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

Michael Oliver Day

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy.

Johannesburg, 2013.

DECLARATION

I declare that this thesis is my own, unaided work, except where specified in the text. It is being submitted for the Degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. This work has not been previously submitted to any other University or academic institution.

_____

(Signature of candidate)

_____ day of _____ 2013

To my parents and my sister Steph,

For their unconditional love and support.

'If Nature here wishes to make a mountain, she runs a range for five hundred miles; if a plain, she levels eighty; if a rock, she tilts five thousand feet of strata on end; our skies are higher and more intensely blue; our waves larger than others; our rivers fiercer. There is nothing measured, small nor petty in South Africa.'

- *Olive Schreiner 1892*

ABSTRACT

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.

ACKNOWLEDGEMENTS

Many people have contributed to the production of this thesis and I therefore have a great deal of thanks to bestow upon all those who have aided me. It is almost certain that I have omitted to mention people who proffered a fertile idea or provided encouragement at important junctures but I would especially like to thank the following individuals for their input.

My foremost gratitude goes to my supervisor, Prof. Bruce Rubidge, whose career this study has been an extension of. I am indebted to him for sharing with me his extensive knowledge of the Karoo but also for his assiduous guidance and encouragement, which has been of the utmost assistance over the past three years.

I would also like to thank the indefatigable Mr Sifelani Jirah for his assistance and company during many weeks spent in the field, particularly whilst undertaking the measurement of so many stratigraphic sections. To this I would like to add the many personalities who have made fieldwork so enjoyable (whether they found fossils or not) and with whom so many fascinating discussions were had, in particular Prof. Bruce Rubidge, Dr Fernando Abdala, Prof. Tom Kemp, Prof. Billy de Klerk, Dr Juan Cisneros, Dr Gabe Bevor, Dr Tyler Lyson, Ms Pia Viglietti and Mr Luke Norton.

I must also thank Dr Ken Angielczyk, Dr Fernando Abdala, Ms Saniye Güven, Prof. Bruce Rubidge, Dr Jörg Fröbisch and Dr Juan Cisneros for their erudite council concerning the identity of fossil specimens. For the same reasons I am grateful to the entire preparation team at the Bernard Price Institute, but in particular Mr Sifelani Jirah, Mr Charlton Dube and Mr Pepson Mukanela. For their help in dealing with existing collections I would like to thank Dr Bernhard Zipfel, Ms Elise Butler, Dr Jennifer Botha-Brink, Prof. Billy De Klerk and Ms Sheena Kaal.

I would also like to acknowledge the efforts of Dr Merrill Van der Walt, whose perseverance in the production of the Beaufort Fossil Vertebrate database provided the resource to make this project possible as a PhD.

Although I was met with practically invariable hospitality throughout my fieldwork, several individuals are deserving of special recognition for providing me not only

with the opportunity to work but also with shelter, once even in their own home. My greatest thanks therefore go to Mr Francois Van Wyk of Celeryfontein, Fraserburg district. Other important figures are Mr and Mrs Kobus Snyman for accommodating a field team on several occasions on the farm Elandsfontein near Merweville, Ms Gay Van Hasselt for the generous use of the Bloukrans homestead and the excellent cheese, Mr David Luscombe for allowing us to stay at Wilgerbos near Laingsurg, Mr and Mrs Dirk and Elsabe Olivier for their hospitality on the farm Puntkraal near Sutherland and Mr Piet Olivier at Driefontein near Victoria West for his conversation and liberal donations of biltong.

I am grateful to Ms Andrea Leenan and the Palaeontological Scientific Trust (PAST), as well as the National Research Foundation (NRF) for their generous financial support during the completion of this thesis.

I must also thank the United States Geological Survey for their extremely useful swatches for Adobe Illustrator, which I incorporated into many of my diagrams.

I would like to thank Dr Jörg Fröbisch, Dr Zubair Jinnah and Prof. Tom Kemp for their input and corrections of this thesis, which have improved in no end.

In a more general but no less important sense, I wish to extend my deepest thanks to all the staff and students of the BPI and at the University of the Witwatersrand who have made the last three years so much fun. Although so many people contributed to the friendly atmosphere, from my perspective particular gratitude is reserved for Ms Aurore Val for her unfailing frindship, but also Dr Fernando Abdala, Dr Vincent Fernandez and Mr Blair McPhee for their wonderfully distracting antics.

Last but not least, I wish to thank David, Nigel and Kelvin from the Postgraduate Club, for providing me with a refreshing beer at the end of a hard day.

TABLE OF CONTENTS

DECLARATION ii

DEDICATION iii

ABSTRACT iv

ACKNOWLEDGEMENTS vi

CHAPTER 1: INTRODUCTION 23

1.1 Introduction to the Thesis 23

1.2 Aims 27

1.3 Structure of the Thesis 28

1.4 Field Area 29

1.4.1 List of geographical terms 29

CHAPTER 2: LITERATURE REVIEW 31

2.1 Lithostratigraphy 31

2.1.1 Early stratigraphic work on the lower Beaufort Group 32

2.1.2 Lithostratigraphy east of 24° E 39

2.1.2.1 Stratigraphic nomenclature 39

2.1.2.2 Thicknesses 41

2.1.3 Lithostratigraphy west of 24° E (South-West) 42

2.1.3.1 Stratigraphic nomenclature: From series to formations 42

2.1.3.2 Stratigraphic nomenclature: Members 44

2.1.3.3 Thicknesses 48

2.1.4 Lithostratigraphy west of 24° E (North-West) 50

2.1.5 Palaeocurrents 51

2.2 Biostratigraphy 53

2.2.1 Early Beaufort Group biostratigraphy 53

2.2.2 Early Subdivision of the *Tapinocephalus* Assemblage Zone 58

2.2.3 Beaufort Group biostratigraphy after 1970 60

2.2.4 Recent subdivision of the *Tapinocephalus* Assemblage Zone 64

2.3 Karoo Basin Development 65

2.4 The Terrestrial Middle Permian 68

2.4.1 Middle Permian tetrapod faunas 69

2.4.1.1 Russia 69

2.4.1.2 China 73

2.4.1.3 Brazil 73

2.4.1.4 Zimbabwe 74

2.4.1.5 Tanzania 75

2.4.2 Dating 75

2.4.2.1 The Russian record 75

2.4.2.2 Radiometric dates from South Africa 78

2.4.3 Relative ages and correlations 79

2.4.3.1 Russia 80

2.4.3.2 China 82

2.4.3.3 Brazil 83

2.4.3.4 Zimbabwe 84

2.4.3.5 Tanzania 85

2.4.3.6 United States 85

2.5 The Marine Late Middle Permian Extinction 86

2.5.1 Recognition of a marine extinction in the late Guadalupian 87

2.5.2 Age of the marine extinctions 88

2.6 A Guadalupian Crisis on Land? 90

CHAPTER 3: MATERIALS AND METHODS 92

3.1 Lithostratigraphy 92

3.1.1 Identification of required stratigraphic sections 92

3.2 Fieldwork 93

3.2.1 Stratigraphic sections 94

3.2.2 Stratigraphic fossil collection 97

3.3 Biostratigraphy 97

3.3.1 Preliminary work 98

3.3.2 Sectors 99

3.3.3 Stratigraphic sections used in each sector 101

3.3.3.1 Victoria West Sector 103

3.3.3.2 Fraserburg Sector 103

3.3.3.3 Sutherland Sector 104

3.3.3.4 Laingsburg Sector 106

3.3.3.5 Merweville Sector 106

3.3.3.6 Leeu-Gamka Sector 107

3.3.3.7 Beaufort West Sector 107

3.3.3.8 Jansenville Sector 108

3.3.3.9 Grahamstown Sector 108

3.3.3.10 Philippolis Sector 109

3.3.4 Calculation of stratigraphic ranges for fossil specimens 109

3.3.4.1 Certain ranges vs. Potential ranges 110

3.3.4.2 Calculation of composite range 111

3.3.4.3 Specimen identification and the exclusion of specimens 113

3.3.4.4 Genera with multiple species 114

3.3.5 Abundance through the stratigraphy 115

3.3.6 Originations, extinctions and generic diversity 115

3.4 Institution Abbreviations 116

CHAPTER 4: LITHOSTRATIGRAPHY OF THE MIDDLE PERMIAN BEAUFORT GROUP 117

4.1 Stratigraphic Sections 117

4.1.1 Northern Cape 117

4.1.1.1 Section 1. Borehole AB1/65, Abrams Kraal 206, Victoria West District 117

4.1.1.2 Section 2. Spuitpoort, Victoria West District 118

4.1.1.3 Section 3. Borehole QU1/65, Quaggasfontein 357, Fraserburg District 121

4.1.1.4 Section 4. Puntkraal, Sutherland District 121

4.1.1.5 Section 5. Ouberg Pass, Sutherland District 123

4.1.1.6 Section 6. Verlatenkloof, Sutherland District 126

4.1.2 Western Cape 128

4.1.2.1 Section 7. Moordenaarskaroo (begins Buffelsrivier 67), Laingsburg District 128

4.1.2.2 Section 8. Wilgerbos, Laingsburg District 129

4.1.2.3 Section 9. Die Skeur, Laingsburg District 132

4.1.2.4 Section 10. Dwyka River, Prince Albert district 133

4.1.2.5 Section 11. Merweville region, Prince Albert and Beaufort West districts 134

4.1.2.6 Section 12. Springfontein, Beaufort West District 135

4.1.2.7 Section 13. Combrinkskraal, Prince Albert District 136

4.1.2.8 Section 14. Botterkraal and Jansenskraal, Prince Albert District 139

4.1.2.9 Section 15. Paalhuis, Beaufort West District 141

4.1.3 Eastern Cape 142

4.1.3.1 Section 16. Klipplaat area, Jansenville District 142

4.1.3.2 Section 17. Coniston, Peninsular and The Grant, Albany District 142

4.1.3.3 Section 18. Bucklands and De Goede Hoop, Albany District 143

4.2 List of Sub-formational Units of the Middle Permian Beaufort Group used in this study 146

4.2.1 Combrinkskraal Member*, Abrahamskraal Formation 147

4.2.2 Leeuvlei Member*, Abrahamskraal Formation 149

4.2.3 Koornplaats Member*, Abrahamskraal Formation 151

4.2.4 'Wilgerbos'/Swaerskraal Member*, Abrahamskraal Formation 153

4.2.5 Moordenaars Member*, Abrahamskraal Formation 155

4.2.6 Karelskraal Member*, Abrahamskraal Formation 157

4.2.7 Kopjesfontein Member*, Abrahamskraal Formation 158

4.2.8 Davidskolk Member*, Abrahamskraal Formation 158

4.2.9 Poortjie Member, Teekloof Formation 158

4.3 Summary 161

CHAPTER 5: STRATIGRAPHIC RANGES OF MIDDLE PERMIAN TETRAPOD GENERA IN THE BEAUFORT GROUP 163

5.1 Amphibians 163

5.2 Parareptiles 164

5.2.1 *Bradysaurus* 165

5.2.2 *Embrithosaurus* 174

5.2.3 *Nochelosaurus* 175

5.2.4 *Broomia* 176

5.2.5 *Eunotosaurus* 178

5.3 Basal Synapsids or 'Pelycosaurs' 179

5.3.1 *Elliotsmithia* 179

5.3.2 *Heleosaurus* 180

5.4 Biarmosuchians 182

5.4.1 *Hipposaurus* 182

5.4.2 *Bullecephalus* 183

5.4.3 *Pachydectes* 186

5.4.4 *Lobalopex?* 187

5.5 Dinocephalians 187

5.5.1 *Australosyodon* 190

5.5.2 *Anteosaurus* 190

5.5.3 *Titanosuchus* 195

5.5.4 *Jonkeria* 199

5.5.5 *Avenantia* 202

5.5.6 *Criocephalosaurus* 202

5.5.7 ***Delphinognathus*** 205

5.5.8 ***Keratocephalus*** 205

5.5.9 ***Mormosaurus*** 207

5.5.10 ***Moschops*** 208

5.5.11 ***Phocosaurus*** 212

5.5.12 ***Riebeeckosaurus*** 214

5.5.13 ***Struthiocephaloides*** 214

5.5.14 ***Struthiocephalus*** 215

5.5.15 ***Struthiocephaloides*** 216

5.5.16 ***Struthionops*** 218

5.5.17 ***Tapinocaninus*** 218

5.5.18 ***Tapinocephalus*** 219

5.5.19 ***Taurocephalus*** 222

5.5.20 ***Styracocephalus*** 222

5.6 Non-dicynodont Anomodonts 225

5.6.1 ***Anomocephalus*** 225

5.6.2 ***Galechirus*** 226

5.6.3 ***Galeops*** 227

5.6.4 ***Galepus*** 228

5.6.5 ***Patranomodon*** 229

5.7 Dicynodonts 229

5.7.1 ***Brachyprosopus*** 230

5.7.2 ***Chelydontops*** 232

5.7.3 ***Colobodectes*** 232

5.7.4 ***Cryptocynodon?*** 236

5.7.5 ***Dicynodontoides*** 237

5.7.6 ***Diictodon*** 238

5.7.7 ***Emydops*** 242

5.7.8 ***Endothiodon*** 244

5.7.9 ***Eodicynodon*** 245

5.7.10 ***Eosimops*** 249

5.7.11 ***Lanthanostegus*** 252

5.7.12 ***Pristerodon*** 253

5.7.13 ***Prosictodon*** 257

5.7.14 ***Robertia*** 257

5.8 Gorgonopsians 261

5.9 Therocephalians 262

5.9.1 ***Lycosuchus*** 263

5.9.2 ***Alopecodon*** 264

5.9.3 ***Glanosuchus*** 265

5.9.4 *Ictidosaurus* 271

5.9.5 *Pardosuchus* 271

5.9.6 *Pristerognathus* 272

5.9.7 *Scylacosaurus* 273

5.9.8 *Ictidosuchoides* 274

5.9.9 *Ictidosuchus* 275

5.9.10 *Hofmeyria* 275

5.9.11 *Blattoidealestes, Crapartinella* and *Simorhinella* 276

5.10 Stratigraphic patterns of higher taxa in the Middle Permian 276

5.10.1 Temnospondyl Amphibians 276

5.10.2 Parareptiles 276

5.10.3 Basal Synapsids 277

5.10.4 Biarmosuchians 277

5.10.5 Dinocephalians 278

5.10.6 Non-dicynodont anomodonts 280

5.10.7 Dicynodonts 280

5.10.8 Gorgonopsians 281

5.10.9 Therocephalians 282

5.11 Summary 283

CHAPTER 6: DISCUSSION 285

6.1 Lithostratigraphy 285

6.1.1 Thicknesses 285

6.1.2 Distribution of Members in the Abrahamskraal Formation 288

6.1.3 Changes to existing geological maps 289

6.2 Middle Permian Beaufort Group Biostratigraphy and Intra- basinal Correlation 290

6.2.1 Indicator taxa 291

6.2.2 Biostratigraphic nomenclature 293

6.2.3 Collecting Bias 296

6.3 Karoo Basin Development 297

6.3.1 The Karoo Basin; Flexural retroarc foreland basin or Ramp Syncline 297

6.3.1.1 Sediment source 298

6.3.1.2 Timing of Cape Fold Belt initiation 300

6.3.1.3 Tectonics 301

6.3.1.4 Sandstone Packages 304

6.3.1.5 Summary 304

6.3.2 Deposition of the Lower Beaufort Group 306

6.4 Middle Permian tetrapod diversity change in South Africa 312

6.4.1 Pareiasaurs 312

6.4.2 Dinocephalians 313

6.4.3 Dicynodonts 314

6.4.4 Therocephalians 315

6.4.5 Tetrapod biodiversity in the *Eodicynodon* and *Tapinocephalus* assemblage zones 316

6.4.6 The end-*Tapinocephalus* AZ extinction and tetrapod biodiversity in the *Pristerognathus* AZ 319

6.4.6.1 Karelskraal Member 319

6.4.6.2 Poortjie Member 320

6.4.7 Magnitude and timing 322

6.4.8 Selectivity 323

6.4.9 The genus *Diictodon* 325

6.5 Middle Permian tetrapod diversity change globally and the Guadalupian extinctions 326

6.5.1 Global tetrapod diversity in the late Middle Permian 326

6.5.2 Timing of the terrestrial extinction 328

6.5.3 Age of the marine extinctions and a global Capitanian extinction event 329

6.5.4 Possible causes 334

CHAPTER 7: CONCLUSIONS 336

7.1 Lithostratigraphy 336

7.2 Biostratigraphy 338

7.3 Basin Development 339

7.4 The end-*Tapinocephalus* AZ extinction in the Karoo Basin 341

7.5 Global Capitanian tetrapod diversity change and the Guadalupian extinction on land 342

CHAPTER8: FUTURE DIRECTIONS 344

REFERENCES 346

APPENDIX 1 (ON CD) INSIDE BACK COVER

APPENDIX 2 (ON CD) INSIDE BACK COVER

LIST OF FIGURES

Figure 1. Map showing tetrapod biozones of the Beaufort Group, South Africa (from Van der Walt *et al.* 2010). 25

Figure 2. Map showing field areaof this study, indicating the geagraphical areas referred to in the text. 30

Figure 3. Global tetrapod bearing terrestrial deposits of Middle Permian age. Ages of stage boundaries taken from ISC (2012). 76

Figure 4. Lithostratigraphic units of the Permian part of the Beaufort Group used in this study. At the member level, only the Poortjie Member of the Teekloof Formation is currently accepted by the South African Committee for Stratigraphy (SACS). 94

Figure 5. Map showing the localities of all stratigraphic sections used in this study. Section localities are 1, AB1/65 Abrahams kraal; 2, Spuitpoort; 3, QU1/65 Quaggasfontein; 4, Puntkraal; 5, Ouberg Pass; 6, Verlatenkloof; 7, Moordenaarskaroo; 8, Wilgerbos; 9, Die Skeur; 10, Dwyka River; 11, Prince Albert Road/Merweville; 12, Springfontein; 13, Combrinkskraal; 14, Jansenskraal; 15, Paalhuis; 16, Klipplaat; 17, The Grant; 18, Bucklands. 96

Figure 6. Map showing the sectors used in the calculation of specimen stratigraphic positions. 1 = Victoria West, 2 = Fraserburg, 3 = Sutherland, 4 = Lainsburg, 5 = Merweville, 6 = Leeu-Gamka, 7 = Beaufort West, 8 = Jansenville, 9 = Grahamstown. 102

Figure 7. Method used in this study to calculate stratigraphic ranges of taxa from the stratigraphic position of individual specimens. A, certain stratigraphic range extremities set by well-placed specimens, extending through the intervening strata; B, certain stratigraphic range extended to the closest 50 m SI of a poorly stratigraphically constrained specimen; C, certain stratigraphic range can only be determined to cover the most exclusive interval between two poorly stratigraphically constrained specimens; D, overlapping potential ranges prevent the recognition of a certain stratigraphic range. 112

Figure 8. Stratigraphic sections from localities in the Northern Cape Province demonstrating fining-upward cycles. Section localities are shown in Figure 5. Sections 1 and 3 after Cole and Wipplinger (2001); Section 6 after Turner (1981). 120

Figure 9. Map showing the traverse of the stratigraphic section measured on the farm Spuitpoort, Victoria West district. 122

Figure 10. Photograph of the Spuitpoort locality looking northwest. The thick sandstones visible in the gully belong to the Poortjie Member of the Teekloof Formation, while the fine-grained strata above the saddle belong to the overlying Hoedemaker Member. The valley floor is most likely Abrahamskraal Formation. 123

Figure 11. Map showing the traverse of the stratigraphic section measured on the farm Puntkraal, Sutherland district. 124

Figure 12. Photograph of the Karelskraal Member as exposed on the farm Puntkraal, Sutherland district (looking north). The Karelskraal Member is well defined in this area; the sandstone at the top of the slope is the basal Poortjie Member sandstone. 125

Figure 13. Photograph of the western slope of Langberg, taken on the farm Puntkraal, Sutherland district. The sandstone at the base of the picture, in the foreground, is the uppermost Poortjie Member sandstone. The sandstones at the top of the mountain belong to the Oukloof Member. 125

Figure 14. Photograph looking south on the farm Puntkraal showing the terraces formed by the Poortjie Member in this area. 126

Figure 15. Map showing the traverse of the stratigraphic section measured at Ouberg Pass, Sutherland district. 127

Figure 16. A comparison of all stratigraphic sections used in this study and the correlation of lithostratigraphic units. Stratigraphic sections are shown in an anti-clockwise direction from the north of the basin. Numbers correspond to the stratigraphic sections mentioned in the text. The localities of each stratigraphic section are shown in Figure 5. 130

Figure 17. Stratigraphic sections measured in the Moordenaarskaroo and Komsberg Mountains in the Western Cape Province demonstrating fining-upward cycles. Section localities are shown in Figure 5. Moordenaarskaroo section after Loock *et al.* (1994). 131

Figure 18. Map showing the traverse of the stratigraphic section measured on the farm Wilgerbos, Laingsburg district. 132

Figure 19. Map showing the traverse of the stratigraphic section measured on the farm Die Skeur, Laingsburg district. 135

Figure 20. Stratigraphic sections measured in the west-central Koup region in the Western Cape Province demonstrating fining-upward cycles. Section localities are shown in Figure 5. Dwyka River section after Vitali (2001); Merweville section after Jirah (2013). 137

Figure 21. Map showing the traverse of the stratigraphic section measured on the farm Springfontein, Beaufort West district. 138

Figure 22. Stratigraphic sections measured in the eastern Koup region in the Western Cape Province, demonstrating fining-upward cycles. Section localities are shown in Figure 5. Combrinkskraal section after Thissen et al. (2010); Paalhuis section after Cole and Wipplinger (2001). 140

Figure 23. Map showing the traverse of the stratigraphic section measured on the farm Jansenskraal, Prince Albert district. 141

Figure 24. Stratigraphic sections measured in Eastern Cape Province, demonstrating fining-upward cycles. Section localities are shown in Figure 5. Klipplaat section after Helber and Gebauer (2001); The Grant and Bucklands sections partly after Mason (2007). 144

Figure 25. Map showing the traverse of the stratigraphic section measured on the farm The Grant, Albany district. 145

Figure 26. Map showing the traverse of the stratigraphic section measured on the farm Bucklands, Albany district. 146

Figure 27. Generalised map showing the surface expression of the members of the Abrahamskraal Formation and the Poortjie Member of the Teekloof Formation. 150

Figure 28. Photograph of the Poortjie Member as exposed on the Nuweveld Escarpment at Springfontein. The large sandstone in the centre of the photograph is the basal Poortjie sandstone and overlies the argillaceous Karelskraal Member here, although in places thick lenticular sandstones occur immediately below the base of the Poortjie Member. 159

Figure 29. Stratigraphic ranges of parareptile and basal synapsid genera in each of the sectors in which they occur. 171

Figure 30. Composite stratigraphic ranges of parareptile and basal synapsid genera in the Middle Permian Beaufort Group. 172

Figure 31. Abundances of higher taxa through the Middle Permian Beaufort Group with *Eunotosaurus* included separately. The abundance of dicynodonts in the upper three SIs is reduced by a factor of 10 due to the great abundance of *Diictodon* in these horizons. 173

Figure 32. Stratigraphic ranges of biarmosuchian and basal anomodont in each of the sectors in which they occur. 185

Figure 33. Composite stratigraphic ranges of biarmosuchian and basal anomodont genera in the Middle Permian Beaufort Group. 186

Figure 34. Stratigraphic ranges of dinocephalian genera in each of the sectors in which they occur. 192

Figure 35. Composite stratigraphic ranges of dinocephalian genera in the Middle Permian Beaufort Group. 193

Figure 36. Abundance of dinocephalian genera through the Middle Permian Beaufort Group. Black = abundance within the certain stratigraphic range of the genus, Grey = abundance values outside of certain stratigraphic range. 197

Figure 37. Stratigraphic ranges of dicynodont genera in each of the sectors in which they occur. 234

Figure 38. Composite stratigraphic ranges of dicynodont genera in the Middle Permian Beaufort Group. 235

Figure 39. Abundance of dicynodont genera through the Middle Permian Beaufort Group. Black = abundance within the certain stratigraphic range of the genus, Grey = abundance values outside of certain stratigraphic range. The abundance of *Diictodon* in the upper three SIs is reduced by a factor of 10 due to the great number of specimens in these horizons. 246

Figure 40. Stratigraphic ranges of therocephalian genera in each of the sectors in which they occur. 268

Figure 41. Composite stratigraphic ranges of therocephalian genera in the Middle Permian Beaufort Group. 270

Figure 42. Stratigraphic ranges of all tetrapod genera from the Middle Permian Beaufort Group, inclusive of temnospondyl amphibians and gorgonopsians. 284

Figure 43a. Stages of Karoo Basin development during the Middle Permian. 310

Figure 43b. Stages of Karoo Basin development during the Middle Permian (cont.). 311

Figure 44. Graph of overall tetrapod generic diversity through the Middle Permian Beaufort Group. Generic diversity reaches its peak immediately before the extinction interval between the *Tapinocephalus* and *Pristerognathus* assemblage zones. 317

Figure 45. Tetrapod generic originations and extinctions through the Middle Permian Beaufort Group. The increase in extinctions and decrease in originations at the top of the *Tapinocephalus* AZ is evident. The last point represents the condensed *Tropidostoma* AZ using data from Smith *et al.* (2012); the large number of originations here is partly the result of the inclusion of gorgonopsian genera but does demonstrate the recovery stage after the end-*Tapinocephalus* AZ extinction. 318

Figure 46. Timing of the extinctions in the terrestrial and marine realms during the late Capitanian. The age of the boundary between the *J. altudaensis* and *J. xuanhanensis* conodont zones in scenario 1 is based on the occurrence of a basalt horizon in the Xiong Jia Chang section, within the *J. altudaensis* conodont zone, and the association of this with the increase in Emeishan volcanism ~262 Ma (Sun *et al.* 2010). The position of the marine extinction interval is based on Bond *et al.* (2010a) and Wignall *et al.* (2009a). Scenario 2 is based only on the distribution of conodont zones presented in the latest Permian Timescale (ISC 2012). Abbreviated conodont genera are *Clarkina postbitteri hongshuiensis* and *Clarkina postbitteri postbitteri*. LOPIN. = Lopingian, Wuchia. = Wuchiapingian. 333

LIST OF TABLES

Table 1. Green's (1888) table of rock characteristics for the rocks of South Africa. 36

Table 2. Sources for the thickness of the Abrahamskraal Formation and Poortjie Member of the Teekloof Formation in each of the sectors used in this study. 105

Table 3. Valid genera from the Middle Permian of South Africa. All Gorgonopsians are excluded on the basis that their taxonomy is in a state of flux. 164

CHAPTER 1: INTRODUCTION

1.1 Introduction to Thesis

The Karoo Supergroup records over 100 million years of sedimentation on the southern margin of Gondwanaland, ranging from Carboniferous glacial deposits to the remnants of Jurassic desert sand dunes (Smith *et al.* 1993). Despite the erosion of huge volumes of material during the Cretaceous Period, uneven uplift and resistant Jurassic volcanic rocks have preserved this remarkable sequence (Partridge and Maud 1987; Partridge 1998) that today provides a window into the Permo-Triassic terrestrial world. It is now well established that the Karoo Supergroup accumulated in a retro-arc foreland basin that formed behind the 'Gondwanides' mountains of southern Gondwanaland; however, the exact dynamics behind the formation of this basin have still only been broadly explored (Catuneanu 1998, 2004; Cole 1992; De Wit & Ransome 1992; Visser 1987, 1992; Visser and Dukas 1979). Nevertheless, the constituent groups of the Karoo, namely the Dwyka, Ecca, Beaufort, Stormberg and Drakensburg groups, all clearly represent successive stages in the filling of the basin.

The Beaufort Group consists of fluvio-lacustrine sediments that began their deposition in the Middle Permian with the emergence of fully terrestrial conditions on the southern margin of the Ecca Sea. Thence, deposition extended into the Middle Triassic where upper Beaufort Group rocks now unconformably underlie the Molteno Formation (du Toit 1954; Green 1888; Hancox 1998; Rubidge 1987). The group itself is separated into the Adelaide and Tarkastad subgroups, which roughly split the group into its Permian and Triassic components (Johnson 1976; Romer 1970). These rocks are of great importance to the world of palaeontology, containing as they do a comprehensive amniote fauna with such temporal continuity as is found nowhere else on earth for this time interval (Rubidge 2005). It was at this time that therapsids came to replace more basal synapsids as the dominant terrestrial vertebrates. The continuity of sedimentation has allowed the observation in the Beaufort Group of vertebrate assemblage zones, of which between eight and ten are recognised today (Hancox 1998; ed. Rubidge 1995; Smith, Rubidge and Van der Walt 2012).

The Middle Permian part of the Beaufort Group, being those rocks found in its lowest reaches, belong to the *Eodicynodon, Tapinocephalus* and *Pristerognathus* faunal assemblage zones (AZ's) (Figure 1; South African Committee for Stratigraphy 1980; Rubidge 2005). This part of the sequence is of particular interest for two main reasons. The first of these is that it preserves one of the earliest therapsid faunas, especially in the *Eodicynodon* and *Tapinocephalus* assemblage zones, and include the earliest dicynodonts, therocephalians and gorgonopsians, as well as the earliest record of pareiasaurian parareptiles (Boonstra 1969; Lucas 2006; Rubidge 1987; Rubidge 2005). Furthermore, the presence in the *Tapinocephalus* AZ of basal synapsids, a tetrapod grade usually associated with the Early Permian, highlights the connection to the earlier, pre-therapsid world (Broom 1937; Reisz and Modesto 2007). Indeed, over the last decade various researchers have discussed the potential existence of a gap in the tetrapod fossil record between the 'pelycosaur'-dominated world of the Early Permian and therapsid-dominated late Middle Permian (Benton 2012; Lucas and Heckert 2001; Lucas 2001, 2002, 2006; Reisz and Laurin 2001, 2002) to which the Beaufort Group fauna is central.

The second reason is the disappearance of dinocephalian therapsids at the top of the *Tapinocephalus* AZ and the more general loss of taxonomic diversity recorded there (Keyser and Smith 1977; Smith and Keyser 1995a). Since the identification of an extinction in the marine realm of China during the Middle Permian, separate from the end-Permian extinction event (Stanley and Yang 1994), a flurry of studies have aimed to clarify its timing, magnitude and causes (e.g. Bond *et al.* 2010a, 2010b; Clapham *et al.* 2009; Ota and Isozaki 2006; Wang, Cao and Wang 2004; Wignall *et al.* 2009a, 2009b). Recently, there has been an interest in correlating the marine and terrestrial realms in order to better assess these factors and investigate the potentially global extent of this extinction (Lucas 2009; Bond *et al.* 2010a). In light of recent radiometric dates recovered for some Permian assemblage zones in the Karoo (Rubidge *et al.* 2013), and given the continuity of the sequence, the Beaufort Group is the best location to make such comparisons.

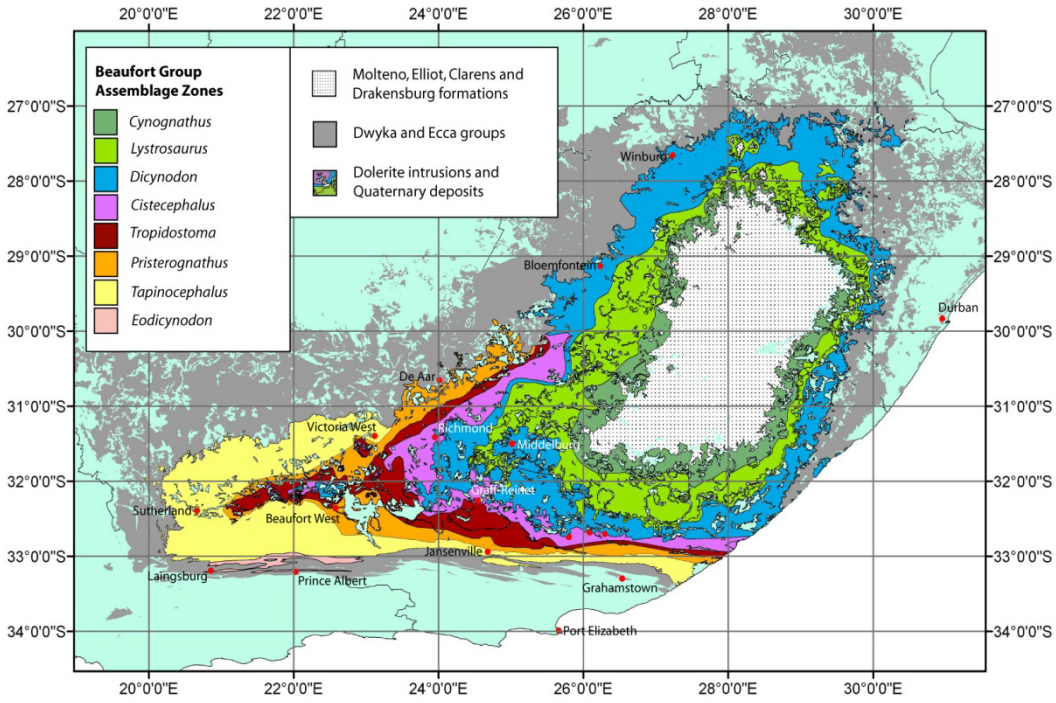


Figure 1. Map showing tetrapod biozones of the Beaufort Group, South Africa (from Van der Walt *et al.* 2010).

This last decade of research has therefore demonstrated the importance of the Middle Permian part of the Beaufort Group to the understanding of therapsid evolution and global biodiversity patterns. Yet, the primary medium for presenting such biodiversity data in a temporal context, i.e. the biostratigraphic scheme, has not been given as much attention for this timeframe as research elsewhere. The *Tapinocephalus* AZ was last discussed thoroughly by Boonstra (1969) and, though subsequent work has established the *Pristerognathus* AZ (Keyser and Smith 1977) and the *Eodicynodon* AZ (Rubidge 1987), the most recent summary still contained a lot of uncertainty (ed. Rubidge 1995). However, collecting and phylogenetic research has undergone considerable leaps since Boonstra's (1969) review, with a great many new taxa having been described from these three zones and numerous others synonymised or declared invalid (e.g. Angielczyk and Rubidge 2010; Modesto *et al.* 1999, 2003; Rubidge and Kitching 2003; Rubidge *et al.* 2006; Sigogneau-Russell 1989; Van den Heever 1987).

Though these circumstances clearly highlight the need for a biostratigraphic review of the Middle Permian in South Africa, the main catalyst for this project was the

recent creation of a GIS-based tetrapod fossil database for the Beaufort Group, which consolidated all collections data from within South Africa and projected the localities in space (Nicolas 2007). This revolutionary work provided the necessary platform from which to launch a comprehensive reassessment of biodiversity change in the Middle Permian Karoo, this being the primary aim of this thesis. Ultimately, this work forms part of a much larger project concerning the lowermost Beaufort Group run by the BPI Palaeontology, soon to become the Palaeosciences Institute, based at the University of the Witwatersrand.

Subsidiary to the biostratigraphic question, but also essential to the acquisition of any meaningful biostratigraphic results, is that of the lithostratigraphy of the basal Beaufort Group. A good number of studies have made increasingly narrow subdivisions of the Middle Permian strata, mainly on the back of commercial exploration (Cole and Wipplinger 2001; Johnson 1976; Jordaan 1990; Keyser and Smith 1977; LeRoux 1985; SACS 1980; Stear 1980) but none have fully incorporated all available data from the literature. In addition, several unpublished stratigraphic sections now exist that post-date the last of these reviews. Because the accuracy of a biostratigraphic model is only as great as the accuracy with which fossil material can be placed in a vertical sequence, a large number of stratigraphic sections would be required. Therefore, in order to provide a robust framework on which to determine the stratigraphic ranges of tetrapod taxa, a thorough reassessment of the lithostratigraphy was a requisite part of this project.

Finally, once both the lithostratigraphy and biostratigraphy had been addressed, it was pertinent to also refine the prevailing theories of development for the Karoo Basin. This forms the lesser of the aims stated below. The Karoo basin has so far only been broadly discussed (Catuneanu, Hancox and Rubidge 1998; Cole 1992) but this section intends only to provide a more specific glimpse of its formation during the late Middle Permian.

1.2 Aims

The primary aims of this project are as follows, with the former involving a data collection exercise and the latter being confined to a discussion of the former data:

1. To create a biostratigraphic record, comprising the ranges of all individual tetrapod genera in the *Eodicynodon*, *Tapinocephalus* and *Pristerognathus* assemblage zones, at a far higher resolution than is currently available. This is to be done using the Beaufort Tetrapod Database of Nicolas (2007), unpublished biostratigraphic data collected as part of the lower Beaufort project run by the BPI Palaeontology, published data on fossil occurrences, and fossil collection in key areas conducted specifically for this research.
2. To use the ranges of individual genera and of higher taxa, combined with the radiometric dates from the Karoo, in order to deduce and record changes in tetrapod biodiversity in the late Middle Permian and quantify the extent of the end-*Tapinocephalus* AZ extinctions. This will then be discussed in a global context and especially with reference to the 'end-Guadalupian Mass Extinction'.

Secondary aims are similarly split between the former, which involves data collection, and the latter, which confined to a discussion based on all data collected:

2 To conduct an holistic review of the existing lithostratigraphic schemes used in the lower Beaufort Group and, particularly at the sub-formational level, use stratigraphic sections from the published literature, unpublished sections measured as part of the wider project run by the BPI Palaeontology and sections specifically measured in the course of this research to trace identifiable units around the basin. This will be done primarily to support biostratigraphic work but will be discussed in its own right.

3 To use the biostratigraphic and lithostratigraphic data collected to discuss the potential course of Karoo Basin development through the late Middle Permian.

1.3 Structure of the Thesis

The second chapter of this thesis intends to review the state of the literature regarding each of the aims in question, but not in the order of precedence stated in the aims above. Naturally, regard for the lithostratigraphy precedes that for the biostratigraphy, which requires the former be known. Similarly, any conclusions drawn about basin development require both these previous areas to be known.

The third chapter deals with the methodology and reasons for the acquisition of data. Here are details of where stratigraphic sections were measured, the sources for those retrieved from the literature, the reasons for supplementary work and a description of the methods used in measurement. It also explains how the fossil dataset was acquired, how stratigraphic heights for individual specimens were recorded, how stratigraphic ranges were calculated, how fossil data was organised geographically into sectors and the justifications for the use of different stratigraphic sections in each of these sectors.

The fourth chapter contains details of the lithostratigraphic sections used in this project, with all appropriate additional information for those measured in the course of this project. A list of valid units used in subsequent chapters in then provided.

The fifth chapter records the stratigraphic ranges of each individual tetrapod genus in the lower three assemblage zones of the Beaufort Group. For the more common taxa, this includes an individual record of their occurrences in each sector, completed by a description of their overall range.

The sixth chapter comprised the discussion of all four aims outlined above. It works through what can be determined about the distribution of deposition in the Karoo Basin form the recognised lithostratigraphic units and then the biostratigraphy of the Middle Permian and its uses in correlating lithostratigraphic units. The formation of the Karoo Basin itself is then discussed in light of the information provided by this thesis. The chapter then addresses biodiversity within the Middle Permian Beaufort Group and the end-*Tapinocephalus* extinction, followed by the global implications of this study.

The seventh chapter presents the conclusions of this thesis in five separate sections and the eighth briefly outlines directions for further work.

1.4 Field Area

The field area is shown in Figure 2. A list of geographical terminology is provided below, the extent of which are indicated in Figure 2.

1.4.1 List of geographical terms

The Koup: a flat area of ground, approximately 120 km wide at its thickest and bordered to the south by the Swartberg Mountains, to the north by the Nuweveld escarpment, the west by the Komsberg escarpment and to the east by a line running south of Beaufort West.

Nuweveld: plateau north of the Nuweveld Mountains.

Nuweveld Mountains: the line of mountains running along the north of the Nuweveld Escarpment.

Nuweveld escarpment: the portion of the Great Escarpment that borders the north of the Koup.

Roggeveld: area of flat ground north of the Komsberg escarpment and contiguous with the Nuweveld in the north-east.

Komsberg Escarpment: the portion of the Great Escarpment that separates the Roggeveld from the Moordenaarskaroo and the northwest part of the Koup.

Swartberg Mountains: northernmost mountains which form part of the Cape Fold Belt and extend from Laingsburg in the west to Willowmore in the east.

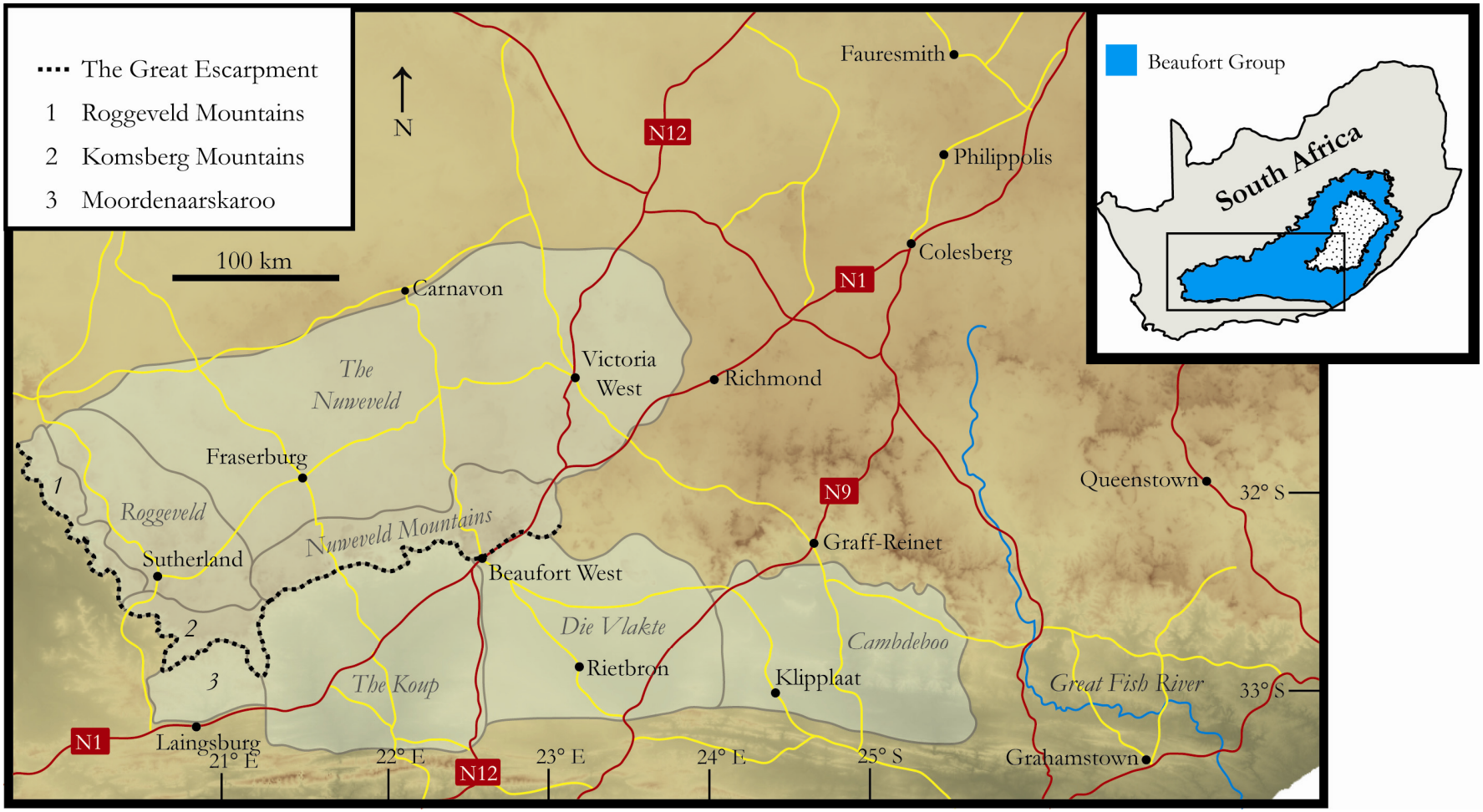


Figure 2: Map showing field area of this study, indicating the geagraphical areas referred to in the text

CHAPTER 2: LITERATURE REVIEW

2.1 Lithostratigraphy

The rocks of the Beaufort Group have been studied for more than 150 years and in that time a great wealth of literature has been produced, documenting the changing opinions of the stratigraphy and sedimentary mechanisms that form the basis of the current paradigm. Much of the early work was conducted by government geologists (e.g. Wyley 1859; Dunn 1873, 1887), with the most remarkable advances being made in the period following the advent of the Geological Survey of South Africa in 1895 (e.g. du Toit 1905; Rogers 1902, 1905; Rogers and du Toit 1909; Rogers and Schwartz 1903). Later, the scramble for uranium led many private sector geologists to contribute to the understanding of these rocks as well (e.g. Jordaan 1990; Keyser and Smith 1977; LeRoux 1985; Stear 1980). In particular, the present definition of the lower Beaufort Group has been most affected by two salient processes: that of reduction, whereby the sequence has been steadily divided into smaller and more manageable stratigraphic units; and the redefinition of the boundary with the underlying Ecca Group.

Despite the work undertaken on the stratigraphy and morphology of the Karoo Basin and particularly the Beaufort Group, there are still many gaps in our understanding. Firstly, as a fluvial sequence, the facies present are very homogeneous compared to those deposited in a marine setting. The stratigraphy displays considerable lateral variation making lithostratigraphic units identified in one area very difficult to correlate with exposures a few tens of kilometres away. Combined with the difficulties associated with folding in the south and poor exposure in the north, the number of lithostratigraphic sections remains low in comparison to the large area covered by the basin.

The distribution of fossil genera is potentially very useful for relative dating of different stratigraphic horizons around the basin and, consequently, in the reconstruction of the Karoo Basin during the Permo-Triassic. In order to use this tool, it is first necessary to understand the stratigraphic makeup of different areas of

the lower Beaufort. This is achieved through the measurement of stratigraphic sections that are then correlated with each other firstly using the distribution of lithostratigraphic units and subsequently through the application of biostratigraphic correlation. This chapter will review the current literature regarding the lithostratigraphy of the lower, Middle Permian part of the Beaufort Group.

2.1.1 Early stratigraphic work on the lower Beaufort Group

The first work of note on the geology of the Cape Colony, now covering the Karoo Supergroup, was that of Andrew Geddes Bain (1856). While working as an engineer on the Queen's Road from Grahamstown to Fort Beaufort in the late 1830s, Bain had taken an interest in geology that persisted for the rest of his life. He continued to work as a road engineer, a profession which took him across the Cape Colony, and during this time made numerous observations of the geology and palaeontology of the region. He produced the first geological map of the Colony in 1852, which was eventually published by the Geological Society of London (Bain 1856). In this he referred to the 'Karoo or Reptiliferous Series,' being the strata above the 'Claystone Porphyry' (Dwyka Conglomerate) that outcrop predominantly in the Great Karoo. This rather inclusive designation included what are now the Ecca and Stormberg Groups as well. Bain considered what are now the lowest part of the Beaufort Group and the uppermost part of the Ecca Group to constitute his 'Second Division' of the Karoo Series. For the next thirty years there persisted the tendency to differentiate the lowest Beaufort rocks from those above based primarily on an absence of fossils. In the Eastern Cape in particular, fossils in the lower Beaufort rocks are much rarer than in younger strata.

