Karoo Supergroup).* South African Committee for Stratigraphy Biostratigraphic Series **1**: Council for Geoscience, 1–46.

RUBIDGE, B.S. & ANGIELCZYK, K. 2009. Stratigraphic ranges of *Tapinocephalus* Assemblage Zone dicynodonts: implications for middle Permian continental biostratigraphy. Abstracts of the 15th biennial meeting of the Palaeontological Society of South Africa. *Palaeontologia africana* **44**, 134–135.

RUBIDGE, B.S., KITCHING, J.W. & VAN DEN HEEVER, J. 1983b. First record of a therocephalian (Therapsida: Pristerognathidae) from the Ecca of South Africa. *Navorsinge van die Nasionale Museum, Bloemfontein* **4**, 229–235.

SACS. 1980. *Statigraphy of South Africa*, Handbook 8. Pretoria, Republic of South Africa Geological Survey.

SEELEY, H.G. 1892. Researches on the structure, organization and classification of the fossil reptilia. VII. Further observations on *Pareiasaurus*. *Philosophical Transactions of the Royal Society* **182**, 311–370.

TATE, R. 1867. On some secondary fossils from South Africa. *Quarterly Journal of the Geological Society* **23**, 142–144.

VAN DER WALT, M., DAY, M., RUBIDGE, B., COOPER, A. & NETTERBURG, I. 2010. A new GIS-based biozone map of the Beaufort Group (Karoo Supergroup), South Africa. *Palaeontologia africana* **45,** 1–5.

VON HUENE, F. 1925. *Die siidafrikanische Karroo-Formation als geologisches und faunisches Lebensbild.* Berlin,Verlag von Gebrfider Borntraeger.

WATSON, D.M.S. 1914a. The zones of the Beaufort Beds of the Karoo System in South Africa. *Geological Magazine, New Series* (Decade IV), 203–208.

WATSON, D.M.S. 1914b. On the nomenclature of the South African pareiasaurians. *Annals of the Magazine of Natural History* **8**, 98–102.

WATSON, D.M.S. 1942. On Permian and Triassic Tetrapods. *Geological Magazine* **79**, 81–116.

WYLEY, A. 1859. Notes of a journey in two directions across the Colony, made in the years 1857–8, with a view to determine the character and order of the various geological formations. *Appendix to Cape of Good Hope Parliamentary Report.* Cape Town, Cape of Good Hope Parliament.