Bain has sometimes been credited with conceiving the term 'Beaufort' to refer to the fossil bearing part of the stratigraphy but, as noticed by Johnson (1976), his 'Beaufort Grit' was in fact a small outlier near Fort Beaufort that was based in lithological grounds. Bain's (1856) stratigraphy was as follows:

Karoo or Reptiliferous (Lacustrine?) Series

4. Reptiles, silicified trees, thin beds of coal

3. Reptiles, Bivalves, Asterophyllites, Lycopodium?

2. Plants and silicified trees

1. Plants

Claystone Porphyry

Soon thereafter, the Geological Surveyor to the Cape Colony, Andrew Wyley, published his own map of the Colony. Here, he defined the 'Coal Measures' that roughly included the modern Beaufort and Stormberg groups (Wyley 1859). These measures were split into three: the 'Upper Coal Measures,' corresponding roughly to the 'Stormberg' Group; the fossil bearing 'Middle Coal Measures'; and, in a similar fashion to Bain's 'Second division', he designated the 'Lower Coal Measures' as the strata above the dark Ecca Shales but below the first appearance of reptile fossils or purple mudstones. This latter division was described as containing 'brown sands', the extent of which was later assigned to the Waterford Formation of the Ecca Group (Johnson 1976). It is also worth noting here that Wyley correlated the 'Stormberg Beds' with the Nuweveld and Roggeveld, which has subsequently proved false. Wyley's (1859) stratigraphy was recorded as:

Coal Measures

3. Upper

2. Middle

1. Lower

Upper Karoo Shale

Trap Conglomerate

Lower Karoo Shale

The stratigraphy of South Africa was summarised in 1867 by T. Rupert Jones within an article primarily authored by Ralph Tate (Tate 1867). This was based mainly on the work of Bain. Jones retained essentially the same units but elaborated upon them, such as by acknowledging that the Ecca continues below the 'Trap Breccia' (formerly Trap Conglomerate/Claystone Porphyry) as observed by Wyley (1859); he also provided names for the divisions of what he called the 'Karoo Series.' The Second Division of Bain therefore became the 'Koonap Beds', although with very little

information other than that they contained 'sandstones and hard shales, with fossil trees...' (Jones In Tate 1867:142). Bain's 'Third Division' is for the first time named the 'Beaufort Beds' and the implication was made that this is due to the situation of Fort Beaufort and Beaufort West on rocks of this unit. The Beaufort Beds are described as 'greenish laminated sandstone, with shale, calcareous bands, and numerous hard nodular masses often containing Dicynodont remains' (Jones In Tate 1867:143). There is a list of the numerous fossils of both reptiles and plants described from the Beaufort Beds up to 1867, and mention is made of Bain's 'Fort-Beaufort Grit' being a coarse sandy horizon near the base of the zone, by then known to contain the dicynodont *Oudenodon*.

Interestingly, he says nothing of red mudstone in the Beaufort Beds, instead defining the overlying 'Stormberg Beds' as 'white and yellowish sandstones, with grey and reddish shales' (Jones In Tate 1867:143). In these beds he mentions dinosaurs and a specimen of *Dicynodon* from the Modder River, a fact which demonstrates that the Stormberg Beds were still thought to continue northward onto the highveld. Jones' (1867) divisions appear thus:

<u>Karoo Series</u>
6. Stormberg Beds
5. Beaufort Beds
4. Koonap Beds
3. Upper Ecca Beds
2. Trap Breccia
1. Lower Ecca Beds

The northern areas of the Cape Colony and Orange Free State remained poorly explored for some time. This is evident in the maps produced by Edward Dunn during his time as a geologist for the Cape government between 1871 and 1886. His first maps are quite generalized (based mostly on previous works) but the newly named 'Dwyka Conglomerate' formed the base of his Triassic strata, while the 'Karoo Beds' were split into upper and lower parts with the Stormberg beds above (Dunn 1873). His later map, based on the previous decade of fieldwork and only published once he had returned to Australia (Dunn 1887), was a magnificent piece of work that made four important observations. Firstly, he separated the Stormberg

Beds out into four divisions: the Coal Measures, the Red Beds, the Cave Sandstone and the Volcanic Beds. These divisions remain more or less intact today, though with a different nomenclature. He also officially declared the Dwyka Conglomerate to be of glacial, not igneous, origin. This lithological unit had gone by many names and was probably one of the most contentious topics for early geologists in South Africa but, after this work, it became generally accepted as a tillite.

Dunn's third important observation was his inclusion of the 'Koonap Beds' into the 'Lower Karoo or Ecca Beds.' This began the convention of allying these strata to the Ecca that was to continue for nearly a century; the lack of fossil reptiles and red mudstone evidently outweighed the increase in sandstone. Dunn's (1887) divisions were as follows:

Stormberg Beds
4. Volcanic Beds
3. Cave Sandstone
2. Red Beds
1. Coal Measures
Upper Karoo Beds
Lower Karoo or Ecca Beds including the Dwyka Conglomerate

Not long after the publication of Dunn's last map, the stratigraphy of the Cape Colony was once again summarised by Alexander Green, who had visited South Africa as a geologist in 1882 (Green 1888). Green did not spend enough time in the Cape to draw his own map, instead contenting himself to provide a synopsis of what had gone before him, spiced with his own experience. He builds heavily on the work of Dunn with some minor alterations: for a start, he recorded a great unconformity between the 'Ecca Beds' and the 'Karoo Beds' in the south, while in the north he considered the 'Kimberley Shales' (now the Tierberg Formation) to be conformable with the overlying Karoo Beds and therefore younger. However, his 'Karoo Beds' remained identical to the 'Upper Karoo Beds' of Dunn (1887). He also replaced the name of the former Coal Measures with the 'Molteno Beds.' Perhaps the most significant contribution was to provide a table of lithological characters for the three upper divisions of the modern Karoo Supergroup. This provided the first

quantifiable set of instructions for differentiating the Ecca, Karoo (later Beaufort) and Stormberg Beds (Table 1).

	Ecca	Karoo	Molteno
Sandy Rocks	Very quartzose, compact, and hard. Marked spheroidal weathering in some.	Much felspathic matter, finely grained, not massive, as a rule. Feeble tendency to spheroidal weathering in some.	Coarse quartzose grits and conglomerates common, often in massive beds.
Clayey Rocks	Mudstones predominate; shales rare.	Shales, few mudstones; red, purple, and mottled beds common.	Shales, few mudstones, grey or dark; red beds rare.
		Sandstones thin compared with the shale bands.	Shale bands for the most part thin compared with the sandstones.

Table 1. Green's (1888) table of rock characteristics for the rocks of South Africa.

A map produced for an article by Schenk (1888) was similar to that of Dunn (1887), but was rather less accurate in its projection. He showed the Ecca Beds in the south reaching as far north as Beaufort West and Graff-Reinet, while neglecting to extend the Beaufort Beds north into the Transvaal. However, he did use the nominal breakdown which placed the Dwyka, Ecca, Beaufort and Stormberg as separate layers within the Karoo Formation, a paradigm that was soon followed by British geologists in the Cape. Interestingly, like Bain, Schenck has been attributed with introducing the term Beaufort for what became the Beaufort Group (Loock *et al.* 1994:187); however, as previously discussed, this was in fact just the reinstatement of the name 'Beaufort Beds' proposed by Jones (In Tate 1867).

By the time the Geological Survey of South Africa was formed in 1895, Seeley (1892a) had already published the first subdivision of the Karoo based on the

occurrence of fossils, but he gave only limited descriptions of their extent having experienced each in a relatively localized area. Seeley's zones two to four were officially acknowledged by Rogers (1903) and Rogers and Schwarz (1903) as the subdivisions of what they termed the 'Beaufort Series' within the 'Karroo [*sic*] System', the latter of which contained the Dwyka, Ecca and Stormberg series as well. Alex du Toit (1905) was the first to acknowledge this in a map in the course of his survey of the Aliwal North-Barkly East district, using Seeley's 'zone of highly specialized Theriodonts' to define the 'Burghersdorp Beds.' This name was erected to describe the upper part of the Beaufort Series that outcropped in the area around Burgersdorp and Aliwal North.

The assiduous geological work that occurred after 1896 led to the publication in 1905 of two text books on the geology of South Africa (Hatch and Corstorphine 1905) and the Cape Colony (Rogers 1905). Their sections on the Karoo System each have merit, albeit in different ways. Both inform the reader that the Beaufort Series consists of sandstone and shale; that calcareous, nodular horizons are present; that 'clay-pebble conglomerates' are found at the base of sandstones; and that the sandstones can be divisible into 'defining' and 'intermediate' forms as posited by Schwartz (1897:15). The latter sandstone types can be equated with the 'channel' and 'crevasse-splay' facies later described by Smith (1989). Both provide a polished geological map of South Africa that clearly shows that the Beaufort Series was known to extend round the Stormberg Series to the north. Apart from underestimating the extent of the Beaufort outcrop in the Orange Free State and northern Natal, they are very similar to modern maps.

Both books had second editions four years later (Hatch and Corstorphine 1909; Rogers and du Toit 1909). This was fortuitous, as by then Broom (1906a, 1906b) had published his updated biostratigraphy for the Beaufort Series; yet, despite this quite significant development, only Rogers and du Toit (1909) incorporated this new information into their volume. In both publications, the 'Lower Beaufort Series' was defined by the first appearance of *Pareiasaurus*, although Rogers and Du Toit do acknowledge a difference in lithology between the north, where a yellow weathering sandstone provided an abrupt lower contact with the Ecca, and the south, where the Ecca became more arenaceous and the boundary more obscure. The Lower Beaufort

Series was now defined as the strata encompassing Broom's *Pareiasaurus*, *Endothiodon* and *Kistecephalus* zones. Similarly, the 'Middle Beaufort Beds' are characterised by *Lystrosaurus*, with some brief mention of 'yellow defining sandstones' in the vicinity of Naauwpoort (Rogers and du Toit 1909:204). It is only for the 'Upper Beaufort or Burghersdorp beds,' incorporating the *Procolophon* and *Cynognathus* beds, that they made specific reference to lithology in their definition. They record that 'the sandstones are yellowish or pale blue in colour, but are somewhat more widely spaced than the sandstones in the lower beds [and] between them are brilliant red and purple shales' (Rogers and du Toit 1909:205). The resulting subdivision of the Beaufort Series therefore was strongly based on biostratigraphy:

Upper Beaufort Series (Burghersdorp beds)

6. Cynognathus beds

5. Procolophon beds

Middle Beaufort Series

4. Lystrosaurus beds

Lower Beaufort Series

3. Kistecephalus beds

2. Endothiodon beds

1. Pareiasaurus beds

The Lower Beaufort Series endured as a name in practice after this. It in essence remained defined by the presence of fossils, although du Toit (1929) did provide a lithological description for its exposure in the area around Griqualand East. The perhaps rather vague suite of facies provided by this author consisted of, 'yellow, feldspathic medium grained sandstones, alternating with green, blue and buff mudstones' (du Toit 1929:10). On the accompanying map, he makes the additional remark that these beds contain '*Dicynodon* and *Glossopteris*' (Cape Sheet 135, Griqualand East; 1 inch =3.8 miles. 1929. Geological Survey South Africa, Pretoria). However, the lower Beaufort Series was still distinguished from the Ecca based on the presence of reptilian fossils until Mountain (1946) proposed the use of the first purple mudstone as the boundary, taking it to be an indicator of some change in the environment.

After this point, it became increasingly common to consider the eastern and western portions of the Lower Beaufort Series separately. As such, the histories of these two regions will be discussed individually in the following sections.

2.1.2 Lithostratigraphy east of 24° E

2.1.2.1 Stratigraphic nomenclature

The area north of Grahamstown had been one of the major influences on Bain and most subsequent geologists of South Africa. However, the nature of the Ecca-Beaufort boundary here had always been an issue of contention. Bain (1856), Wyley (1859) and Jones (In Tate 1867) had all recognised that a stretch of more arenaceous strata existed above the typical Ecca shales but below the beds of red and purple mudstones or the presence of fossil reptiles, viz. the 'Koonap Beds' of Jones (In Tate 1867). This unit was assigned to the Ecca by Dunn (1873) on the basis it lacked fossil reptiles and from then on had been considered as such. Above this, the Lower Beaufort Beds extended up to the base of the *Lystrosaurus* zone (Broom 1906a) and the 'very massive bed of whitish sandstone' (du Toit 1929:10), which together distinguished the Middle Beaufort Beds.

The Ecca-Beaufort boundary in this region proved malleable in the absence of a well defined lithological boundary, a fact which led Mountain (1946) to institute the appearance of red and purple mudstones as the lower boundary of the Beaufort Series. The 'Koonap Beds' therefore remained as the 'Upper division' of the Ecca Series. However, Mountain (1946:20) was fully aware of the affinities that these rocks had with the overlying Beaufort strata, stating that:

> *…a feature suggestive of the succeeding Beaufort series is observed in the increasing development of greenish mudstones. The uppermost Ecca series shows the advent of bluish-green quartzitic sandstone in thin bands, while the mudstones in places acquire a deep bluish green tint in contrast to the olive green and drab colour of the mudstones commonly found at lower horizons.*

These observations proved decisive for Johnson (1966) in his reappraisal of the Karoo sequence in which he assigned these beds, now using the official nomenclature, to his Koonap Formation, within the 'Beaufort Group.' He also subdivided the former Lower Beaufort Series into the Middleton and Balfour Formations. This followed Mountain (1946), who noted that the red and purple coloured mudstones were more common towards the base of the old Lower Beaufort series; Johnson upheld this observation and so named the Middleton Formation for strata with a greater content of red mudstone, which occurred in the middle of what he later called the 'Adelaide Subgroup' (Johnson 1976).

The Adelaide Subgroup encompassed the Koonap, Middleton and Balfour formations but, at the same time, Johnson (1976) removed the lowest part of the Koonap Formation, placing it instead within the Ecca as the 'Waterford Formation.' This decision was based on the lithological criteria devised by the South African Committee for Stratigraphy (SACS) the year before (Johnson *et al.* 1975), and heralded the dismemberment of Bain's Second Division, one hundred and twenty years after its original conception. This new stratigraphic nomenclature was later accepted for the Lower Beaufort Group outcropping east of 24° E (SACS 1980).

Since then, a couple of slight alterations have been made to the SACS stratigraphic scheme in the east. Firstly, in the explanation to sheet 3224 (Graff-Reinet), Hill (1993) admits to using an arenaceous zone to map the base of the Middleton Formation. The presence of an interval of greater relative sandstone content coinciding with the first purple mudstone is mentioned by Johnson (1976) and this obviously proved far easier to follow, especially where outcrop was poor. As Johnson and le Roux (1994) use the increase in purple mudstones in their explanation of Sheet 3326 (Grahamstown), the base of the Middleton Formation may therefore be defined by two separate criteria in these two areas. Secondly, the Waterford Formation of the Ecca Group has now been recognised north of Grahamstown; formerly, the Waterford Formation was shown to pinch out south of Middleton (map sheet: Republic of South Africa 3324, Port Elizabeth, 1:250 000 Geological Series 1991) but now between 80–210 m of the lowest Koonap Formation east of Middleton has been attributed to it (Mason 2007; Rubidge *et al.* 2011).

2.1.2.2 Thicknesses

The question of sequence thickness has long proved troublesome for geologists in the Karoo. Du Toit (1954:291) described it with enduring applicability when he wrote that 'owing to the great breadth of outcrop, the low dip and the abundance of dolerite, it is difficult to obtain satisfactory estimates for the thickness.' Nevertheless, estimates were made as early as 1859 when Wyley (1859) gave an approximate thickness of 1500 feet (457.2 m) and 1700 feet (518 m) for his Lower and Middle Coal Measures, respectively. This was a conservative estimate, as Rogers and Du Toit (1909) record a thickness of 6000 feet (1829 m) for the Beaufort Series and du Toit (1954:291) gives a thickness of 9000 feet (2743 m) for the lower Beaufort Series near Jansenville, the latter being essentially equivalent to the Middle Coal Measures alone.

In the east, Mountain (1946) referred to a thickness of 9000 feet (2743 m) for the lower Beaufort sediments (i.e. above the first purple mudstone) but this was probably taken from du Toit (1954) as he provided no details. For the upper Ecca division, which is equivalent to the modern Koonap Formation, the same author calculated a thickness of 4150 feet (1265m) near Committee's Drift and 3950 feet (1204 m) on the farm Bucklands. Johnson (1976) gave similar thicknesses for this formation, varying between 1250 m and 1450 m for the Koonap Formation from Committee's Drift to south of Cookhouse but recorded a sharp reduction in thickness at Waterford, down to 220m; however, he acknowledged that the top of the Koonap Formation is recognised by the first occurrence of purple mudstone, a feature which is controlled by local environmental factors and therefore liable to vary laterally. The much thinner Koonap Formation at Waterford therefore does not indicate a genuinely lesser amount of sediment deposition, but merely a difference in the position of this marker. Later, Johnson and Le Roux (1994) gave average heights for the Adelaide Subgroup formations in the Grahamstown area: 1300 m for the Koonap Formation, 1600 m for the Middleton Formation and 2000 m for the Balfour Formation.

More recently, several small scale studies have re-examined the thickness of the lowest Beaufort Group at localities in the southern Karoo. A section measured near Klipplaat in the Eastern Cape Province by Helber and Gebauer (2001) supplied the first comprehensive image of the Koonap Formation. This revealed a thickness of

2560 m for the formation in this area, considerably more than had been found further to the east. Mason (2007) subsequently re-measured detailed sections along the Great Fish River north of Grahamstown, in the same area worked by Mountain (1946). This study was primarily aimed at deciphering the nature of the Ecca-Beaufort boundary and as such only encompassed the Koonap Formation up to the first purple mudstone. Mountain (1946) had noted that several small purple mudstone layers did occur below the horizon after which such colouration became common; nevertheless, the thickness of 1180 m found on the farm Bucklands by Mason (2007), comes very close to that of Mountain (1946) on the same farm, which stood at 1204 m.

2.1.3 Lithostratigraphy West of 24° E (South-West)

2.1.3.1 Stratigraphic nomenclature: from series to formations

From the beginning, Bain (1856) had recognised the substantial outcrop of fossiliferous rocks in the Great Karoo with the designation of its eponymous sequence. In the course of the twentieth century, during the search for minerals and especially oil in the rocks of the Karoo Supergroup, the Great Karoo has become by far the most studied area due to the excellent outcrop there. The first specific work on the area began with the Geological Survey, and more specifically with the report on the area by Rogers and Schwarz (1903). Although Dunn (1873) had placed Jones' (1867) 'Koonap beds' in the Lower Karoo (Ecca) Series, Rogers and Schwarz reported its absence in the Great Karoo and that the Beaufort Series here sat directly on the Ecca. They also drew attention to the lack of an unconformity between these two series, contrary to the observations of Green (1888). However, the distinction between the Ecca and the Beaufort series remained obscure. Hatch and Corstorphine (1905, 1909) mentioned that Beaufort sandstones differed from those of the Ecca by having no spheroidal weathering, as well as reiterating the greater frequency of 'purple or brownish red' mudstones. Rogers and Du Toit (1909:203) make no mention of lithological characters, instead taking the base of the Beaufort Series to be the 'lowest stratum containing *Pareiasaurus*,' as had been done before.

This definition was maintained by most subsequent geologists at the Geological Survey and was used in the production of Cape map sheet 5 (Laingsburg) (Rogers 1925). Although he admitted that dinocephalians were known from the Ecca and that 'it is likely that future discoveries will prove the boundary between the Ecca and Beaufort beds...to be still less satisfactory than it now is' (Rogers 1925:20), he continued to be reticent concerning lithological characters. Rogers (1925:19) in fact wrote that 'lithologically there is little difference between the rocks of the two formations,' and only ventures to posit that 'the hard red-weathering sandstones like those frequently found in the Beaufort beds in the dry Karroo [sic] climate are much less abundant in the Ecca beds.'

It ultimately fell upon Blignaut *et al.* (1948), whilst mapping the Skoorsteenberg area, to adopt the incoming of reddish and purplish mudstones as the base of the Beaufort series, devised by Mountain (1946) for these strata in the Eastern Cape. The boundary was therefore defined as the 'first purple shale' (Blignaut *et al.* 1948:9). While it was accepted that this was rather arbitrary, they remark that 'the zone in which it occurs is a thin one'. It was certainly a far more reliable and consistent marker than the appearance of *Pareiasaurus*. They went on to describe lithological disparities that had so eluded Rogers (Blignaut *et al.* 1948:9):

> *The shales that are now assigned to the Ecca are green and blue, generally finely bedded, and weather in pencil-like fragments. Those assigned to the Beaufort are purple and blue and weather into blocky fragments. Sandstones in the upper part of the Ecca are often mottled and contain fairly numerous inclusions of brown weathering, marly rock. Those in the lower part of the Beaufort are rarely mottled, and the brown-weathering, marly lenses are rare. Further, above the purple shale nodules of pink and green quartz and calcite are found, but they are not found below it. While limestone nodules and chert lenses are almost absent from the Ecca, as now defined, they occur frequently in the Beaufort.*

Of the facies they described the 'chert,' or siliceous shales that resemble chert, are of particular interest. The feature most remarkable to these authors was that these rocks form thin bands that can be traced for many miles at the same level in the stratigraphy and which, when they finally taper out, are often replaced by another only slightly above or below it. They found the origin of these beds hard to explain; however, they do mention that 'the absence of rounding in many of the quartz

fragments and the freshness of the feldspars indicate that the material could not have been transported far' (Blignaut *et al.* 1948:13). Subsequent work showed these to be formed by reworked volcanic tuff (Martini 1974). These 'chert' bands were later recognised in the Merweville area by Rossouw and de Villiers (1953), both these men having been involved in mapping the Skoorsteenberg.

Rossouw and de Villiers (1953) in fact identified most of the 'chert' in the Merweville area as occurring simply as lenses of silicified argillaceous rocks, being not much different from the other facies present other than by containing higher levels of silica. They did, however, describe several marker 'chert' bands. The other stratigraphic horizon they observe is the Poortjie Sandstone, which has remained an important horizon and is one of the few stratigraphic members of the Beaufort Group west of 24° E that were officially recognised by SACS (1980).

It was only in the late seventies that a significant increase in research in the area began, this time in the interests of uranium exploration. Kubler (1977), while conducting a study on Uranium mineralisation, found that the strata of the western Karoo were too homogenous to realistically subdivide. Soon after, Keyser and Smith (1977) proposed the subdivision of the western Beaufort into a lower Abrahamskraal Formation and upper Teekloof Formation, the latter of which was distinguished by several lithological characters including a greater ratio of mudstone to sandstone and a greater abundance of red and purple mudstones. They also correlated the Abrahamskraal Formation with their Dinocephalian and *Pristerognathus-Diictodon* assemblage zones. While the boundary between the two formations originally sat just above the Poortjie sandstone, it was soon transferred to the base of that unit in order to correspond better with the change in mudstone colouration (Johnson and Keyser 1979).

2.1.3.2 Stratigraphic nomenclature: Members

Due to the flat-lying nature of the beds further north of the Nuweveld Escarpment and the relatively lesser content of sandstone in the Teekloof Formation, this unit was more easily subdivided into members. Turner (1979) saw the expression of a fining up cycle in the western Beaufort with three facies associations: the high-

sinuosity lower facies (at the base of the Abrahamskraal Formation), the low sinuosity facies association (at the top of the Abrahamskraal Formation) and the floodplain facies association, corresponding to the entire Teekloof Formation. Within the otherwise mudstone dominated upper Teekloof Formation he identified an arenaceous zone that he called the Oukloof Member, after its exposure in that pass to the north-west of Beaufort West. This member was also linked to the *Aulacephalodon-Cistecephalus* Assemblage Zone. A member including the Poortjie Sandstone was also proposed, Turner's 'Paalhuis Member', but this was rejected in favour of the name Poortjie Member shortly thereafter (Johnson and Keyser 1979; SACS 1980).

Due to this and the recognition elsewhere in the lower Beaufort Group of fining-upward allocycles (Visser and Dukas 1979; Winter and Venter 1970), the use 'sandstone packages' (intervals of greater relative sandstone content, often manifesting as a higher frequency and thickness of constituent sandstone beds) as marker horizons became more common from this point onwards. These packages were linked to fining-upwards allocycles in the Beaufort Group. Stear (1980) described seven such cycles in the Lower Beaufort, the lower five of which made up the Abrahamskraal Formation. Each megacycle contained a sandstone rich lower part and mudstone rich upper part; he gave the name Moordenaars Member to the arenaceous portion of his megacycle five, which has since been traced as far west as Leeu-Gamka and round to Fraserburg in the north (Cole and Wipplinger 2001; Stear 1980). Stear (1980:40) failed to make any further subdivisions of the Abrahamskraal Formation, explaining this and the lack of any previous such proposals as 'probably because most of the Abrahamskraal Formation is not adequately exposed for detailed investigation.' In addition, he provided names for the argillaceous members above and below the Oukloof Sandstone, being the Steenkampsberg and Hoedemaker members, respectively.

The Abrahamskraal Formation was subsequently elevated to the status of Subgroup by Turner (1981) and split into two formations; the lower, sand dominated Lootskloof Formation and the higher Verlatenkloof Formation. This paper continued to advocate the Paalhuis Member as a discreet sandstone package, inclusive of the Poortjie sandstone horizon, and introduced the similarly arenaceous

Jakhal's Valley Member just below this. However, as discussed by Cole and Wipplinger (2001), these members are shown to be exposed at the top of Verlatenkloof Pass where they both in fact form part of the more continuous Moordenaars Member. At this locality, these latter authors include the Lootskloof Formation and the lower 80m of the Verlatenkloof Formation within the Waterford Formation of the Ecca Group, a decision which is not beyond doubt.

Le Roux (1985) favoured the retention of the Abrahamskraal Formation but found only three allocycles within it. Unlike Stear (1980), he provided an almost complete nomenclature for the alternating arenaceous and argillaceous parts of each cycle, which is now the accepted paradigm for the south-western Karoo (Cole and Wipplinger 2001). Utilising borehole data as well as surface and photogeological exploration, he accepted the genuineness the Moordenaars Member as the arenaceous part of his allocycle 3 and proposed the name Karelskraal Member for the argillaceous part of this cycle, below the Poortjie Member of the Teekloof Formation. The allocycle below was split into the arenaceous Koornplaats Member, which outcrops on the farm Koornplaats 41 in the Moordenaarskaroo, and the argillaceous Wilgerbos Member, appearing along to Wilgerbos River on the farm Elandsfontein 257 in the northern Koup. The Koornplaats Member, according to Le Roux (1985:34), 'underlies the Buffels River region [in the Moordenaarskaroo]...as well as large parts of the Koup Karoo.' Stear (1980) had thought the Moordenaars Member to underlie much of the Moordenaarskaroo, Merweville and the northern Koup, but had also pointed out that this unit was folded below an argillaceous zone in most of the area to the east of Leeu-Gamka, possibly the Karelskraal Member of LeRoux. The Koornplaats Member is therefore not as well exposed in western Koup, while to the North, Cole and Wipplinger (2001) trace it through Verlatenkloof and perhaps as far as Ouberg Pass.

The lowest allocycle comprises the sandstone packages of the Combrinkskraal Member, best exposed along the Gamka River north of Prince Albert, and the argillaceous Leeuvlei Member, after the eponymous farmstead on the farm Leeuwenvalley 50 north of Laingsburg. Le Roux (1985) did not comment on the distribution of these members, although in his description of the stratigraphy of the Drie Vaderlansche Rietvalleyen 49 he stated that the DR-3 deposit (within the

Koornplaats Member) was situated only a few hundred metres from the Ecca-Beaufort contact.

The placement of the contact between the Ecca and Beaufort groups was again reconsidered around this time. Fossils had been found in what was known as the Ecca since the early 20th century (e.g. Barry 1974**;** Rogers and du Toit 1909), despite the presence of reptilian fossils being one of the defining features of the Beaufort strata. With the work of SACS (1980), this criterion combined with certain other lithological characters was officially recognised as distinguishing the Ecca Group from the Beaufort Group and so led to the lowering of the boundary to below the first purple mudstone (Theron 1983). In the SACS (1980) report, the boundary was considered to reflect the change from deposition in a marine environment to a terrestrial, fluvial one. This was refined by Rubidge (1987, 1988) to correspond to the transition from subaqueous to sub-aerial deposition; the contact was therefore lowered again, reducing the thickness of the Waterford Formation of Johnson (1976).

A couple of other studies followed Le Roux (1985), namely Wadley and Hoffman (1986) and Jordaan (1990), which proposed further stratigraphic schemes for the south-western Karoo. Wadley and Hoffman (1986) were working in the Moordenaarskaroo where they identified four members/facies of the Abrahamskraal Formation. The upper, mostly argillaceous unit they called the Verlatenkloof Facies for its outcrop on that pass, which was underlain by the Koornplaats member, retained from Le Roux (1985). Below this, the DR-3 Facies, containing the eponymous uranium anomaly, was now considered separate from the Koornplaats Member. The basal arenaceous unit they named the Klipgat Facies. They did not, however, provide detailed descriptions for any of their units.

Jordaan (1990) conducted a rather comprehensive study utilising multiple sections from around the south-western Karoo. His scheme was based on a rather distinct set of fining-upwards cycles: he recognised only one in the Abrahamskraal Formation, consisting of the lower, arenaceous Combrinkskraal Member and overlying argillaceous Leeu-Gamka Member. He, like Turner (1979, 1981), recognised a single sandstone package equivalent to the Paalhuis Member, inclusive of both the Moordenaars and Poortjie members. This scheme was not adopted by subsequent

researchers but several of his stratigraphic sections have been used by subsequent workers (Cole and Wipplinger 2001; ed. Rubidge 1995).

The first review of these existing stratigraphic regimes was conducted for the Moordenaarskaroo by Loock *et al.* (1994). These authors accepted that of Le Roux (1985), mapping out the area around the Buffels river north of Laingsburg. Initially, according to Cole and Wipplinger (2001), Loock (1993) had confirmed the existence of two distinct sandy members, constituting the Koornplaats and DR-3 members; however, in the later publication the DR-3 sandstone is considered too small to warrant member status and is instead included within the argillaceous Leeuvlei Member as merely a prominent sandstone. Other than this Cole and Wipplinger (2001) remain fairly faithful to the scheme of Le Roux (1985).

A further review was conducted for the Council for Geosciences (Cole and Wipplinger 2001), this time directly in the interests of prospecting for uranium and molybdenum. This report also adopts the scheme of Le Roux (1985) for the south-western Karoo, with only minor modification in that they elevate the DR-3 Sandstone to the level of member and reduce the extent of the Koornplaats Member in a similar fashion to Loock (1993). Although most of the members discussed by them have not yet been accepted by SACS, this report provides the most up-to-date stratigraphic nomenclature for the south-western Karoo.

2.1.3.3 Thicknesses

The thicknesses of stratigraphic units in the west were investigated by Rossouw and de Villiers (1953). Here the thickness of the Lower Beaufort beds was discovered to vary laterally as well as reducing towards the north. Along the southern boundary of the Koup, they found a maximum thickness of 7000 feet (2133.6 m) from the first purple mudstone to the Poortjie sandstone at Elandsberg, near Prince Albert Road. Further to the east they recorded 5680 feet (1731 m) and 5950 feet (1814 m) for the same interval on the farms Blauuw Krantz and Groot Waterval, respectively. In support of the truncation for the Beaufort towards the north, they refer to the borehole SA 1/66 where the Beaufort rocks amount only to some 1480 feet (451 m).

Both Keyser and Smith (1977) and Turner (1979) gave an approximate maximum thickness for the Abrahamskraal Formation of 1800 m based on the work of Rossouw and de Villiers (1953), apparently from the latter's measurement at the Groot Waterval syncline. Apart from discounting the measurement from Elandsberg, Keyser and Smith (1977) also included the Poortjie sandstone in the Abrahamskraal Formation; Rossouw and de Villiers did not include this in their measurement. Turner (1981) also incorporated the Poortjie Sandstone — here as part of his Paalhuis Member — in his Abrahamskraal Subgroup, for which he found a maximum thickness of only around 1100 m.

The Poortjie Sandstone itself appears to thin towards the east, from around 260 m west of Merweville to 160 m in the vicinity of Beaufort West (Stear 1980). This author does not give a locality from which he took his western thickness, but he likely took the thickness around Beaufort West from Turner (1979). Cole and Wipplinger (2001) re-measured Turner's section at Paalhuis and retrieved a thickness of 182.4 m for the Poortjie Member there.

After the Poortjie Member was included within the Teekloof Formation (Johnson and Keyser 1979), the thickness of the Abrahamskraal Formation was reduced correspondingly; indeed, Stear (1980) arrived at a thickness of 1400 m for this formation near Leeu-Gamka. However, when Loock *et al.* (1994) measured the Abrahamskraal Formation in the Moordenaarskaroo they recorded a much greater thickness of 2210 m. This figure surpassed all measurements taken in the previous two decades but, remarkably, was not far off the thickness measured at Elandsberg by Rossouw and de Villiers forty years earlier, albeit in a different locality.

The Abrahamskraal Formation in the south has been re-measured twice more in recent years: at the farm Combrinkskraal, north of Prince Albert, Western Cape Province (Thissen, Ronge and Marpmann 2010) and at Prince Albert Road some 30 km further west (Jirah 2009). The former produced a thickness of 1865 m from the first purple mudstone to the base of the Poortjie Member, as mapped in that area. Combined with the thickness found by Rubidge (1988) for the Abrahamskraal Formation below the first purple mudstone at this locality, being this author's Lithofacies Association 3, the total thickness for the Abrahamskraal Formation at Combrinkskraal would be 2468 m.

Jirah (2009), similarly, produced a section from the first purple mudstone up to the base of the Poortjie Member. This produced a thickness of 1860 m, uncannily close to that of the same unit at Combrinkskraal; furthermore, a subsequent measurement of the Abrahamskraal Formation below the first purple mudstone revealed a thickness of 606 m (Jirah pers. comm. 2011), only 3 m off the measurement for the same interval at Combrinkskraal. The thickness at Prince Albert Road has also now been extended up to the Poortjie Member on the escarpment in the north, thereby adding a further 80m to the total (Jirah pers. comm. 2011). If this is correct, then the total thickness for the Abrahamskraal Formation at Prince Albert Road would be 2575 m, representing the greatest value for this interval yet measured.

2.1.4 Lithostratigraphy West of 24° E (North-West)

The lower Beaufort in the north-western part of the basin has been relatively overlooked as the outcrop is poor when compared to the south. In the Nuweveld region the topography and the bedding are flat, making the stratigraphy almost inscrutable. As such, while Abrahamskraal Formation rocks of *Tapinocephalus* AZ age are known to outcrop there, little attention has been paid to any differences in stratigraphy.

Two SOEKOR borehole cores provide some insight into the structure of the north-western Beaufort rocks (Cole and Wipplinger 2001). These two cores, QU1/65 and AB1/65, show that the Abrahamskraal Formation thins drastically towards the north. There appears to be a slight thinning towards the east as well. Cole and Wipplinger also made surface observations, including the recognition of a south-easterly palaeocurrent direction, and subsequently devised a separate stratigraphic scheme applicable for the north-western extent of the Abrahamskraal Formation.

This scheme provided names for only arenaceous intervals, but identified three in core QU1/65 from a site just north of Fraserburg. The lower two members, named the Kopjesfontein and Davidskolk members after the respective farms where they outcrop, have a south-easterly palaeocurrent direction, implying a north-western source area. At Fraserburg, these members are 60.5 m and 116 m thick respectively, with the former occurring about 40 m from the base of the Beaufort Group. The

third sandstone package here was correlated with the Moordenaars Member in the south, of which 81.5 m is present in the core (Cole and Wipplinger 2001). The entire thickness of Abrahamskraal Formation rocks preserved immediately north of Fraserburg is therefore 507 m.

Further east but only marginally further north, at Paardeberg, the authors found the Kopjesfontein Member to be absent in core AB1/65, presuming it to have pinched out. Here the Davidskolk Member is situated only 50 m above the base of the Beaufort. In addition, as the Moordenaars Member could not be traced north-east Fraserburg, the upper sandstone package here was named the Loxton Member as it can be seen in outcrop near that town. At Paardeberg, the Davidskolk and Loxton members are 97.5 m and 57.5 m thick, respectively, and the entire Abrahamskraal Formation is 390 m thick.

North-east of Victoria West, the stratigraphy becomes harder to record. The lowest Beaufort rocks as far north as Philippolis have been attributed to the Abrahamskraal Formation (Welman *et al.* 2001), while Cole and Wipplinger (2001) record the eastern Middleton Formation as being present to the east of Victoria West. In the absence of core logs, it is hard to support the lithostratigraphic affinity of the lower Beaufort rocks between Victoria West and Philippolis to any known unit; however, they can be attributed to the *Pristerognathus* Assemblage Zone (Welman *et al.* 2001).

2.1.5 Palaeocurrents

Various authors have made records of palaeocurrent direction throughout the Beaufort Group. Only the two broad-scale studies will be discussed here as, between them, they include readings extracted from a wide number publications and that would hardly be bettered here. The first of these was pioneered by Theron (1975) in which he used 11,000 readings from 1,000 localities around the main Karoo basin. On the resulting map, the author identified a predominant north-westerly current direction emanating from the south-east of the basin in the vicinity of what is now Port Elizabeth. As vector strengths emanating from the south-east were also highest, he proposed that this was the primary source area for the Karoo. In addition, he

noticed that the western part of the basin displayed a more northerly current direction and that along the southern rim in this area the flow was almost due east, a phenomenon explained by the presence in the western part of the basin of an embayment and the influence of syndepositional folding related to the Cape Fold Orogeny. Here, vector strengths were low and were attributed to either a low palaeoslope or conflicting input directions. However, Theron admitted that the density of readings was highest in the Free State, where he was based, and lowest in the area west of 24°E.

Cole and Wipplinger (2001) improved on this greatly by increasing their sample size to 38,000 readings, taken overwhelmingly from publications subsequent to 1973 (Cole and Wipplinger 2001:224). By concentrating on the basin west of 24°E, these authors discovered a south-easterly palaeocurrent direction in the north-west of this area. They found that the south-easterly palaeocurrents were restricted to two arenaceous units in the north-west that formed the lower part of the Abrahamskraal Formation there, namely the Kopjesfontein and the Davidskolk members. Overall, three palaeocurrent directions were identified: a north-western which was dominant east of 24°E; a north-eastern, dominant in the western part of the basin; and the south-eastern which occurs as a sliver along the north-west lower boundary of the Beaufort Group (Cole and Wipplinger 2001: figure 2.1).

These studies combine to produce a clear picture of overall palaeocurrent structure in the Karoo Basin. The predominance of northward flow directions indicates that the source area for the majority of the basin was primarily in the south. Further, the basin west of 24°E was also affected by the north-west branch of the Cape Fold Belt which contributed to produce a more easterly flow direction in this area (Cole and Wipplinger 2001; Theron 1975).

2.2 Biostratigraphy

The interest in the fossil remains of the Beaufort Group and their relationship to the lithostratigraphy goes back as far as the earliest geological studies in South Africa. In fact, the two are inextricably linked; when Bain first described the stratigraphy of the Cape Colony, he used the presence of fossil reptiles as a defining character for the upper division, which he named the 'Karoo or Reptiliferous Series' (Bain 1856). The fossil content was recognised as often unique to certain strata by subsequent geologists, with Jones (In Tate 1867) observing the abundance of reptilian bones in the 'Beaufort Beds' and their much greater scarcity in the overlying 'Stormberg Beds'. Since then, the highest resolution subdivisions of the mostly undifferentiated fluvial sediments of the Beaufort Group have been biostratigraphic (e.g. Keyser and Smith 1977; ed. Rubidge 1995).

2.2.1 Early Beaufort Group biostratigraphy

The first palaeontologist to officially propose a stratigraphic division of faunas from what would become the Karoo Supergroup was Seeley (1892a). In his article, primarily on *Pareiasaurus*, he describes a division of the fossiliferous rocks into five 'zones'. The second zone is that of pareiasaurians, which he indicates to 'extend from south of Fraserburg Road Station 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 1892a:312). Although he does not explicitly mention it, this corresponds to the northern part of the Koup region of the Western Cape Province today. It also corresponded to the lower part of the 'Upper Karoo Beds' as drawn by Dunn (1887), a work that Seeley used extensively in this article. Seeley's (1892a) complete list of zones, the middle three of which occur in what is now the Beaufort Group, was:

5. Zone of zanclodonts
4. Zone of highly specialised theriodonts
3. Zone of dicynodonts
2. Zone of pareiasaurians

1. Mesosaurian zone

This biostratigraphic organisation of fossil occurrences was subsequently used by palaeontologists and geologists to supplement the lithostratigraphy. Rogers (1903) and Rogers and Schwartz (1903) grouped the middle three zones into a division they called the 'Beaufort Series', based upon Dunn's 'Upper Karoo Beds' (Dunn 1873). Du Toit (1905) further recognised that the zone of specialised theriodonts corresponded to a lithologically distinct interval of red beds he called the 'Burghersdorps Beds [*sic*]'. This tripartite zonal grouping for the Beaufort Series was then adopted by the two important textbooks that were independently produced three years later, Rogers (1905) and Hatch and Corstorphine (1905).

Shortly thereafter, a new subdivision of the Beaufort Series was introduced by Broom (1906a, 1906b) that was quite innovative and still forms the basis of the biostratigraphic system used today. In Broom's view, there were six biozones in the Beaufort Series, rather than three. The 'Upper Beaufort Beds' were subdivided into the upper '*Cynognathus* Beds' and lower '*Procolophon* Beds', which were likely equivalent to the 'Burghersdorp Beds' of du Toit (1905). Below this the '*Lystrosaurus* Beds' comprised the middle subdivision of the 'Beaufort Beds', while the 'Lower Beaufort Beds' consisted of the lower '*Pareiasaurus* Beds', now followed by the *Endothiodon* and *Kistecephalus* [*sic*] beds. As the preceding paragraph indicates, Broom certainly mixed his terminology but, here using 'Series' for larger stratigraphic units and 'Beds' for biozones, his biostratigraphic scheme was thus:

<u>Upper Beaufort Series</u>
6. *Cynognathus* Beds
5. *Procolophon* Beds
<u>Middle Beaufort Series</u>
4. *Lystrosaurus* Beds
<u>Lower Beaufort Series</u>
3. *Kistecephalus* Beds
2. *Endothiodon* Beds
1. *Pareiasaurus* Beds

Until this point, the lithostratigraphic subdivision of the Beaufort Series below the 'Burghersdorp Beds' of du Toit (1905) had been stymied by the homogeneity of the strata and had only been roughly split biostratigraphically into the *Pareiasaurus* and *Dicynodon* 'zones'. Broom's six-fold subdivision became an important method of identifying the level of Lower Beaufort strata, being readily adopted in the second edition of Rogers' book on the geology of the Cape Colony (Rogers and du Toit 1909), and was not greatly improved upon for many years.

Very little alteration was made to this paradigm until the work of Kitching (1970); however, several interim publications are worth noting. D. M. S. Watson, who had himself visited the Karoo, found Broom's (1906a, 1906b) biozone designations to be correct but inadequate in detail and so provided a thorough description of them all (Watson 1914a). He further clarified the definition of the 'zones' (reverting to Seeley's terminology) through the suite of reptiles found in each, the geographical extent of the exposures and the personalities involved in collecting each level. Watson's (1914a:203) account of the '*Pareiasaurus* Zone' (soon to become the '*Tapinocephalus* 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 mentions 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. Importantly, this author 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.

Above the *Pareiasaurus* zone, Watson (1914a:204) writes that:

> *The* Endothiodon *Beds, that are seen in the field to follow those of the* Pareiasaurus *zone...have never yielded any Pareiasaurian remains and no Deinocephalians. There are*

many Therocephalia, particularly Gorgonopsids...[and] numerous large Endothiodons and all the Dicynodons are very small.

Even at this stage a distinct faunal turnover at the top of the '*Pareiasaurus* zone' was evident.

Another of the bountiful observations made by Watson was that more the armoured species of pareiasaur were found in the '*Cisticephalus* [*sic*] zone', mentioning the genus *Propappus*. He also mentions that in the east of the Cape Province, the presence of the type locality of *Pareiasaurus* at Blinkwater would suggest the presence of the eponymous zone but that '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* zone form' (Watson 1914a:207).

Such an observation was quickly developed and after re-examining the British Museum's pareiasaur material decided that the name '*Pareiasaurus* zone' was misleading, as that genus was indeed a '*Cistecephalus* zone' form, and that in any case pareiasaurs were known from both zones (Watson 1914b). 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. His breakdown therefore became:

6. *Cynognathus* zone
5. *Procolophon* zone
4. *Lystrosaurus* zone
3. *Kistecephalus* zone
2. *Endothiodon* zone
1. *Tapinocephalus* zone

The tremendous usefulness of creating a map to display the area of exposure for each of these biozones was not lost on Robert Broom. In an article detailing the type specimens acquired by the American Museum of Natural History from him, Broom (1915) followed Watson's example and included a map of his biozones. He did not, however, heed the recommendations of Watson's (1914b) work and so continued to use the '*Pareiasaurus* zone'.

Perhaps more pertinent is that Broom considered the ornamented pareiasaur *Propappus* to occur in the '*Endothiodon* zone', rather than in the '*Cistecephalus* zone' as reckoned by Watson (1914a) who, on the contrary, believed the '*Endothiodon* zone' to be devoid of pareiasaurs. However, Broom (1915:107) continued further and mentioned two intra-zonal patterns of distribution: firstly, 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'; secondly, in the '*Cistecephalus* zone', where he simply stated that 'the lower beds are characterised 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 also appear to be gross overestimations for the upper zones. It is likely they were very rough guesses. For instance, 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) re-designation for the lowest Beaufort biozone, adopting the name '*Tapinocephalus* zone'. Other than this there was little deviation from the existing scheme, although he does provide another map. Thereafter, no publications made any further reference to the distribution of faunas outside this biostratigraphic paradigm until 1942, when Watson wrote a summary of Permian and Triassic tetrapods (Watson 1942). Here, while retaining the existing biozones, he recognised several patterns regarding the distribution of taxa within those zones 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 and only small toothless dicynodonts. The B zone in his view 'probably contain[s] only small Endothiodonts of different genera and yield also Dicynodons of medium size' (Watson 1942:111). He also finds a similar pattern in the *Cistecephalus* zone, finding there a lower A zone that contains *Cistecephalus* itself

and a B zone which is dominated by 'large Dicynodons...and advanced Gorgonopsids.' He even postulates the existence of a C zone containing diverse therocephalians, but does not include this on his diagram (Watson 1942:115). The '*Tapinocephalus* zone' again remains unchanged, the apparent disappearance in pareiasaurs and dinocephalians apparently providing a very natural boundary.

2.2.2 Early subdivision the *Tapinocephalus* Assemblage Zone

The first observed differences in tetrapod fossil taxa within the *Tapinocephalus* Zone (now with the latter word capitalised) only occurred several years later, strangely enough during the production of a geological map of the Merweville area (Rossouw and de Villiers 1953). This map covered the area cited by all previous authors as the primary outcrop area for the *Tapinocephalus* Zone and Rossouw and de Villiers made extensive lists of the fossil specimens found in the region. They then used their understanding of regional stratigraphic heights 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 round Merweville.

The lower zone lies below and immediately above what they term the 'Droëfontein chert', while the upper zone surrounds the 'Green "chert" and Poortjie sandstone' (Rossouw and de Villiers 1953:59). Between these two they loosely designate an intermediate zone. It is astonishing that from relative abundances of taxa within each zone these authors then draw several important and enduring conclusions about faunal distribution 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 mention a 'phenomenal' increase in dicynodont abundance from the lower to upper zones. Rossouw and 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 sub-equal in abundance, pareiasaurs half as common.

1. Zone of the Droëfontein 'chert'

Pareiasaurs and dinocephalians dominant and sub-equal in abundance, dicynodonts moderately abundant.

Such a division was expanded, if not directly acknowledged, by Boonstra (1969), who had been working on the *Tapinocephalus* Zone since the late 1920s. Boonstra didn't question the name of the zone itself but he did record in this publication some opinions on its integrity. Like Rossouw and de Villiers (1953), Boonstra determined there to be three subdivisions within the *Tapinocephalus* Zone but, conversely, these were different in composition and not lithologically constrained.

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 and de Villiers (1953), Boonstra (1969) considered pristerognathid therocephalians to decline in abundance into the middle division.

Most radically, Boonstra's upper division is characterised by the disappearance of most families and the severely reduced abundance of those that remained. The only taxa he records within this division are dicynodonts, hipposaurids, galesuchids, pristerognathid therocephalians and the parareptile *Eunotosaurus*, representing a 63% loss of families. This work therefore displays for the first time the point at which dinocephalians and the early pareiasaurs disappear, along with the faunal composition immediately succeeding it.

This upper division, before the *Endothiodon* Zone fauna appeared but with an apparent absence of dinocephalians and pareiasaurs, was later to be developed but not before the first major restructuring of the Beaufort Group biostratigraphy since Broom (1906a, 1906b).

2.2.3 Beaufort Group biostratigraphy after 1970

After collecting throughout the Beaufort Group for since 1945, Kitching (1970) became the first palaeontologist to challenge the Broomian paradigm. The biozone nomenclature was in the most part retained but the lithostratigraphic interval covered by most was modified and both the *Endothiodon* and *Procolophon* zones were discarded. The former became absorbed into the '*Cistecephalus* zone' (again in lower case) 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 reaches 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 was, as we have seen, 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.'

The former *Procolophon* zone was now absorbed into the '*Lystrosaurus* zone', as had been suggested by Hotton and Kitching (1963), while the *Cynognathus* zone remained in its former state. Kitching referred matters of the *Tapinocephalus* zone to Boonstra (1969) and does not implement any further subdivision of that biozone. In terms of its geographic distribution, Kitching (1970) now confined the *Tapinocephalus* Zone to the very south-west 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) zonal breakdown 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 reference also included a map of these localities which were represented symbolically by biozone.

Soon after Kitching's (1977) publication, Keyser and Smith (1977) published another biostratigraphic division of the Beaufort Group, which for the first time was closely integrated with their proposed lithostratigraphic units. This was primarily aimed at the south-west 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.

This scheme differed from that of Kitching (1977) in several important areas, especially in nomenclature. The '*Cynognathus* Zone' was renamed for the more common dicynodont genus *Kannemeyeria*. The '*Daptocephalus* Zone', while maintaining its integrity, was renamed the *Dicynodon* Assemblage Zone (AZ) because the former genus had been synonymised with the latter (Cluver and Hotton 1981). The name '*Cistecephalus* Zone' was discarded due to its confusing history of use, as well as its uneven occurrence; instead, Keyser and 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 similarly dropped that genus as an index fossil in favour of the dicynodont *Tropidostoma*; this they did because they considered *Endothiodon* to be relatively rare and as 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 support this designation with lithological characteristics.

Keyser and Smith (1977) also formally subdivided the *Tapinocephalus* Zone, based partly on the work of Rossouw and 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 and 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 abundances of taxa through the Dinocephalian Assemblage Zone, Keyser and Smith (1977:18, figure 3.1) only acknowledge some change for *Embrithosaurus,* which becomes less abundant in its upper division.

Keyser and Smith's (1977) biozone designations are 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

Rubidge (1984, 1987, 1988) and Rubidge *et al.* (1983), working on the lower contact of the Beaufort Group in the south-west Karoo basin, then extended the Abrahamskraal Formation down into what had previously been considered to be Ecca Group rocks to a stratigraphic horizon he 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 recognised an entirely new biozone comprising a therapsid fauna dominated by *Eodicynodon* and 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 map of the entire Beaufort Group, rather than just the south-west of 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

With the exception that a tripartite division of the *Cynognathus* Assemblage Zone is now often accepted (Abdala *et al.* 2005; Hancox *et al.* 1995; Hancox 1998; Neveling *et al.* 1999; Shishkin 1995), this is the accepted biostratigraphic scheme for the Beaufort Group.

2.2.4 Recent Subdivision of the *Tapinocephalus* Assemblage Zone

Loock *et al.* (1994), working on the *Tapinocephalus* AZ to the north of Laingsburg in the Western Cape Province, linked the stratigraphic ranges of taxa with lithostratigraphic units in this area, thereby creating the first union of litho- and biostratigraphy within the *Tapinocephalus* AZ. These authors found strong support for the idea of Rossouw and 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. They also found this change in abundance coincided with the boundary of the Koornplaats and Wilgerbos members of the Abrahamskraal Formation. While they did not collect thoroughly in the uppermost part of the *Tapinocephalus* AZ, the assumption would be that its upper 540m were dominated by dicynodonts, if this portion was homogeneous as suggested by Boonstra (1969).

Loock *et al.* (1994) also observed decreases in abundance within other taxa. Unlike Rossouw and de Villiers (1953), Boonstra (1969) or Keyser and Smith (1977), they found pareiasaurs to be equally common in the upper and lower divisions of their field area. However, these results, while novel, were based on a fossil sample collected over only a few field seasons. The primary merit of the study lies in its association of lithostratigraphy with fossil occurrence and in that it has remained, until now, 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 and Rubidge 2010; Modesto *et al.* 2002; Modesto *et al.* 2003) as well as the morphological and stratigraphic review of existing ones (e.g. Angielczyk and Rubidge 2009, 2012) has contributed to a subdivision of the *Tapinocephalus* AZ based on the appearance of small dicynodonts (Angielczyk and Rubidge 2012; Rubidge and Angielczyk 2009).

Rubidge and Angielczyk (2009) suggest that *Eodicynodon* occurs up to 1100m above the base of the Abrahamskraal Formation, while *Diictodon* only appears at 1900m. They indicate that *Robertia* first appears above the range of *Eodicynodon* but below that of *Diictodon* but are reticent to state where *Colobodectes* would fit in as it does not occur in the south of the basin. Angielczyk and Rubidge (2010), on the other hand, provide

a stratigraphic ordering for the first appearances of the small dicynodonts. This is as follows:

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. This forms the basis of the biostratigraphic approach to this project.

2.3 Karoo Basin Development

In comparison to the lithostratigraphy and palaeontology, the overall depositional history of the Karoo Basin itself has been rather neglected. The first substantial mention of a possible scenario for the basin's formation was made by A.H. Green (1888), building on all work done prior to that in the Cape Colony, combined with his own extensive work. Du Toit (1937) recognized the Gondwanaland-wide continuation of the Cape Fold Mountain chain in his reconstruction of that supercontinent but otherwise little progress was made until the latter half of the Twentieth Century.

Lock (1978, 1980) studied the Cape Fold Mountains and first suggested the role of subduction in the formation of this structure. He had recognised that subduction explained the formation of a continuous mountain chain coinciding with the southern margin of Gondwanaland; yet he also noted that in South Africa there existed a geographic separation between the continental margin of Gondwanaland and the Cape Fold Mountains. He explained this by positing the adherence of the subducting slab to the underside of the continental crust, a process termed 'flat-plate subduction.' The unusual inland nature of the mountain belt was later attributed to a zone of weakness which has resulted from crustal thinning during deposition of the Cape Supergroup (Tankard *et al.* 1982).

The Karoo Basin itself is mostly taken to have formed as a result of isostatic subsidence associated with the Cape Fold Orogeny, being classified as a retroarc foreland basin (Catuneanu 1998; Cole 1992; de Wit and Ransome 1992; Johnson 1991; Lock 1980). The end of Cape Supergroup deposition in the Carboniferous was followed by a hiatus of many millions of years, which is probably related to the early uplift of this region (Visser 1987) before Karoo Supergroup sedimentation began north of the mountain range. The source of the sedimentary infill of the early Karoo Basin would be expected to come from the incipient Cape Fold Mountains but it seems that a granitic or recycled orogen was the provenance of the Ecca and Lower Beaufort Groups (Anderson 2004; Johnson 1991). This supports the presence of land south of the Cape Fold Mountains where subduction related volcanism in the volcanic arc could provide appropriate sediment and, perhaps, suggests that the orogenic front was very far south leaving much of the Cape Supergroup uneroded until Middle Beaufort times (Cole 1992; Johnson 1991). However, it has been proposed that the subduction subduction trench was situated not much further than 500 km to the south of the modern Cape Fold Mountains, which restricts the position of the volcanic arc to less than that distance.

Hälbich (1983) recorded phases of metamorphism in the Cape Fold Belt and dated the termination of these phases, with the first ending some 292 million years ago (Ma). The influence of tectonics on the formation of the Karoo Basin was never subsequently in question, only the extent of that influence was. Most researchers considered that only large-scale stratigraphic horizons were the direct result of tectonic activity and proposed that below the Katberg Formation, all arenaceous packages were due to an increase in mechanical weathering (Cole 1992; Cole and Wipplinger 2001; Johnson 1991; Turner 1985). This included the Poortjie Member of the Teekloof Formation (Turner 1985).

Climatic studies of the Karoo Basin have provided mixed results. Several studies undertaken in the Eastern Cape Province have indicated a humid climate throughout the Lower Beaufort up until deposition of the Katberg Formation (Catuneanu and Bowker 2001; Johnson 1976; Stavrakis 1980), while in the south-western part of the basin an arid climate has been proposed for the entire deposition of the Beaufort Group there (Smith 1990; Stear 1980). The increase in aridity in the west has been

suggested as the cause behind deposition of the Poortjie Member (Cole and Wipplinger 2001). This work suggests a distinct east–west difference in climate within the Karoo Basin, at least during deposition of the Lower Beaufort before the eastern part of the basin developed an arid climate as well (Smith *et al.* 1993).

A primary tectonic cause for the formation of the Poortjie Member was ruled out because of the lack of coarser material, such as is evident in the Katberg Formation (Cole 1992; Cole and Wipplinger 2001; Johnson 1991). However, Cole and Wipplinger (2001) did posit that differential subsidence played an important role in the formation of the younger members of the Teekloof Formation, with increased subsidence leading to the deposition of the more argillaceous units and quiescence to the more arenaceous ones. Such an hypothesis had been proposed by Allen (1978), whereby low subsidence rates lead to the reworking of sediments and a relative increase in sandstone. This would be accentuated by the basin-ward movement of coarse deposits during periods of quiescence as less accommodation space would be available in the proximity of the orogen (Flemings and Jordan 1989). The sandstone-rich stratigraphic members of the lower Beaufort Group have also been attributed to allocyclic processes (e.g. Smith 1989; Stear 1980).

Greater tectonic controls on sedimentation in the Karoo Basin were suggested by Catuneanu *et al.* (1998). In this scenario, the Karoo Basin was described as demonstrating reciprocal flexural responses to orogenic loading with out-of-sync sequence deposition in areas either proximal or distal to the orogen, in this case the Cape Fold Mountains. The effects of tectonic processes were also extended to account for sub-formational sandstone packages as well as larger-scale stratigraphic units (Catuneanu and Bowker 2001; Catuneanu and Elango 2001). Both these latter studies focused on the Lower Beaufort Group in the Eastern Cape and mention that the palaeoclimate throughout the sequence appears stable, ruling out climatic controls on stratigraphy.

The foreland basin model for the Karoo Basin does not exclusively rest on direct orogenic loading. Dynamic subsidence is accepted as a secondary factor and it has been pointed out that only dynamic subsidence could account for the large size of Karoo Basin (Catuneanu *et al.* 1998; Pysklywec and Mitrovica 1999). This phenomenon is accepted by an alternative hypothesis to the flexural model, that of a

ramp syncline. This proposes the Karoo Basin formed by the broader, more rigid subsidence of basement blocks in response to mantle flow produced by subduction (Tankard *et al.* 1982; Tankard *et al.* 2009). This model accepts the formation of the Cape Fold Belt only in the Triassic, near the end of Karoo sedimentation, supported by the first occurrence of recycled sediments from the Cape Supergroup in the earliest Triassic Katberg Formation of the Beaufort Group (Johnson 1991). Furthermore, the ramp syncline model utilises geophysical evidence that suggests the northward termination of units along fault boundaries and that the difference in the composition of these basement blocks would prohibit a uniform flexural movement.

2.4 The Terrestrial Middle Permian

Beyond the Karoo Basin, there are sedimentary basins of Middle Permian age that have yielded tetrapod faunas. The number of localities that have produced similarly aged assemblages to those of South Africa have increased notably in recent years, both in Gondwana and Laurasia (Cheng and Li 1997a, 1997b; Cisneros *et al.* 2012; Malabarba *et al.* 2003; Langer 2000; Simon *et al.* 2010). These studies have provided a greater dataset for exploring Middle Permian biodiversity changes and contributed to the confirmation of the global extinction of dinocephalians and an overall biotic crisis on land at this time (Lucas 2009).

Given its continuity and rich fossil fauna, the Beaufort Group is crucial to the understanding of Middle Permian terrestrial biosphere but this can only be properly explored in context. This section aims to examine the current literature regarding Middle Permian terrestrial tetrapod faunas.

2.4.1 Middle Permian tetrapod faunas

2.4.1.1 Russia

The Middle Permian fossil tetrapod fauna of Russia has been known since the 18th Century, although it was only in the mid 19th Century that the fossils began to be properly described (e.g. Kutorga 1838; von Eichwald 1846). These publications coincide with the first discoveries of tetrapod fossils in South Africa, although it would be some time before the faunas were compared (Owen 1876). The Russian material was at first discovered through mining activity in the Copper Sandstones to the west of the Ural Mountains but, as a result of targeted palaeontological collecting, tetrapod fossils have since been found in a broad arc extending as far north as the Mezen River, east of Archangel. Today, the Russian sequence represents the most speciose Middle Permian fauna outside South Africa (Battail 2000; Rubidge 2005).

Since the mid 20th Century, the Russian Permian faunas of the Copper Sandstones have been separated into four 'zones' (Efremov 1940). This was altered by later workers (e.g. Chudinov 1969, 1983; Efremov and V'jushkov 1955) who accepted three zones: a lower dinocephalian fauna, best represented by the Ocher locality (Zone 1); an upper dinocephalian fauna, best represented by the Isheevo locality (Zone 2); and a pareiasaurian-gorgonopsian fauna, represented by several localities such as Kotel'nich and Sokolki (Zone 3) (see Modesto and Rybczynski 2000). Of these, zones 1 and 2 are securely of Middle Permian age and are therefore of interest here (Rubidge 2005 and references therein).

Above zones 1 and 2, the rather broad Zone 3 probably corresponds to the Late Permian (Battail 2000; Modesto and Rybczynski 2000). In the lower part of the Kotel'nich locality, probably the oldest of the former Zone 3 localities, the presence of cynodonts (Hopson and Kitching 1972; Tatarinov 1987), the presence of the dicynodont *Australobarbarus* (a close relative of *Tropidostoma*) (Angielczyk and Kurkin 2003b; Kurkin 2000) and the absence of dinocephalians, suggests an early Late Permian age, equivalent to the *Tropidostoma* Zone of South Africa (Rubidge 2005). Alternatively, the presence of the scylacosaurid therocephalian *Scylacosuchus* (Battail and Surkov 2000) and the rather basal pareiasaur *Deltavjatia* (Lee 2000; Modesto and

Rybczynski 2000) may suggest a correlation with the *Pristerognathus* AZ of South Africa, in the latest Middle Permian (Benton 2012). However, as the purported scylacosaurid *Hexacynodon* is found securely in the latest Permian Vyazniki Assemblage (Modesto and Rybczynski 2000; Abdala *et al.* 2008), the presence of scylacosaurids seems not to be a good indicator of Middle Permian affinities in Russia and so, contrary to Benton (2012), the Kotel'nich fauna and younger are considered here as Late Permian and therefore not discussed in detail.

In addition, an older, early Kazanian fauna that contains some of the oldest therapsids has been reported in Russia at various sites in the Copper sandstones of Bashkorostan (see Modesto and Rybczynski 2000). Therapsids from strata assigned to the lower Kazanian include the anteosaurid *Microsyodon* (Ivakhnenko 1995; Kammerer 2010); the dinocephalian genus *Brithopus*, which was formerly seen as an anteosaurid but is in fact a probable estemmenosuchid (Kammerer 2010); and the problematic, potentially dinocephalian family Phreatosuchidae (Battail and Surkov 2000; Efremov 1954; Modesto and Rybczynski 2000).

Given the redefinition of absolute ages for the Russian continental stages, the actual age of these fossils is uncertain. If this horizon falls within the Roadian stage, then it would indeed represent one of the earliest therapsid faunas, though it could equally fall within the early Wordian. Furthermore, the fossil material currently known from all localities of this age is very poorly preserved and was collected over a diffuse area (Modesto and Rybczynski 2000). Therefore, until better material is found and the stratigraphy more clearly defined, this early fossil fauna will remain enigmatic.

Ocher (Ochyor or Ezhovo) fauna

The Ocher fauna, discovered at a locality in the western Perm Krai, was first fully recognized in the 1950s and since then has come to represent one of the main Middle Permian Russian faunal assemblages (e.g. Chudinov 1969, 1983; Efremov and V'jushkov 1955; Rubidge 2005). In the past the Ocher fauna was attributed to the late Kazanian (Battail 2000) or perhaps straddling the boundary of the Kazanian and the Tatarian (Modesto and Rybczynski 2000) but, since the shift in temporal correlations made by Wardlaw *et al.* (2004) and the resultant linkage of the Russian

units with the global timescale (Resolutions 2006), most authors now accept a Wordian age for this assemblage (Abdala *et al.* 2008; Benton 2012; Fröbisch 2009; Rubidge 2005).

The Ocher fauna contains the fossils of several therapsid groups, including dinocephalians (see Battail 2000; Rubidge 2005). Of these, the basal tapinocephalian estemmenosuchids are known from several genera including *Estemmenosuchus*, *Anoplosuchus*, *Molybdopygus* and *Zopherosuchus* (Battail and Surkov 2000). Anteosaurids are represented securely by *Archaeosyodon*; older publications also recognise the genus *Chthamaloporus* (e.g. Battail 2000; Battail and Surkov 2000) but this genus is not mentioned by Kammerer (2010) in his review of the Anteosauridae. Biarmosuchians are represented by *Biarmosuchus*, *Eotitanosuchus* and *Ivantosaurus*, while the basal anomodont *Otsheria* also occurs at Ocher. Other taxa have been named from this locality, such as several genera of enigmatic group Pthinosuchia, but much of this fossil material is poor and is therefore of dubious identity (Battail 2000).

Belebey fauna

The Belebey locality in Bashkorostan, which has produced relatively few fossil taxa and very few therapsids, is of relevance as it is usually considered similar in age to the Ocher complex (Chudinov, 1983; Modesto and Rybczynski 2000; Battail 2000); most recently, it has been placed within the Kazanian (as it is defined now) suggesting that it may be slightly older than Ocher (Benton 2012) but this has yet to be corroborated. The Belebey fauna mostly consists of platyoposaurid temnospondyls, the nycteroleterid parareptile *Nycteroleter* and the bolosaurid parareptile *Belebey* (Modesto and Rybczynski 2000); other taxa include the poorly known bolosaurid *Davletkulia* (Ivakhnenko 1991a), the nycteroleterid *Rhiphaeosaurus* (Lee 1995) and the 'biarmosuchid' *Phthinosaurus* (Efremov 1940; Sigogneau-Russell 1989), all of which are represented by poorly preserved and incomplete material.

Isheevo fauna

The early Tatarian 'Zone 1' fauna of Russia, typified by the locality at Isheevo in the Republic of Tatarstan, is known in particular for its suite of dinocephalian therapsids. Of these, the best known is probably the tapinocephalid dinocephalian *Ulemosaurus*, which is currently the only tapinocephalid found in Russia. Chudinov (1983) considered that this genus was a junior synonym of the South African form *Moschops* but, more recently, its validity has been maintained as it differs from *Moschops* in several key features (Güven pers. comm. 2012). Other dinocephalians from this assemblage are all anteosaurids, the largest being *Titanophoneus*, which is known from two species (Kammerer 2010). The smaller *Syodon* also occurs in strata of this age, as does *Notosyodon* (Chudinov 1968; Kammerer 2010).

The Isheevo fauna has also been given attention in recent years for its basal anomodonts (e.g. Fröbisch 2008, 2009); both *Venjukovia* and *Ulemica* have been found in the early Tatarian. The fauna also includes the seymoriamorph *Enosuchus* and the parareptile *Lanthanosuchus*.

Mezen fauna

The Mezen fauna is more difficult to place temporally. This assemblage is less constrained to a single site, rather being a series of localities situated along the Mezen River in the north of Russia, and contains taxa that link it with both the Isheevo and Ocher faunas. Amniote fossil taxa known from the Mezen fauna inlcude the parareptiles *Nyctiphruretus*, *Macroleter*, *Nycteroleter*, *Bashiroleter* and *Lanthaniscus*; the therapsids '*Biarmosuchus'* and *Niaftasuchus*; the caseid *Ennatosaurus*; and the varanopids *Mesenosaurus* and *Pyozia* (Anderson and Reisz 2004; Battail 2000; Lozovsky 2005; Reisz and Berman 2001).

Ivakhnenko (1991b) observed that the Mezen fauna was difficult to correlate with either Ocher or Isheevo. This was echoed by Modesto and Rybczynski (2000), who recorded that Mezen shared closely related genera with several other Russian faunal assemblages of varying age; however, they also indicated that most Russian palaeontologists consider the most exposed svita (formation) to be lower Tatarian in

age and therefore coeval with Isheevo. Indeed, as the Mezen Basin is so large, it is possible that the lower Mezen fauna is still contemporaneous with the Ocher fauna, as presented in Benton (2012). The assignment of an age for the Mezen fauna in confounded further by the presence of the parareptile *Macroleter* in North America, where it occurs in rocks of early Middle Permian or late Early Permian age (Lucas 2002; Reisz and Laurin 2001, 2002).

2.4.1.2 China

The Middle Permian in China has not been extensively studied but recent work has revealed several important genera that occur in the Xidagou Formation, near Dashankou in Gansu Province. This assemblage has similarities with the Russian faunas in the presence of the bolosaurid *Belebey*, as well as the basal anteosaurid *Sinophoneus* (Battail 2000; Cheng and Li 1997a). Specimens assigned to the genus *Stenocybus* were firstly thought to represent a family of dinocephalians (Cheng and Li 1997b), then a basal anteosaurid (Battail 2000) but, most recently, *Stenocybus* has been considered a junior synonym of *Sinophoneus* (Kammerer 2010).

The Xidagou Formation has also produced the basal anomodont *Biseridens*. This genus was initially described as an eotitanosuchid (Li and Cheng 1997) but it was later suggested that it resembled the Russian anomodont *Ulemica* (Battail 2000). This was confirmed by Liu, Rubidge and Li (2010), who described several more newly discovered and better preserved specimens.

One of the most interesting tetrapods from the Xidagou Formation is *Raranimus*, which has been described as the most basal therapsid but is based on only one fragmentary specimen (Liu *et al.* 2009).

2.4.1.3 Brazil

Dinocephalian teeth from the families Titanosuchidae and Anteosauridae have been found at the Posto Queimado locality in the Rio do Rasto Formation of the Parana Basin, southern Brazil (Langer 2000). The dinocephalian presence was very recently

supplemented by the discovery of the anteosaurid *Pampaphoneus*, represented by a well preserved skull (Cisneros *et al.* 2012).

Pareiasaurs also occur in the Rio do Rasto Formation, namely the genus *Provelosaurus* from Bage Aceguà (Araujo 1985; Lee 1997) and Posto Queimado (Malabarba *et al.* 2003). This form was described by Lee (1997) to fall intermediate between the early, large species from the *Tapinocephalus* AZ and the later, more heavily armoured pareiasaurs of the *Cistecephalus* AZ in South Africa.

The basal anomodont *Tiarajudens*, which is closely related to the South African genus *Anomocephalus*, has also been recovered from the Posto Queimado locality (Cisneros *et al.* 2011). Several sites have yielded temnospondyl remains (Langer 2000).

2.4.1.4 Zimbabwe

Dinocephalian fossils have been known from Zimbabwe for some time, although the number of specimens recovered there is very low. The most complete fossil specimen was a tapinocephalid skull referred to *Criocephalus gunyankaensis*, retrieved from the Busi Valley in northern Zimbabwe (Boonstra 1946, 1969; King 1988); this skull has been lost and the species declared a *nomen nudum* (Güven pers. comm.). More recently, further dinocephalian remains attributed to the Anteosauridae and Tapinocephalidae have been found in the Madumabisa Mudstones in the north-west of the country (Lepper *et al.* 2000). This latter material is very fragmentary, consisting mostly of isolated teeth, but more recently the Madumabisa Mudstones have also produced a partial tapinocephalid skull that is closely allied to *Avenantia* (Munyikwa 2001).

Other than dinocephalians, a probable pristerognathid therocephalian is mentioned by Boonstra (1969) as coming from Zimbabwe, though no details are provided.

2.4.1.5 Tanzania

Recent collecting in the Ruhuhu Formation of southern Tanzania has revealed the presence of tapinocephalid dinocephalians there (Simon *et al.* 2010); however, as the only elements so far retrieved are isolated teeth, identification beyond family level is not possible.

2.4.2 Dating

2.4.2.1 The Russian record

Traditionally, determining of age of terrestrial Middle Permian deposits has relied heavily on the Russian record. More recently, the Russian scheme has declined in use with the increasing influence of the well-dated marine stages of the USA and China (e.g. Harland *et al.* 1990; Wardlaw *et al.* 2004) and the realization that the Russian units may be temporally variable (Steiner 2006). The recent extraction of radiometric dates from most Permian biozones of the Beaufort Group in South Africa has greatly aided in age assessment there (Rubidge *et al.* 2013) but, currently, the Russian paradigm is still used extensively. This is primarily due to the magnetostratigraphic and marine biostratigraphic work which has been undertaken throughout the Russian, which until now was the only way of correlating the terrestrial and marine sequences of this period. As a result, in order to understand the age designations for Middle Permian terrestrial faunas, it is essential to have some understanding of the Russian stratigraphic system and its relation to the current global marine timescale (International Commission on Stratigraphy 2012; Figure 3).

The pertinent part of the Russian stratigraphic scheme comprises the Kazanian, Tatarian and Urzhumian stages. The first two stages, along with the older Ufimian, were first proposed as constituting the 'Upper Permian' of the Russian sequence (Neachaev 1915), a period which in modern terms would extend from the latest Early Permian to the base of the Triassic. While the Kazanian and Tatarian have persisted into modern usage, the Ufimian has fallen from favour in recent years; it has been argued that it represents a genuinely definable stage in the Urals by

Lozovsky *et al.* (2009) but these authors also confine it to the Early Permian. As such, it is not considered here.

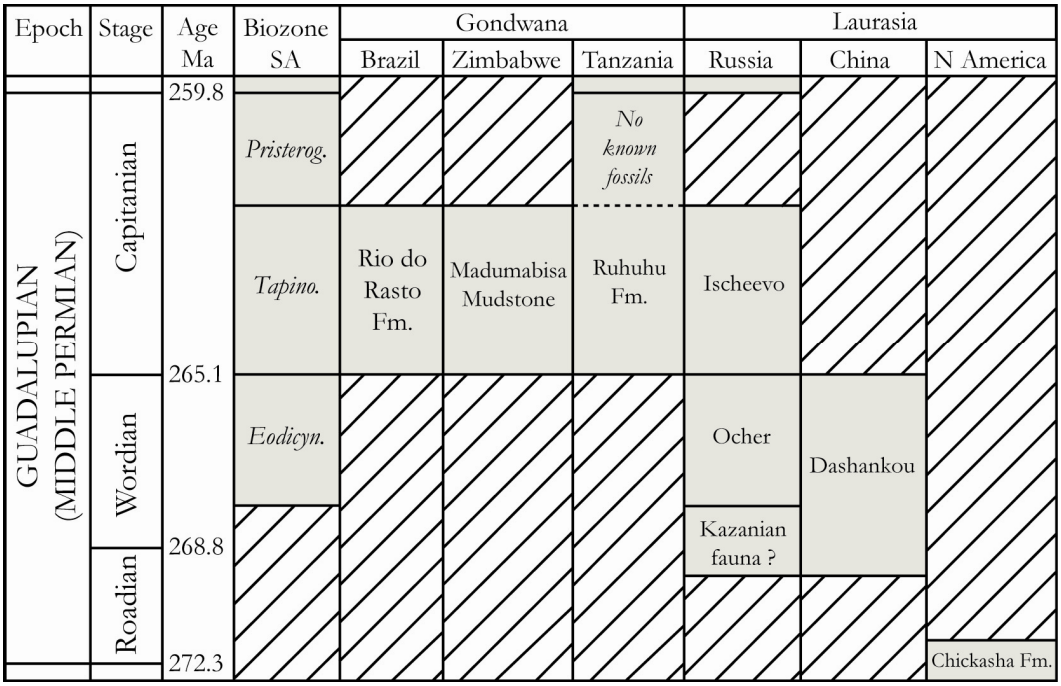


Figure 3. Global tetrapod bearing terrestrial deposits of Middle Permian age. Ages of stage boundaries taken from ISC (2012).

Of particular significance is that the quality and accuracy of absolute ages assigned to all Permian units, as well as the correlation between different schemes, have varied greatly up until now. While I omit to discuss the deep history of Permian chronology, it is important to bear in mind that dates provided in older literature will disagree significantly with more recent ones.

The Kazanian

Currently, the Kazanian is considered to be equivalent to the Roadian Stage and perhaps the oldest part of the Wordian, extending from 272.3 to around 268.8 Ma (Benton 2012; ICS 2012; Resolutions 2006). The first correlations of Russian sequences with those in the USA found the Kazanian to be equivalent to the Wordian (Ruzhencev 1962), but a Roadian correlation is now supported by the discovery of Roadian ammonoids in the Kazanian of Russia (Leonova 2007).

While this is not contested, Leven and Bogoslovskaya (2006) point out that the upper and lower boundaries of the Roadian are poorly defined in their type area and should therefore not replace the Russian scheme in Boreal realm. These authors also cast doubt on the reliability of conodont-based correlation between the Roadian and Kazanian, citing apparent discrepancy in the range of certain genera and the absence of conodonts altogether at important localities. They therefore rely more primarily on ammonoid correlations.

Other forms of dating for the Kazanian are not readily available: radiometric dates have not been extracted from terrestrial rocks here and palaeomagnetic studies prove fruitless as the Roadian falls within the 'Kiaman Superchron', a period of stable reversed polarity extending from the Carboniferous to the Middle Permian (Steiner 2006). The reliance on imperfect biostratigraphic dating therefore ensures that the boundaries remain uncertain (Leven and Bogoslovskaya 2006).

The Urzhumian and Tatarian

The Russian continental scheme has changed quite drastically in its definition in the past decade. The switch to the use of the global marine timescale by many recent authors (e.g. Fröbisch 2009; Rubidge 2005) has been followed by a change in the Russian nomenclature to better fit the global marine timescale. The Tatarian itself used to form the latest temporal unit of the old 'Late Permian' (e.g. Baud *et al.* 1996) but after work by Gradstein *et al.* (2004), in which the Middle Permian was introduced, the Tatarian was considered to correspond only to the Capitanian and latest Wordian. Since 2006 (Resolutions 2006), the convention is to consider the Tatarian as equivalent to the marine Capitanian, Wuchiapingian and Changhsingian stages (see also Benton 2012; Menning *et al.* 2006).

Previous to the work of Resolutions (2006), the Tatarian was placed as immediately succeeding the Kazanian (Battail 2000; Modesto and Rybczynski 2000); however, the Russia nomenclature was changed so that the Urzhumian horizon, which had formerly been part of the Tatarian stage, was now separated out as an independent unit, roughly equivalent to the Wordian stage (Resolutions 2006; Menning *et al.* 2006; Figure 3). Together with the Kazanian, this stage formed the Biarmian series that was

equivalent to the Roadian and Wordian stages of the Lopingian epoch (Middle Permian).

The upper boundary of the Urzhumian, and hence the base of the Tatarian, is correlated with the upper boundary of the Wordian primarily through magnetostratigraphy (see Menning *et al.* 2006); more specifically, the end of the stable Carboniferous-Permian reversed polarity 'Kiaman Superchron,' termed the 'Illawara reversal' (IR), allegedly occurs in both the latest Wordian (Burov *et al.* 2002 In Menning *et al.* 2006; Glenister *et al.* 1999; Menning *et al.* 2001, 2005 In Menning *et al.* 2006) and the latest Urzhumian (formerly in the lower Tatarian) (Khramov 1963). However, the most recent studies of Russia magnetostratigraphy in the Tatarian type area were still pre-2006 and as such place the IR more generally in the early Tatarian (Gialanella *et al.* 1997; Menning and Jin 1998).

2.4.2.2 Radiometric dates from South Africa

In their explanation to sheet 198 of Merweville, Rossouw and De Villiers (1953) mention the presence of 'chert' layers in the Lower Beaufort Group rocks that outcrop in that area. These siliceous horizons remained enigmatic until later identified as ash tuffs (Martini 1974), but were only sampled for radiometric dating in 1998 (Rubidge *et al.* 2013). As a result of this, a suite of TIMS Ur-Pb dates from zircons are now available for most Permian faunal assemblage zones of the Beaufort, from the *Pristerognathus* Assemblage Zone up to the *Dicynodon* Assemblage Zone.

When these dates are compared to the global marine timescale, the lower *Pristerognathus* Assemblage Zone is of mid-Capitanian age at 261.24 Ma, while the base of the *Tropidostoma* Assemblage Zone is approximately 260 Ma, placing it on the Capitanian-Wuchiapingian boundary (Rubidge *et al.* 2013). Such results have had a great influence on our understanding of Middle Permian faunal chronology and are of particular importance as they constrain the top of the *Tapinocephalus* AZ to the mid- or upper Capitanian (Figure 3). Through biostratigraphic correlation, this then impacts the potential ages of other Middle Permian therapsid faunal assemblages from outside South Africa.

2.4.3 Relative ages and correlations

Both the Russian and South African fossil assemblages had first appeared in the literature in the early 19th Century but the first comparison between them was only conducted several decades later, when Russian material was brought to England by English miners working in Russia (Owen 1876). In the early 20th Century, Broom (1906b) observed that the fossil genera of the *Gordonia* Beds of Scotland had similarities with those from the *Pareiasaurus* (now *Tapinocephalus*) AZ and that the Russian fossils formed an intermediary between them.

Von Huene (1940) was the first to compare global Permo-Triassic faunas using both the South African biostratigraphy and the newly devised biostratigraphic scheme devised for the Russian faunas (Efremov 1940). In this, Von Huene correlated the newly recognized Russian Zone II (*Titanophoneus*) and lower part of the Zone III (Pelycosaurier) with the *Tapinocephalus* Zone. He also recognised that the *Geika* fauna (*Gordonia* of Broom) from Scotland correlated better with the Late Permian Russian pareiasaurian Zone IV and *Cistecephalus* AZ.

Correlation of the Russian, South African and American records was discussed by Watson (1942). This author found the Russian dinocephalians of Zones I and II to be more primitive than the South African forms, and therefore considered them to be older. As a consequence, the Russia Zone III ('Pelycosaurian') was correlated with the *Tapinocephalus* AZ, although Watson acknowledges that the Mezen fauna, which had been attributed to the Russian Zone II, shared few taxa in common with either South Africa or other Russian zones. An older age for the typical Russian Zone II (the Isheevo fauna) than for the *Tapinocephalus* AZ was accepted by Boonstra (1969), who also indicated that by the late 1960s the only countries known to possess equivalent assemblages to *Tapinocephalus* AZ were Russia and Zimbabwe. Anderson and Cruickshank (1978) and Li (2001) also agreed that the Russian dinocephalian zones were older than the *Tapinocephalus* Zone.

The discovery of a more primitive therapsid fauna from the *Eodicynodon* AZ in South Africa (Rubidge 1987, 1988, 1991; Rubidge and Hopson 1996), combined with the discovery of basal genera from the *Tapinocephalus* AZ (Modesto and Rubidge 2000; Modesto, Rubidge and Welman 1999), led later authors to rather correlate the

Eodicynodon and *Tapinocephalus* assemblage zones with the Ocher and Isheevo faunas of Russia, respectively (Battail 2000; Lucas 2006; Rubidge 2005).

Middle Permian therapsid faunas recognised in Brazil, China and Tanzania have all been compared with either or both the South African and Russian assemblages (Barbarena *et al.* 1985; Cheng and Li 1997a, 1997b; Cisneros *et al.* 2011, 2012; Langer 2000; Malabarba *et al.* 2003; Simon *et al.* 2010) and so all terrestrial Middle Permian faunas can be correlated with the Beaufort Group of South Africa (Figure 3).

This section reviews the literature concerning correlations of Middle Permian therapsid faunas.

2.4.3.1 Russia

The Russian Ocher fauna is correlated by most recent authors with the *Eodicynodon* AZ of South Africa (Battail 2000; Benton 2012; Lucas 2009; Rubidge 2005), although Lucas (2009) accepts a slightly older age for the *Eodicynodon* AZ. The primary similarity between the two assemblages lies in the shared presence of basal anteosaurid dinocephalians and basal anomodonts (Rubidge 2005).

In terms of absolute ages, both the Russian Dinocephalian Zone I (Ocher fauna) and the *Eodicynodon* Assemblage Zone of South Africa are placed in the Wordian stage of the Guadalupian epoch (Middle Permian) (Benton 2012; Rubidge 2005; Figure 3). Previously, this would have corresponded to the late Kazanian in the Russian continental chronology but is now considered within the Urzhumian (Resolutions 2006; Menning *et al.* 2006; Benton 2012). Alternatively, if the *Eodicynodon* Assemblage Zone is younger than the Dinocephalian Zone I (e.g. Abdala *et al.* 2008) then it's possible that the *Eodicynodon* AZ is of late Wordian age, while the Dinocephalian Zone I remains in the early Wordian. Conversely, Fröbisch (2009) considers the Ocher fauna to be coeval with the upper *Eodicynodon* AZ and that the latter spans the Wordian, though this is likely based on the more general scheme of Rubidge (2005). Despite minor disagreement, a Wordian age for the *Eodicynodon* AZ and the Dinocephalian Zone 1 of Russia is therefore generally accepted (Figure 3), which is

not inconsistent with a mid-Capitanian age for the lowest *Pristerognathus* AZ (Rubidge *et al.* 2012).

The Dinocephalian Zone II (Isheevo fauna) of Russia is now similarly equated with the *Tapinocephalus* AZ of South Africa (Battail 2000; Benton 2012; Lucas 2009; Rubidge 2005). This is supported by a greater amount of evidence than for the older two biozones as a result of targeted stratigraphic collecting in South Africa conducted by the BPI Palaeontology; several taxa are present in both these assemblages, including anteosaurid and tapinocephalid dinocephalians, biarmosuchians, scylacosaurid therocephalians and basal anomodonts (see Rubidge 2005 and references therein).

The Isheevo fauna was previously attributed to the early Tatarian (e.g. Modesto and Rybczynski 2000; Battail 2000) but using the modern stratigraphic definitions (Resolutions 2006) its age is now less secure, being considered to occur in either the late Urzhumian or early Tatarian (Benton 2012), equivalent to the Wordian-Capitanian boundary. However, the *Tapinocephalus* AZ of South Africa is almost certainly constrained to the early Capitanian based on a late Capitanian age for the base of the overlying *Pristerognathus* AZ (Rubidge *et al.* 2013). Despite the discrepancy in their proposed ages, the strong correlations between the Isheevo and *Tapinocephalus* AZ faunas suggest an early Capitanian age for the Ischeevo fauna (Figure 3).

The Kotel'nich fauna, which occurs in the Severodvinian Gorizont as it outcrops along the Vyatka River, is considered to be younger than Isheevo (Battail 2000; Benton 2012; Lucas 2009; Rubidge 2005); however, there is no consensus as to its absolute age. Battail (2000) places Kotel'nich in the Late Tatarian, lumping it with *Scutosaurus*-bearing faunas typical of the Late Permian of Russia. Lucas (2005b) does not mention Kotel'nich, but correlates the potentially later *Proelginia* fauna to his Hoedemakeran Land Vertebrate Faunachron (LVF), which immediately succeeds the Gamkan LVF in which the Isheevo fauna occurs. Golubev (2005) accepts an earliest Late Permian age for the Kotel'nich fauna, assigning it to the *Deltavjatia* tetrapod Assemblage Zone in Russia.

Lucas (2009) accepted the presence of an unconformity between the Isheevo and Kotel'nich faunas in the Tatarian (Lozovsky *et al.* 2001) and, based on the presence of the Illawara reversal just above this unconformity and the first appearance of *Dicynodon* just above that, suggested a possible *Dicynodon* AZ correlation for the Kotel'nich and later Permian faunas in Russia. However, the utility of *Dicynodon* in intercontinental correlation has been questioned due to the broad criteria used in the identification of the genus in the past (Angielczyk and Kurkin 2003a). This was countered by Lucas (2005a), who argued that this was erroneous as a result of the excessive use of cladistics but, at the same time, stated that *Dicynodon* in Russia is restricted to 'a relatively narrow interval' (Lucas 2005a:195), equivalent to the late Tatarian, or the latter part of the Late Permian. If *Dicynodon* is present in Russia, then it occurs later than the Kotel'nich assemblage.

Benton (2012) correlates Kotel'nich with the *Pristerognathus* AZ, while Rubidge (2005) found the Kotel'nich fauna best correlated with the *Tropidostoma* AZ of South Africa, in the early Wuchiapingian. This latter correlation was supported by Golubev (2005). A *Pristerognathus* AZ correlation probably draws on the presence of scylacosaurid therocephalians (Battail and Surkov 2000) but, as these are present in the latest Permian Vyatskian Gorizont as well, it appears scylacosaurids do not become extinct at the end of the Middle Permian in Russia and are therefore are not indicative of that time period in Russia. The presence of the burnetiamorph *Proburnetia*, the armoured pareiasaur *Deltavjatia*, the cynodonts *Nanocynodon* and *Uralocynodon* and the dicynodont *Australobarbarus* (Angielczyk and Kurkin 2003b; Kurkin 2000) are most consistent with a *Tropidostoma* AZ correlation, within the Late Permian (Rubidge 2005). Therefore, it is more likely that Kotel'nich falls within the Late Permian and that the *Pristeroganthus* AZ is absent in Russia, falling within the unconformity reported between the Ischeevo and Kotel'nich assemblages (Lozovsky *et al.* 2001; Figure 3).

2.4.3.2 China

The Dashankou fauna from the Xidagou Formation of China was at first correlated with the *Eodicynodon* AZ of South Africa and Ocher fauna of Russia, based on the

presence of the bolosaurid *Belebey* and the basal anteosaurids *Stenocybus* and *Sinophoneus* (Battail 2000). This author also first recognized the anomodont affinities of *Biseridens*. Further comparison by Li (2001) determined that the Xidagou Formation shared more families in common with Isheevo in Russia than with the *Eodicynodon* AZ; he considered both the Dashankou and Isheevo faunas to potentially predate the *Eodicynodon* AZ based on the presence of archaic taxa in both and the lack of several derived taxa found in South Africa.

Rubidge (2005) reverted to the correlation of the Dashankou fauna with the *Eodicynodon* AZ and Ocher fauna of Russia, while Lucas (2006) included Dashankou in his Gamkan faunachron, coeval with the *Tapinocephalus* AZ. The subsequent discovery of the stem therapsid *Raranimus* in the Xidagou Formation prompted a shift to an even earlier, pre-*Eodicynodon* AZ age for this formation (Liu *et al.* 2009). According to these authors, the presence of this genus, along with the concurrence of the dissorophoid temnospondyl *Anakamacops* with bolosaurids, suggested a Roadian age for the Xidagou Formation. This would make the Dashankou Formation the earliest therapsid bearing assemblage; however, the description of *Raranimus* is based on a single, incomplete specimen. The age of Dashankou, though probably one of the oldest therapsid-bearing faunas, is therefore currently uncertain.

2.4.3.3 Brazil

The first known localities of the Rio do Rasto Formation were initially correlated with the Tatarian; more specifically, the '*Endothiodon'* bearing rocks of the Serra do Cadeado were equated with the '*Cistecephalus* Zone' of Kitching (1977) and the *Pareiasaurus* bearing Aceguá locality was equated with the South African '*Daptocephalus* Zone' (Barbarena *et al.* 1985). The discovery of dinocephalian teeth at the Posto Queimado locality led Langer (2000) to erect a third assemblage for Brazil which he equated broadly with the *Eodicynodon* and *Tapinocephalus* assemblage zones of South Africa.

Malabarba *et al.* (2003) diverged from this after the discovery of the pareiasaur *Provelosaurus* at Posto Queimado. They argued that the concurrence of pareiasaurs and dinocephalians occurs only in the *Tapinocephalus* AZ of South Africa and

therefore the correlation of the Posto Queimado fauna could be refined to only this former zone. They added that the presence of *Provelosaurus* at Posto Queimado and Aceguá suggested a *Tapinocephalus* AZ correlation for the latter assemblage as well. While Malabarba *et al.* (2003) do not specifically mention it, Lee (1997:277) states that the name *Provelosaurus* was erected because this genus was 'morphologically intermediate between the large, loosely armoured pareiasaurs and the heavily armoured dwarf forms.' Such an observation is not inconsistent with their correlations.

Most recently, the discovery of the basal anomodont *Tiarajudens* (Cisneros *et al.* 2011) and the anteosaurid *Pampaphoneus* (Cisneros *et al.* 2012) in the Rio do Rasto Formation has confirmed the correlation of part of this unit with the *Tapinocephalus* AZ. Indeed, *Tiarajudens* and the South African genus *Anomocephalus* are very similar (Cisneros *et al.* 2011). Although there is little connection in the literature between the Brazilian faunal localities and the internal lithostratigraphic breakdown of the Rio do Rasto Formation (with the exception of *Pampaphoneus*, which is attributed to the Morro Pelado Member), it is highly likely that both *Tiarajudens* and *Pampaphoneus* come from the same level as the Posto Queimado fauna as together they are typical of the *Tapinocephalus* AZ (Figure 3).

2.4.3.4 Zimbabwe

The Madumabisa Mudstones have not produced a great deal of fossil tetrapod material but the Upper Madumabisa Mudstone has yielded definitive dinocephalian remains of the families Anteosauridae and Tapinocephalidae (Lepper *et al.* 2000). This included a specimen that may be similar to the *Tapinocephalus* AZ genus, *Avenantia* (Munyikwa 2001). A specimen of *Criocephalosaurus* was allegedly found in northern Zimbabwe (Boonstra 1946, 1969) but no stratigraphic information was provided and the specimen is now lost (Güven pers. comm.). It is therefore clear that the *Tapinocephalus* AZ has a correlative fauna in the middle part of the Madumabisa Mudstone of Zimbabwe, although the nature of the Zimbabwean fauna is unknown apart from the presence of dinocephalians.

2.4.3.5 Tanzania

Von Huene (1940) correlated the 'Lower Bonebed' of the Ruhuhu system with the '*Cistecephalus'* and '*Endothiodon'* zones of South Africa based on the presence of *Endothiodon* in that unit (Haughton 1932). Atteridge *et al.* (1964) reported further specimens of *Endothiodon* in the area and Cox (1964) attributed them to the Ruhuhu Formation. A Middle Permian component in Songea Group of Tanzania was therefore not recognized until the very recent discovery of dinocephalian teeth in the Ruhuhu Formation (Simon *et al.* 2010). Based on the preservation of the fossils, it was also proposed that the *Endothiodon* material previously assigned to the Ruhuhu Formation was in fact more likely to have been found in the basal Usili Formation (Sidor *et al.* 2010). The presence of dinocephalians in the Ruhuhu Formation and of *Endothiodon* in the overlying Usili Formation would be consistent with a *Tapinocephalus* AZ correlation for at least part of the Ruhuhu Formation (Simon *et al.* 2010).

2.4.3.6 United States

While Olson (1965) had compared the Mezen fauna of Russia with the Chickasha Formation fauna of the Oklahoma, this was based on the alleged presence of therapsids in the Chickasha Formation; this material has subsequently been suggested to represent basal synapsids (Sidor and Hopson 1995). As such, the synapsids faunas of the United States were considered limited to the Early Permian and the existence of a stratigraphic hiatus was proposed between the basal synapsid dominated Early Permian and therapsid dominated Middle Permian, termed 'Olson's gap' (Lucas and Heckert 2001).

However, recent research has challenged the existence of 'Olson's gap.' Reisz and Laurin (2001) described the parareptile *Macroleter* from the Chickasha Formation and used this, along with the presence of varanopids and caseids and the lack of therapsids, to correlate the Chickasha Formation with the Mezen fauna of Russia. This supported Olson's (1965) correlation and suggested a late Middle Permian age for the Chickasha Formation. Lucas and Heckert (2001) and Lucas (2001) refuted this on the basis of two dates: firstly, that the Blaine Formation in Oklahoma, which overlies the Chickasha Formation and the other fossiliferous terrestrial Permian

units, is dated to the latest Kungurian or perhaps the earliest Roadian; and secondly, that the Russian Mezen fauna could be constrained to the late Wordian through correlations within Russia and magnetostratigraphic studies (see Lucas 2001 and references therein).

Reisz and Laurin (2002) responded with somewhat of a compromise, suggesting that although the Chickasha and Mezen faunas were not strictly coeval, they represented part of the same varanopid and caseid dominated terrestrial vertebrate fauna; this 'varanopid-caseid dominated terrestrial vertebrate fauna' was proposed to encompass the Roadian and Wordian stages, with the Chickasha Formation representing the earliest representative example and Mezen the latest. Lucas (2001) had admitted that a Roadian age for the Chickasha Formation was possible and more-or-less accepted an early Roadian age for what became the latest part of his Littlecrotonian LVF (Lucas 2006).

Most recently, it has been proposed that there is no tangible hiatus in between the Chickasha fauna and the earliest therapsid faunas of Russia and South Africa (Benton 2012). The existence of 'Olson's gap,' or at least its extent, is therefore uncertain, as is a Middle Permian age for the youngest American terrestrial Permian.

2.5 The Marine Late Middle Permian Extinction

Beyond the terrestrial realm, great advances have been made in the study of marine biodiversity change in the late Middle Permian (Bond *et al.* 2010a, 2010b**;** Clapham *et al.* 2009; Isozaki *et al.* 2004; Ota and Isozaki 2006; Stanley and Yang 1994; Wignall *et al.* 2009a, 2009b). The addition of data concerning the marine realm allows the most comprehensive assessment of biodiversity change in the Lower Beaufort Group to be made, as well as the assessment of global biodiversity trends. The marine record also has important implications for terrestrial environments in terms of extinction mechanisms, as the coincidence of extinctions on land and in the oceans can provide constraints on potential causes.

As marine data is primarily of interest as an aid to understanding the major terrestrial biodiversity patterns, i.e.extinctions, this section focuses on the marine extinctions recorded in the late Guadalupian (late Middle Permian) of China and Japan.

2.5.1 Recognition of a marine extinction in the late Guadalupian

A drop in marine taxonomic diversity (richness) at the end of the Middle Permian, separate from the end-Permian extinction event, was first formally recognised only in the early nineties (Stanley and Yang 1994). This loss of taxonomic diversity affected invertebrate taxa, primarily calcareous algae, fusilinacean foraminiferans, corals and brachiopods (e.g. Shen and Shi 1996; Wang and Sugiyama 2000; Wignall *et al.* 2009a) and, by the 2000s, had attracted a great deal of attention.

An extinction close to the end of the Guadalupian was subsequently observed at several localities in East Asia, including Chaotian in Sichuan Province, central China (Isozaki *et al.* 2004; Lai *et al.* 2008); at Penglaitan in Guangxi Province, southern China (Kaiho *et al.* 2005); and at Kamura on Kyushu Island, Japan (Ota and Isozaki 2006). All studies of Chinese localities record particular extinctions of fusilinacean foraminiferans across the upper boundary of the Maokou Formation, which is invariably associated with a change from carbonate to siliceous mud deposition. In mid-Panthalassa, the extinction is reported to occur below the identified base of the Wuchiapingian, at the base of a 'barren interval' in the upper Iwato Formation and Upper Member of the Akasaka Limestone (Ota and Isozaki 2006). This 'barren interval' is not associated with a facies change, unlike the shelf environments in modern mainland China. Where these studies do agree is in the relatively rapid nature of the extinction.

Shen and Shi (1996) recorded an extinction of brachiopods within the Capitanian at sites in southern China, during which 87% of species were lost. This was later elaborated upon at the Guadalupian-Lopingian boundary GSSP (Global boundary Stratotype Section and Point) at Penglaitan where the brachiopod extinction was recorded as occurring well within the Capitanian, below that of conodonts, ammonoids and fusilinid foraminiferans (Shen and Shi 2009). Similarly, Wang and Sugiyama (2000) recognised a serious loss of taxonomic richness in corals, especially

in tabulates, between the Moakouan and Wuchiapingian subseries (around the Guadalupian-Lopingian boundary). Wang and Sugiyama (2000:291) emphasise the magnitude of this taxonomic diversity loss, stating that 'this event eliminated 75.6% of families, 77.8% of genera and 82.2% of coral species.'

Clapham *et al.* (2009) attribute the apparent loss of taxa in the late Guadalupian to a decrease in originations, leading to a more gradual drop in taxonomic diversity from the Wordian to the end of the Permian. According to these authors, only fusilinaceans suffered from a drastic extinction 'event'. Bond *et al.* (2010a) compiled various sections from southern China, including at Xiong Jia Chang in Guizhou province, and demonstrated that an extinction horizon for fusilinacean foraminiferans coincided with the boundary of the *J. altudaensis* and *J. prexuanhanensis*/*J. xuanhanensis* conodont zones, in the mid-Capitanian. This was closer to the brachiopod extinction horizon identified by Shen and Shi (1996, 2009). Bond *et al.* (2010a) also rejected a gradual drop in taxonomic diversity, instead highlighting that a drop in originations would be sufficient to cause a mass extinction and that the low resolution of Clapham *et al.*'s (2009) study obscured the extinction event in the Capitanian.

2.5.2 Age of the marine extinctions

While many publications accept a marine extinction at the Guadalupian–Lopingian boundary (e.g. Isozaki 2009; Isozaki *et al.* 2004; Jin *et al.* 2006; Kaiho *et al.* 2005; Lai *et al.* 2008; Ota and Isozaki 2006; Stanley and Yang 1994), this is not universally accepted. In the initial identifications of a distinct Middle Permian extinction, its position was reported at the end of the Guadalupian (Stanley and Yang 1994) or within the late Middle Permian, more specifically referred to as the 'pre-Lopingian benthic crisis' (Jin *et al.* 1994).

An extinction within rather than at the end of the Guadalupian was supported by Shen and Shi (1996, 2009) based on brachiopod extinctions well within the Maokou Formation at Penglaitan. Wang and Sugiyama (2001) supported this by identifying several drops in the species richness of rugose corals in the Guadalupian, with most

species extinct by the *Jinogondolella postserrata* condont zone; this conclusion pushed back the potential onset of late Guadalupian marine extinctions to the early Capitanian (ISC 2012). Fusilinacean foraminiferans were more generally considered to undergo an extinction in the latest Maokou Formation (latest Capitanian) culminating in a maximum low in taxonomic diversity at the Guadalupian-Lopingian boundary (e.g. Yang *et al.* 1999; Yang, Jiarun and Guijun 2004).

Alternatively, an extinction at the Guadalupian-Lopingian boundary (GLB) was supported by the distribution of foraminiferans and calcareous algae at Chaotian (Lai *et al.* 2008). At Penglaitan, an extinction was posited for the earliest Lopingian, based on the relative abundances of fossil fragments belonging to different taxa, as well as the unfossiliferous nature of rocks in the lower Wuchiapingian (Kaiho *et al.* 2005).

The most recent work at various localities in southern China has preferred a mid-Capitanian age for the Guadalupian extinction, drawing on the above data as well as new observations on the distributions of foraminiferans and calcareous algae in southern China (Wignall *et al.* 2009a, 2009b; Bond *et al.* 2010a). These studies also draw on the use of carbon isotope data as a means of correlating geographically separated stratigraphic sections. Wang *et al.* (2004) had recorded a negative Carbon isotope excursion immediately above the boundary, defined as the first appearance of the conodont *Clarkina posthitteri posthitteri* (Henderson 2002). Isozaki *et al.* (2007) also found a negative carbon excursion in the basal Wuchiapingian, beginning in their 'barren interval' and reaching a trough in the presence of the Wuchiapingian fusiline *Codonofusiella*. However, after further work in western Guizhou Province, Wignall *et al.* (2009a) recorded a more pronounced negative carbon excursion in the mid-Capitanian *J. prexuanhanensis/xuanhanensis* conodont zone, above the fusilinacean extinction horizon. This was used to correlate other Chinese sections, based primarily on the carbon isotope curve from Xiong Jia Chang (Wignall *et al.* 2009a; Bond *et al.* 2010b). Bond *et al.* (2010b) also correlated the southern Chinese sections with the carbon isotope curve at Kamura in Japan (Isozaki *et al.* 2007) and therefore considered the Kamura extinction to occur in the mid-Capitanian, at the base of the *J. altudaensis* conodont zone. This would bring the range of the Wuchiapingian fusilinaceans *Codonofusiella* and *Reichelina*, which are present in the basal Mitai and Itchihashi formations, down to the mid-Capitanian.

Despite the growing consensus of a mid-Capitanian age for the late Guadalupian marine extinction event, absolute dates for the late Capitanian conodont zones and, indeed, the GLB itself are not yet available. Shen *et al.* (2010) accept an age of ~259 Ma for the GLB based on the current suite of radiometric dates for the Emeishan volcanic that are present throughout southern China. The base of the Capitanian is better constrained to about 265.3 ± 0.2 Ma, based on TIMS dates from ash bed 20m below the base of the Capitanian in the Guadaloupe Mountains, USA (Bowring *et al.* 1998). Therefore, 'end-Guadalupian extinctions' in marine faunas have been recorded from between the *J. Postserrata* conodont zone at ~264 Ma (Wang and Sugiyama 2001) and the earliest Lopingian ~259 Ma (Kaiho *et al.* 2005).

2.6. A Guadalupian Crisis on Land?

Taxonomic turnover at the end of the *Tapinocephalus* AZ was described, if not unequivocally recognized, by Watson (1914a) in his elaboration on the biozones erected by Broom (1906b). Both these works indicate the lack of dinocephalians in the succeeding '*Endothiodon* Zone,' while Watson also refers to the dearth of pareiasaur fossil material in the lower part of this zone, before the appearance of *Pareiasaurus*. Rossouw and De Villiers (1953) elaborated on this by recording a decrease in the abundance of dinocephalians and pareiasaurs higher in the stratigraphy, within the *Tapinocephalus* Zone as it was then.

The position of the dinocephalian disappearance was refined by Boonstra (1969), who re-described an upper division of the *Tapinocephalus* AZ in which no dinocephalians or pareiasaurs were present. This division was later formally recognized as distinct from the newly dubbed Dinocephalian AZ on the basis it was characterized by an impoverished Dinocephalian AZ fauna, in particular the absence of dinocephalians (Keyser and Smith 1977; Smith and Keyser 1995a). Keyser and Smith (1977:17) also gave a lithostratigraphic position for top of their Dinocephalian AZ, which 'coincides with an extensive green "chert" band about 120m below the arenaceous Poortjie horizon'. In their figure 3.1 (Keyser and Smith 1977:18), it appears clear that a significant turnover of taxa occurs between what is now the *Tapinocephalus* AZ and the base of the *Tropidostoma* AZ.

The first attempt to quantify the tetrapod turnover at the end of the *Tapinocephalus* AZ in terms of an end-Guadalupian extinction was by Retallack *et al.* (2006). They espoused a significant extinction of terrestrial tetrapods and plants in South Africa and linked this event to a similar plant extinction recorded in Antarctica. An end-Guadalupian age was supported based on chemostratigraphic correlation (carbon isotope) with GLB sections in China. However, this study suffered from several critical flaws. Data regarding the tetrapod extinctions were presumably taken indirectly from Rubidge (ed. 1995), in which the stratigraphic ranges of most *Tapinocephalus* AZ genera were arbitrarily attached to biozone boundaries. Similarly, plant spore ranges were based collated from various sources but included data from the Beaufort Group (Anderson 1977) where the extraction of palynomorphs is notoriously difficult; these palaeofloral stratigraphic ranges are therefore highly conjectural (Nicoletti pers. comm. 2012). Furthermore, the veracity of the chemostratigraphic correlations was questioned by Lucas (2009) and Bond *et al.* (2010a) as they were based on only a few points and do not fit the Carbon isotope curves from China very well.

Lucas (2009) documented the extinction at the end of the *Tapinocephalus* AZ, in which he calculated a generic diversity loss of 73%. However, this too was based on the *Tapinocephalus* AZ as a single unit. As such, few conclusions could be drawn about the form or rate of the extinction.

The turnover in tetrapod faunas in the upper *Tapinocephalus* AZ is now recognised as an important time in late Palaeozoic tetrapod evolution (e.g. Lucas 2009) but it is still poorly understood. The primary problem lies in the lack of a detailed stratigraphic distribution for the tetrapod genera, as has been done for marine taxa in China (e.g. Lai *et al.* 2008; Wignall *et al.* 2009a, 2009b; Bond *et al.* 2010b). Temporal correlations with the marine extinctions have been made but so far these are based on insufficient data. A high resolution biostratigraphic review of Middle Permian tetrapods is therefore required; the Beaufort Group of South Africa is suitable as it is fossiliferous, records a continuous period of sedimentation and is now constrained by radiometric dates (Rubidge *et al.* 2013).

CHAPTER 3: MATERIALS AND METHODS

3.1 Lithostratigraphy

3.1.1 Identification of required stratigraphic sections

The first consideration was to address the lithostratigraphy throughout the study area (Figure 1). As a study of the Middle Permian part of the Beaufort Group, the geological formations of interest are the Abrahamskraal Formation and Poortjie Member of the overlying Teekloof Formation west of 24° E and the Koonap Formation and lower Middleton Formation east of 24°E (Figure 4). Stratigraphic sections were retrieved from publications and from unpublished student projects. These were: Cole and Wipplinger (2001) (Northern Cape); Helber and Gebauer (2001) (Klipplaat); Jirah (2009, 2013) (Merweville); Jordaan (1990) (various localities); Loock *et al.* (1994) (Moordenaarskaroo); Mason (2007) (Great Fish River); Rubidge (1988, Unpublished data) (various localities); Stear (1980) (Combrinkskraal); Thissen *et al.* (2010) (Combrinkskraal); Turner (1981) (Verlatenkloof); and Vitali (2001) (Prince Albert Road). Figure 5 shows the localities of these sites.

Despite the number of sections available, several gaps were identified where the lithostratigraphy was either unknown or in need or refinement. In order to gain a sufficiently complete understanding of the structure of the Middle Permian Beaufort strata throughout the study area, additional sections were required. Suitable localities were identified using Google Earth (Figure 5). These were, in a clockwise direction:

1. The farm Jansens kraal, Prince Albert district, Western Cape
2. The farm Die Skeur, Laingsburg district, Western Cape
3. Ouberg Pass, Sutherland district, Northern Cape
4. The farm Puntkraal, Sutherland district, Northern Cape
5. The farm Spuitpoort, Victoria West district, Northern Cape

In addition, several sections in the literature were re-measured or supplemented (Figure 5). These were:

1. The farms Bucklands and De Goede Hoop, Albany district, Eastern Cape – The section of Mason (2007) was extended from first purple mudstone up to the base of the Middleton Formation.

2. The farms Coniston and The Grant, Albany district, Eastern Cape – The section of Mason (2007) was extended from first purple mudstone up to the base of the Middleton Formation.

3. The farm Springfontein, Beaufort West district, Western Cape – The section of Jirah (2009, 2013) was extended up to the Oukloof Member of the Teekloof Formation to provide a well bounded section for the Middle Permian strata of the Beaufort Group at its thickest point.

4. The farm Wilgerbos, Laingsburg district, Western Cape – The section of Jordaan (1990) was re-measured after the scepticism shown by Cole and Wipplinger (2001) of the thicknesses portrayed by Jordaan (1990).

After stratigraphic sections had been prepared from around the basin, they were standardised in Adobe Illustrator and the different stratigraphic units from the literature critically examined. Sandstone packages were identified in section and were traced out between localities using Google Earth and through field observations.

3.2 Fieldwork

As part of a larger investigation of the lower boundary of the Beaufort Group, a great deal of fieldwork has already been undertaken by Bruce Rubidge and his students in support of this project. This investigation has measured important stratigraphic sections as well as provided crucial biostratigraphic information through the targeted stratigraphic collection of tetrapod fossils, which are now curated at either the National Museum, Bloemfontein or the Bernard Price Institute for Palaeontology, Johannesburg. Several of the stratigraphic sections measured over the last 30 years have remained unpublished and are presented here for the first time, as

is much of the biostratigraphic information; therefore, this work must be acknowledged as a contributing part of the data collection for this thesis.

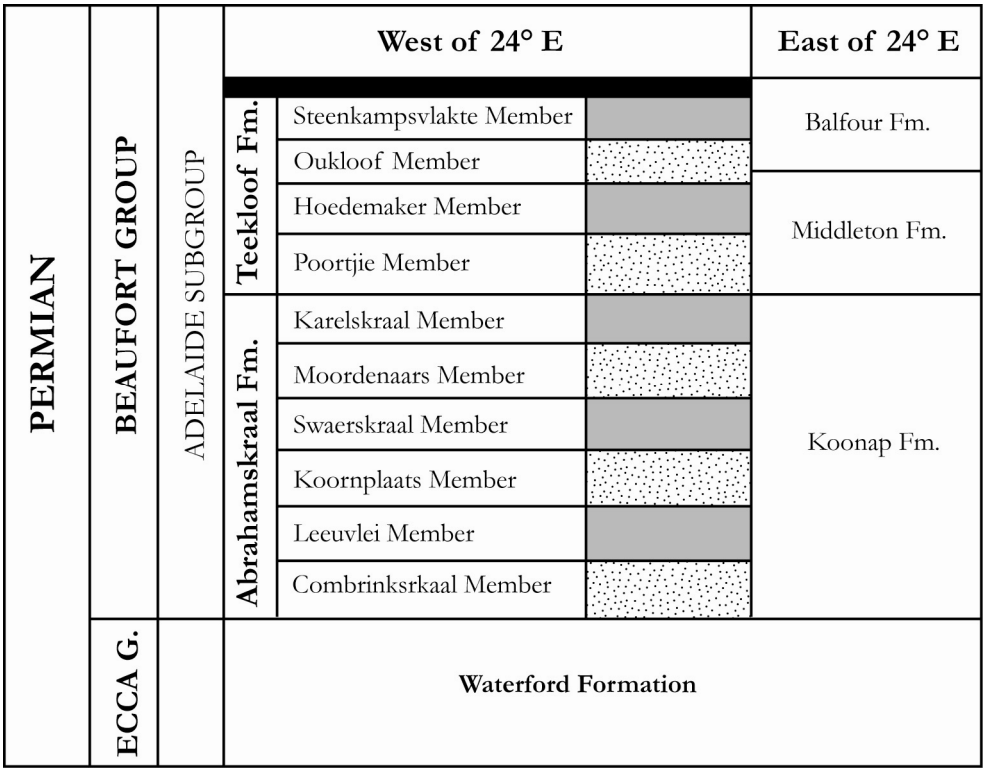


Figure 4. Lithostratigraphic units of the Permian part of the Beaufort Group used in this study, South Africa. At the member level, only the Poortjie Member of the Teekloof Formation is currently accepted by the South African Committee for Stratigraphy (SACS).

3.2.1 Stratigraphic sections

Stratigraphic sections were measured during the course of several trips between 2010 and 2012. All sections were measured using a Jacob's staff and Abney level in conjunction with a clinometer. With the exception of sections measured on the farms Seekoegat and Wilgerbos, both of which are situated along the folded southern margin of the basin, the dip of strata was generally low with little disruption. At these two localities, tectonic folds were recognised and compensated for.

In the western part of the basin, sections were ideally measured up to the top of the Poortjie Member of the Teekloof Formation; however, this was possible only on the farm Springfontein, in the northern Koup (Figure 5). Elsewhere, sections were

restricted to a narrower part of the stratigraphy but were still measured as they provided useful information, at least at a local level.

Several instances of this occur. At the Wilgerbos locality the Poortjie Member is not present; however, its placement half way between the Moordenaarskaroo and the Koup allows the better comparison of the stratigraphy of each of these regions. The Poortjie Member is present at Die Skeur, some 30km to the north of Wilgerbos, and a section was measured here to provide a direct measurement for the distance between the base of this member and the floor of the Koup. At Ouberg Pass the top of the escarpment belongs to the mid-Abrahamskraal Formation but this can be correlated with the section at Verlatenkloof (Cole and Wipplinger 2001; Turner 1981) and thence with the section measured in the Moordenaarskaroo (Loock *et al.* 1994). Similarly, while the section at Puntkraal encompasses only the uppermost Abrahamskraal Formation and Poortjie Member, it can be correlated with the Moordenaarskaroo and, in conjunction with section at Ouberg Pass, provides stratigraphic information for the whole of the Roggeveld.

The Abrahamskraal Formation in the north-western part of the basin proved practically impossible to measure due to the low relief, low angle of dip, large distances and the subsequent lack of continuous exposure. As such, for the Fraserburg area data from SOEKOR borehole QU1/65 was used, as described by Cole and Wipplinger (2001). At Victoria West, a section was measured on the farm Spuitpoort, which encompassed a 120 m of Beaufort rocks that were mapped as Abrahamskraal Formation. Although this section was isolated, the missing thickness to the Ecca-Beaufort boundary was approximated using GPS altitudes, which was possible given the near horizontal dip of strata in the area.

Because only broad-scale lithostratigraphic units are considered here and the thickness of the Abrahamskraal Formation exceeds 2000 m in the south of the basin, facies units less than 1m in thickness were ignored. In the case where units less than 1m in thickness were found in abundance, the majority facies was recorded. The sedimentology of the lower Beaufort Group has been addressed in several specific studies (e.g. Kubler 1977; Smith, 1981, 1987, 1989, 1990; Stear 1980) and is not discussed further here.

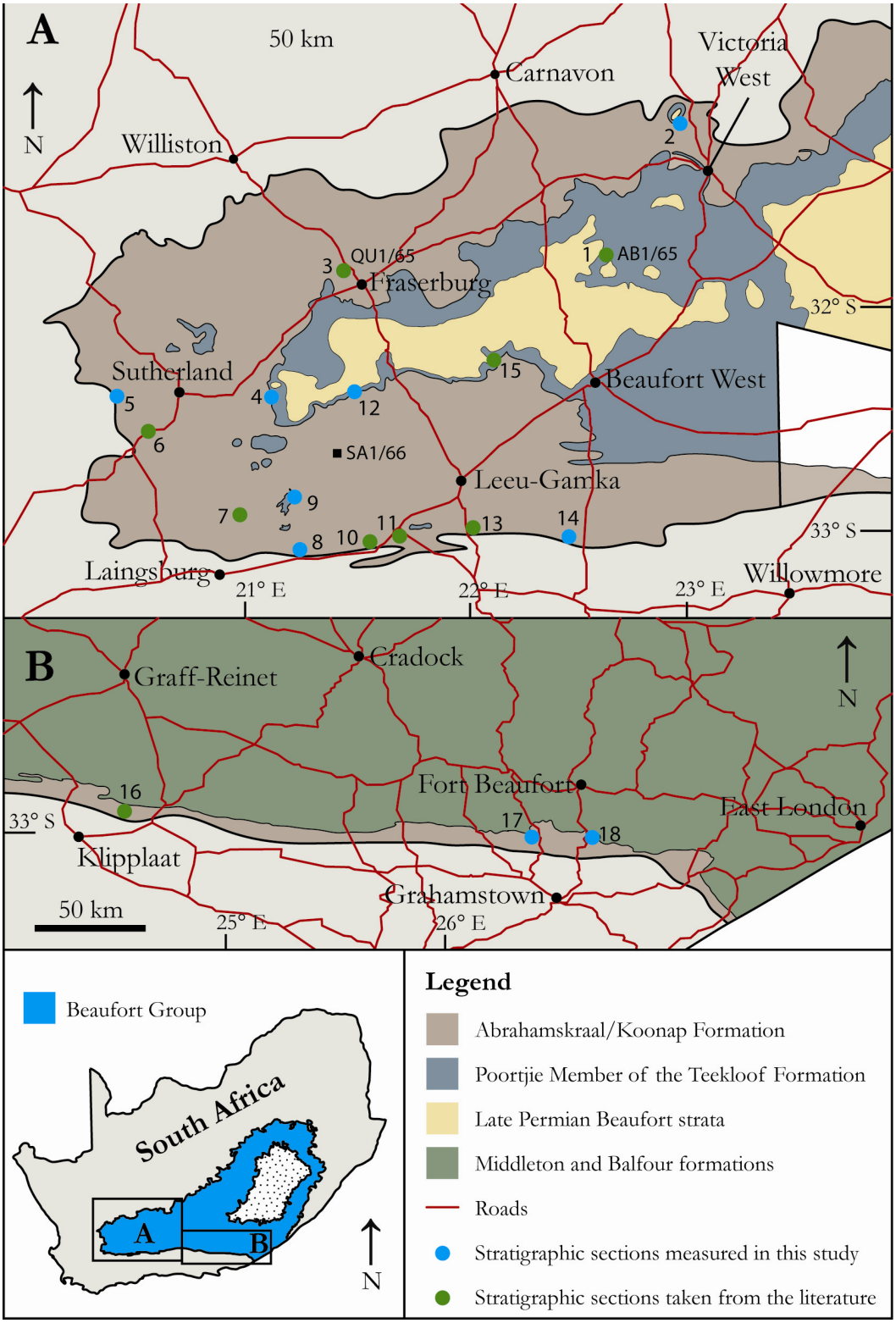

A
50 km
N
Williston
Carnavon
Victoria West
2
1 AB1/65
3 QU1/65
Fraserburg
32° S
Sutherland
15
Beaufort West
4
5
12
6
SA1/66
Leeu-Gamka
7
9
11
13
14
8
10
33° S
Laingsburg
21° E
22° E
23° E
Willowmore
B
Graff-Reinet
Cradock
N
16
Fort Beaufort
East London
33° S
17
18
Klipplaat
Grahamstown
50 km
25° E
26° E
Beaufort Group
South Africa
A
B
N
Legend
Abrahamskraal/Koonap Formation
Poortjie Member of the Teekloof Formation
Late Permian Beaufort strata
Middleton and Balfour formations
Roads
Stratigraphic sections measured in this study
Stratigraphic sections taken from the literature

Figure 5. (previous page). Map showing the localities of all stratigraphic sections used in this study. Section localities are 1, AB1/65 Abrahms kraal; 2, Spuitpoort; 3, QU1/65 Quaggasfontein; 4, Puntkraal; 5, Ouberg Pass; 6, Verlatenkloof; 7, Moordenaarskaroo; 8, Wilgerbos; 9, Die Skeur; 10, Dwyka River; 11, Prince Albert Road/Merweville; 12, Springfontein; 13, Combrinkskraal; 14, Jansenskraal; 15, Paalhuis; 16, Klipplaat; 17, The Grant; 18, Bucklands.

3.2.2 Stratigraphic fossil collection

Fossil collection was undertaken during the annual fieldtrip run by the BPI Palaeontology to the lower Beaufort, for the years 2010, 2011 and 2012. In the first two years, tetrapod fossils were collected from the upper Abrahamskraal Formation and Poortjie Member in an area of the northern Koup, namely the farms Elandsfontein, Klipbankskraal, Bullekraal and Springfontein (Figure 5); all are within the Beaufort West district, Western Cape Province. During the 2012 field season, collecting was conducted in the uppermost Abrahamskraal Formation and lower Poortjie Member on the farm Puntkraal, Sutherland district, Northern Cape Province. Both areas possessed good exposure the *Tapinocephalus* AZ-*Pristerognathus* AZ boundary, where the highest biostratigraphic resolution was required. The stratigraphic position of all fossil specimens was recorded and stratigraphic sections were measured at each of the two regions.

All fossil specimens are now curated at the BPI Palaeontology, Johannesburg.

3.3 Biostratigraphy

In order to review the stratigraphic range of each tetrapod genus in the Abrahamskraal Formation and Poortjie member, three conditions would ideally need to be met: 1) a thorough understanding of the lithostratigraphy these units throughout the basin, 2) a robust taxonomic framework for Middle Permian tetrapods and 3) the re-identification of all fossil collections based on the most recent taxonomic work. The first criterion was met to a sufficient standard through fieldwork and from the literature, as described above. For some taxa, like

dicynodonts, the latter two criteria are mostly met; however, for others, especially the gorgonopsians and temnospondyls, the taxonomy is still in a state of flux. Importantly though, the taxonomic state of most taxa has changed significantly the last holistic biostratigraphic review (ed. Rubidge 1995).

3.3.1 Preliminary work

The primary task of the study involved the determination of the stratigraphic provenance of each individual tetrapod fossil specimen collected from the Middle Permian Beaufort rocks. This was achieved with the use of the Beaufort Fossil Vertebrate (BFV) GIS database (Nicolas 2007), which allowed each fossil locality to be plotted in geographic space. The GIS data was imported into .kmz format and thence into Google Earth from where the surface geology could be seen. All fossil specimens used in this analysis are listed in the Appendix 2(CD).

The Surface expression of each stratigraphic level was determined in several stages. Initially, 1:250 000 geological maps for the relevant regions were consulted (map sheet: Republic of South Africa 3122, Victoria West, 1:250 000 Geological Series 1992; map sheet: Republic of South Africa 3120, Williston, 1:250 000 Geological Series 1992; map sheet: Republic of South Africa 3220, Sutherland, 1:250 000 Geological Series 1983; map sheet: Republic of South Africa 3222, Beaufort West, 1:250 000 Geological Series 1979; map sheet: Republic of South Africa 3224, Graff-Reinet, 1:250 000 Geological Series 1994; map sheet: Republic of South Africa 3326, Grahamstown, 1:250 000 Geological Series 1996). These maps show the stratigraphy only at formation level, so a review of the existing sub-formational stratigraphic paradigms was necessary (see Chapters 4 and 6). The stratigraphic nomenclature of Le Roux (1985) and Loock *et al.* (1994) was chosen and this study uses a modified version of these schemes (Figure 4). It is these units that are referenced throughout the interpretation of the biostratigraphy.

From the localities of available lithostratigraphic sections, horizons of known level were traced out laterally from where sections were measured to surrounding areas, both in the field and using Google Earth. This allowed the surface expression of sub-formational units to be determined. The surface mapping of Jirah (2009) and Thissen

et al. (2010) was particularly useful in this respect. The increasing error in the tracing of units with distance from a section locality was incorporated into the accuracy of stratigraphic heights provided for each specimen, i.e. those specimens found furthest from stratigraphic section traverses have higher uncertainty in their stratigraphic provenance and so are attributed to a wider stratigraphic interval.

3.3.2 Sectors

A vertical stratigraphic section was required on which to plot the stratigraphic horizon of each fossil specimen. As the lithostratigraphy of the Lower Beaufort Group has long been known to vary laterally in thickness and in structure (e.g. Johnson 1976; Jordaan 1990; Keyser and Smith 1977), the same sections could not be used for specimens retrieved from across the whole basin. Accordingly, the Karoo Basin was split into sectors, each of which could be represented by a single stratigraphic section that approximated that of the whole sector (Figure 6). The sector names are associated with a town in the area for clarity, though this does not imply that any stratigraphic sections were measured in the immediate vicinity of the town; Laingsburg and Grahamstown occur close to, but not within, their eponymous sectors.

Sectors were generally the smallest areas that were possible. While lateral variation in stratigraphy certainly occurs on a finer scale within each sector, limitations were imposed on sector size by the availability of outcrop on which to measure complete stratigraphic sections for the Middle Permian Beaufort strata. Examples of this are the interior of the basin, where the lowest Beaufort Group strata are in the sub-surface only; the north-west of the basin, where dolerite intrusions and low topography obscure the stratigraphy; and in the south-central part of the basin, in particular the area known as Die Vlakte, where alluvium obscures large swathes of ground and tectonic folding makes the extrapolation of any one horizon inaccurate (Figure 1). In addition, time restrictions prevented the measuring of more sections. The resolution portrayed here is considered to be sufficiently accurate for this project. Where variation in the lithology was noted within a sector, and the erection

of a new sector was unfeasible, this was taken into account when assigning stratigraphic positions to fossil specimens from the area in question.

Once the position of a sector was established, the definition of sector areas attempted to follow the geology where possible. The boundary between the Beaufort West Sector and the Leeu-Gamka Sector follows an apparent increase in mudstone in the eastern Koup, a phenomenon previously noted by Stear (1980). Similarly, the boundary between the Merweville and Laingsburg sectors is placed within the western Koup; this is because a stratigraphic section measured on the farm Die Skeur in the Laingsburg district demonstrated the lithostratigraphy of the Abrahamskraal Formation in the western Koup to be more similar to that of the Moordenaarskaroo than the Merweville Sector. The boundary between the Fraserburg and Victoria West sectors in the north and the Merweville, Leeu-Gamka and Beaufort West sectors in the south follows close to the Great Escarpment. This was intended to pass through the youngest Beaufort rocks and thereby ensuring the outcrop of the Poortjie Member within each sector.

Sector 8 is rather wide, which is due to the paucity of stratigraphic sections from this part of the Eastern Cape Province. Because of the position of Die Groot Vlakte, there is not sufficient outcrop in the western half of sector 8 to measure a stratigraphic section there. Despite the stratigraphic transition at 24°E, this area is included in sector 8 as the only fossils reported in this region are in much greater proximity to the section measured at Klipplaat than to that measured at Jansenskraal.

The Eastern Cape region has a particular dearth of measured stratigraphic sections. However, few fossils have been found between Klipplaat and Rietbron and for this reason, combined with the lack of outcrop, this area was divided between adjacent sectors (Figure 6). As the majority of this area lies closer to the eastern sector (Jansenville) than to the western sector (Beaufort West) and the geological map indicate the exposure of the Koonap/Abrahamskraal Formation better fits the condition in the southeast of the basin, a greater proportion of the south-central basin was included in the Jansenville Sector.

The stratigraphic sections used in each sector were in a few cases taken from the published literature but were mostly derived from unpublished student projects or

were measured during the course of this study. Because few localities possessed an uninterrupted succession of Middle Permian Beaufort rocks, coverage of the Abrahamskraal and Koonap formations was given priority over that of the Poortjie Member or lower Middleton Formation; the reasons for this were that the Abrahamskraal and Koonap Formations represented the majority of the Middle Permian Beaufort succession and that these units varied in thickness to a greater degree than the younger units. Furthermore, the Poortjie Member is exposed in a salient of younger rocks into the Abrahamskraal Formation, corresponding roughly to the Nuweveld Mountains (Figure 6). Due to the restricted area of outcrop for this unit, stratigraphic sections measured through the Poortjie Member are therefore shared with a sector to the north and south.

As a result of the priority given to the Abrahamskraal and Koonap formations and the incompleteness of the stratigraphic record at single localities, the stratigraphic sections provided for each sector are mostly composites, i.e. in the Beaufort West Sector, the Abrahamskraal Formation and Poortjie Member were not measured at the same locality. The thickness provided for the Poortjie Member in each sector is considered to be representative of that area and, at the coarse resolution necessitated by the great thicknesses measured in the Abrahamskraal Formation, small lateral differences in thickness are negligible.

3.3.3 Stratigraphic sections used in each sector

The sources of the measured stratigraphic section used in each sector and the thicknesses obtained for each of the major lithostratigraphic units are illustrated in Table 2 and the localities of all stratigraphic sections are illustrated in Figure 5. Justification for the composite stratigraphic sections used in each sector is provided in the following section, in a clockwise direction from the east.

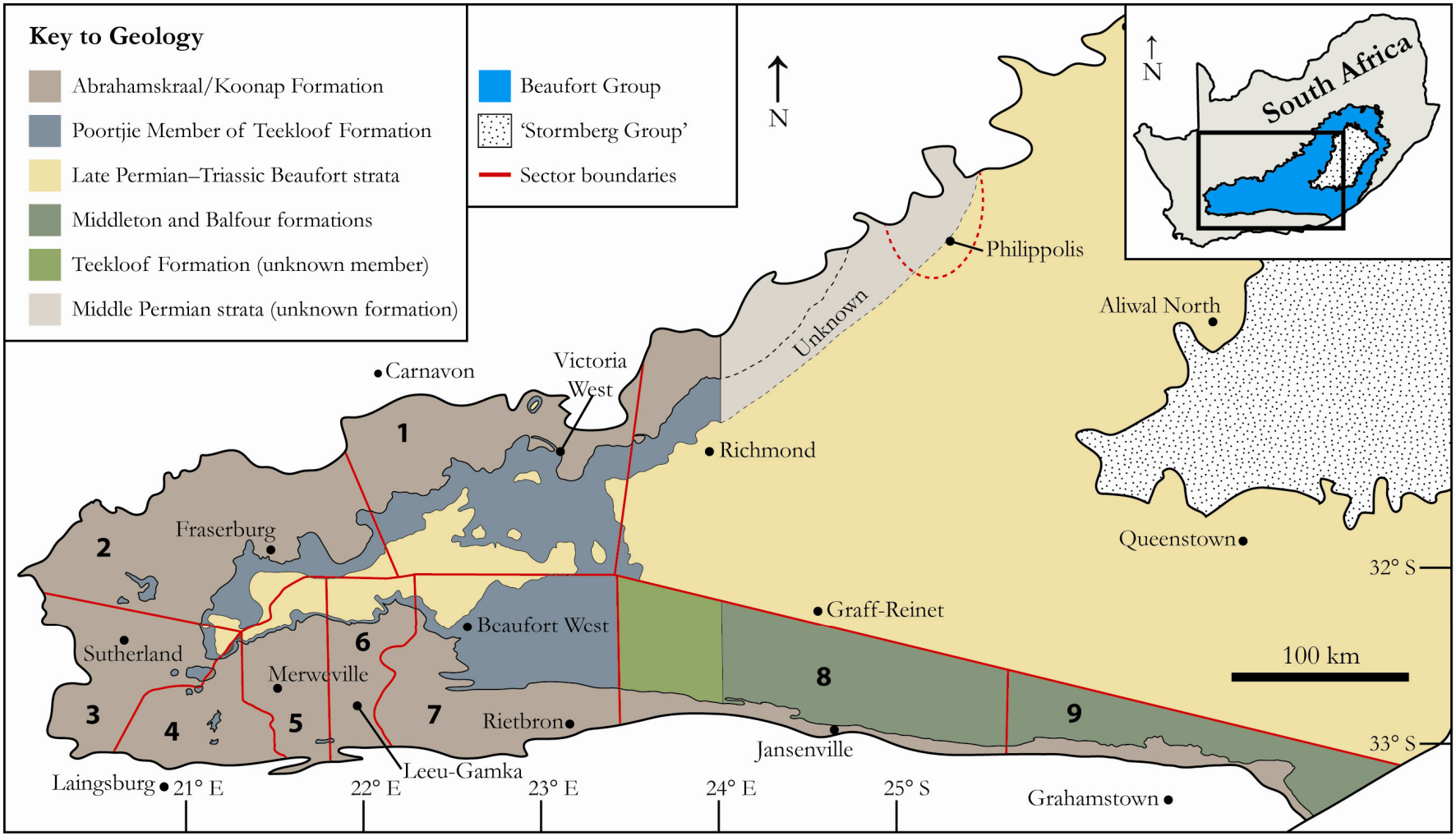


Figure 6. Map showing the sectors used in the calculation of specimen stratigraphic positions. 1 = Victoria West, 2 = Fraserburg, 3 = Sutherland, 4 = Lainsburg, 5 = Merweville, 6 = Leeu-Gamka, 7 = Beaufort West, 8 = Jansenville, 9 = Grahamstown.

3.3.3.1 Victoria West Sector

Because of the flat topography on the Nuweveld and the large size of the sector, this stratigraphic section was difficult to assemble. It is based on the work of Cole and Wipplinger (2001), who described the Beaufort Group rocks in core from SOEKOR borehole AB1/65. This borehole was drilled on the farm Paardeberg, Victoria West district, Northern Cape Province, in the south of the Victoria West Sector. Cole and Wipplinger (2001) recorded a total thickness for the Abrahamskraal Formation at Paardeberg of 392 m but field investigation of the Abrahamskraal Formation in the northern part of the sector has revealed that it is far thinner there, perhaps less than 50 m in thickness (see 4.1.1.1 and 4.1.1.2).

Due to this northward thinning of the Abrahamskraal Formation, the surface exposure of the Abrahamskraal Formation throughout most of the sector is probably within 50 m of the base of the Poortjie Member. However, there is also an element or eastwards thinning in the Abrahamskraal Formation: the Ecca-Beaufort boundary is known to become younger in a north-east direction (Rubidge 2005; Rubidge and Angielczyk 2010; Rubidge, Hancox and Catuneanu 2000), which means the lowermost Abrahamskraal Formation strata exposed in the north-west of the sector are therefore likely to be further below the Poortjie Member than those exposed in the north-east of the sector. As a result, it is accepted here that exposure of the Abrahamskraal Formation is 1) within 50m of the base of the Poortjie Member throughout the entire eastern and southern portions of the Victoria West Sector and 2), no more than 150 m below the Poortjie Member in the north-west of the Victoria West Sector.

The Stratigraphic section for the Poortjie Member in this sector was measured for this thesis on the farm Spuitpoort, Victoria West district, Northern Cape Province, and was found to be 120 m thick (see 4.1.1.2)

3.3.3.2 Fraserburg Sector

Because of the flat topography in this sector, this stratigraphic section was also based on the work of Cole and Wipplinger (2001), who described the stratigraphy of the

Beaufort Group rocks in core from SOEKOR borehole QU1/65, which was drilled on the farm Quaggas fontein, Fraserburg district, Northern Cape Province. These authors determined the Abrahamskraal Formation rocks present in the core to be 507 m thick. Field investigation of the site revealed less than 50 m of sediments above the level of the borehole and the base of the Poortjie Member as mapped (map sheet: Republic of South Africa 3120, Williston, 1:250 000 Geological Series 1989). Therefore, the Abrahamskraal Formation is approximately 557 m in the southern part of this sector (see 4.1.1.3).

The stratigraphic section for the Poortjie Member was measured for this thesis on the farm Springfontein in the Beaufort West district, Western Cape Province and is 115 m thick (see 4.1.2.5). Although this section was measured in the Merweville Sector, the Poortjie Member is not well exposed near Fraserburg and the Springfontein locality is very close to the south-central boundary of Fraserburg Sector (Figure 5).

3.3.3.3 Sutherland Sector

This stratigraphic section was based on the work of Turner (1981), who measured the Abrahamskraal Formation at Verlatenkloof Pass, Northern Cape Province; however, the position of the Ecca-Beaufort boundary is taken from Cole and Wipplinger (2001). According to these latter authors, Abrahamskraal Formation strata present in the pass were found to be 926 m thick. Because of the disruption in continuity within the Abrahamskraal Formation in this sector caused by the Roggeveld plateau (Figure 5), the top of Verlatenkloof Pass was correlated with the Moordenaarskaroo using Google Earth to an horizon approximately 600 m below the base of the Poortjie Member. The missing upper 600 m of the Abrahamskraal Formation at Verlatenkloof was extrapolated across from the section of Loock *et al.* (1994) in the Moordenaarskaroo and a total thickness of 1526 m was therefore calculated for the Abrahamskraal formation in this sector (see 4.1.1.6).

The Poortjie Member was measured for this thesis in the eastern Sutherland Sector on the farm Puntkraal, Sutherland district, Northern Cape Province, and was found to be 164 m thick (see 4.1.1.4).

Sector	Unit	Thickness (m)	Locality	Source
1. Victoria West	Abrahamskraal Fm	150	Abrahamskraal (SOEKOR AB1/65), Victoria West district; Spuitpoort, Victoria West district	Cole and Wipplinger (2001), this study
	Poortjie Member	100	Spuitpoort, Victoria West district	this study
2. Fraserburg	Abrahamskraal Fm	550	Quaggasfontein (SOEKOR QU1/65), Fraserburg district	Cole and Wipplinger (2001)
	Poortjie Member	119	Springfontein, Beaufort West district	this study
3. Sutherland	Abrahamskraal Fm	1550	Klipbanksrivier, Sutherland district	Turner (1981)
	Poortjie Member	162	Puntkraal, Sutherland district	this study
4. Laingsburg	Abrahamskraal Fm	2210	Buffelsfontein, Laingsburg district	Loock et al (1994)
	Poortjie Member	162	Puntkraal, Sutherland district	this study
5. Merweville	Abrahamskraal Fm	2575	Tuinkraal, Prince Albert district	Jirah (2012)
	Poortjie Member	119	Springfontein, Beaufort West district	this study
6. Leeu-Gamka	Abrahamskraal Fm	2468	Combrinkskraal, Prince Albert district	Rubidge (1988), Thissen *et al.* (2010)
	Poortjie Member	182	Paalhuis, Beaufort West district	Cole and Wipplinger (2001)
7. Beaufort West	Abrahamskraal Fm	2151	Botterkraal, Prince Albert district	Rubidge (1988), this study
	Poortjie Member	160	Paalhuis, Beaufort West district	Cole and Wipplinger (2001)
8. Jansenville	Koonap Fm	2330	De Draai, Jansenville district	Gebauer (2001), Helber (2001)
9. Grahamstown	Koonap Fm	1415	Coniston, Albany district	Mason (2007), this study

Table 2. Sources for the thickness of the Abrahamskraal Formation and Poortjie Member of the Teekloof Formation in each of the sectors used in this study

3.3.3.4 Laingsburg Sector

The stratigraphic section was primarily taken from the work of Loock (1993) and Loock *et al.* (1994). These authors measured a thickness of 2210 m for the Abrahamskraal Formation from the Ecca-Beaufort boundary on the farm Buffelsrivier, Laingsburg district, Western Cape Province, up to the base of the Poortjie Member as mapped on the farm Gatsberg (map sheet: Republic of South Africa 3220, Sutherland, 1:250 000 Geological Series 1983; see 4.1.1 Section 7).

The Poortjie Member in this sector was measured for this thesis on the farm Puntkraal, Sutherland district, Northern Cape and was found to be 164 m thick (see 4.1.1.4). Although this section was measured in the adjacent Sutherland Sector, it is considered to be representative of the Poortjie Member in the Laingsburg Sector because the Puntkraal locality is situated close to the northern boundary of Laingsburg Sector, where the Poortjie Member is exposed (Figure 5).

3.3.3.5 Merweville Sector

This stratigraphic section was primarily taken from the work of Jirah (2013). A total thickness of 2575 m was determined for the Abrahamskraal Formation up to the base of the Poortjie Member as mapped, beginning on the farm Tuinkraal in the Prince Albert district, Western Cape Province and being completed on the farm Springfontein in the Beaufort West district (map sheet: Republic of South Africa 3220, Sutherland, 1:250 000 Geological Series 1983; see 4.1.1 Section 11). Formerly, Jirah (2009) had measured 1860 m for the Abrahamskraal Formation between the first purple mudstone and the Poortjie Member as mapped on Elandskop, east of Prince Albert Road; his more recent work suggests a greater thickness for the Abrahamskraal Formation when measured up to the Poortjie Member at the escarpment (Jirah 2013) and it is this that is used here.

The Poortjie and Hoedemaker members were measured for this thesis, continuing from the section of Jirah (2013) on the farm Springfontein, and were found to be 115 m and 151 m thick, respectively (see 4.1.2.6).

Because the Abrahamskraal Formation was at its thickest in this sector, this stratigraphic section was chosen to bear the composite ranges for each individual genus.

3.3.3.6 Leeu-Gamka Sector

This stratigraphic section was partly taken from the work of Rubidge (1988), who measured 604 m from the Ecca-Beaufort boundary up to the first purple mudstone on the farm Combrinkskraal, Prince Albert district, Western Cape Province. This was continued at the same locality by Thissen *et al.* (2010), who measured a further 1864 m for the Abrahamskraal Formation up to the base Poortjie Member as is indicated on the Beaufort West sheet (map sheet: Republic of South Africa 3222, Beaufort West, 1:250 000 Geological Series 1979), primarily on the farms Combrinkskraal and Bloukrans. A total thickness of 2468 m is therefore recorded for the Abrahamskraal formation in this sector (see 4.1.2.7).

The Poortjie Member in this stratigraphic section was taken from Cole and Wipplinger (2001) and was measured as 182 m thick on the farm Paalhuis, Beaufort West district, Western Cape Province, in the northern part of this sector (see 4.1.2.9).

3.3.3.7 Beaufort West Sector

This stratigraphic section was partly taken the work of Rubidge (1988), who measured 330 m from the Ecca-Beaufort boundary up to the first purple mudstone on the farm Botterkraal, Prince Albert district, Western Cape Province; this was then extended by 1821.5 m in this study from the first purple mudstone up to the base of the Poortjie Member as mapped on the farm Jansenskraal, Prince Albert district, Western Cape Province (map sheet: Republic of South Africa 3322, Oudtshoorn, 1:250 000 Geological Series 197; see 4.1.2.8).

The section for the Poortjie Member in this sector was taken from Cole and Wipplinger (2001) and was measured on the farm Paalhuis, Beaufort West district, Western Cape Province, which is situated to the west of Beaufort West within the

Leeu-Gamka Sector. This section was used as no more complete stratigraphic section for the entire Poortjie Member could be measured to the east of this point, but it is considered to be sufficiently representative of the member in this area. The Poortjie Member portrayed here is therefore 182 m thick (see 4.1.2.9).

1.3.3.8 Jansenville Sector

This stratigraphic section was based on the work of Helber and Gebauer (2001), who measured a thickness of 2330m for the Koonap Formation as mapped on the farms De Draai and Waterfall in the Jansenville district, Eastern Cape Province (map sheet: Republic of South Africa 3224, Graaff-Reinet, 1:250 000 Geological Series 1993; see 4.1.3.1). The section for the lower Middleton Formation used for this sector was measured nearby, on the farm Hilary, by Rubidge (Unpublished data).

3.3.3.9 Grahamstown Sector

This stratigraphic section was based on the work of Mason (2007), who measured a thickness of 1145 m for a part of the Koonap Formation from the Ecca-Beaufort boundary up to the first purple mudstone of the Beaufort Group. This was measured on the farm Coniston, Albany district, Eastern Cape Province (see 4.1.3.2). This stratigraphic section was supplemented for this thesis by measuring from the first purple mudstone up to the top of the Fish River Rand and the base of the Middleton Formation as mapped (map sheet: Republic of South Africa 3326, Grahamstown, 1:250 000 Geological Series 1996). This added a further 270 m to the Koonap Formation as measured by Mason (2007) (see 4.1.3.2). As so few fossils have been collected from the lower Middleton Formation in this sector, no stratigraphic section was measured for this unit.

3.3.3.10 Philippolis Sector

Although some *Tapinocephalus* or *Pristerognathus* AZ genera have been found in the southern Free State, the stratigraphy there is very poorly understood. Accordingly, these specimens are mentioned directly in the text and are not included in the supplementary data within the context of a sector.

3.3.4 Calculation of stratigraphic ranges for fossil specimens

Once the lithostratigraphic work was accomplished, the stratigraphic provenance of each specimen could be determined. The accuracy of these assignments varied depending on 1) the quality of the provenance data provided for the specimen, 2) the stratigraphic distance exposed in the vicinity of the locality and 3) the distance of the fossil locality from a measured stratigraphic section. At a few localities, especially in the lowest Beaufort rocks, specimens had been measured in precisely and include GPS coordinates; however, for most specimens only a farm name was provided by the collections catalogues and Beaufort Vertebrate Fossil database (Nicolas 2007). In such instances the exact locality is unknown and specimen can only be considered to originate somewhere within the farm boundaries. Where the area of a farm contains the exposure of a wide stratigraphic interval, the stratigraphic provenance of the fossil is only poorly constrained. As stratigraphic members were recorded in section and were thence extrapolated laterally, the error in tracing units increased with distance from a section locality. Therefore, even when a specimen had accurate GPS coordinates its origin was not necessarily attributable to a specific stratigraphic horizon.

In order to facilitate the assignment of a stratigraphic range for each specimen, the Middle Permian strata (Abrahamskraal Formation and Poortjie Member of the Teekloof Formation in the west; the Koonap and basal Middleton Formation in the east) were divided into 50 m stratigraphic intervals (SIs). This resolution is the most reasonable compromise between accuracy and manageability, considering the thicknesses involved (<2600 m) and the relatively poor stratigraphic information of the majority of specimens. The thicknesses of the stratigraphic sections representing each sector do not, of course, fit exactly with 50 m intervals. In this case, the

thickness was extended or reduced to the nearest 50 m boundary. The one exception to this rule is in the Merweville Sector: in this stratigraphic section the Abrahamskraal Formation was 2575 m thick, which fell exactly in the middle of a 50 m interval; as such, an interval of 25 m was used for the uppermost interval of the Abrahamskraal Formation.

The Poortjie Member varies between 115–180m throughout the study area. This is divided into 3 SIs, which for the sake of consistency correspond to the lower, middle and upper parts of the member throughout the study area. These are considered separate from those of the Abrahamskraal Formation. The contact between the Abrahamskraal Formation and Poortjie Member of the Teekloof Formation therefore always represents the boundary between two SIs.

Using the Beaufort Fossil Vertebrate database locality information, as projected onto satellite imagery in Google Earth, the stratigraphic position of each specimen was then calculated. A few specimens could be constrained to a single 50 m SI but more commonly it could be assigned only to a broader stratigraphic range, encompassing two or more 50 m SIs. In these cases, a specimen was given a 'potential range' rather than an exact position. The distinction between 1) the 'certain presence' of a specimen within a 50 m SI and 2) the 'possible presence' of a specimen in any one 50 m SI within a range is important.

Specimens from collections outside South Africa, which were therefore not included on the Beaufort Fossil Vertebrate database, were considered on an *ad hoc* basis. This was usually because these specimens represented a significant number of those assigned to a particular genus. Alternatively, a specimen in a foreign collection was the holotype of a genus and was therefore an important specimen to include.

3.3.4.1 Certain ranges *vs.* potential ranges

When calculating the 'certain' stratigraphic range of a taxon in a sector, the stratigraphically highest and lowest definite occurrences were determined in one of three ways: firstly, as the distance between the highest and lowest reliably identified specimens, for which the stratigraphic provenance could be constrained to a single

50 m SI (Figure 7, A). Secondly, if the 'potential range' of a specimen fell outside the most exclusive interval as calculated above, then the 'certain range' was extended from the established stratigraphic range to the closest 50 m SI of the 'potential range' (Figure 7, B). If no specimens could be constrained to a single 50 m SI but at least two specimens possessed non-overlapping 'potential ranges', then the 'certain range' was taken to be the most exclusive interval that included at least one 50 m SI from each range (Figure 7, C). If no specimens could be constrained to a single 50 m SI and all ranges overlapped each other, then no 'certain range' could be determined (Figure 7, D).

3.3.4.2 Calculation of composite range

Once the ranges of specimen had been calculated within their respective sectors, a composite biostratigraphic section was created representing the ranges of all genera in the Abrahamskraal Formation and lower Teekloof Formation. This required the Abrahamskraal Formation at its thickest and therefore adopted the stratigraphic section measured in the Merweville Sector (4.1.1 Sections 10 and 12, see Table 2).

Because the base of the Abrahamskraal Formation has been demonstrated to be diachronous (Rubidge 2005; Rubidge and Angielczyk 2010; Rubidge, Hancox and Catuneanu 2000), the base of the Poortjie Member was used throughout the study area as a relatively time-constant horizon; this was done because the base of the Poortjie Member is more consistently coincident with the *Tapinocephalus-Pristerognathus* AZ boundary (ed. Rubidge 1995). Although the position of this boundary is actually not well defined, it is currently the most reliable way of correlating between sectors than any other stratigraphic horizon in the region. Sectors were therefore compared based on the position of the base of the Poortjie Member. Once this was done, the stratigraphic position of all specimens of a taxon throughout the south-west of the basin could be compared and a composite range calculated using the method described above (see 3.3.4.1 above).

A

1500-1549	1550-1599	1600-1649	1650-1699	1700-1749	1750-1799	1800-1849	1850-1899
	1						
					1		

B

1500-1549	1550-1599	1600-1649	1650-1699	1700-1749	1750-1799	1800-1849	1850-1899
1							
		1					
				0.33	0.33	0.33	

C

1500-1549	1550-1599	1600-1649	1650-1699	1700-1749	1750-1799	1800-1849	1850-1899
0.33	0.33	0.33					
				0.33	0.33	0.33	

D

1500-1549	1550-1599	1600-1649	1650-1699	1700-1749	1750-1799	1800-1849	1850-1899
	0.25	0.25	0.25	0.25			
		0.2	0.2	0.2	0.2	0.2	
	?	?	?	?	?	?	

Figure 7. Method used in this study to calculate stratigraphic ranges of taxa from the stratigraphic position of individual specimens. A, certain stratigraphic range extremities set by well-placed specimens, extending through the intervening strata; B, certain stratigraphic range extended to the closest 50 m SI of a poorly stratigraphically constrained specimen; C, certain stratigraphic range can only be determined to cover the most exclusive interval between two poorly stratigraphically constrained specimens; D, overlapping potential ranges prevent the recognition of a certain stratigraphic range.

3.3.4.3 Specimen identification and the exclusion of specimens

The identity status of specimens used in this analysis falls into one of three categories:

1. Specimens whose identifications were known to be valid due to recent research; these were included.

2. Specimens whose identifications were taken directly from museum catalogues via the Beaufort Fossil Vertebrate database (Nicolas 2007); these were included unless there were grounds to consider them unreliable.

3. Specimens whose identifications were considered spurious; these were excluded.

Specimens in the first category are those that were identified in the literature or had been assigned an identification subsequent to the creation of the Beaufort Fossil Vertebrate database (Nicolas 2007). In a few cases, these identifications had pre-dated this database but were not updated on the collection catalogues of the participating institutions. It was primarily from publications that identifications for specimens curated outside South Africa were obtained. All identifications from the most recent literature and from recent updates to museum catalogue identifications were considered to supersede the identity data on the Beaufort Fossil Vertebrate database. The identifications of specimens used in this thesis are shown in Appendix 2.

If a specimen that had not been directly re-identified recently, then its identity data were taken from the Beaufort Fossil Vertebrate database. These identifications, while not the most secure, were accepted and included unless there was specific reason to doubt their validity.

This was particularly evident in the case of *Pristerognathus*, where a taxonomic review has cast doubt on the identification of many specimens referred to this genus (Van den Heever 1987): this review only dealt with a subset of therocephalian fossil specimens and, despite the conclusion that most referrals to *Pristerognathus* were erroneous, large numbers of specimens unseen by Van den Heever remain identified as *Pristerognathus* on the Beaufort Fossil Vertebrate database. A similar case is the

pareiasaur *Embrithosaurus*, for which the generic diagnosis was recently altered (Lee 1997). This makes all specimens not directly listed as referred specimens in that publication of dubious identity. Other reasons for specimen exclusion included a general disagreement among current researchers as to the validity of particular genera. This was the case for gorgonopsians and temnospondyls, whose taxonomy is still in a state of flux.

Specimens were occasionally re-identified by the author but this was usually restricted to the ruling-out of existing generic assignments, rather than providing new ones. Cursory identifications made by the author were used to support pre-existing identifications but were excluded if found to be different from the catalogue.

As regards identification, there was an exception to the third category for some taxa: specimens that could not be identified to genus level but could be confidently placed within a family of higher taxon (e.g. scylacosaurid therocephalian indet.) were included in the analyses of the higher taxa. As such, the total number of individuals used for higher taxa will usually be greater than for their constituent genera.

The second reason to exclude a specimen concerned the accuracy of its stratigraphic position. A specimen was excluded from the calculation of 'certain ranges' if it could not be constrained to a stratigraphic interval of 500 m and was excluded almost entirely if it could not be constrained to a stratigraphic interval of 1000 m or less; however, if a specimen's entire potential range fell outside of the 'certain range' of its genus as calculated without it, then the 'certain range' of the genus was extended by the minimum interval to accommodate the outlier specimen (Figure 7, C).

The status of each genus is discussed in more detail in Chapter 5.

3.3.4.4 Genera with multiple species

In this study, all genera are considered as monospecific. This is partly as it reduces the number of taxa involved to a manageable level. However, the primarily reason is to obviate any confusion as a result of the rampant splitting in early therapsid taxonomy. Many more species than genera have been described for taxa yet to undergo re-evaluation; within the Dinocephalia, for instance, eight species have been

described for *Jonkeria* alone, of which many are represented by only a single specimen. Recent taxonomic revisions have tended to greatly reduce the number of valid species when compared to older literature (Kammerer 2010; Kammerer *et al.* 2011; Van den Heever 1987). In light of this and the difficulty of discriminating species level distinctions within incomplete fossil genera, individual species are not considered in this study.

3.3.5 Abundance through the stratigraphy

In order to calculate the abundance of any one genus in each 50 m SI, every specimen was given a value of 1 which was subsequently divided over the number of 50 m SIs that the specimen may have come from, i.e. a specimen known to occur within one SI will give a value of 1 to that level, whereas a specimen constrained only to four SI's (200 m) would give a value of 0.25 to each 50 m SI. When all specimens of the genus were considered, the sum of each 50 m interval then gave an approximate abundance at that level.

The distinction between 'certain' and 'potential' ranges was particularly important here. When calculating the abundance for a genus, each 50 m SI that falls within its certain range is recorded as being genuine, while abundances in 50 m SIs that are within the 'potential range' only are illustrated separately. These abundances in the uncertain part of the range were retained to avoid the loss of data. Therefore, the total abundance is equal to the number of specimens, whether they fall within the 'certain range' or not.

3.3.6 Originations, extinctions and generic diversity

The number of originations and extinctions that occur within each 50 m SI were recorded, as was the total generic diversity in each SI. This was used to create a generic diversity curve for tetrapods through the Abrahamskraal Formation and the Poortjie Member of the Teekloof Formation.

When calculating generic diversity through the stratigraphy, only the 'certain ranges' of genera were used as their 'potential ranges' frequently extended beyond the probable limits of the genuine range of the genus. While conservative, the use of a genus' 'certain range' only is therefore considered most reflective of actual trends in taxonomic diversity.

Several genera were excluded from the calculations of generic diversity for several reasons. These were:

1. Those genera represented by single specimens of uncertain provenance (*Cryptocynodon*, *Taurocephalus*, *Riebeeckosaurus* and *Struthionops*)

2. Those genera known only from the Eastern Cape, which probably correlate with the *Eodicynodon* AZ but are uncertain (*Lanthanostegus* and *Pachydectes*).

Although the stratigraphic position of these taxa is uncertain, the exclusion of the three dinocephalian taxa may reduce the apparent extinction rate in the upper *Tapinocephalus* AZ; however, the number of tapinocephalid genera is likely to be reduced in the near future (Güven pers. comm. 2012). The impact of these exclusions may therefore be less than it would currently appear.

3.4 Institution Abbreviations

AMNH, American Museum of Natural History, New York; BP, Bernard Price Institute for Palaeontology, Johannesburg; CGS, Council for Geoscience, Pretoria; FMNH, Field Museum of Natural History, Chicago; MMK, McGregor Museum, Kimberly; NHMUK, Natural History Museum, London; NMQR, National Museum, Bloemfontein; ROZ, Roy Oosthuizen collection, now at the South African Museum, Cape Town; SAM, Iziko South African Museum, Cape Town; TM, Transvaal Museum (now Ditsong Museum of Natural History), Pretoria; UMZC, University Museum of Zoology, Cambridge; UT, University of Tübingen, Tübingen.

CHAPTER 4: LITHOSTRATIGRAPHY OF THE MIDDLE PERMIAN BEAUFORT GROUP

4.1 Stratigraphic Sections

The first section of this chapter lists the stratigraphic sections used in the interpretation of the lithostratigraphy throughout the Middle Permian Beaufort Group. Many stratigraphic sections have been taken from the literature covering various portions of the Abrahamskraal Formation and Poortjie Member of the Teekloof Formation. They are therefore often supplemented by measurements conducted during the course of this project. Where stratigraphic sections were measured in at the same locality, they are generally described in the same entry; conversely, where two stratigraphic sections were measured at different localities, they are described separately, even if together they provide coverage for the entire Middle Permian sequence within one area. Where stratigraphic sections were measured for this thesis, more details about the locality are provided than for those taken from the literature.

Note: Lithostratigraphic members within the Abrahamskraal and Teekloof Formation are not yet accepted by SACS, with the exception of the Poortjie Member. Of the members summarised at the end of this chapter, those marked with an * are not accepted by SACS.

4.1.1 Northern Cape

4.1.1.1 Section 1. Borehole AB1/65, Abrams Kraal 206, Victoria West District

Starts: 31°48.08' S, 22°37.08'

Abrahamskraal Formation thickness in section: 390 m

Poortjie Member thickness in section: >54 m

In the vicinity of Victoria West, the only existing evidence for the lithostratigraphic structure of the Abrahamskraal Formation is the log of SOEKOR borehole AB1/65 from Abrams kraal 206, near Paardeberg (Figure 5), which was described by Cole and Wipplinger (2001). The core provides a complete measurement of the Abrahamskraal Formation south-west of Victoria West but only partially samples the overlying Poortjie Member. Cole and Wipplinger record a thickness of 390 m for the Abrahamskraal Formation at this locality (Figure 8). Within it, they recognise two sandstone packages: the lower Davidskolk Member, which is 97.5 m thick, and the Loxton Member, which is 58 m thick and is separated from the overlying Poortjie Member by 37 m of finer rocks (Cole and Wipplinger 2001). The surface rocks at Abrams kraal belong to the Poortjie Member and therefore this unit is not completely represented in this section (map sheet: Republic of South Africa 3122, Victoria West, 1:250 000 Geological Series 1992).

4.1.1.2 Section 2. Spuitpoort, Victoria West District

Starts: 31°10.581' S, 22°59.382' E

Abrahamskraal Formation thickness in section: ≤45 m

Poortjie Member thickness in section: 120 m

Given the significant degree of northward thinning known to occur in the western Karoo (Cole and Wipplinger 2001), the Abrahamskraal Formation at the Ecca-Beaufort boundary north of Victoria West should be thinner than at Abrams kraal 206. To confirm this, a section was measured on the farm Spuitpoort, on the Vosburg road around 28 km north of Victoria West (Figure 5; Figure 9). Beaufort Group strata are well exposed on a hillside near the northern boundary of this farm that is capped by a large dolerite sill. The strata exposed on the lower part of the hill are mapped as Abrahamskraal Formation, whereas the upper part of the hillside is mapped as belonging to the Hoedemaker Member of the Teekloof Formation (map sheet: Republic of South Africa 3122, Victoria West, 1:250 000 Geological Series 1992); presumably, the Poortjie Member was considered to be absent.

The lower part of the hillside, that mapped as Abrahamskraal Formation, is 120 m thick and consists of eight thick sandstones set within finer grained rocks; conversely, the upper part of the hillside (mapped as Hoedemaker Member of the Teekloof Formation) is almost exclusively mudrock (Figure 8; Figure 10). A layer of creamy, black speckled rock approximately 20 cm thick was identified 16 m below the division between these two units, which was identified as an ash tuff. This was sampled and after subsequent TIMS analysis, zircons within this rock produced a radiometric age of 260.9 Ma (Rubidge pers. comm.2012), which is consistent with a mid-*Pristerognathus* AZ age (Rubidge *et al.* 2013). The presence of large sandstone beds and a *Pristerognathus* AZ age therefore identify this unit as the Poortjie Member of the Teekloof Formation.

The thickness of the Abrahamskraal Formation at the Spuitpoort locality is less secure. The strata exposed on the hillside are obscured by dolerite dykes between Spuitpoort and the Ecca-Beaufort boundary to the north, while the low dip of the strata in the region and the presence of soil make the measurement of a stratigraphic section on the flat ground practically impossible. However, in light of the low dip, a rough estimate of thickness was achieved through the use of GPS altitude readings. These indicated a difference of approximately 45 m between the base of the sandstone package at Spuitpoort (Figure 8) and the Ecca–Beaufort boundary as mapped on the farm Rheboksfontein, 10 km to the north (Figure 9; map sheet: Republic of South Africa 3122, Victoria West, 1:250 000 Geological Series 1992).

The presence of the Abrahamskraal Formation north of Victoria West is attested by the discovery of an anteosaurid dinocephalian (BP/1/5591) immediately above the Ecca-Beaufort boundary on the farm Rheboksfontein; this is secure as, currently, anteosaurids are known only from the upper Abrahamskraal Formation (see 5.5.2). The Abrahamskraal Formation must therefore occupy at least the lower portion of the approximately 45 m interval below the base of the sandstone package exposed at Spuitpoort. This confirms the northward attenuation of the Abrahamskraal Formation (Cole and Wipplinger 2001).

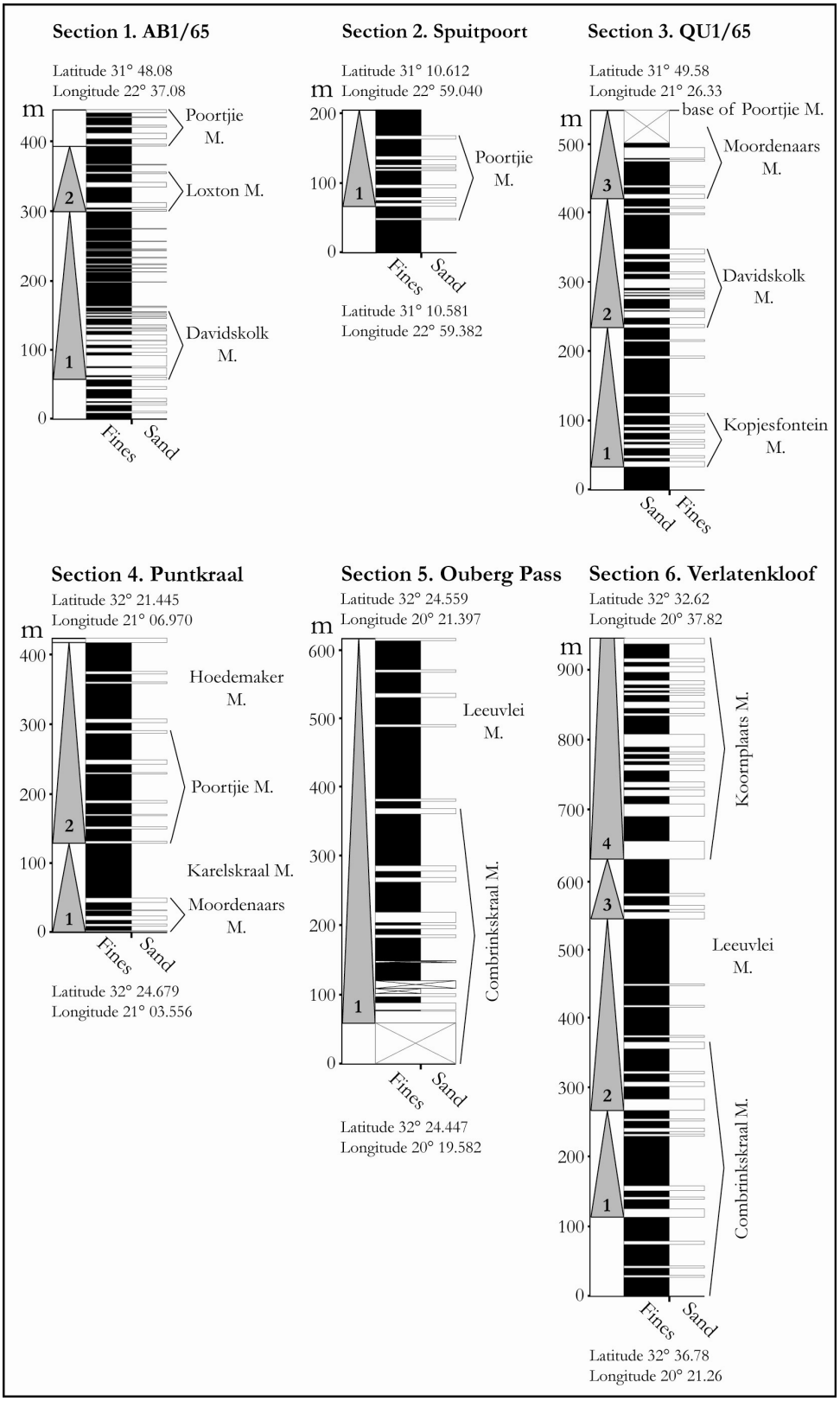


Figure 8. Stratigraphic sections from localities in the Northern Cape Province demonstrating fining-upward cycles. Section localities are shown in Figure 5. Sections 1 and 3 after Cole and Wipplinger (2001); Section 6 after Turner (1981).

4.1.1.3 Section 3. Borehole QU1/65, Quaggasfontein 357, Fraserburg District

Starts: 31°49.58' S, 21°26.33' E

Abrahamskraal Formation thickness in section: ~550 m

Poortjie Member thickness in section: n/a

112 km west of borehole AB1/65 is the site of SOEKOR borehole QU1/65, on the farm Quaggasfontein, north of Fraserburg (Figure 5). The core from this borehole was also logged by Cole and Wipplinger (2001), who recorded within it 505 m of Abrahamskraal Formation rocks (Figure 8). Because the borehole was drilled into Abrahamskraal Formation surface rock, it does not record the entire Formation at this locality; however, field observation of the area suggests that no more than 50 m of rock separates the surface horizon at the site of the borehole from the base of the Poortjie Member as mapped on the same farm, 4.5 km to the southwest (map sheet: Republic of South Africa 3120, Williston, 1:250 000 Geological Series 1989). Therefore, added to the 505 m described by Cole and Wipplinger (2001), the Abrahamskraal Formation at this point in the basin is approximately 550 m thick.

Within the Abrahamskraal Formation at Quaggasfontein, Cole and Wipplinger (2001) recognised three sandstone packages. The lower two, measuring 61 m and 115 m, were attributed to the Kopjesfontein and Davidskolk members, respectively. The upper package, of which 80 m was preserved at the top of the core, was attributed to the Moordenaars Member (Cole and Wipplinger 2001).

4.1.1.4 Section 4. Puntkraal, Sutherland District

Starts: 32° 24.679' S, 21° 03.556' E

Abrahamskraal Formation thickness in section: upper 128 m

Poortjie Member thickness in section: 164 m

In order to provide a good stratigraphic section for the Poortjie Member at its westernmost exposure, a stratigraphic section was measured on the farm of Puntkraal, which lies at the western end of the Nuweveld Mountains around 39 km

east of Sutherland (Figure 5). The lithostratigraphy at Puntkraal is easily interpreted: a package of sandstones in the upper Abrahamskraal Formation is evident in the western part of the farm, which is separated from the overlying Teekloof Formation by an argillaceous unit 78 m thick (Figure 8; Figure 11). This argillaceous unit forms a distinct topographic 'step' that can be traced for 10 km between Bontberg and the farm Die Kuile to the south, corresponding to the mapped base of the Teekloof Formation (Figure 12; map sheet: Republic of South Africa 3220, Sutherland, 1:250 000 Geological Series 1983). These two units form a single fining-upward cycle (Figure 8).

A sandstone package interpreted to represent the Poortjie Member of the Teekloof Formation is exposed on a series of terraces that extend from the top of the step near Puntkraal farmstead up to lower slopes of Langberg (Figure 13, 14). The Poortjie Member is therefore well constrained at this locality, being 164 m thick.

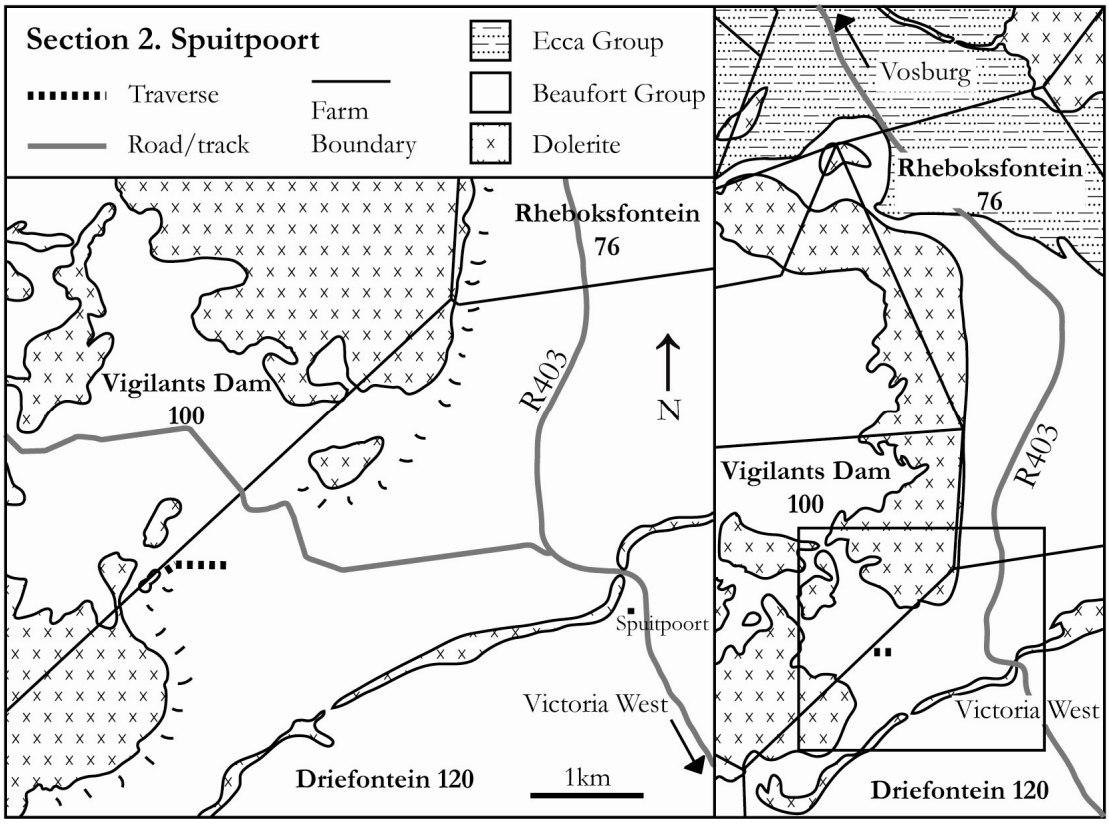


Figure 9. Map showing the traverse of the stratigraphic section measured on the farm Spuitpoort, Victoria West district.



Figure 10. Photograph of the Spuitpoort locality looking northwest. The thick sandstones visible in the gully belong to the Poortjie Member of the Teekloof Formation, while the fine-grained strata above the saddle belong to the overlying Hoedemaker Member. The valley floor is most likely Abrahamskraal Formation.

4.1.1.5 Section 5. Ouberg Pass, Sutherland District

Starts: 32°24.447' S, 20°19.582' E

Abrahamskraal Formation thickness in section: lower 617 m

Poortjie Member thickness in section: n/a

Ouberg Pass is situated on the escarpment between the Roggeveld and the Tanqwa Karoo, approximately 28 km west of Sutherland (Figure 5). A stratigraphic section was measured at this locality to understand the lithostratigraphy on the western escarpment and provide better stratigraphic constraints for fossil specimens found in the vicinity Sutherland (Figure 15). At Ouberg Pass, 617 m of Beaufort Group strata

are present in a single upwards fining cycle (Figure 8), the top of which has been correlated with the lower Koornplaats Member in the Moordenaarskaroo (Cole and Wipplinger 2001). Through the tracing of this sandstone horizon using Google Earth, this correlation is supported here, which indicates the exposure of the Koornplaats, Wilgerbos and Moordenaars members on the Roggeveld between the western escarpment and the Nuweveld Mountains at Puntkraal (Figure 5).

Sandstone is more abundant in the lower 230 m of this section and only a single fining upward cycle is present (Figure 8). No fossil material has yet been found on the lower arenaceous unit that could provide an age for it but two specimens of the dicynodont *Colobodectes* have been recovered from the top of Ouberg Pass; however, these are the lowest known individuals of that genus and therefore provide poor time constraints on the rocks below.

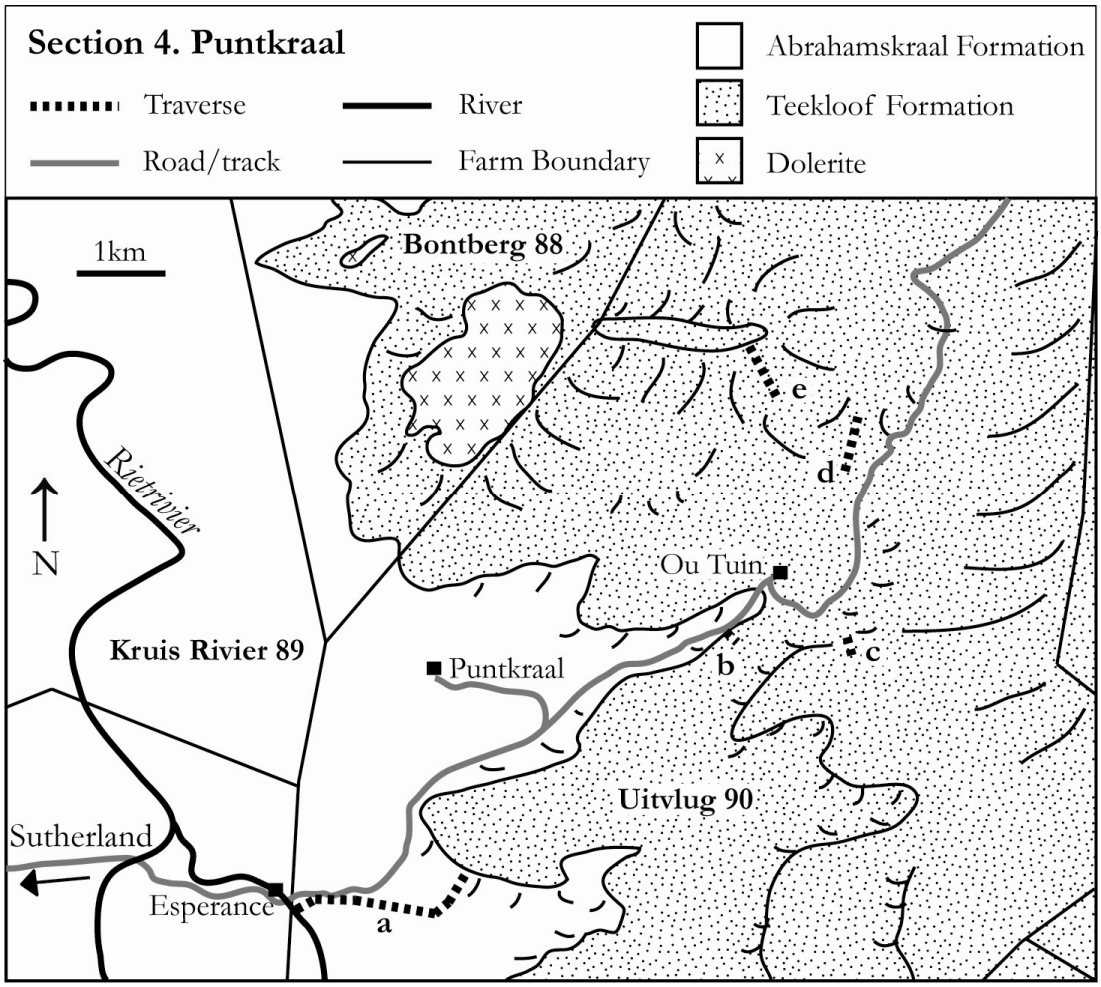


Figure 11. Map showing the traverse of the stratigraphic section measured on the farm Puntkraal, Sutherland district.

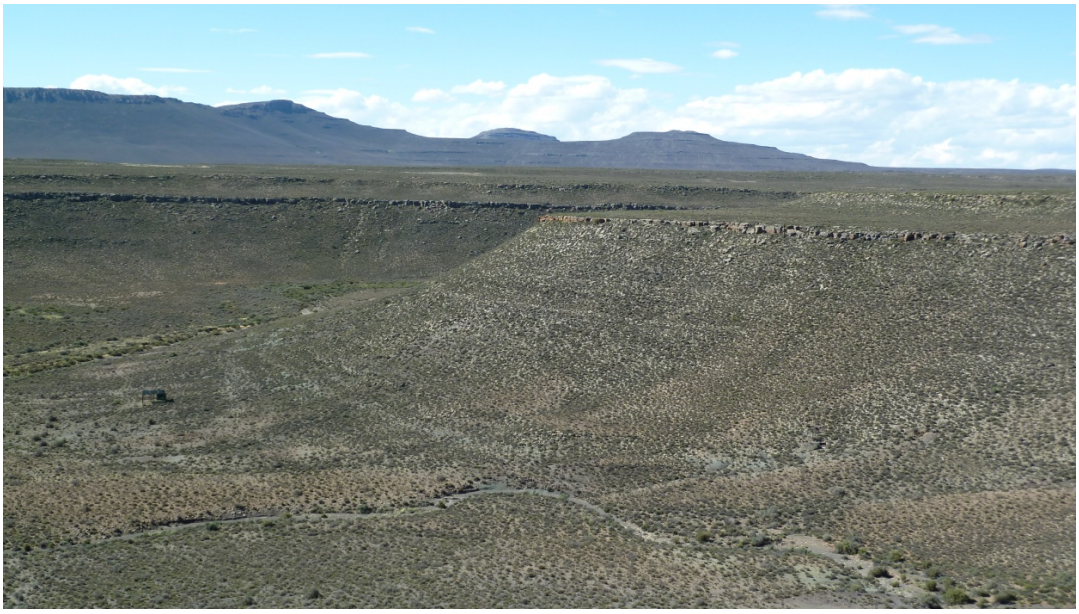


Figure 12. Photograph of the Karelskraal Member as exposed on the farm Puntkraal, Sutherland district (looking north). The Karelskraal Member is well defined in this area; the sandstone at the top of the slope is the basal Poortjie Member sandstone.

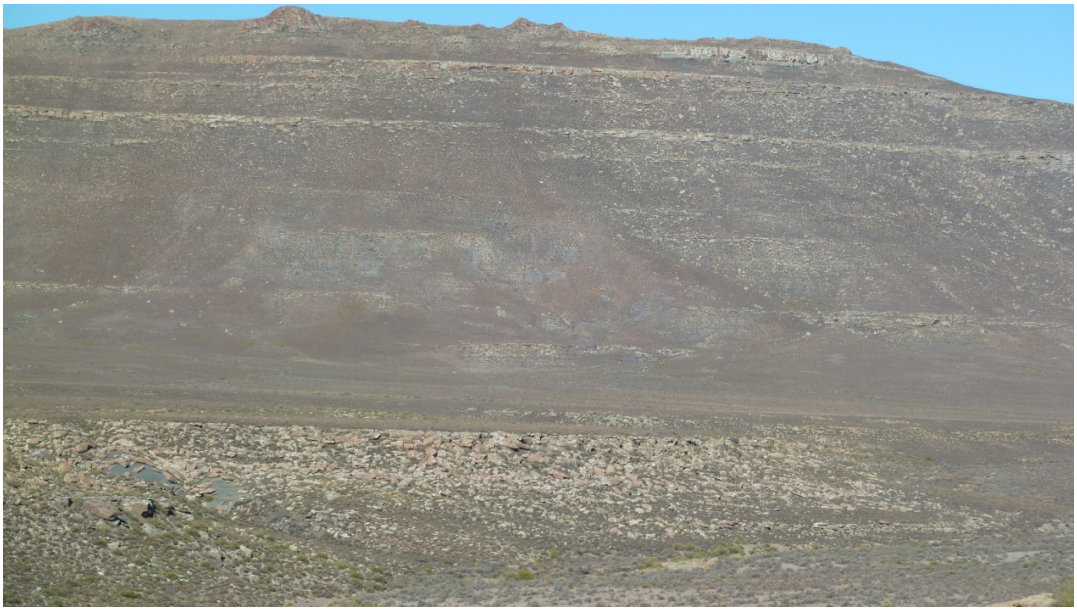


Figure 13. Photograph of the western slope of Langberg, taken on the farm Puntkraal, Sutherland district. The sandstone at the base of the picture, in the foreground, is the uppermost Poortjie Member sandstone. The sandstones at the top of the mountain belong to the Oukloof Member.

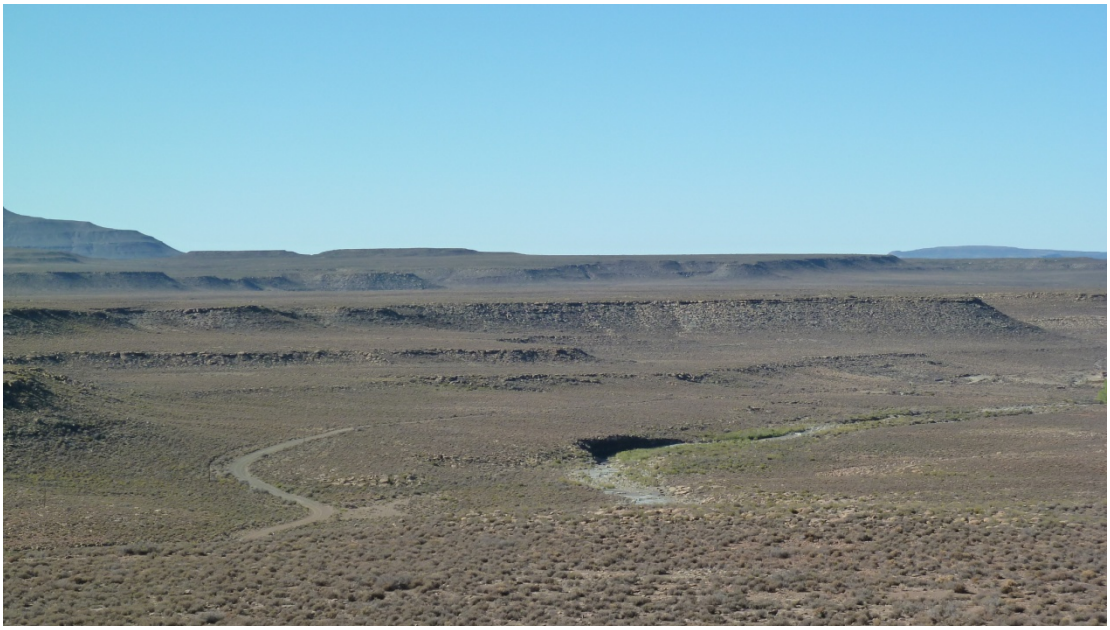


Figure 14. Photograph looking south on the farm Puntkraal showing the terraces formed by the Poortjie Member in this area.

4.1.1.6 Section 6. Verlatenkloof, Sutherland District

Starts: 32°36.78' S, 20°21.26' E

Abrahamskraal Formation thickness in section: lower 926 m

Poortjie Member thickness in section: n/a

Verlatenkloof is situated only 17 km south of Ouberg Pass and is the site of a stratigraphic section measured by Turner (1981), which was subsequently reinterpreted by Cole and Wipplinger (2001) (Figure 5). This section records a greater portion of the Abrahamskraal Formation than at Ouberg Pass, with a total thickness of 934 m, and the strata comprise three complete upwards-fining cycles with 300 m of the arenaceous part of a fourth at the top (Figure 8). At this locality, the lowest 110 m of the Abrahamskraal Formation are actually very argillaceous, so the base of the first complete fining-upward cycle only occurs at that level.

The lower part of the Abrahamskraal Formation at Verlatenkloof is more arenaceous than in the Moordenaarskaroo and does not correlate exactly with this section

(Figure 16). This may be partly due to the resolution used by Loock *et al.* (1994) in the Moordenaarskaroo. However, it is possible to see that at Verlatenkloof, the lower fining-upward cycles of the Abrahamskraal Formation are considerably thinner than along the southern boundary of the basin; for instance, the first cycle is only 155 m thick and the second only 360 m thick.

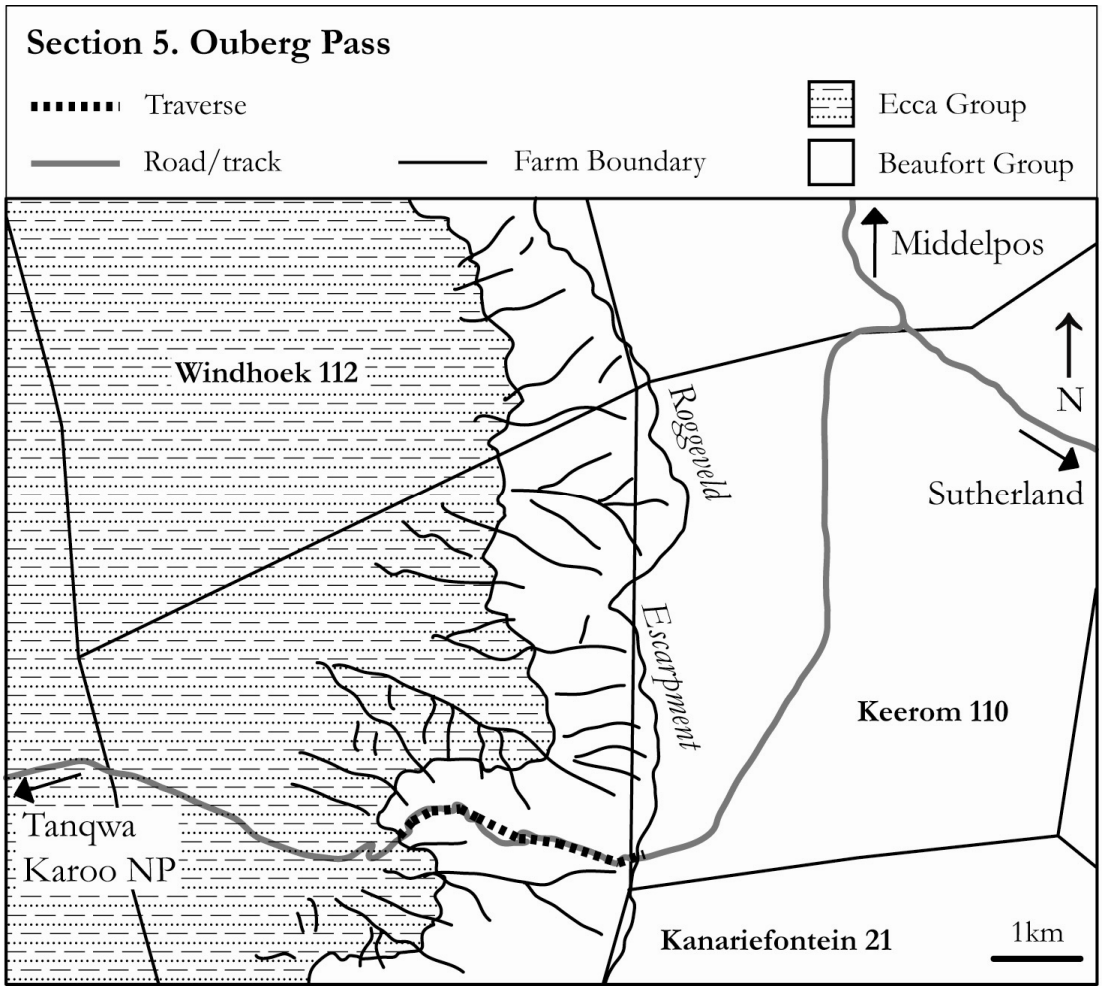


Figure 15. Map showing the traverse of the stratigraphic section measured at Ouberg Pass, Sutherland district.

The thickness of the missing Abrahamskraal Formation strata at Verlatenkloof Pass was calculated by using Google Earth to trace the sandstone at the top of the Pass southeast along the Komsberg Escarpment to the Moordenaarskaroo. The traced horizon intercepted the stratigraphic section measured in the Moordenaarskaroo about 600 m below the base of the Poortjie Member, within the upper Koornplaats Member. This indicates a missing 600 m of rock at the top of the Verlatenkloof

stratigraphic section, which would make the original thickness of the Abrahamskraal Formation at this locality 1534 m.

4.1.2 Western Cape

4.1.2.1 Section 7. Moordenaarskaroo (begins Buffelrivier 67), Laingsburg District

Starts: approximately 32° 7.242' S, 20° 54.664' E

Abrahamskraal Formation thickness in section: 2210 m

Poortjie Member thickness in section: lower 45 m

Building on the work of LeRoux (1985), the studies in this area by Loock (1993) and Loock *et al.* (1994) have provided the most influential nomenclature for the stratigraphy of the Abrahamskraal Formation. The stratigraphic section was measured across the Moordenaarskaroo, from the Ecca-Beaufort boundary in the south to the base of the Poortjie Member a mapped on Gatsberg and on the Komsberg escarpment (Figure 5; map sheet: Republic of South Africa 3220, Sutherland, 1:250 000 Geological Series 1983). This stratigraphic section provides a complete measurement of the Abrahamskraal Formation of 2210 m (Loock *et al.* 1994; Figure 17).

Loock (1993) originally recognised three coarsening-upwards cycles in the Moordenaarskaroo, which conflicted with the three upwards-fining cycles identified by Le Roux (1985). Subsequent stratigraphic sections measured on the farms Wilgerbos (4.1.2.2) and Die Skeur (4.1.2.3) at a higher stratigraphic resolution have identified a more typical fluvial fining-upwards pattern (Figure 17), contrary the observations of Loock (1993). Moreover, comparison with Wilgerbos suggests that five fining-upward cycles are present in the Moordenaarskaroo, comprising three sandstone packages (Figure 17).

4.1.2.2 Section 8. Wilgerbos, Laingsburg District

Starts: 33° 06.477' S, 21°14.602' E

Abrahamskraal Formation thickness in section: lower 2274 m

Poortjie Member thickness in section: n/a

A stratigraphic section was measured on the farm Wilgerbos, between Laingsburg and Prince Albert Road, to record the nature of the lithostratigraphy between the Moordenaarskaroo and Prince Albert Road (Figure 5). The Abrahamskraal Formation is exposed between the farm Grootfontein, just to the north of the N1 road, and the hill to the east of the Wilgerbos farmstead (Figure 18). Several large folds pass through the south of this locality in an east-west direction becoming gentler towards the north but these were taken into consideration.

The Wilgerbos locality records the majority of the Abrahamskraal Formation and that which is present represents an intermediate between the stratigraphy to the east and west (Figure 16). Correlation with the stratigraphic section at Die Skeur (4.1.2.3) suggests that approximately 75 m of rock is missing between the top of the stratigraphic section at Wilgerbos and the base of the Poortjie Member. As the stratigraphic section at Wilgerbos records 2274 m of Abrahamskraal Formation strata, the original thickness of the Abrahamskraal Formation at this locality is approximately 2350 m (Figure 17).

The stratigraphic section of the Abrahamskraal Formation at Wilgerbos measured for this thesis shows close similarities with the section of Jordaan (1990), with the exception that it is 200 m thicker. This differs from most of Jordaan's other stratigraphic sections that have caused concern for significantly overestimating thicknesses (Cole and Wipplinger 2001:7). The Abrahamskraal Formation at Wilgerbos shows four fining-upwards cycles, with the possibility that the arenaceous base of a fifth is present in the uppermost part of the section (Figure 17). If 75 m of strata is considered missing between the top of this stratigraphic section and the base of the Poortjie Member, the fifth fining-upward cycle can be no more than 150 m thick.

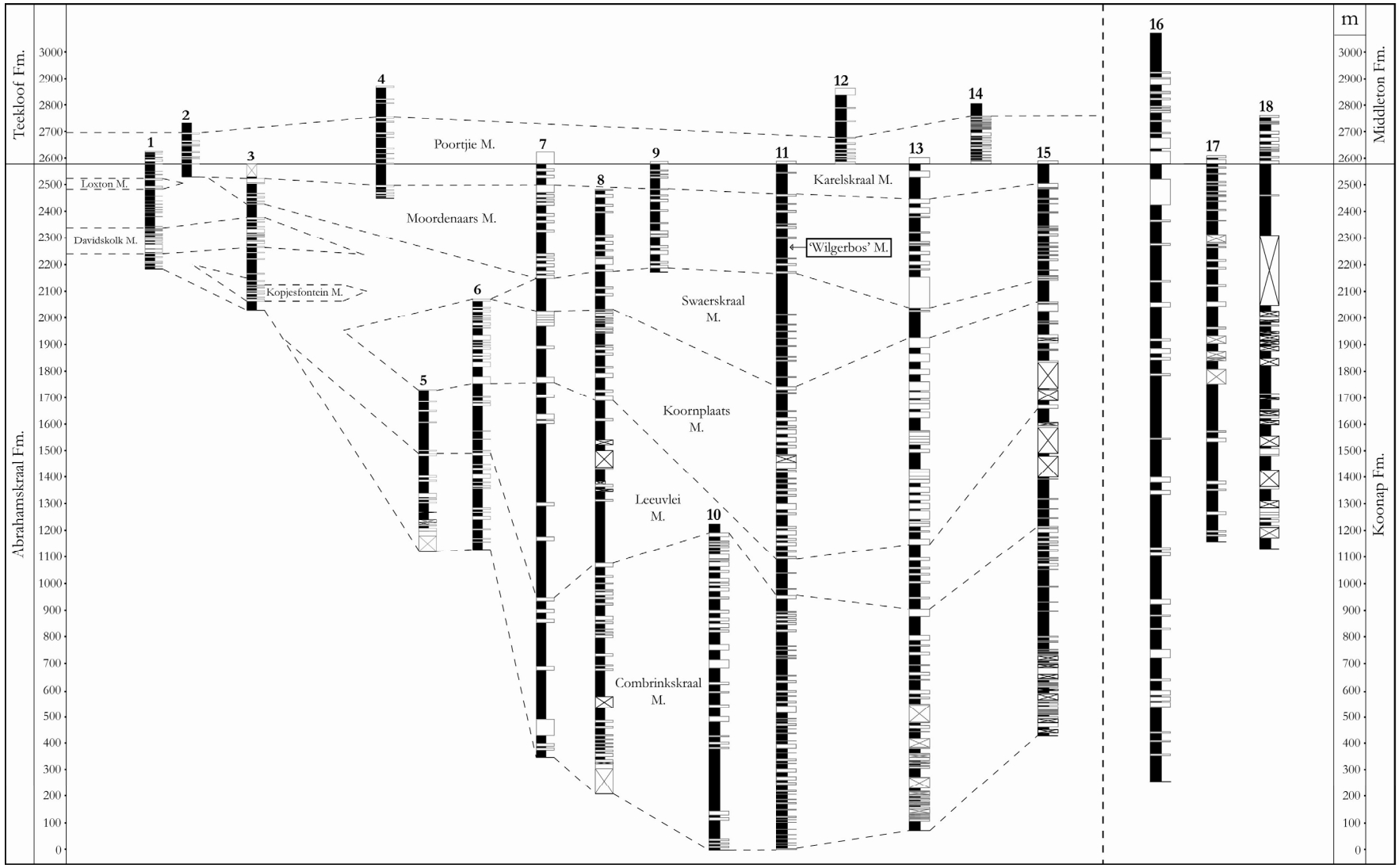


Figure 16. A comparison of all stratigraphic sections used in this study and the correlation of lithostratigraphic units. Stratigraphic sections are shown in an anti-clockwise direction from the north of the basin. Numbers correspond to the stratigraphic sections mentioned in the text. The localities of each stratigraphic section are shown in Figure 5.

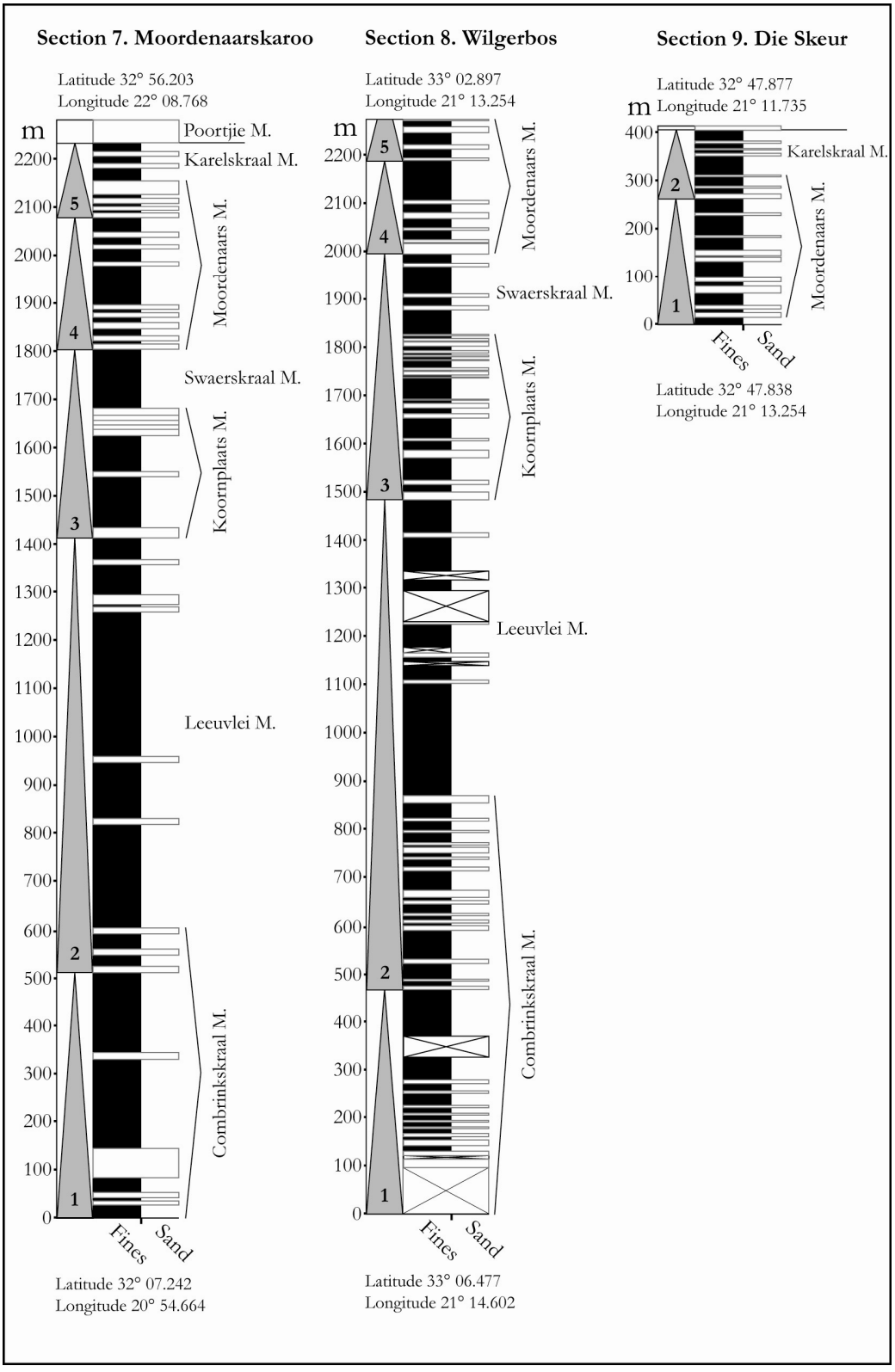


Figure 17. Stratigraphic sections measured in the Moordenaarskaroo and Komsberg Mountains in the Western Cape Province demonstrating fining-upward cycles. Section localities are shown in Figure 5. Moordenaarskaroo section after Loock *et al.* (1994).

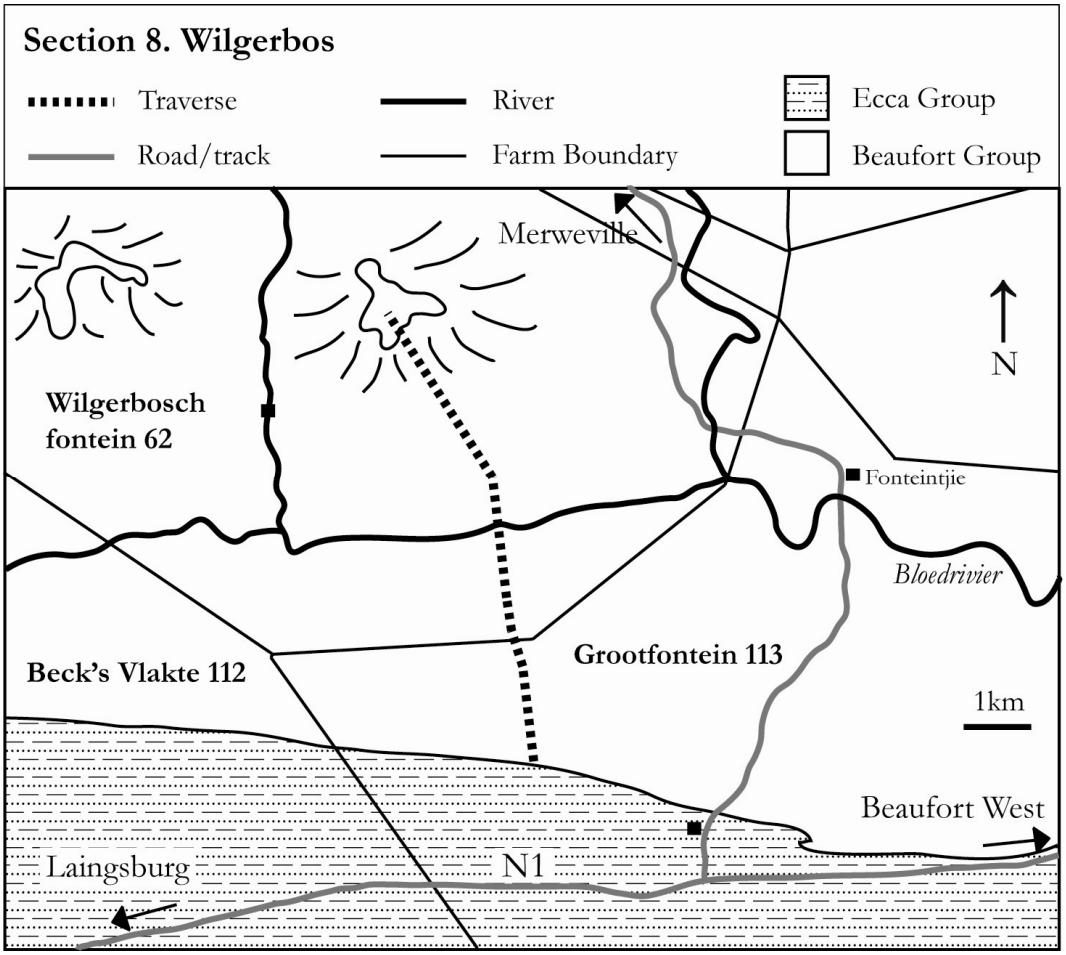


Figure 18. Map showing the traverse of the stratigraphic section measured on the farm Wilgerbos, Laingsburg district.

4.1.2.3 Section 9. Die Skeur, Laingsburg District

Starts: 32°47.838' S, 21° 13.127' E

Abrahamskraal Formation thickness in section: upper 402 m

Poortjie Member thickness in section: lower 8 m

A stratigraphic section was measured on the farm Die Skeur on the western border of the Koup in order to determine the distance between the base of the Poortjie Member and the floor of the Koup itself, as well as provide information on the upper Abrahamskraal Formation that was absent at the Wilgerbos locality (Figure 5; Figure 19). The section was measured up to the base of the Poortjie Member as mapped but the section was measured from a point 924 m above sea level, about 275

m above the lowest point in the western Koup (map sheet: Republic of South Africa 3220, Sutherland, 1:250 000 Geological Series 1983). Perhaps two fining-upward cycles are present in the 400 m of the Abrahamskraal Formation recorded in the stratigraphic section at Die Skeur (Figure 17). The thickness indicates that the Abrahamskraal Formation strata that outcrop in the western Koup are constrained to be between 400–675 m below the base of the Poortjie Member of the Teekloof Formation.

4.1.2.4 Section 10. Dwyka River, Prince Albert district

Starts: 33° 05.907' S, 21° 35.133' E

Abrahamskraal Formation thickness in section: 1225 m

Poortjie Member thickness in section: n/a

A stratigraphic section was measured along the Dwyka River by Vitali (2001), 15 km southwest of Prince Albert Road (Figure 5); this was intended to investigate the lowermost Beaufort Group in this area and so only the lower 1225 m of the Abrahamskraal Formation were measured (Figure 19). The Abrahamskraal Formation is relatively high in sandstone at this locality but an argillaceous interval between 140 m and

375 m above the base of the Abrahamskraal Formation shows similarities with the Moordenaarskaroo (4.1.2.1) and Wilgerbos (4.1.2.2) localities, indicating the presence of at least one fining-upward cycle (Figure 19; Figure 16).

4.1.2.5 Section 11. Merweville region, Prince Albert and Beaufort West districts

Starts: 33° 01.750' S, 21° 41.068' E

Abrahamskraal Formation thickness in section: 2560 m

Poortjie Member thickness in section: n/a

The stratigraphic section of the Abrahamskraal Formation in the Merweville area was primarily measured on the farm Tuinkraal in the Prince Albert district, but the upper few hundred metres were traced north through Merweville and the section was completed on the farm Springfontein in the Beaufort West district (Jirah 2009, 2013; Figure 5); the section was measured up to the base of the Teekloof Formation as mapped (map sheet: Republic of South Africa 3220, Sutherland, 1:250 000 Geological Series 1983). At 2575 m, it is the greatest thickness reached by the Abrahamskraal Formation anywhere in the basin and four fining-upwards cycles are five fining-upward cycles are present, as is the case further west (Figure 19). The lower two are less well defined than those higher in the Abrahamskraal Formation, but the finer parts of these cycles can be distinguished by the lack of the thick sandstones bodies typical of the arenaceous packages. These intervals occur 635–815 m and 955–1090 m above the base of the Abrahamskraal Formation.

The third fining-upward cycle is quite extended at Prince Albert Road, with both the lower sandstone package and the upper argillaceous interval having a combined thickness of 1075 m between 1090 m and 2165 m above the base of the Abrahamskraal Formation. This is significantly more than their equivalents to the west (Figure 16). The upper two fining-upward cycles of the Formation are similar to their equivalents in the Moordenaarskaroo and at Wilgerbos. Overall, the lower two thirds of the Abrahamskraal Formation in the Merweville area are rather arenaceous.

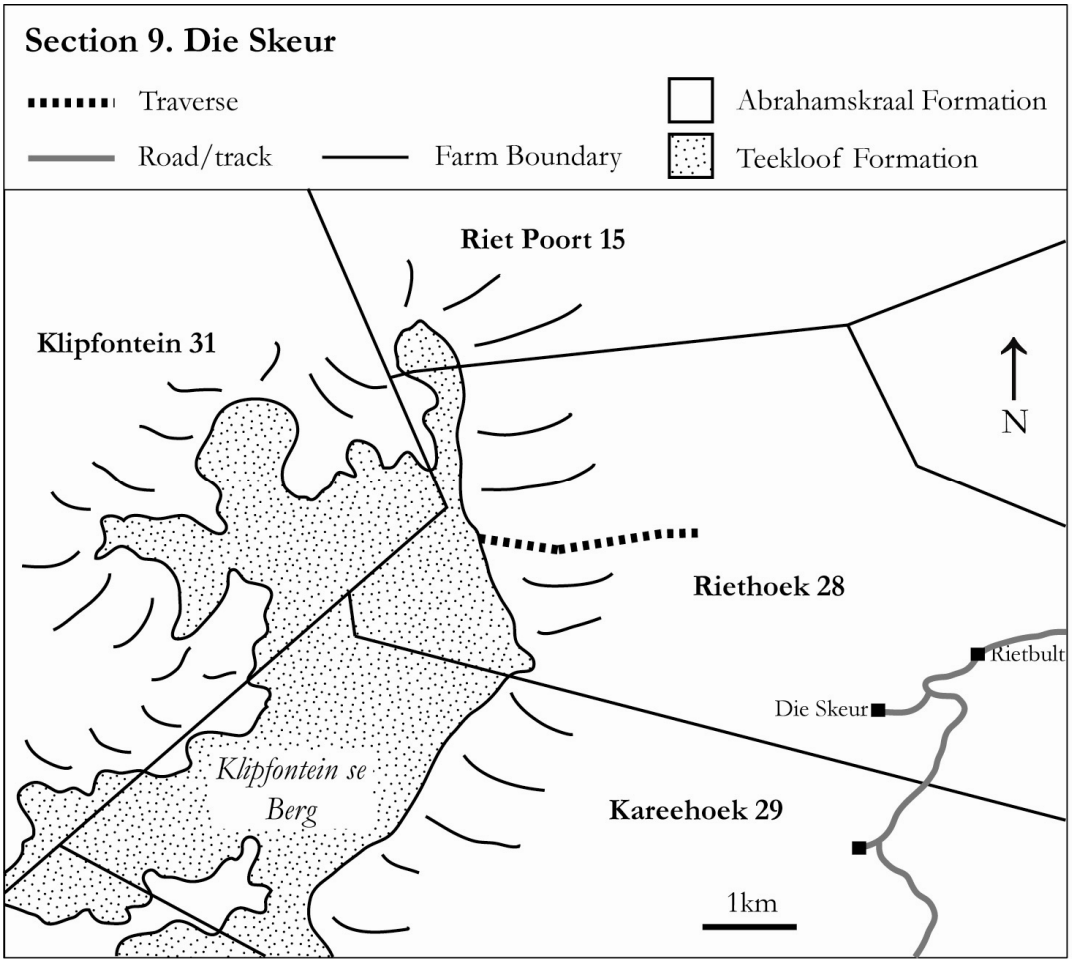


Figure 19. Map showing the traverse of the stratigraphic section measured on the farm Die Skeur, Laingsburg district.

4.1.2.6 Section 12. Springfontein, Beaufort West District

Starts: 32° 21.870' S, 21° 26.961' E

Abrahamskraal Formation thickness in section: n/a

Poortjie Member thickness in section: 103 m

The stratigraphic section measured on the farm Springfontein, north of Merweville, followed on directly from the section measured by Jirah (2013) and encompassed the lower Teekloof Formation from the base of the Poortjie Member to the base of the Oukloof Member, which outcrops at the top of the escarpment at this locality (Figure 5; Figure 20). The primary purpose of this section was to record the thickness of the Poortjie Member in the western Koup. Stear (1980) had stated a thickness of over 200 m for the Poortjie Member in this part of the basin but he cited no

evidence and such a thickness is not substantiated here; in fact, the lower sandstone package identified to be the Poortjie Member on the farm Springfontein was found to be only 102 m thick (Figure 19). The overlying argillaceous interval interpreted as the Hoedemaker Member is 152 m thick at this locality and together these two members correspond to single fining-upwards cycle, above the five already observed in the underlying Abrahamskraal Formation (4.1.2.5).

4.1.2.7 Section 13. Combrinkskraal, Prince Albert District

Starts: 33° 1.354' S, 21° 59.947' E for Rubidge (1988) and 33° 0.896' S, 22° 0.633' E for Thissen *et al.* (2010)

Abrahamskraal Formation thickness in section: 2468 m

Poortjie Member thickness in section: n/a

The Abrahamskraal Formation at Combrinkskraal has been measured several times but the most recent stratigraphic section can be composed using the work of Rubidge (1988), who measured the Abrahamskraal Formation from its base up to the first purple mudstone, and that of Thissen *et al.* (2010), who measured from the first purple mudstone up to the base of the Poortjie Member as mapped near the Combrinkskraal farmstead (Figure 5; map sheet: Republic of South Africa 3222, Beaufort West, 1:250 000 Geological Series 1979). At this locality, the Abrahamskraal Formation is 2468 m thick and is even more arenaceous than recorded in the Merweville area to the west (Figure 21); this is particularly noticeable in the upper third of the Abrahamskraal Formation, which makes sandstone packages hard to distinguish. Jordaan (1990) had achieved a very similar thickness for his stratigraphic section at Combrinkskraal but had found it to be rather less arenaceous than Thissen *et al.* (2010). Jordaan does, however, recognise an increase in sandstone abundance in the central part of the Abrahamskraal Formation at this locality.

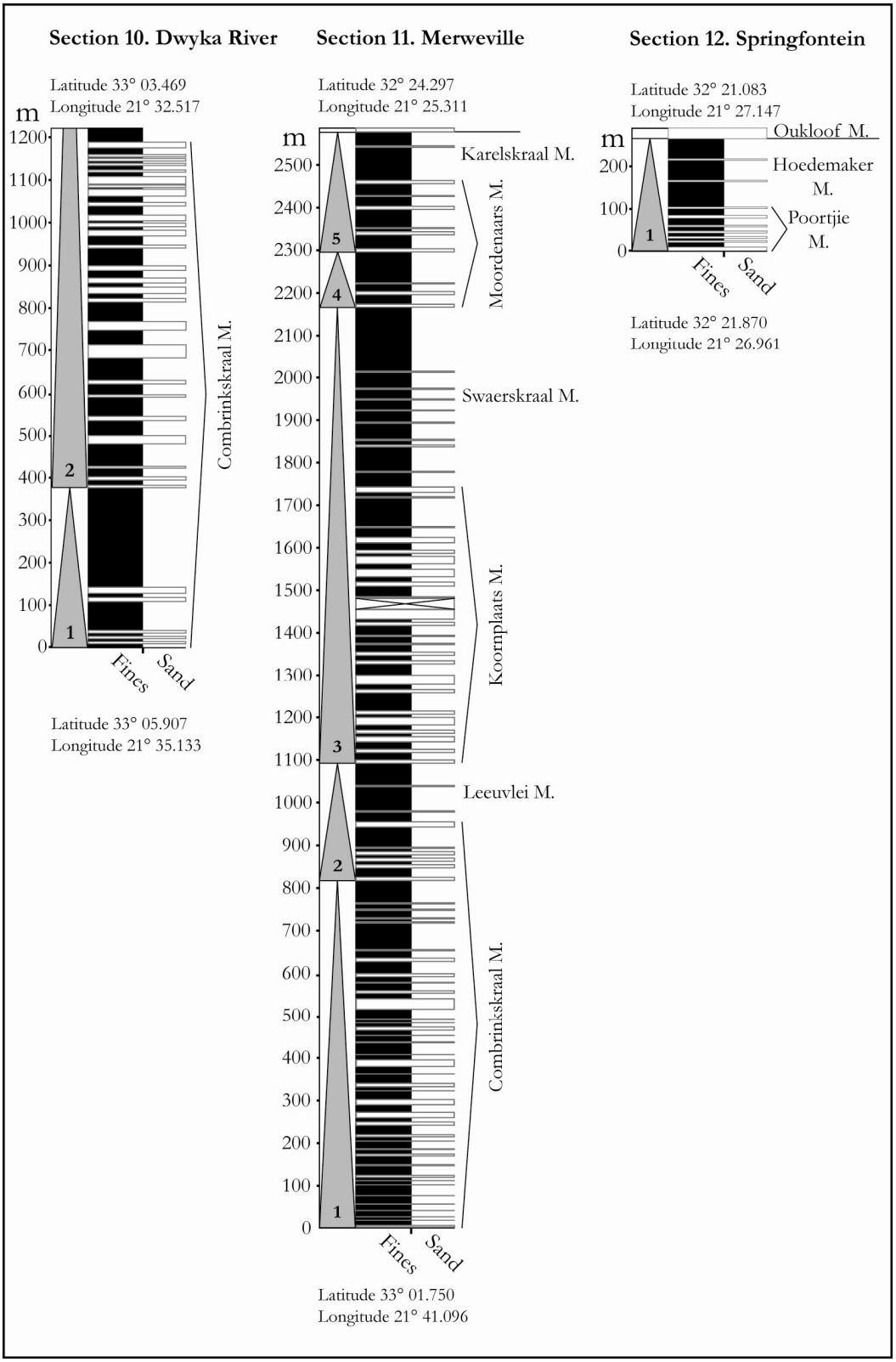


Figure 20. Stratigraphic sections measured in the west-central Koup region in the Western Cape Province demonstrating fining-upward cycles. Section localities are shown in Figure 5. Dwyka River section after Vitali (2001); Merweville section after Jirah (2013).

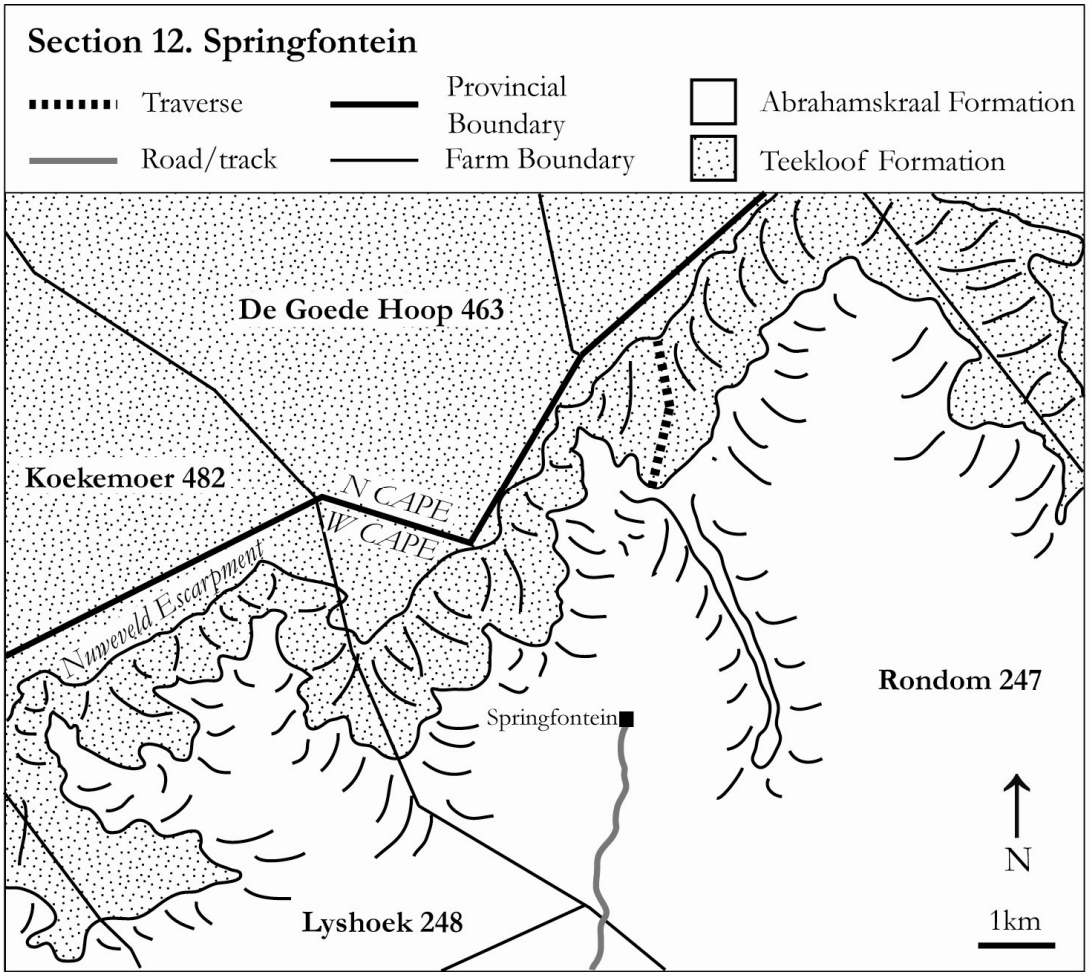


Figure 21. Map showing the traverse of the stratigraphic section measured on the farm Springfontein, Beaufort West district.

Jordaan (1990) assigned the majority of the Abrahamskraal Formation to his 'Combrinkskraal Member' and only the top few hundred metres to the argillaceous 'Leeu Gamka Member.' This interpretation is understandable given the appearance of the sequence here. The stratigraphy at this locality is in general is hard to interpret and fining-upwards cycles not clear. However, the sandstone package in the central part of the Abrahamskraal Formation at Combrinkskraal, between about 1085–1850 m above its base, has a similar position to the base of fining-upward cycle 3 in the Merweville area (Figure 16). Below the base of the this package, the sandstone content remains relatively evenly distributed, although a more argillaceous interval between 830–1085 m that may possibly delineate the top of the Combrinkskraal Member (Figure 21). Only two fining-upward cycles are therefore evident in the Abrahamskraal Formation at this locality.

4.1.2.8 Section 14. Botterkraal and Jansenskraal, Prince Albert District

Starts: 33° 05.444' S, 22° 24.124' E for Rubidge (1988) and 33° 03.824' S, 22° 24.085' E for this study

Abrahamskraal Formation thickness in section: 2152 m

Poortjie Member thickness in section: n/a

A stratigraphic section was required in the eastern Koup for use in both the litho- and biostratigraphic interpretation of the Abrahamskraal Formation and the locality at Jansenskraal proved the most suitable locality (Figure 5). The Abrahamskraal Formation from its base to the first purple mudstone had been measured on the farm Botterkraal by Rubidge (1988) and in the course of this study was continued up to the base of the Poortjie Member as mapped on the farm Jansenskraal (Figure 22; map sheet: Republic of South Africa 3322, Oudtshoorn, 1:250 000 Geological Series 1979). By combining these two sections, the Abrahamskraal Formation is calculated to be 2152 m thick at this locality, which is thinner than at Combrinkskraal (4.1.2.7) or at Merweville (4.1.2.5) (Figure 16). The sequence is also considerably more argillaceous than in the central Koup. Stear (1980) mentioned that the Moordenaars Member dipped below a mud-rich unit in the eastern Koup but it appears that this phenomenon is related more to an overall decrease in sandstone content in this part of the basin.

Two upward-fining cycles are clearly visible in the lower Abrahamskraal Formation in the Jansenskraal area: the first extends from the base of the Abrahamskraal Formation up to 640 m and a second from that horizon up to perhaps 1235 m, although lack of exposure mid-formation makes the top of this second cycle hard to identify with confidence (Figure 21). From 1160–1635 m above the base of the Abrahamskraal Formation there appears to be a sandstone package forming the base of a third fining-upward cycle, in a similar fashion to the Abrahamskraal Formation in the central Koup. Above the upper limit of this sandstone package to the base of the Teekloof Formation there is a generally low proportion of sandstone but a sandstone package is recognisable in section between 1713–2080 m above the base

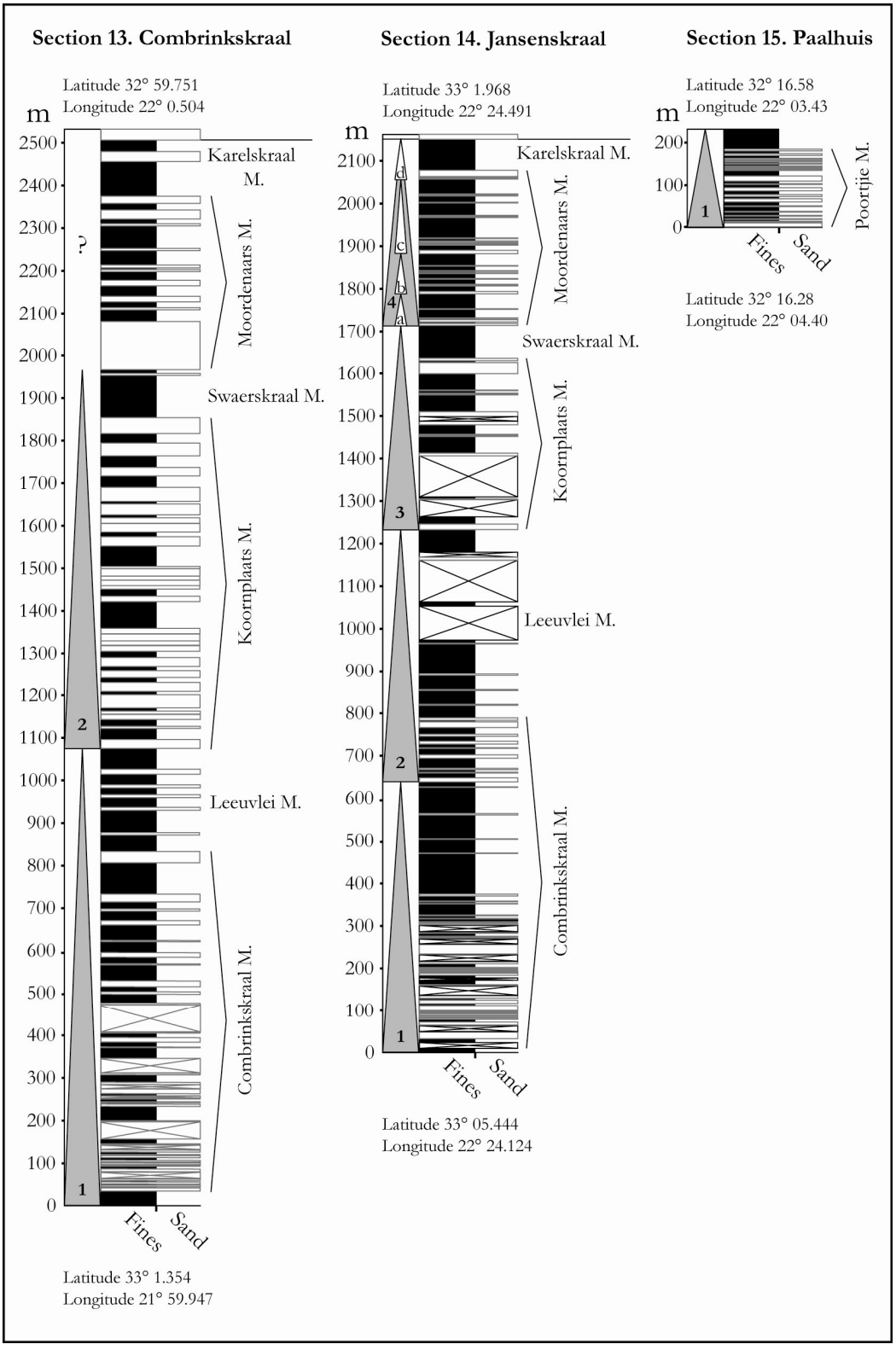


Figure 22. Stratigraphic sections measured in the eastern Koup region in the Western Cape Province, demonstrating fining-upward cycles. Section localities are shown in Figure 5. Combrinkskraal section after Thissen et al. (2010); Paalhuis section after Cole and Wipplinger (2001).

of the Abrahamskraal Formation. This upper package appears to consist of three lower order fining-upward cycles (Figure 21).

4.1.2.9 Section 15. Paalhuis, Beaufort West District

Starts: 32° 16.28' S, 22° 04.40' E

Abrahamskraal Formation thickness in section: n/a

Poortjie Member thickness in section: 182 m

This stratigraphic section was measured on the farm Paalhuis in the Beaufort West district by Cole and Wipplinger (2001) and provides a thickness for the Poortjie Member of the Teekloof Formation in the eastern Koup (Figure 5). At 182.4 m, the Poortjie Member is thicker at this locality than anywhere else that it has been measured (Figure 21).

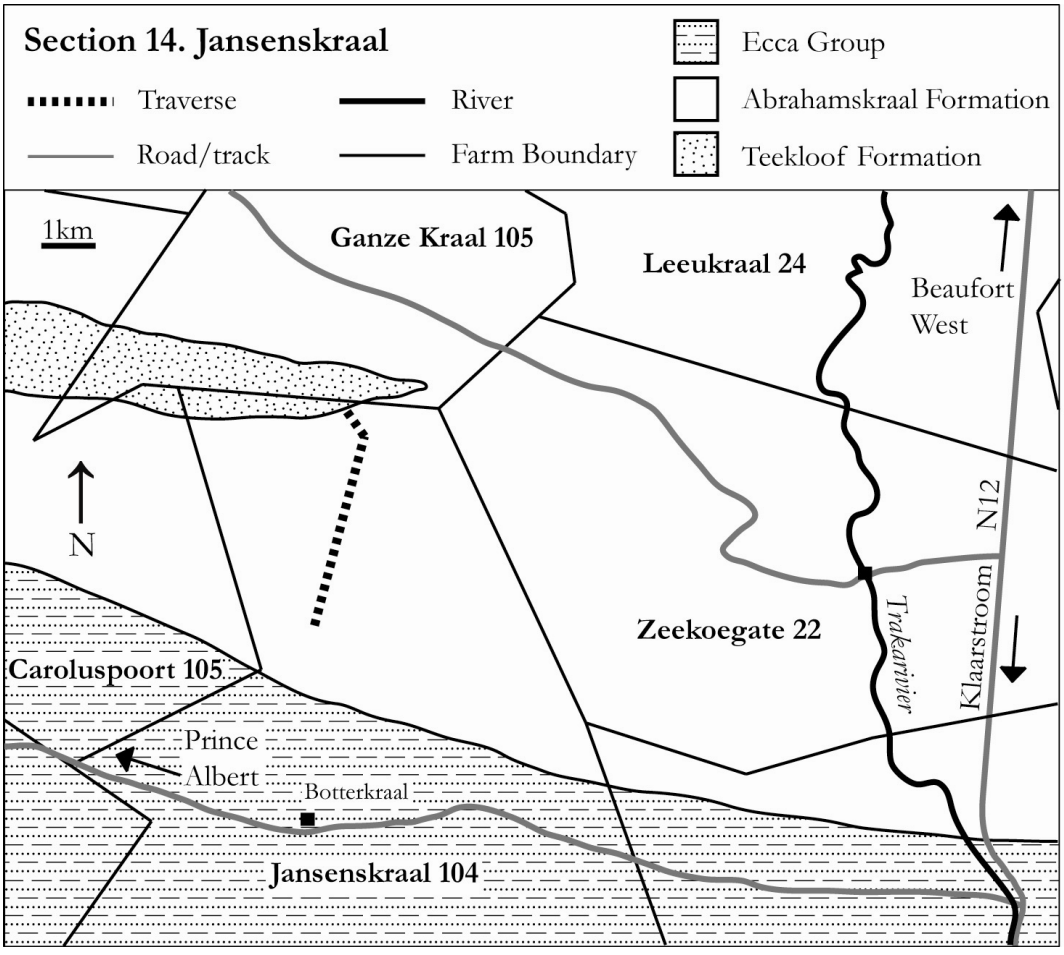


Figure 23. Map showing the traverse of the stratigraphic section measured on the farm Jansenskraal, Prince Albert district.

4.1.3 Eastern Cape

4.1.3.1 Section 16. Klipplaat area, Jansenville District

Starts: 32° 58.136' S, 24° 27.337' E

Koonap Formation thickness in section: 2330 m

In the Eastern Cape, east of 24° E, the stratigraphic subdivision for the Middle Permian part of the Beaufort Group includes the Koonap and Middleton Formations, of which the Koonap Formation is a lateral equivalent to the Abrahamskraal Formation (Hill 1993; Johnson 1976; SACS 1980). Northeast of Klipplaat, a stratigraphic section measured by both Helber and Gebauer (2001) provides a thickness for the Koonap Formation and represents the only documented stratigraphic section of the lower Beaufort rocks between the Great Fish River and the eastern Koup (Figure 5).

The Koonap Formation at Klipplaat was measured to be 2330 m thick by Helber and Gebauer (2001) but internally there is little in the way of clear stratigraphic subunits or fining-upward cycles (Figure 23); the only features of possible interest are an interval of closely packed sandstones between 280–340 m above the base of the formation and a sandstone dominated unit at 2170–2265 m, near its upper boundary (Figure 23). Overall, the composition of the Koonap Formation in this part of the basin consists overwhelmingly of fine-grained rocks.

4.1.3.2 Section 17. Coniston, Peninsular and The Grant, Albany District

Starts: 33° 05.960' S, 26°24.932 E

Koonap Formation thickness in section: 1420 m

The easternmost stratigraphic sections come from north of the Great Fish River in the Albany district. Mason (2007) measured a stratigraphic section of the Koonap Formation up to the first purple mudstone on the farms Coniston and The Grant, which was subsequently continued in the course of this study up to the base of the

Middleton Formation as mapped (map sheet: Republic of South Africa 3326, Grahamstown, 1:250 000 Geological Series 1996; Figure 24). In total, the Koonap Formation at this locality is only 1420 m thick (Figure 23), considerably less than in the vicinity of Klipplaat to the west.

The Koonap Formation at this locality is also overwhelmingly dominated by mudrocks and the first purple mudstone occurs higher at this locality than any known point further west, at 1150 m above the base of the Formation. Unlike at Klipplaat, two possible fining-upward units are visible in section, the lower of which extends from the base of the Koonap Formation to around 885 m and second from 885 m up to the base of the Middleton Formation (Figure 23). Within this upper cycle, sandstone bodies become thinner above 1150 m from the base of the Koonap Formation.

4.1.3.3 Section 18. Bucklands and De Goede Hoop, Albany District

Starts: 33° 05.427' S, 26° 40.255' E

Koonap Formation thickness in section: 1445 m

Middleton Formation thickness in section: lower 185 m

Mason (2007) measured the Koonap Formation from its base up to the first purple mudstone on the farm Bucklands, 24 km to the east of The Grant (Figure 5). This stratigraphic section was also continued up to the base of the Middleton Formation as mapped (Figure 24; map sheet: Republic of South Africa 3326, Grahamstown, 1:250 000 Geological Series 1996). At 1450 m, the Koonap Formation on the farm Bucklands is very similar in thickness to the same formation at The Grant (4.1.3.2), as is the internal lithostratigraphy where visible (Figure 23). A fining-upwards cycle is evident at Bucklands in the lower 860 m of the Koonap Formation, which is not much less than the 885 m recorded at The Grant, but above this horizon a 165 m gap obscures an interval what would be expected to contain the lower part of the second fining-upward cycle. The first occurrence of purple mudstone also matches closely the position observed at The Grant, which at this locality occurs 1180 m

above the base of the Koonap Formation. This stratigraphic section indicates a relative uniformity in the Koonap Formation in the vicinity of the Great Fish River.

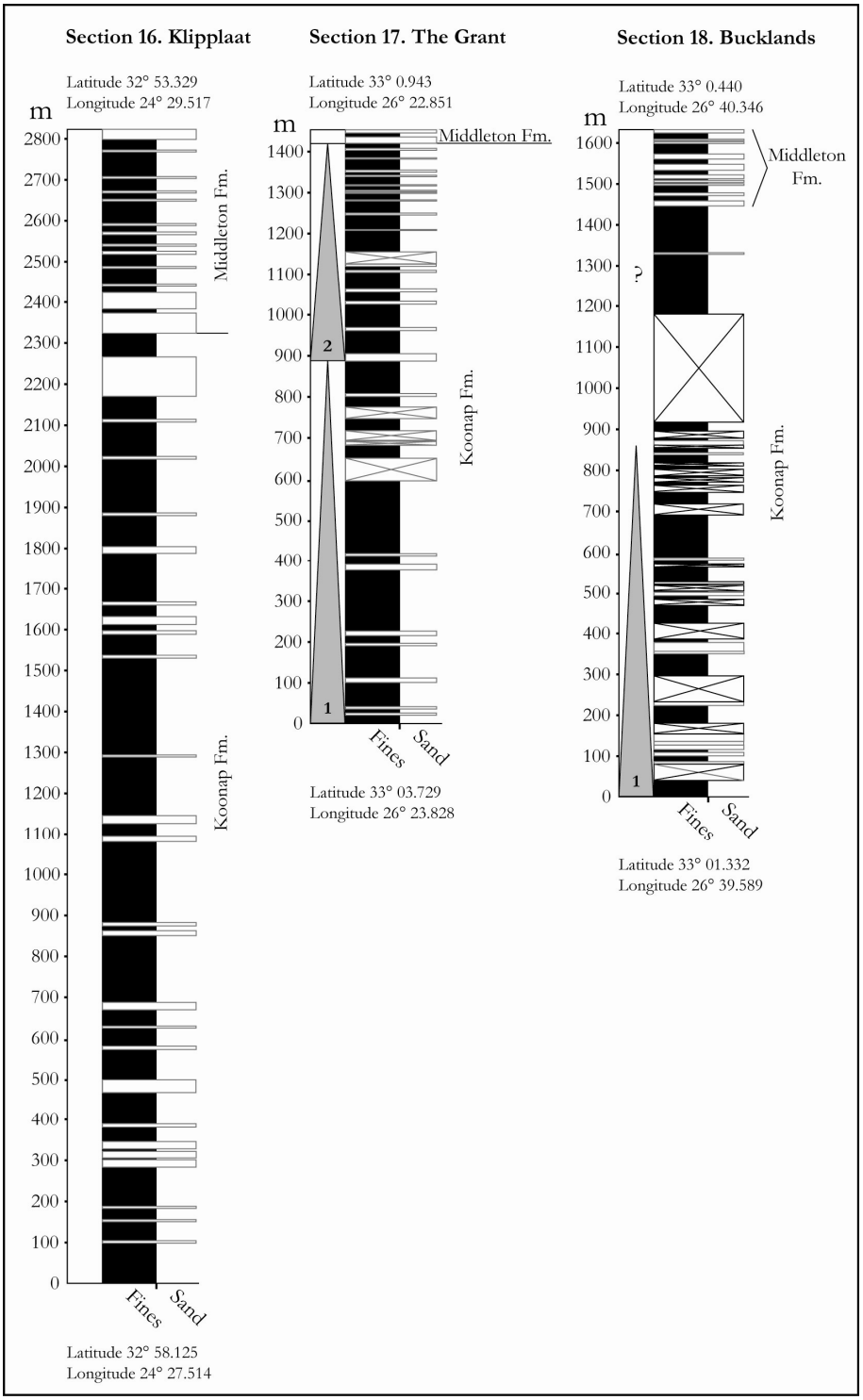


Figure 24. Stratigraphic sections measured in Eastern Cape Province, demonstrating fining-upward cycles. Section localities are shown in Figure 5. Klipplaat section after Helber and Gebauer (2001); The Grant and Bucklands sections partly after Mason (2007).

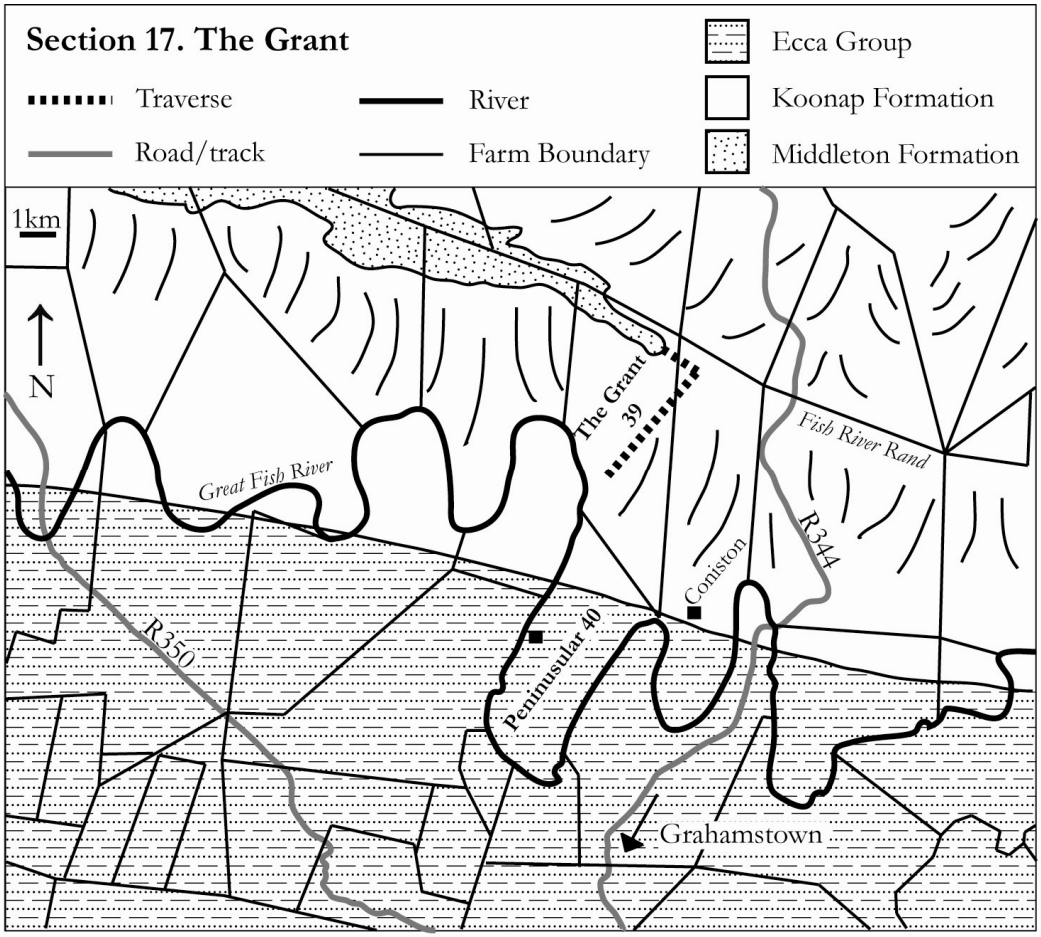


Figure 25. Map showing the traverse of the stratigraphic section measured on the farm The Grant, Albany district.

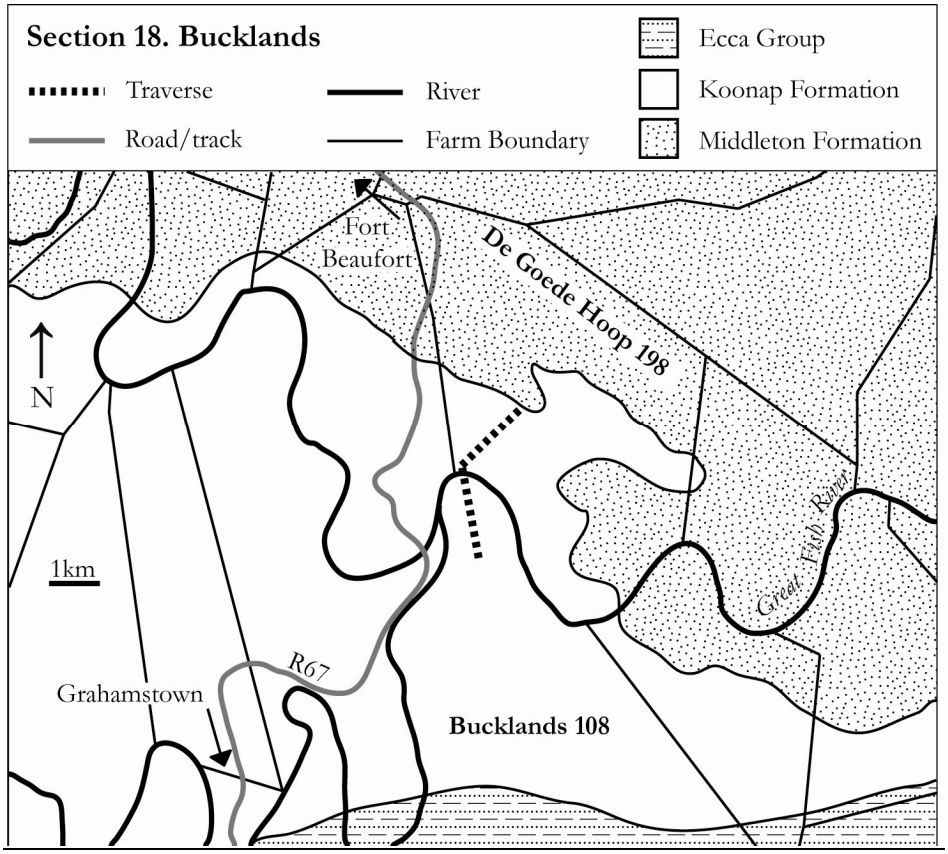


Figure 26. Map showing the traverse of the stratigraphic section measured on the farm Bucklands, Albany district.

2.2 List of Sub-formational Units of the Middle Permian Beaufort Group used in this study

This section provides details on the sub-formational lithostratigraphic units within the Middle Permian Beaufort Group that are found to be have the greatest utility. This is based on their presence in individual stratigraphic sections and the traceability of the units between different parts of the basin. Most of these units occur in the southwest of the basin, where stratigraphic sections are densest, but some are also restricted to the northwest. While new observations have been made regarding the south-western part of the basin as a result of recently collected data, the units in the northwest defined by Cole and Wipplinger (2001) are accepted in their existing form.

The Koonap Formation, east of 24° E, has a higher proportion of fine-grained rocks than the southwest of the basin. The Formation is rather homogenous in the Jansenville area (4.1.3.1) but there is some evidence for fining-upward cycles at localities along the Great Fish River (4.1.3.2 and 4.1.3.3); however, these cycles are not considered sufficient to form the basis of any further stratigraphic subdivision of the Koonap Formation as they are weakly developed and cannot be traced on the surface.

Although this section technically constitutes part of the discussion, it is necessary to present it here as the units discussed below are used in the biostratigraphic interpretations of Chapter 5.

Stratigraphic units marked with an * are not accepted by SACS.

4.2.1 Combrinkskraal Member*, Abrahamskraal Formation

The Combrinkskraal Member is the name applied to the series of sandstone packages in the lowest part of the Abrahamskraal Formation and is recorded in the literature from the farm Combrinkskraal itself as far northwest as Verlatenkloof Pass in the Northern Cape (Cole and Wipplinger 2001; Le Roux 1985). Although defining the Combrinkskraal Member, Le Roux himself gave little information about the distribution or thickness of this unit. Jordaan (1990) recognised the Combrinkskraal Member to be 2100 m thick at the farm Combrinkskraal, encompassing almost the entire Abrahamskraal Formation. Such a thickness is largely the result of the much greater proportion of sandstone in the Abrahamskraal formation in the central Koup, and is unlikely to correspond to the sandstone packages mentioned by LeRoux (1985) (Figure 21). Loock *et al.* (1994), conversely, recognised this member to be only 550 m thick in the Moordenaarskaroo (4.1.2.1) and also that it was separated from younger sandstone packages by a distinct argillaceous interval. When correlated laterally, the Combrinkskraal Member as recognised in the Moordenaarskaroo corresponds to a similar unit at the Wilgerbos locality, where it encompasses 1 ½ fining upwards cycles (Figure 16). This relationship to fining-upward cycles can be applied across most of the south-western basin and so is a useful definition for the Combrinkskraal Member.

The Combrinkskraal Member is clearly visible in the stratigraphic section measured at Wilgerbos (4.1.2.2), where the unit is 860 m thick. At this locality, it consists of the first fining-upward cycle and the arenaceous lower part of a second, which leads to an argillaceous break between 280–465 m above the base of the Abrahamskraal Formation. This interval has an equivalent in the Moordenaarskaroo, albeit on a reduced scale (Figure 16). Further east, the Combrinkskraal Member becomes more difficult to trace: at Dwyka River (4.1.2.4), the argillaceous interval at the top of the first fining-upward cycle is distinct, but the sandstone package above continues up to the top of the section at 1225 m. This would imply the Combrinkskraal member is at least 1225 m thick at Dwyka River. At Prince Albert Road (4.1.2.5), the upper boundary of the Combrinkskraal Member can be placed at 955 m above the base of the Abrahamskraal Formation, at the top of the second sandstone package (Figure 19).

At Combrinkskraal (4.1.2.7), the identification of fining-upward cycles is rather hindered by the greater amount of sandstone in the Abrahamskraal Formation in this part of the basin. An argillaceous interval within the lower Abrahamskraal Formation is not apparent but there is a relatively sandstone deficient interval between 830–1010 m above the base of the formation. This corresponds approximately to the top of the Combrinkskraal Member at Prince Albert Road and so it is here accepted that the lower 830 m of the Abrahamskraal Formation at Combrinkskraal represents the Combrinkskraal Member (Figure 21).

In the eastern Koup at Jansenskraal (4.1.2.8), two distinct fining-upwards cycles are again present in the lower part of the Abrahamskraal Formation. If measured from the top of the arenaceous part of cycle 2, this provides a thickness of 790 m for the Combrinkskraal Member at this locality (Figure 21). The Combrinkskraal Member is hereby recognised in the eastern Koup for the first time.

To the north, the Combrinkskraal Member has been recorded at Verlatenkloof (4.1.1.6) by Cole and Wipplinger (2001). These authors recorded a thickness of 130 m for this unit, which they indicate to be separated from the base of the Abrahamskraal Formation by about 30 m of fine grained rocks. However, if the Combrinkskraal Member is considered to constitute the first fining-upward cycle and the arenaceous portion of the second cycle, then the Combrinkskraal Member at

Verlatenkloof would be 365m thick (Figure 8). This would be consistent with the base of the Koornplaats Member being situated at 630 m above the base of the Abrahamskraal Formation at this locality.

The presence of the Combrinkskraal Member at Ouberg Pass (4.1.1.5) is less certain, primarily as only a single fining-upward megacycle is recorded. The top of Ouberg Pass has been correlated with the base of the Koornplaats Member (Cole and Wipplinger 2001), which would suggest that the lower arenaceous base of the Abrahamskraal Formation at this locality belonged to the Combrinkskraal Member. Given the proximity of Ouberg Pass to Verlatenkloof, the stratigraphy should not be drastically different, and therefore the sandstone package in the lower 370 m of the Abrahamskraal Formation is assumed to represent the Combrinkskraal Member. This is its most northerly occurrence yet recorded. The distribution of this unit is shown in (Figure 25).

4.2.2 Leeuvlei Member*, Abrahamskraal Formation

The Leeuvlei Member has been officially recognised only in the Moordenaarskaroo, where it forms the relatively argillaceous interval between the top of the Combrinkskraal Member at 550 m and the base of the Koornplaats Member at 1410 m above the base of the Abrahamskraal Formation (Loock 1993**,** Loock *et al.* 1994; Figure 17). On the farm Wilgerbos (4.1.2.2), this unit forms the argillaceous upper part of the second fining-upward cycle and is 615 m thick. By the definition of Loock (1993) and Loock *et al.* (1994), the Leeuvlei Member does contain several prominent sandstones, including the thick DR-3 sandstone, but at Wilgerbos this interval is distinctively free of large sandstone bodies (Figure 17). At Prince Albert Road (4.1.2.5), the Leeuvlei Member is reduced to only 135 m (Figure 19), while at Combrinkskraal (4.1.2.7), a relatively argillaceous interval occurs in a similar stratigraphic position, 830 m above the base of the Abrahamskraal Formation. This interval is approximately 180 m thick but appears to correspond to the upper part of the first fining-upward cycle (Figure 21). In the eastern Koup at Jansenskraal (4.1.2.8), this interval has a clearly defined base 790 m above the base of the Abrahamskraal Formation

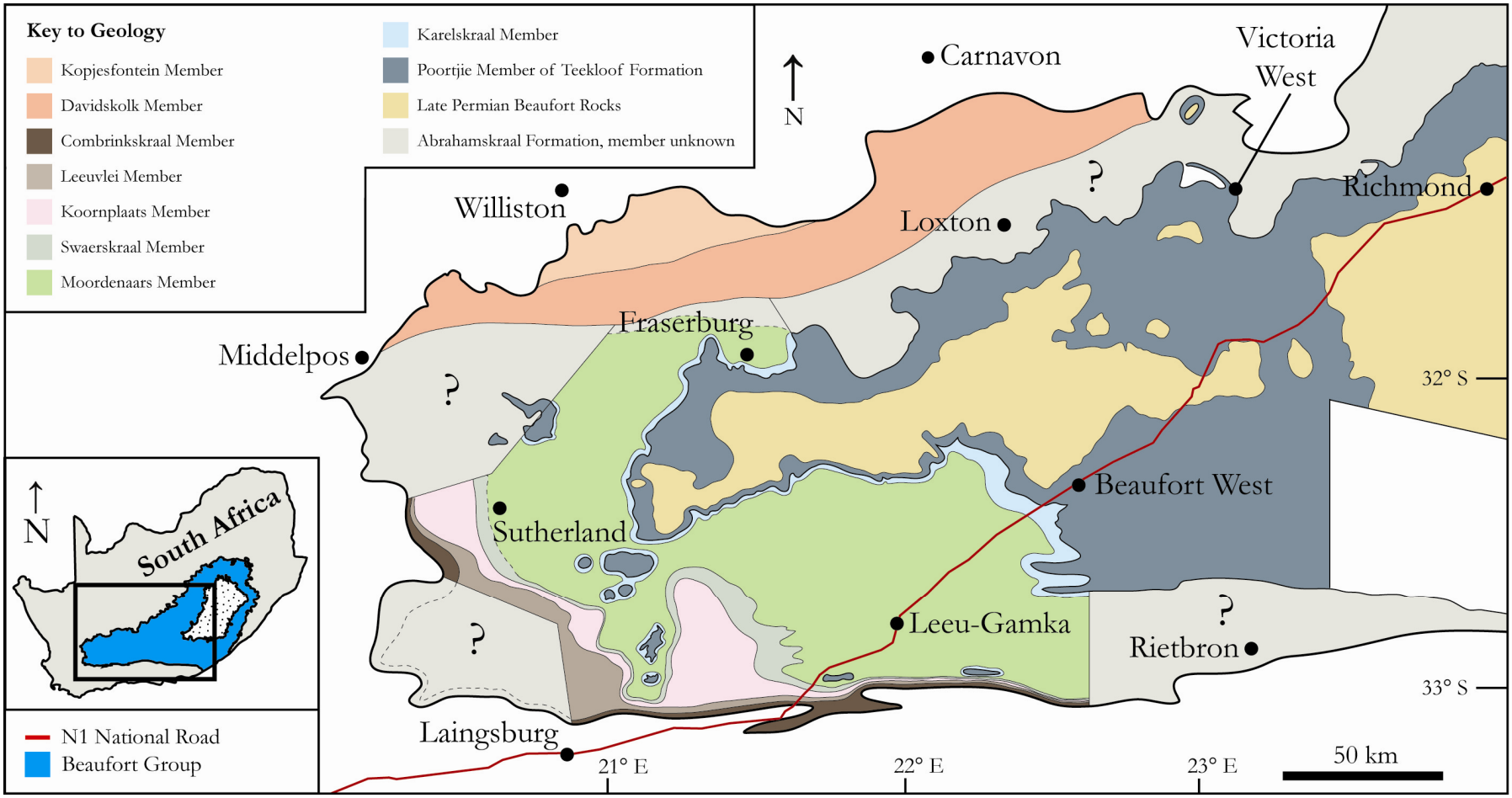


Figure 27. Generalised map showing the surface expression of the members of the Abrahamskraal Formation and the Poortjie Member of the Teekloof Formation.

but a less well constrained upper boundary due to lack of outcrop (Figure 21); it may be as thick as 445 m.

To the north-west, the Leeuvlei Member at Verlatenkloof (4.1.1.6) has a thickness of 265 m. This extends from the top of the Combrinkskraal Member at 360 m to the base of the Koornplaats Member at 625 m above the base of the Abrahamskraal Formation at this locality (Figure 8). Similarly, as the top of Ouberg Pass has been correlated with the base of the Koornplaats Member (Cole and Wipplinger 2001) and the Combrinkskraal occupies the lower 370 m of the Abrahamskraal Formation at that locality, the Leeuvlei Member there is approximately 230 m thick (Figure 8).

As the lower strata north of Ouberg Pass belong to the south-east fluvial transport system (Cole and Wipplinger 2001), the Leeuvlei Member cannot be traced any further north than this and so is restricted to the southwest of the Karoo Basin (Figure 25).

4.2.3 Koornplaats Member*, Abrahamskraal Formation

The Koornplaats Member was originally defined as the arenaceous lower portion of the second fining-upward cycle of the Abrahamskraal Formation (Le Roux 1985). It was first recognised in a stratigraphic section by Loock (1993) and Loock *et al.* (1994), in the central part of the Abrahamskraal Formation in the Moordenaarskaroo (4.1.2.1); however, the resolution of the Loock *et al.*'s (1994) stratigraphic section is quite low and fining-upward cycles are difficult to interpret from it. The stratigraphic section measured at Wilgerbos (4.1.2.2) provides a higher resolution image of the lithostratigraphy in this part of the basin. At this locality it is clear that the sandstone package that correlates with the Koornplaats Member as identified in the Moordenaarskaroo in fact forms part of the third fining-upward cycle, 1485 m above the base of the Abrahamskraal Formation (Figure 16; Figure 17). Closer inspection of the Moordenaarskaroo stratigraphic section suggests that the presence of a fining-upward cycle within the Combrinkskraal Member at that locality is probable, indicating that the Koornplaats Member in its type area also represents the base of the third fining-upward cycle (Figure 17).

A thick arenaceous unit occurs in the central Abrahamskraal Formation at Prince Albert Road (4.1.2.5), which forms the basal portion of the third fining-upwards cycle of the Abrahamskraal Formation (Figure 19). In this sense, it can be considered as a correlate of the Koornplaats Member in the Moordenaarskaroo. At 655 m, the Koornplaats Member at Prince Albert Road is rather thicker than the Koornplaats Member at Wilgerbos, where it is only approximately 360 m thick. This difference seems primarily due to the earlier onset of the third fining-upward cycle at Prince Albert Road, the base of which occurs 1090 m above the base of the Abrahamskraal Formation.

The greater proportion of sandstone at Combrinkskraal (4.1.2.7) obscures much of the cyclicity in the Abrahamskraal Formation at this locality but a particularly sandstone rich package is clearly present in central part of the formation between 1085–1850 m above its base. As with the lower units, a correspondence with fining-upward cycles exhibited elsewhere in the south-western part of the basin does not occur, but the base of this unit closely corresponds to the base of the Koornplaats Member at Prince Albert Road. It is therefore accepted to be the Koornplaats Member and, at 765 m, represents the greatest thickness that this member achieves.

The Koornplaats Member is weakly developed at Jansenskraal (4.1.2.8) and its lower boundary is obscured by lack of outcrop. Despite this, the presence of four fining-upward cycles is evident and the first large sandstone above the second cycle appears 1235 m above the base of the Abrahamskraal Formation (Figure 21). Although surrounding strata are obscured, this is tentatively accepted here as the base of the third fining-upward cycle at this locality, and hence the base of the Koornplaats Member. The top of this sandstone package is situated 1635 m above the base of the Abrahamskraal Formation at Jansenskraal and therefore indicates a tentative thickness of 400 m for the Koornplaats Member in the eastern Koup.

To the north, the Koornplaats Member has been recorded at Verlatenkloof (Cole and Wipplinger 2001). These authors ascribe only a 36 m thick package of three sandstone bodies to the Koornplaats Member, while they assign the thick, arenaceous interval in the upper 300 m of the Verlatenkloof section to the Moordenaars Member. Correlation of the sandstone forming the top of Verlatenkloof Pass with the Moordenaarskaroo using Google Earth and field

observation found that this horizon intercepted the uppermost Koornplaats Member, approximately 600m below the Teekloof Formation (Figure 16). Such a correlation suggests that the arenaceous package at the top of Verlatenkloof Pass represents the greater part of the Koornplaats Member, contrary to Cole and Wipplinger (2001), and that the top of Verlatenkloof Pass is ~600 m below the base of the Poortjie Member.

This interpretation is more consistent with the complete stratigraphic section in the Moordenaarskaroo as, if the upper 300 m of the Verlatenkloof did represent part of the Moordenaars Member, then it would require one of two alternatives: 1) that the Moordenaars Member was approximately 900 m thick (equivalent to half the Abrahamskraal Formation at Verlatenkloof when the missing upper portion is extrapolated from the Moordenaarskaroo) or 2) that only 150 m of rock are exposed on the Roggeveld between the top of Verlatenkoof Pass and the base of the Poortjie Member at Puntkraal (Figure 5). As such, the Koornplaats Member is recognised as occupying the upper 300 m of the Verlatenkloof stratigraphic (Figure 8).

The top of Ouberg Pass has also been correlated with the lowest sandstone of the Koornplaats Member (Cole and Wipplinger 2001:7). This further supports the assignment of the upper 300 m of Verlatenkloof to the Koornplaats Member as the thickness of the section at Ouberg is similar to the thickness of strata the below the upper sandstone package in the Verlatenkloof stratigraphic section (Figure 16). Cole and Wipplinger (2001) note that the Koornplaats Member pinches out somewhere north of Verlatenkloof and the correlations supported here indicate that this occurs further north than Ouberg Pass. The Koornplaats Member is therefore distributed in an arc around the southwest of the basin, including the western Koup and parts of the central Moordenaarskaroo (Figure 25).

4.2.4 'Wilgerbos'/Swaerskraal Member*, Abrahamskraal Formation

The Wilgerbos Member was originally defined by Le Roux (1985) for an argillaceous unit that outcrops along the Wilgerbos River on the farm Elandsfontein 257 in the northern Koup (this is not to be confused with the farm Wilgerbos in the south-western Koup, near Laingsburg (Figure 5). This name was then applied to the

argillaceous portion of Le Roux's (1985) second fining-upward megacycle. On this basis, Loock (1993) and Loock *et al.* (1994) recognised this unit in the Moordenaarskaroo as a 120 m thick mudstone-dominated interval separating the Koornplaats and Moordenaars members. However, this correlation is now brought into question.

The interval identified with the 'Wilgerbos Member' in the Moordenaarskaroo is evident in the stratigraphic section measured at Wilgerbos (4.1.2.2), in the south-western Koup, where the interval corresponds to the argillaceous portion of the third fining-upward cycle, 1825–1995 m above the base of the Abrahamskraal Formation (Figure 17). Although this horizon cannot be adequately traced on the surface between Wilgerbos and Prince Albert Road (4.1.2.5), a thick argillaceous interval representing the upper part of the third fining-upward cycle is well defined at this latter locality (Figure 19). This interval, between 1745 m and 2170 m above the base of the Abrahamskraal Formation, corresponds to the 'Mudstone B' and uppermost 'Arenaceous Unit A' of Jirah (2009, 2013), which he mapped as being exposed along the southern margin of the basin at Prince Albert Road and along the western edge of the Koup. Conversely, the argillaceous interval exposed on the banks of the Wilgerbos River at Elandsfontein corresponds to the 'Mudstone H', which is higher in the stratigraphy and represents the argillaceous portion of the fourth fining-upward cycle. The equivalence of the 'Wilgerbos Member' as recorded in the Moordenaarskaroo (Loock *et al.* 1994) with the 'Mudstone B' and upper 'Arenaceous Unit A' of Jirah (2013) is further supported by the stratigraphic section measured at Die Skeur (4.1.2.3): this section indicates that at least 400 m of rock separates the base of the western Koup from the Poortjie Member (Figure 17), which places the 'Wilgerbos Member' within the argillaceous portion of the third fining-upward cycle, not within the fourth (Figure 16). Accordingly, the 'Wilgerbos Member' as recorded in the Moordenaarskaroo is hereby declared invalid and the name **Swaerskraal Member** suggested in its place, after the farm in the Moordenaarskaroo where Loock *et al.* (1994) recorded its clear outcrop.

At 170 m, the Swaerskraal Member at Wilgerbos is slightly thicker than in the Moordenaarskaroo. However, the unit becomes substantially thicker moving westwards to Prince Albert Road, where it achieves a thickness of 425 m (Figure 19).

At Combrinkskraal (4.1.2.7), the Swaerskraal Member may be represented by a 115 m thick interval of argillaceous rocks occurring immediately above the thick Koornplaats Member, 1850–1965 m above the base of the Abrahamskraal Formation (Figure 21). In the eastern Koup, at Jansenskraal (4.1.2.8), the weak development of sandstone packages makes the recognition of the Swaerskraal Member more difficult; however, it probably corresponds to an 80 m mudrock interval above the last thick sandstone of the Koornplaats Member, between 1635–1715 m above the base of the Abrahamskraal Formation (Figure 21).

To the north of the Moordenaarskaroo, the Swaerskraal Member is not present on any of the stratigraphic sections included in this study; it presumably outcrops above the Koornplaats Member in the western Roggeveld, at least to the south of Sutherland. It is otherwise restricted to the south of the basin and the Moordenaarskaroo (Figure 25).

4.2.5 Moordenaars Member*, Abrahamskraal Formation

The Moordenaars Member is the most widespread of the Abrahamskraal Formation subunits. Unlike most of the other members, it was first proposed by Stear (1980) as incorporating the package of sandstones outcropping over much of the Moordenaarskaroo, although his stratigraphic section showed the unit as exposed along the Gamka River in the central Koup. The exact locality where Stear (1980) measured his section is not clear, but the unit was subsequently recognised by LeRoux (1985) in cores from the southwest Karoo Basin and by Loock (1993) and Loock *et al.* (1994) in outcrop in the Moordenaarskaroo (4.1.2.1). In this area, the Moordenaars Member consists of a complete fining-upward cycle and the arenaceous lower portion of a second, thereby representing two distinct sandstone packages, although Loock *et al.* (1994) do not acknowledge this (Figure 17). It has a thickness of 360 m, between 1800–2160 m above the base of the Abrahamskraal Formation.

The Moordenaars Member is not completely recorded at Wilgerbos (4.1.2.2) but is clearly visible in the upper 280 m of the stratigraphic section, corresponding to the fourth and lower part of the fifth fining-upward cycles at this locality. Correlation with the stratigraphic section at Die Skeur (4.1.2.3) suggests that only 75 m of strata

are missing at the top of the Wilgerbos section, while extrapolation from the Moordenaarskaroo based on a 350 m thickness for the Moordenaars Member would indicate150 m of missing strata. The Moordenaars Member at Wilgerbos is therefore probably thinner than in the Moordenaarskaroo.

In the Merweville area (4.1.2.5), the Moordenaars Member is a clearly defined, 290 m thick set of sandstone packages 2175–2465 m above the base of the Abrahamskraal Formation and corresponds to the fourth and lower part of the fifth fining-upward cycles at this locality (Figure 19). While the stratigraphic section measured by Thissen *et al.* (2010) at Combrinkskraal (4.1.2.7) does not show an obvious fining-upward sequence in the upper Abrahamskraal Formation, a sandstone package equivalent to the Moordenaars Member may be present. A large and perhaps anomalous sandstone interval 1965–2080 m above the base of the Abrahamskraal Formation probably represents the lower part of a Moordenaars Member (Figure 21).

At Jansenskraal in the eastern Koup, the Moordenaars Member is very weakly developed and contains a high proportion of fine grained rocks. A distinct sandstone package, 365 m thick, does extend between 1715–2080 m above the base of the Abrahamskraal Formation but does appear to consist of three small fining-upward cycles and the base of a fourth (Figure 21). This is unlike its presence elsewhere but it is possible that the reduction in overall sandstone content highlights lower order cyclicity, which is not visible when sandstone content is high at the resolution used in this study.

The Moordenaars Member is also apparent north of the escarpment, having been traced as far northeast as Fraserburg where it occurs in the upper 82 m of the borehole core at Quaggasfontein (4.1.1.3) (Cole and Wipplinger 2001). At this locality the Member is decidedly thinner than in the south of the basin, being between 82 m and 130 m thick (Figure 8). The Moordenaars Member is not present in the stratigraphic sections at either Verlatenkloof, contrary to Cole and Wipplinger (2001), or at Ouberg Pass, but the tracing of sandstone horizons from its known exposure in the Moordenaarskaroo using Google Earth and field observation suggests that it is exposed on the Roggeveld to the east of Sutherland (Figure 25). The stratigraphic section measured at Puntkraal identifies the eastern limit of its exposure on the Roggeveld as the base of the Nuweveld Mountains. Although the

Moordenaars Member has not been traced further north than Fraserburg, the Loxton Member may be a continuation of it (Cole and Wipplinger 2001).

In the south, the Moordenaars Member is well exposed in the north of the Moordenaarskaroo. It also outcrops over much of the eastern and central Koup: Evidence for this comes from the surface mapping of Jirah (2009), who recorded the boundary of his subunits 'B' and 'C' as extending approximately between Prince Albert Road and Merweville. As the Moordenaars Member encompasses subunits C–S of Jirah (2009, 2013), this indicates the exposure of the Moordenaars Member to the east of the Prince Albert Road-Merweville road (Figure 25).

4.2.6 Karelskraal Member*, Abrahamskraal Formation

The Karelskraal Member was another of the names first proposed by LeRoux (1985) for an argillaceous interval that occurs immediately below the Poortjie Member of the Teekloof Formation, defined at Karelskraal Pass in the northwest Koup. This unit was recorded in the Moordenaarskaroo (4.1.2.1) by Loock *et al.* (1994), where it is 70m thick (Figure 17), and may correspond to the upper 130 m of the Abrahamskraal Formation at Die Skeur (4.1.2.3; Figure 17). The Karelskraal Member is evident in the Merweville stratigraphic section (4.1.2.5) as a distinct, almost exclusively mudstone interval corresponding to the upper 110 m of the Abrahamskraal Formation (Figure 19). At Combrinkskraal (4.1.2.7) it is perhaps over 100 m thick, while at Jansenskraal in the eastern Koup (4.1.2.8) it is again a distinct, 70 m thick argillaceous interval immediately below the base of the Teekloof Formation (Figure 21

To the north the Karelskraal Member is well defined at Puntkraal (4.1.1.4), where it achieves a thickness of 78 m (Figure 8). At this locality, the Karelskraal Member is clearly visible as a geographical 'step' separating the sandstones of the Moordenaars Member of the Abrahamskraal Formation and the Poortjie Member of the Teekloof Formation (Figure 12); this can be traced in a north-south direction along the western edge of the Nuweveld Mountains. The Karelskraal Member is not recorded further north than this (Figure 25) and Cole and Wipplinger (2001) mention that '[in the northwest of the basin] the Poortjie Member is usually less than 50 m above the

Moordenaars or Loxton Members and, in places, it is difficult to define boundaries...' This indicates the much reduced significance of the Karelskraal Member north of Puntkraal.

4.2.7 Kopjesfontein Member*, Abrahamskraal Formation

The south-east fluvial transport and the units that comprise it are restricted to the north-western part of the Karoo Basin and have been described exclusively by Cole and Wipplinger (2001). The lowest of these, the Kopjesfontein Member, is only known in section at Quaggasfontein (4.1.1.3), although its outcrop has allegedly been traced through the northwest corner of the basin, in the vicinity of Williston (de Beer pers. comm. 1986 in Cole and Wipplinger 2001:10; Figure 25). In particular, it is recorded to outcrop on the farm Kopjesfontein, in the Fraserburg district. The Kopjesfontein Member is accepted here without modification.

4.2.8 Davidskolk Member*, Abrahamskraal Formation

The Davidskolk Member, which is the youngest of the southeast fluvial transport system units, was described by Cole and Wipplinger (2001) in section at both Quaggasfontein (4.1.1.3) and at Abrams kraal (4.1.1.1; Figure 5). At both these localities, the Davidskolk Member occurs in subcrop, either in the middle of the Abrahamskraal Formation (at Quaggasfontein; Figure 8) or in the lower part of the formation, just above the Ecca-Beaufort boundary (at Abrams kraal; Figure 8). The extent of its outcrop is greater than the Kopjesfontein Member, which Cole and Wipplinger (2001) describe as extending from the vicinity of Middelpos to Pampoenpoort, where the unit pinches out against the Ecca Group (Figure 25).

4.2.9 Poortjie Member, Teekloof Formation

The Poortjie Member of the Teekloof Formation, despite its significance as a traceable lithostratigraphic unit in the south-western Beaufort Group, has been measured in stratigraphic section at only a few localities. The westernmost of these is

at Puntkraal (4.1.1.4), at the western end of the Nuweveld Mountains (Figure 5). At Puntkraal, the base of the Poortjie Member is well defined by the underlying Karelskraal Member of the Abrahamskraal Formation. The top of the Poortjie Member is marked by the top of the eighth laterally continuous sandstone body, 164 m above its base (Figure 8). Above this point the sandstone bodies, while being in places locally thick, are more limited in lateral extent and are therefore considered to be consistent with the Hoedemaker Member.

Further east, on the Great Escarpment at Springfontein (4.1.2.6), the base of the Poortjie Member is also quite clear; a thick sandstone does occur in the upper Abrahamskraal Formation on part of this farm but, like at Puntkraal, this is not laterally continuous (Figure 26). The Poortjie Member at Springfontein is 103 m thick and has a well defined upper boundary, which coincides with the top of the seventh major sandstone body (Figure 19). The Member is thinner at this locality than in any other stratigraphic section.



Figure 28. Photograph of the Poortjie Member as exposed on the Nuweveld Escarpment at Springfontein. The large sandstone in the centre of the photograph is the basal Poortjie sandstone and overlies the argillaceous Karelskraal Member here, although in places thick lenticular sandstones occur immediately below the base of the Poortjie Member.

At Paalhuis (4.1.2.9) the Poortjie Member is 182 m thick as measured by Cole and Wipplinger (2001). In their stratigraphic section, seven or eight significant sandstone horizons are evident, as to the west, but the thickness of the Member is greater at this locality than elsewhere in the basin.

Northeast of Paalhuis, the Poortjie Member is next recorded in stratigraphic section on the farm Abrams kraal (4.1.1.1), in borehole AB1/65 (Cole and Wipplinger 2001). As the Poortjie Member is exposed on the surface at this locality, only its lower 54 m are recorded.

The Poortjie Member has also been measured as far northwest as Spuitpoort (4.1.1.2), to the north of Victoria West (Figure 5). At this locality the top of the Member is clearly defined by the distinct lack of sandstone bodies in the argillaceous unit above (Figure 10). The lower boundary of the Poortjie Member is less clear as the base of the package extends to the flat ground at the base of the hill; however, the presence of an anteosaurid dinocephalian (BP/1/5591) close to the base of the Beaufort Group to the north of Spuitpoort indicates the presence of the Abrahamskraal Formation below this unit. Because only approximately 45 m of rock are present between the base of the stratigraphic section at Spuitpoort and the Ecca-Beaufort boundary (4.1.1.2), the base of the Poortjie Member is probably close to the base of the stratigraphic section; it is therefore approximately 120 m thick at this locality and consists of nine sandstone bodies. If this is so, then it does not indicate any significant distal thinning of the Poortjie Member.

The Poortjie Member is exposed over much of the southern Nuweveld Plateau, to the north of the Nuweveld Mountains (Figure 25). The unit also outcrops in a thin strip along the eastern Roggeveld and the Great escarpment. The strata exposed on the Great Escarpment dip gently eastwards and so the base of the Poortjie Member reaches the level of the Koup low ground at Beaufort West, after which it is exposed over the eastern boundary of the Koup and much of the western portion of Die Vlakte.

4.3. Summary

In the south-western salient of the Karoo Basin, the Abrahamskraal Formation is far easier to assess stratigraphically south of the Great Escarpment because of the greater relief, the better exposure and the lack of dolerite intrusions. Furthermore, the southern region also possesses a far thicker sequence where all strata demonstrate an east-north-easterly palaeocurrent direction (Cole and Wipplinger 2001).

Only slight changes have been made to the existing lithostratigraphic nomenclature for the Abrahamskraal Formation and its sub-divisions (LeRoux 1985; Loock *et al.* 1994), which were otherwise accepted (Figure 4). More specifically, the miscorrelation of the argillaceous part of the third fining-upward in the Moordenaarskaroo with the 'Wilgerbos Member' of Le Roux (1985), as exposed in the northern Koup, has been recognised and rectified (see 4.2.4). The Swaerskraal Member, as suggested above, is visible in section in the Koup at the Prince Albert Road (4.1.2.5) and at Jansenskraal (4.1.2.8). The other units are mostly traceable in section across the south-western basin south of the escarpment (Figure 16), but there are notable exceptions: At Dwyka River (4.1.2.4), the Abrahamskraal Formation becomes very arenaceous and, due to the incompleteness of the stratigraphic section at this locality, it is hard to identify the subdivisions present. At Combrinkskraal (4.1.2.7), the high sandstone content obscures the fining-upwards cycles and even the sandstone packages are not obvious, especially in the upper part of the Abrahamskraal Formation. In the eastern Koup, at Jansenskraal (4.1.2.8), the lack of exposure in the middle of the Abrahamskraal Formation makes the extent of the Koornplaats Member hard to define.

The Abrahamskraal Formation reaches its greatest thickness in the central Koup, at Prince Albert Road and Combrinkskraal, and is thinner both to the east (Jansenskraal) and to the west (Figure 16). The Abrahamskraal Formation is also more arenaceous in the central Koup, particularly in the middle of the Formation (Figure 16). At Jansenskraal, in the eastern Koup, it is particularly argillaceous.

In the north of the escarpment, little additional information has been provided, with the exception of the retrieval of a radiometric date from the farm Spuitpoort (4.1.1.2), north of Victoria West, and the subsequent recognition of the Poortjie

Member there. As a result, the section measured here demonstrates that the Abrahamskraal Formation is very thin north of Victoria West and presumably pinches out entirely not far to the north east, although the lithostratigraphy to northeast of Victoria West is mostly uncertain. Conversely, the Abrahamskraal Formation becomes thicker towards the west, following the work of Cole and Wipplinger (2001). The two sandstone packages of the southwest fluvial transport system recognised at Fraserburg (4.1.1.3) and the lateral continuation of the upper Davidskolk Member at Abrams kraal (4.1.1.1), in the Victoria West district, are taken directly from these authors. The interplay between the units restricted to the north and those of the south has not been addressed in this study.

In the east, the identification of subunits in the Koonap Formation was not successful. Although two fining-upward cycles were recognised at the two localities along the Great Fish River (4.1.3.2 and 4.1.3.3), the Koonap Formation is mostly very argillaceous and the arenaceous packages of the sequence are not identifiable in the field. Further work in the Eastern Cape may uncover other characteristics that are useful indicators for the subdivision of this formation, but none are described here.

CHAPTER 5: STRATIGRAPHIC RANGES OF MIDDLE PERMIAN TETRAPOD GENERA IN THE BEAUFORT GROUP

This chapter describes the stratigraphic range of each valid genus from the lower three vertebrate assemblage zones of the Beaufort Group. Amphibians and parareptiles are considered first, after which synapsid higher taxa are considered in phylogenetic order as recorded by Rubidge and Sidor (2001). A short history of each genus is provided, while the complete list of genera considered valid is contained in Table 3. The stratigraphic ranges of all individual specimens are shown in Appendix 1.

5.1 Amphibians

Temnospondyl amphibians are some of the most common Permian tetrapods from many localities around the world and form a significant part of the tetrapod fauna in the Triassic of South Africa, to the point of having considerable biostratigraphic utility (Hancox *et al.* 1995). However, in the Permian part of the Beaufort Group only one family, the Rhinesuchidae, is present (Damiani 2004; Nicolas 2007); furthermore, the Middle Permian hosts only two described temnospondyl genera, *Rhinesuchus whaitsi* and *Rhinesuchoides tenuiceps*, both of which are known restricted to the *Tapinocephalus* AZ (Damiani 2004). Because temnospondyls are such a minor part of the fauna in the Middle Permian Beaufort Group and their taxonomy is so poorly understood (Damiani and Rubidge 2003), the taxon is only briefly discussed here.

Rhinesuchus whaitsi was described by Broom (1908a) and since then various temnospondyl remains from the lower three Beaufort Group assemblage zones have been assigned to this genus. Further species, such as *R. beaufortensis* (Boonstra 1940) and *R. rubidgei* (Broom 1948), were designated but the former was synonymised with *R. whaitsi* by Schoch and Milner (2000) and the latter with *Rhinesuchoides tenuiceps*. The genus was recognised as monospecific by Damiani and Rubidge (2003) and only five specimens were referred to it, including two unnumbered and one with poor provenance data. Specimens referred to *Rhinesuchus whaitsi* by Damiani and Rubidge

(2003) all probably occur in the *Tapinocephalus* AZ but SAM-PK-3009, which can only be determined to come from the vicinity of Beaufort West, may have been found in the *Pristerognathus* AZ. Smith and Keyser (1995a) show the genus present from the base of the *Tapinocephalus* AZ.

Genus	Taxon	Genus	Taxon
Bradysaurus	Parareptilia	*Anomocephalus*	Anomodontia
Embithosaurus	Parareptilia	*Patranomodon*	Anomodontia
Eunotosaurus	Parareptilia	*Galechirus*	Anomodontia
Broomia	Parareptilia	*Galeops*	Anomodontia
Nochelosaurus	Parareptilia	*Diictodon*	Dicynodontia
Heleosaurus	Pelycosauria	*Robertia*	Dicynodontia
Elliotsmithia	Pelycosauria	*Eodicynodon*	Dicynodontia
Bullecephalus	Biarmosuchia	*Eosimops*	Dicynodontia
Lobalopex	Biarmosuchia	*Colobodectes*	Dicynodontia
Hipposaurus	Biarmosuchia	*Pristerodon*	Dicynodontia
Pachydectes	Biarmosuchia	*Prosictodon*	Dicynodontia
Tapinocephalus	Dinocephalia	*Emydops*	Dicynodontia
Anteosaurus	Dinocephalia	*Lanthanostegus*	Dicynodontia
Moschops	Dinocephalia	*Endothiodon*	Dicynodontia
Mormosaurus	Dinocephalia	*Dicynodontoides*	Dicynodontia
Criocephalosaurus	Dinocephalia	*Chelydontops*	Dicynodontia
Struthiocephalus	Dinocephalia	*Brachyprosopus*	Dicynodontia
Tapinocaninus	Dinocephalia	*Cryptocynodon*	Dicynodontia
Struthiocephaloides	Dinocephalia	*Lycosuchus*	Therocephalia
Struthionops	Dinocephalia	*Pristerognathus*	Therocephalia
Phocosaurus	Dinocephalia	*Alopecodon*	Therocephalia
Riebeeckosaurus	Dinocephalia	*Glanosuchus*	Therocephalia
Keratocephalus	Dinocephalia	*Pardosuchus*	Therocephalia
Jonkeria	Dinocephalia	*Ictidosaurus*	Therocephalia
Titanosuchus	Dinocephalia	*Scylacosaurus*	Therocephalia
Australosyodon	Dinocephalia	*Ictidosuchoides*	Therocephalia
Delphinognathus	Dinocephalia	*Hofmeyria*	Therocephalia
Taurocephalus	Dinocephalia		
Avenantia	Dinocephalia		
Styracocephalus	Dinocephalia		

Table 3. Valid genera from the Middle Permian of South Africa. All Gorgonopsians are excluded because their taxonomy is in a state of flux.

Rhinesuchoides tenuiceps is known only from the holotype as described by Olson and Broom (1937) and one recently referred specimen, RC 73 (Damiani and Rubidge 2003; Schoch and Milner 2000). Only the holotype, FMNH UC 1519, can be attributed to the Middle Permian: according to Olsen and Broom (1937:619), its provenance was simply '*Tapinocephalus* zone, 2 miles east of Stinkfontein,' which was identified as Stinkfontein in the Prince Albert district (Leeu-Gamka sector) by Damiani and Rubidge (2003). Smith and Keyser (1995a) recognise the presence of this genus in the *Tapinocephalus* AZ, probably based only on the holotype, but erroneously refer to it as *Rhinesuchus tenuiceps*.

The genera discussed above have received little attention and the Middle Permian temnospondyls of South Africa require a serious review before their biostratigraphy can be meaningfully considered. This review is currently being undertaken (Marsicano pers. comm.) but temnospondyls are not discussed further in this study.

5.2 Parareptiles

The parareptiles recovered from the Middle Permian part of the Beaufort Group are mostly pareiasaurs. The taxonomic history of the pareiasaurs is remarkably complex. The name 'Pareiasauria' was first used by Seeley (1888), although pareiasaurs as we know them now had been known earlier. While the first pareiasaur specimen to be described in the literature was from Germany (von Meyer 1857), the specimen that was later described by Owen as *Pareiasaurus serridens* (Owen 1876a) was in fact discovered in 1838 by Andrew Geddes Bain and, as such, represents one of the earliest South African fossils.

Initially, *Pareiasaurus* was allied to the dinosaurs (Owen 1876a) but later, and for much of the 20th Century, the taxon was included in the now paraphyletic group 'Cotylosauria' (e.g. Boonstra 1969; Kitching 1977). Pareiasaurs are now nested securely within the Parareptilia (e.g. Lee 1995; Müller and Tsuji 2007). The group is well represented in South Africa but is restricted to the Middle and Late Permian, not surviving the end-Permian mass extinction (Rubidge 2005). The Middle Permian genera from South Africa, which are large and lightly armoured, are the oldest and

most basal pareiasaurs known (Lee 1997) and, within the Beaufort Group, there is an apparent disjunction between these forms and the more heavily armoured Late Permian pareiasaurs (Watson 1914b; Smith and Keyser 1995b).

The second taxon of parareptiles present in the Middle Permian of South Africa is the millerettids. The millerettids are very rare in the Middle Permian and are represented by a single species of *Broomia*. In addition, the genus *Eunotosaurus* occurs in the Middle Permian but it has an uncertain taxomony and is considered separately.

5.2.1 ***Bradysaurus***

The eldest pareiasaur genus from the *Tapinocephalus* AZ is *Bradysaurus*. Its origins lie in the confusion in late 19th Century pareiasaur nomenclature, which began with description of *Pareiasaurus bombidens* (Seeley 1888) and *Pareiasaurus baini* (Seeley 1892a) for specimens collected from the lower Beaufort Group in the vicinity of Beaufort West. Because of the great number of pareiasaur fossils being retrieved from these strata, this led to Seeley (1892a) and later Broom (1906a, 1906b) to erect an assemblage zone based on the presence of *Pareiasaurus*. However, Watson (1914b) recognised morphological differences between *Pareiasaurus serridens* and the pareiasaurs from the '*Pareiasaurus* Zone', which led him to propose the name *Bradysaurus baini* to absorb all material collected lower in the stratigraphy that had previously been assigned to *Pareiasaurus baini*.

Haughton and Boonstra (1929) transferred *P. bombidens* to *Bradysaurus seeleyi* and simultaneously erected a number of genera, many of which were later synonymised with *Bradysaurus*. By the late 1960s, Boonstra (1969) reduced the number of pareiasaur genera again but in the process added a further two species to *Bradysaurus*, thereby recognising a total of four species. Most recently, Lee (1997) accepted the validity of only two species of *Bradysaurus*, *B. baini* and *B. seeleyi*. However, the genus is not differentiated in this study on the basis of species, rather the genus being considered as one. This is primarily due to the vast amount of pareiasaur material in museum collections that is assigned to *Bradysaurus* but which was not identified by Lee (1997) in the course of his taxonomic revision.

Stratigraphically, Keyser and Smith (1977) use *Bradysaurus* '*bombidens'* as an indicator species for their Dinocephalian AZ, while Smith and Keyser (1995a) used the presence of *Bradysaurus* along with *Tapinocephalus* in their definition of the *Tapinocephalus* AZ. The genus is considered to be present throughout the *Tapinocephalus* AZ and into the lower part of the *Pristerognathus* AZ (Smith and Keyser 1995a, 1995b; Smith *et al.* 2012).

Range in the Beaufort West sector

Twelve specimens attributed to *Bradysaurus* are known from the Beaufort West sector. The stratigraphically lowest occurrence is SAM-PK-K7665, from the farm Varsfontein in the Prince Albert district. This farm is situated upon the Abrahamskraal Formation, where strata 1750–2000 m above the base of the Formation are exposed and which constrains the provenance of the specimen to this stratigraphic interval. Two further specimens from the southern Koup margin, BP/1/298 and SAM-PK-1208, have broader potential stratigraphic provenance and may have been collected in a lower horizon. *Bradysaurus* is certainly present from 2000 m above the base of the Abrahamskraal Formation in this sector.

The stratigraphically highest specimen is SAM-PK-4999, from the farm Grootfontein, just to the west of that Beaufort West. This farm is situated on a stratigraphic interval that extends from the upper Abrahamskraal Formation to the Oukloof Member of the Teekloof Formation but the vast majority of the farm, and the flattest parts, expose rocks of the upper Abrahamskraal Formation and lower Poortjie Member. This specimen is therefore most likely constrained stratigraphically to the boundary between the Abrahamskraal and Teekloof formations. The certain stratigraphic range of *Bradysaurus* in this sector extends from the mid-Moordenaars Member up to the base of the Teekloof Formation (Figure 27).

Range in the Leeu-Gamka sector

This sector contains the greatest number of *Bradysaurus* specimens, with thirty-six recorded on the BFV database (Nicolas 2007). The stratigraphically lowest specimens

of this genus with adequate stratigraphic provenance data are six specimens from the farm Abrahamskraal in the Prince Albert district. These can be constrained to an interval 1700–2100 m above the base of the Abrahamskraal Formation in this sector.

The stratigraphically highest specimen is SAM-PK-12080, from the farm Grantham in the Beaufort West district. This is constrained to the uppermost 50 m of the Abrahamskraal Formation, thereby providing a definite range of *Bradysaurus* in this sector from the SI 2050–2100 m above the base of the Abrahamskraal Formation up to the base of the Teekloof Formation.

Range in the Merweville sector

The twenty-nine specimens of *Bradysaurus* known from the Merweville sector are mostly constrained to a similar stratigraphic interval. The stratigraphically lowest specimen is probably SAM-PK-12015 from the farm Buffelsvlei in the Beaufort West district. This specimen can be constrained to the interval 1950–2200 m above the base of the Abrahamskraal Formation in this sector, equivalent to the upper half of the Swaerskraal Member or lowest Moordenaars Member.

The stratigraphically highest specimen is NHMUK 49426, from the farm Palmietfontein in the Beaufort West district. This farm is situated along the foot of the escarpment and is therefore situated on exposure of the upper 75 m of the Abrahamskraal Formation and perhaps the Poortjie Member. The definite range of *Bradysaurus* in this sector is therefore from the base of the Moordenaars Member to the upper Karelskraal Member.

Range in the Laingsburg sector

This sector contains the stratigraphically lowest occurrence of *Bradysaurus* in the basin. This is SAM-PK-11940, from the farm Vereniging in the Laingsburg district, which can be constrained quite broadly to an interval 1300–1650 m above the base of the Abrahamskraal Formation in this sector. The stratigraphically low extent of this potential range is due to the presence of a rather severe anticline that intersects

the southern part of this farm. The interval corresponds to the upper Leeuvlei member and the lower Koornplaats Member.

The highest specimens in this sector are two from the farm Klipfontein in the Moordenaarskaroo, a farm which exposes mostly Moordenaars Member but also has some exposure of the Poortjie Member on the hill to the south. These specimens are therefore constrained to occur between 1950 m above the base of the Abrahamskraal Formation and the lowest Poortjie Member. The definite stratigraphic range of *Bradysaurus* in the Laingsburg sector is therefore between the mid-Koornplaats Member and the base of the Moordenaars Member of the Abrahamskraal Formation.

Range in the Sutherland sector

Only one specimen of *Bradysaurus* is recorded from the Verlatenkloof sector. SAM-PK-9355, from the farm Roggenkloof in the Sutherland district, is constrained to between 1050–1200 m above the base of the Abrahamskraal Formation, in the upper Swaerskraal or lowest Moordenaars Member.

Range in the Fraserburg sector

Only a single specimen of *Bradysaurus* is recorded from the Fraserburg sector as well. SAM-PK-11948 was found on the farm Roxana, in the Fraserburg district to the north-east of that town. This specimen is constrained to occur in an interval 250–400 m above the base of the Abrahamskraal Formation in this sector, which equates to an interval from the upper Davidskolk Member up to the base of the Moordenaars Member.

Range in the Jansenville sector

The one specimen attributed to *Bradysaurus* from the Jansenville sector was collected on the farm Kafferskraal or Kaffir's Berg in the Pearston district. CGS JP56 was assigned to the *Pristerognathus* AZ by Nicolas (2007) but the associated fauna contains

no indicator taxa. The locality is situated well within the Middleton Formation in this sector with reference to the 1:250 000 geological map (map sheet: Republic of South Africa 3224, Graff-Reinet, 1:250 000 Geological Series 1993) and therefore the biozone designation of Nicolas (2007) is considered dubious. The generic identification of the specimen may also be incorrect.

Overall stratigraphic range

The stratigraphically lowest occurrence of *Bradysaurus* is no higher than the upper Koornplaats Member in the Laingsburg sector, while its stratigraphically highest certain occurrence is in the uppermost Abrahamskraal Formation in the Beaufort West sector. When correlated with the Abrahamskraal Formation at its thickest point based on the distance below the base of the Teekloof Formation, this corresponds to an interval around 2000–2575 m above the base of the Abrahamskraal Formation, between the mid-Swaerskraal Member and the base of the Poortjie Member (Figure 28).

This corresponds to the majority of the *Tapinocephalus* AZ as currently defined by the range of the advanced tapinocephalid dinocephalians. The genus is relatively common, accounting for the vast majority of pareiasaur occurrences and with its greatest abundance in the upper Swaerskraal and lower Moordenaars members of the Abrahamskraal Formation (Figure 29). There are fewer specimens of *Bradysaurus* in the uppermost horizons of the Abrahamskraal Formation, but it remains an important part of the fauna until the base of the Poortjie Member.

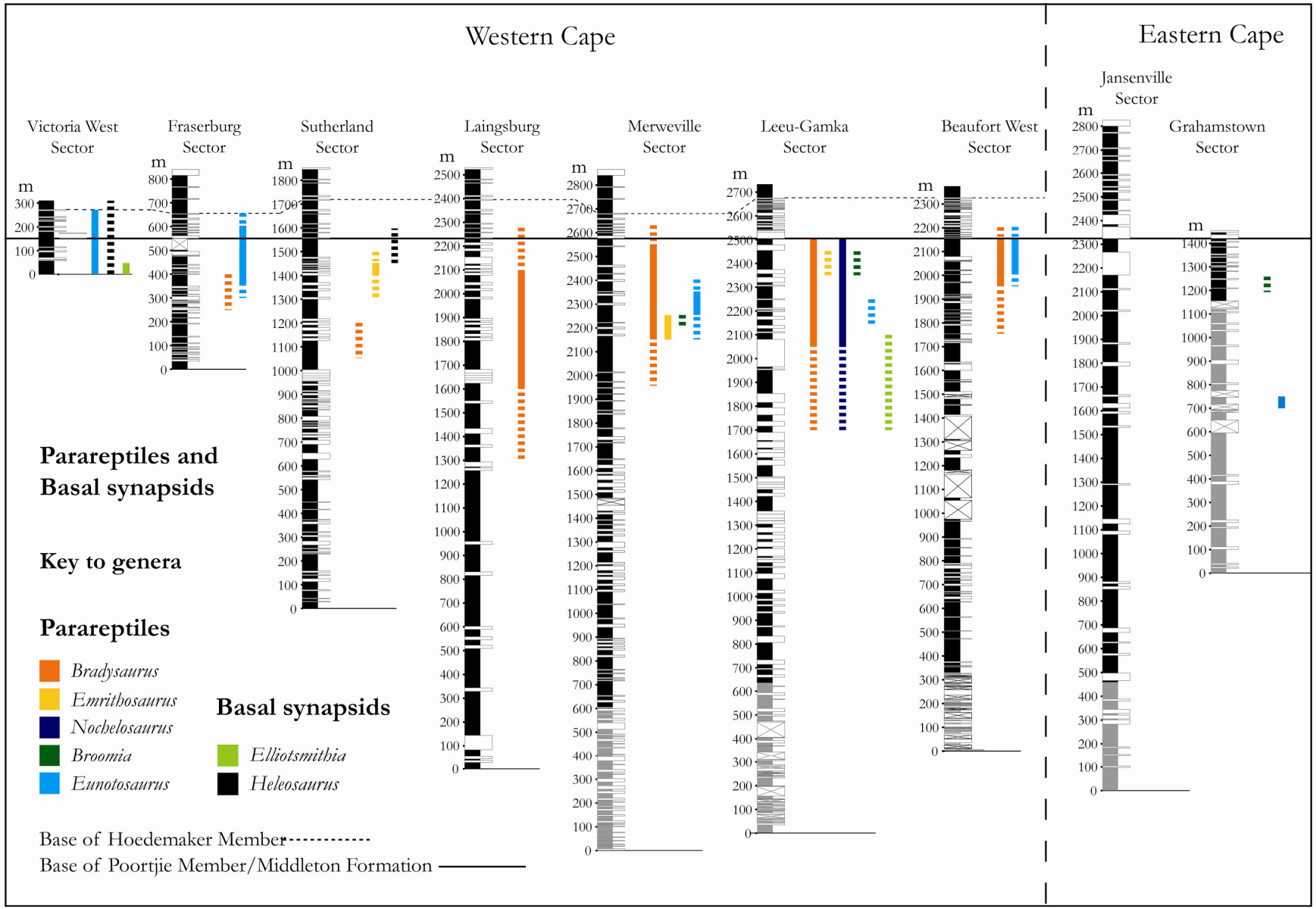


Figure 29. Stratigraphic ranges of parareptile and basal synapsid genera in each of the sectors in which they occur.

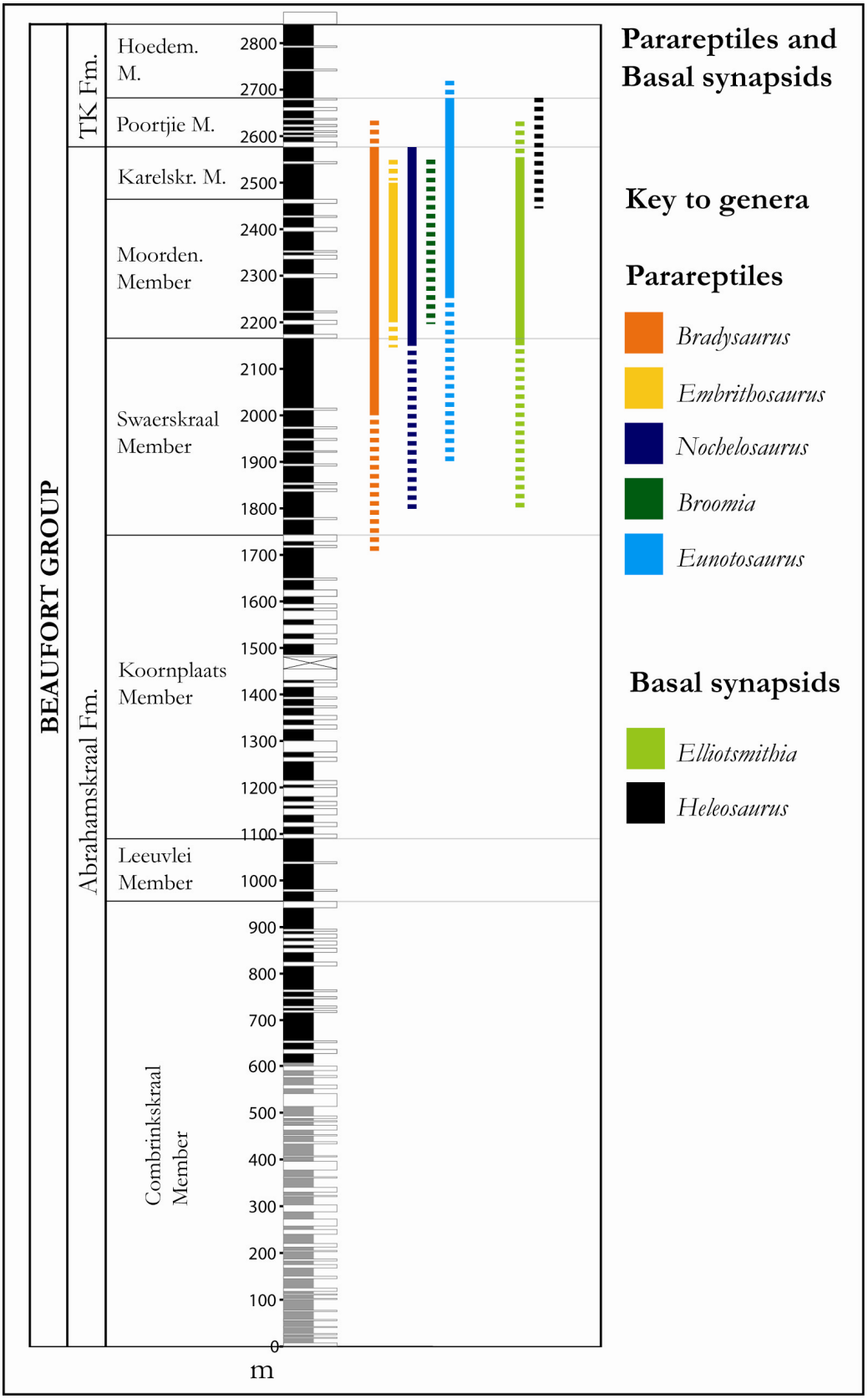


Figure 30. Composite stratigraphic ranges of parareptile and basal synapsid genera in the Middle Permian Beaufort Group.

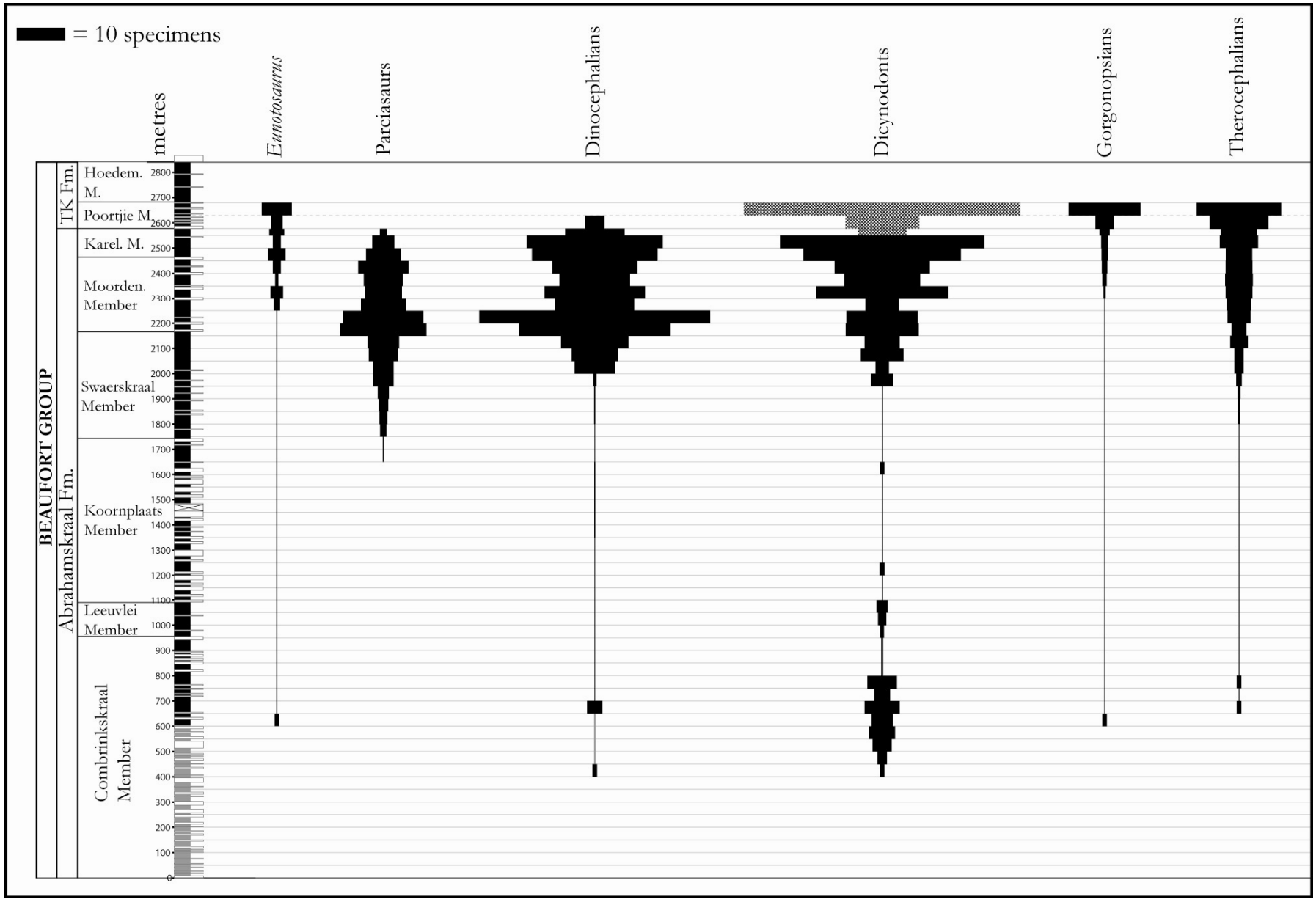


Figure 31. Abundances of higher taxa through the Middle Permian Beaufort Group, except with pareiasaurs and *Eunotosaurus* included separately. The abundance of dicynodonts in the upper three SIs is reduced by a factor of 10 due to the great abundance of *Diictodon* in these horizons.

5.2.2 *Embrithosaurus*

Like *Bradysaurus*, the genus *Embrithosaurus* was described for a specimen that had previously been assigned to *Pareiasaurus* (Watson 1914b). Similarly, the genus was erected after Watson (1914b) noted significant morphological differences between SAM-PK-8034 and more complete material referred to *Pareiasaurus serridens*. *Embrithosaurus* was accepted as valid by later workers with one species, *E. schwartzi* (e.g. Boonstra 1969; Kitching 1977; Lee 1997).

Lee (1997) maintained the genus but found that all the characters originally used by Watson (1914b) to differentiate the holotype from that of *Bradysaurus* were taphonomic artefacts. He therefore redefined the genus based on his own observations and designated four referred specimens. Given the redefinition of the defining characters for *Embrithosaurus*, most specimens identified as *Embrithosaurus* in existing collections are here considered to be spurious, other than those listed by Lee (1997). An additional specimen, BP/1/7213, was recently collected during fieldwork for this project and is included in this analysis.

Keyser and Smith (1977) used *Embrithosaurus* as a defining genus for their Dinocephalian AZ, while Smith and Keyser (1995a) illustrate *Embrithosaurus* to occur throughout the *Tapinocephalus* AZ and into the lower portion of the *Pristerognathus* AZ. Most recently, Smith *et al.* (2012) record only a single specimen of *Embrithosaurus* in the *Pristerognathus* AZ.

The stratigraphically lowest specimens of *Embrithosaurus* identified by Lee (1997) are SAM-PK-8034 and SAM-PK-K324 from the farms Hogeveld and Seekoevallei, respectively; both localities are in the Beaufort West district of the Merweville sector and both specimens can be constrained to the same stratigraphic interval, 2150–2250 m above the base of the Abrahamskraal Formation in that sector (Figure 27). The first appearance of *Embrithosaurus* is therefore in the lower part of the Moordenaars Member.

The stratigraphically highest specimens both occur between 50–150 m below the base of the Poortjie Member in their respective sectors. NHMUK R7782, from the farm Hottentotsrivier in the Beaufort West district (Leeu-Gamka sector), was tentatively assigned to *Embrithosaurus* by Lee (1997). The second specimen is

BP/1/7213, which is a nearly complete skeleton for the farm Kuilenburg, north of the Die Puts farmstead in the Sutherland district (Sutherland sector). One of the specimens mentioned by Lee (1997), CGS R338, could not be found on the catalogues of the Council for Geoscience and so its locality is unknown (Ellen de Kock pers. comm. 2012). The definite range of *Embrithosaurus* is therefore approximately restricted to the Moordenaars Member, in the *Tapinocephalus* AZ (Figure 28).

5.2.3 *Nochelosaurus*

Nochelosaurus was the most recently described of the South African Middle Permian pareiasaurs, which, along with several other genera, was erected in an attempt by Haughton and Boonstra (1929) to streamline pareiasaur taxonomy. Two other genera described in that same publication, *Dolichopareia angusta* and *Brachypareia watsoni*, were both synonymised with *Nochelosaurus* by Lee (1997), though *Dolichopareia* had previously been assigned to *Bradysaurus* (Boonstra 1969).

Originally, two species of *Nochelosaurus* were described by Haughton and Boonstra (1929) but a genotype was not designated. The first described species, *N. strubeni*, was later considered to be a *nomen vanum* by Lee (1997); however, rather than abandoning the genus *Nochelosaurus*, Lee (1997:248) maintained it due to its well established position, stating that 'a less disruptive approach, followed here, is to nominate the second species as the type species of *Nochelosaurus* [*N. alexanderi*].' As a result, this author recognised three specimens; the holotype, SAM-PK-6239, and referred specimens SAM-PK-6239 and SAM-PK-6240, which all represent the species *N. alexanderi*.

Similarly to the situation in *Embrithosaurus*, Lee (1997) found that several characters used in the original definition of *Nochelosaurus* were not genuine, specifically in its distinction from *Bradysaurus*. He described a few characters in support of its validity, particularly in the pelvis, but acknowledged its otherwise close resemblance to *Bradysaurus seeleyi*.

Being prior to Lee's (1997) work, *Nochelosaurus* was not recognized by Smith and Keyser (1995a) as being present in the *Tapinocephalus* AZ. However, the most recent published list of *Tapinocephalus* AZ genera does recognise one specimen (Smith *et al.* 2012). Of the specimens identified by Lee (1997), the designated holotype, SAM-PK-6239, and referred specimen SAM-PK-6238 were collected on the farm Boesmanskop in the Beaufort West district (Leeu-Gamka sector), to the west of that town. The stratigraphic horizon of these specimens can be constrained to the uppermost Abrahamskraal Formation, probably within 50 m of the base of the Poortjie Member (Figure 27). The third specimen, SAM-PK-6240, was found rather lower in the stratigraphy, being found on the farm Abrahamskraal in the Prince Albert district (Leeu-Gamka sector). This latter can be constrained to between 1700–2100 m above the base of the Abrahamskraal Formation in this sector.

The certain stratigraphic range of *Nochelosaurus* therefore occupies the upper Abrahamskraal Formation, throughout the Moordenaars and Karelskraal members of the Formation at its thickest point (Figure 28).

5.2.4 *Broomia*

The millerettids are considered by most authors to be one of the most basal parareptilian groups (e.g. Müller and Tsuji 2007) if not the most basal one (e.g. Laurin and Reisz 1995, Rieppel and Reisz 1999). The family is best represented in the Late Permian *Dicynodon* AZ, but one genus, *Broomia*, has been described from the *Tapinocephalus* AZ (Watson 1914c). Due to the poor state of preservation of the holotype, NHMUK R4065, and the fact that there was only a single representative specimen, *Broomia perplexa* was taxonomically mobile throughout the 20th Century. A better description was undertaken by Thommasen and Carroll (1981), who concluded that based on characters of the palate, the genus was indeed a millerettid.

Cisneros *et al.* (2008) described a second specimen of *Broomia* from the Eastern Cape Province and ascribed the former uncertainty in the taxonomic affinities of *Broomia* to the lack of a skull roof in the holotype. They supported its inclusion within the Millerettidae based on additional cranial and postcranial features provided by the new

specimen, BP/1/6222. A potential third specimen of *Broomia*, BP/1/6881, has also recently been collected in the central Koup but this is only tentatively assigned to the genus.

Stratigraphically, Smith and Keyser (1995a) describe *Broomia* as occurring in the central part of the *Tapinocephalus* AZ but the most recent list of *Tapinocephalus* AZ genera omits *Broomia* entirely (Smith *et al.* 2012). The holotype, NHMUK R4065, was found on the farm Hottentots rivier in the Beaufort West district (Leeu-Gamka sector), at the foot of the Nuweveld Escarpment. The most inclusive area for the name Hottentots rivier, government farm 296, covers exposure of the upper Abrahamskraal Formation and much of the Teekloof Formation but, in the area surrounding the farmstead of that name, only an interval of the upper Abrahamskraal Formation is exposed (map sheet: Republic of South Africa 3220, Sutherland, 1:250 000 Geological Series 1983). As such, the specimen can most probably be constrained to an interval 50–150 m below the base of the Poortjie Member (Figure 27).

The potential specimen, BP/1/6881, was collected on the farm Rietfontein, in the Beaufort West district south of Merweville (Merweville sector). This specimen is well stratigraphically constrained to occur in the SI 2200–2250 m above the base of the Abrahamskraal Formation in this sector, within the lower Moordenaars Member.

BP/1/6222 was collected on the farm The Grant, in the Albany district of the Eastern Cape (Grahamstown sector). Cisneros *et al.* (2008) report it to occur 1705 m above the Ecca-Beaufort boundary, but this was incorrect; it was actually found in an horizon 1200 m above the base of the Koonap Formation, or 245 m below the base of the overlying Middleton Formation. Because the Koonap Formation is likely equivalent to the Abrahamskraal Formation (Hill 1994; Day *et al.* 2013) and the boundary of the *Tapinocephalus* and *Pristerognathus* assemblage zones is situated close to the base of the Middleton Formation, *Broomia* can therefore be constrained to upper *Tapinocephalus* AZ in this sector. The overall stratigraphic range of the genus can approximated to the interval 2200–2550 m above the base of the Abrahamskraal Formation at its thickest point (Figure 28).

5.2.5 *Eunotosaurus*

The genus *Eunotosaurus* has had an uncertain taxonomic history and there is still no consensus on its phylogenetic position. It was originally described by Seeley (1892b) for a specimen from the farm Weltevreden, in the Prince Albert district (Merweville sector), and, although he recognised some similarity to testudine morphology, it was Watson (1914d) that first speculated that *Eunotosaurus* might be an ancestor of modern testudines. Later research placed the genus within the Parareptilia (Gow 1997; Keyser and Gow 1981). *Eunotosaurus* was considered to be a synapsid by Lee (1993) but Modesto (2000) agreed with Gow (1997), finding the genus formed a sister group with the Procolophonomorpha within the Parareptilia. Müller and Tsuji (2007) and Tsuji and Müller (2009) concluded that *Eunotosaurus* was most likely a sister taxon to the Millerettidae and as such, was one of the most basal parareptiles. Cisneros *et al.* (2008) went further and identified *Eunotosaurus* as a millerettid but, most recently, Lyson *et al.* (2010) found *Eunotosaurus* to form a clade with extinct turtle genera, suggesting that this genus is not a millerettid and may be an ancestor of modern testudines as originally proposed by Watson (1914d).

Concerning the stratigraphic range of *Eunotosaurus*, Day *et al.* (2013) found that it is constrained to a 450 m interval inclusive of the upper part of the *Tapinocephalus* AZ and the *Pristerognathus* AZ. They record thirty-eight specimens in their analysis, the stratigraphically lowest of which are NMQR 3514 and NMQR 3515, from the farm Die Bad in the Beaufort West district (Merweville sector). These can be constrained to a stratigraphic interval 2150–2300 m above the base of the Abrahamskraal in this sector, approximately equivalent to the lower Moordenaars Member (Figure 27). The stratigraphically highest specimen is CGS CM45, from the farm Esterville in the Victoria West district (Victoria West sector). According to Day *et al.* (2013), the specimen appears to have been found in the lowest Hoedemaker Member, although there is enough inaccuracy in the map coordinates provided by the CGS catalogue to suggest its potential occurrence in the uppermost Poortjie Member, which outcrops nearby.

Eunotosaurus thus has a definite stratigraphic range that extends from middle Moordenaars Member of the Abrahamskraal Formation to the base of the

Hoedemaker Member of the overlying Teekloof Formation (Figure 28). This corresponds to the upper *Tapinocephalus* AZ and the *Pristerognathus* AZ.

5.3 Basal synapsids or 'Pelycosaurs'

Traditionally known from the Early Permian of North America and Europe, basal synapsids have also been found in the Middle Permian of South Africa. Two genera from the Beaufort Group are now considered valid, both of which belong to the family Varanopidae (Dilkes and Reisz 1996; Reisz and Modesto 2007).

A specimen referred to only as varanopid indet., SAM-PK-K10407, has been reported from the lower Poortjie Member of the Teekloof Formation on the farm La-de-da, Beaufort West district (Modesto *et al.* 2011). This is the youngest record of a 'pelycosaur' grade synapsid; however, the GPS coordinates provided for this specimen suggest that it in fact occurs within the uppermost Abrahamskraal Formation (Karelskraal Member) because the locality is situated stratigraphically below a prominent sandstone bed that is mapped as the base of Teekloof Formation (see map sheet: Republic of South Africa 3222, Beaufort West, 1:250 000 Geological Series 1979). Further investigation is required to confirm this but, as no explanation for the disagreement with the geological map is provided by Modesto *et al.* (2011), it is here considered to belong to the Karelskraal Member of the Abrahamskraal Formation, in the upper *Tapinocephalus* AZ.

5.3.1 *Elliotsmithia*

This genus was first described by Broom (1937) for a specimen in the Transvaal Museum, TM 1483, that had allegedly been discovered by Van Hoepen some twenty years previously. It was immediately recognised as a basal synapsid, although the description is brief because, as Broom (1937:300) explains, 'the matrix is very hard, and it is not only difficult to remove it, but in places it is almost impossible to distinguish the matrix from the bone.' *E. longiceps* was noted to have similarities with the previously described genus *Anningia*.

The status of *Elliotsmithia* as a basal synapsid was not challenged, with the exception of Watson (1957), and most authors accepted Romer and Price's (1940) observation that the genus most resembled American 'pelycosaurs' of the family Varanopidae (e.g. Boonstra 1969). Kitching (1977) recorded *Elliotsmithia* as a tentative millerettid but Reisz (1986) again concluded that the genus was a 'pelycosaur,' although he admitted it could not be placed with confidence in the Varanopidae. After further preparation of the holotype, Dilkes and Reisz (1996) confirmed that *Elliotsmithia* was a varanopid and the genus was later found to form an outgroup to the American varanopids *Aerosaurus*, *Varanops* and *Varanodon* (Reisz, Dilkes and Berman 1998)

During this time, *Elliotsmithia* was known from only the holotype; however, a second specimen was described by Modesto *et al.* (2001a), which preserved additional characters, suggesting *Elliotsmithia* is more closely related to the Russian form *Mesenosaurus* and the American form *Mycterosaurus*.

The holotype, TM 1483, was discovered on the farm Abrahamskraal, in the Prince Albert district (Leeu-Gamka sector), which constrains the stratigraphic position of the specimen to an interval 1700–2100 m above the base of the Abrahamskraal Formation in this sector (Figure 27). The second specimen, BP/1/5678, was collected on the farm Alarmkraal in the Carnavon district (Victoria West sector), very close to the base of the Abrahamskraal Formation in this sector.

The stratigraphic range of *Elliotsmithia* cannot be clearly defined, but it is certainly present in the Moordenaars Member and of the Abrahamskraal Formation at its thickest point (Figure 28).

5.3.2 *Heleosaurus*

When Broom (1927:227) wrote, 'the specimen which I am about to describe, though only a badly-weathered and imperfect skull**,** is one of the most important fossils discovered in South Africa for many years', he was speaking of his newly erected 'pelycosaur' genus *Anninigia*. This genus is now invalid but, had he known, he could have written this twenty years earlier. Broom (1907) had described a small reptile, *Heleosaurus scholtzi*, for specimen SAM-PK-1070, which at the time he considered to

be an eosuchian. Although the genus was later determined to be a basal diapsid (e.g. Benton 1985; Carroll 1976), the most recent work has identified it securely as a varanopid (Reisz and Modesto 2007).

As noted by Reisz and Modesto (2007), the holotype has poor locality information as Broom (1907:31) merely refers to some fossils recovered by his student T. J. R. Scholtz 'in the neighbourhood of Victoria West.' Reisz and Modesto (2007) acknowledge that Kitching (1977) chose to place this locality within the lower part of his *Cistecephalus* AZ, now the *Tropidostoma* AZ, but themselves considered it more likely that the specimen came from the *Tapinocephalus* AZ. Approximately 40% of rock outcrop in the vicinity of Victoria West exposes the Abrahamskraal Formation, with most of the remainder exposing the Poortjie Member of the Teekloof Formation (see map sheet: Republic of South Africa 3122, Victoria West, 1:250 000 Geological Series 1989). Victoria West is situated close to the boundary of these two units and therefore the stratigraphic provenance of SAM-PK-1070 cannot be constrained to a narrower interval than the uppermost Abrahamskraal Formation or the Poortjie Member of the Teekloof Formation (Figure 27).

A second specimen of *Heleosaurus* was recently described, which comprises four juvenile individuals and one adult (Botha-Brink and Modesto 2007). The specimen originates on the farm Beukesplaas, in the Fraserburg district (Fraserburg sector), which straddles the boundary of the Abrahamskraal and Teekloof formations. Botha-Brink and Modesto (2007) attribute the specimen, SAM-PK-K8305, to the uppermost Abrahamskraal Formation, which would support a *Tapinocephalus* AZ origin for the type specimen as well.

Because the Abrahamskraal Formation is very thin in the region around Victoria West, it is probable that both specimens were found in the uppermost Abrahamskraal Formation and, consequently, the uppermost *Tapinocephalus* AZ.

5.4 Biarmosuchians

These basal therapsids have good representation in the Beaufort Group, although most genera are known from only a single specimen. Three genera have been described from the Middle Permian of South Africa (Smith *et al.* 2012) and a specimen of a fourth, Late Permian genus is currently being described.

5.4.1 *Hipposaurus*

Hipposaurus was the first to be described of the South African biarmosuchians (Haughton 1929) and was initially considered to be a primitive gorgonopsian (Boonstra 1969; Sigogneau 1970; Watson and Romer 1956). Sigogneau-Russell (1989) later reported that there was controversy over the position of *Hipposaurus* within the Gorgonopsia but in this same publication erected the infra-order Biarmosuchia for the most basal genera, founded on the recommendation of Hopson and Barghusen (1986). In this taxon she placed the families Biarmosuchidae, Hippoasuridae, Ictidorhinidae and Burnetiidae, with the Hipposauridae consisting of *Hipposaurus* and the genus *Lycaenodon* (Sigogneau-Russell 1989). Since then, the discovery of additional biarmosuchian genera has resulted in a rather uncertain phylogenetic position of this taxon within the clade.

Hipposaurus is the best represented of the biarmosuchians, with five specimens attributed to it on the BFV database (Nicolas 2007). Smith and Keyser (1995a, 1995b) considered the stratigraphic range of the genus to extend across the entire *Tapinocephalus* and *Pristerognathus* assemblage zones but Smith *et al.* (2012) acknowledge its presence only in the *Tapinocephalus* AZ. This is supported here, as all specimens can be constrained to the upper Abrahamskraal Formation.

The stratigraphically lowest specimen, BP/1/6879, was recently discovered on the farm Rietfontein, in the Beaufort West district of the central Koup (Merweville sector). This specimen is well constrained to the SI 2200–2250 m above the base of the Abrahamskraal Formation in this sector, within the lower Moordenaars Member (Figure 30).

Three others specimens come from similar stratigraphic horizons: NMQR 3006, from the farm Seekoegat in the Prince Albert district (Beaufort West sector), was found in an anticline north of the homestead and is therefore constrained to between 1800–2050 m above the base of the Abrahamskraal Formation in this sector. The holotype, SAM-PK-8950, and the referred specimen SAM-PK-9081 both come from the farm Klein Koedoeskop, in the Beaufort west district (Beaufort West sector), and are constrained to an interval 2000–2100 m above the base of the Abrahamskraal Formation. These stratigraphic intervals correspond to the upper Moordenaars Member and Karelskraal Member in the upper Abrahamskraal Formation in this part of the basin.

A fifth specimen, SAM-PK-K252, was collected on the farm Rietfontein, in the Prince Albert district (Beaufort West sector). Because of the complicated nature of tectonic folding in the area, the stratigraphic horizon of this specimen is poorly constrained to between 1550 m above the base of the Abrahamskraal Formation at the lowest and the mid-Poortjie Member of the Teekloof Formation. The coordinates supplied on the BFV database (Nicolas 2007) suggest it occurs in the upper Abrahamskraal Formation.

The certain stratigraphic range of *Hipposaurus* can be constrained to the interval 2200–2500 m above the base of the Abrahamsrkaal Formation at its thickest point, equivalent to the Moordenaars Member and lower Karelskraal Member of that formation (Figure 31).

5.4.2 *Bullacephalus*

Found in 1992 by James Kitching, specimen BP/1/5387 was only described a decade later as the biarmosuchian *Bullacephalus jacksoni* (Rubidge and Kitching 2003), with close affinities to the Burnetiidae as defined by Signoneau-Russell (1989). This was slightly reinterpreted by Sidor *et al.* (2004) and Smith *et al.* (2006), who placed the genus in a clade consisting of *Bullacephalus*, *Burnetia* and *Niuksenitia*, nested within the Burnetiidae.

Bullacephalus is represented by only a single specimen, BP/1/5387, which was found on the farm Middelstevlei, in the Laingsburg district (Laingsburg sector). According to Rubidge and Kitching (2003), the specimen was found approximately 500 m above the Ecca-Beaufort contact; however, the farm Middelstevlei is situated on exposure only of the Leeuvlei Member and the lowest Koornplaats Member of the Abrahamskraal

Formation (Loock *et al.* 1994: figure 2). Furthermore, the stratigraphically lowest rocks on this farm presumably occur above the Leeuvlei sandstone (Loock *et al.* 1994: figure 3) as the farm Leeuvlei occurs to the south.

Because Kitching's original hard-copy map and Loock *et al.* (1994: figure 2) place the specimen locality in the south of the farm, half way between the farms Middelstevlei and Leeuvlei, and given the close proximity of the former farmstead to the DR-3 sandstone, the fossil must occur between the Leeuvlei sandstone and the DR-3 sandstone as defined by Loock *et al.* (1994). This equates to a stratigraphic interval 950–1250 m above the base of the Abrahamskraal Formation in this sector but, given the exact coordinates for the locality, half-way between these two farms, the specimen most likely occurs half-way between the two lithostratigraphic units. The specimen was therefore most likely collected around 1100 m above the base of the Abrahamskraal Formation, in the upper Leeuvlei Member (Figure 30). When the distance below the Poortjie Member is correlated with the Abrahamskraal Formation at its thickest point, this indicates a stratigraphic position within the upper Koornplaats Member (Figure 31).

5.4.3 *Pachydectes*

Pachydectes elsi is known from one specimen, BP/1/5735, from the Eastern Cape Province. In their description and phylogenetic analysis, Rubidge *et al.* (2006) found *Pachydectes* to be closely related to *Bullacephalus* within the Burnetiidae, which was supported by Sidor and Smith (2007).

The holotype of *Pachydectes* was collected on the farm Môrester, in the Jansenville district (Jansenville sector). The outcrop on this farm is poor and the exact

stratigraphic position of the specimen could not be ascertained (Rubidge pers. comm. 2012); however, based on the thickness of the Koonap Formation in the area (see 4.1.3.1) and the position of the locality on the geological map (map sheet: Republic of South Africa 3224, Graff-Reinet, 1:250 000 Geological Series 1993), the specimen can be constrained to a stratigraphic interval 800–1000 m above the base of the Koonap Formation in this sector (Figure 30). Given the thickness of the Koonap Formation in this sector and the potential equivalence of this unit to the Abrahamskraal Formation in the south-western part of the basin (Day *et al.* 2013; Hill 1994), such a stratigraphic position probably corresponds to the upper Combrinkskraal member of the Abrahamskraal Formation at its thickest point (Figure 31).

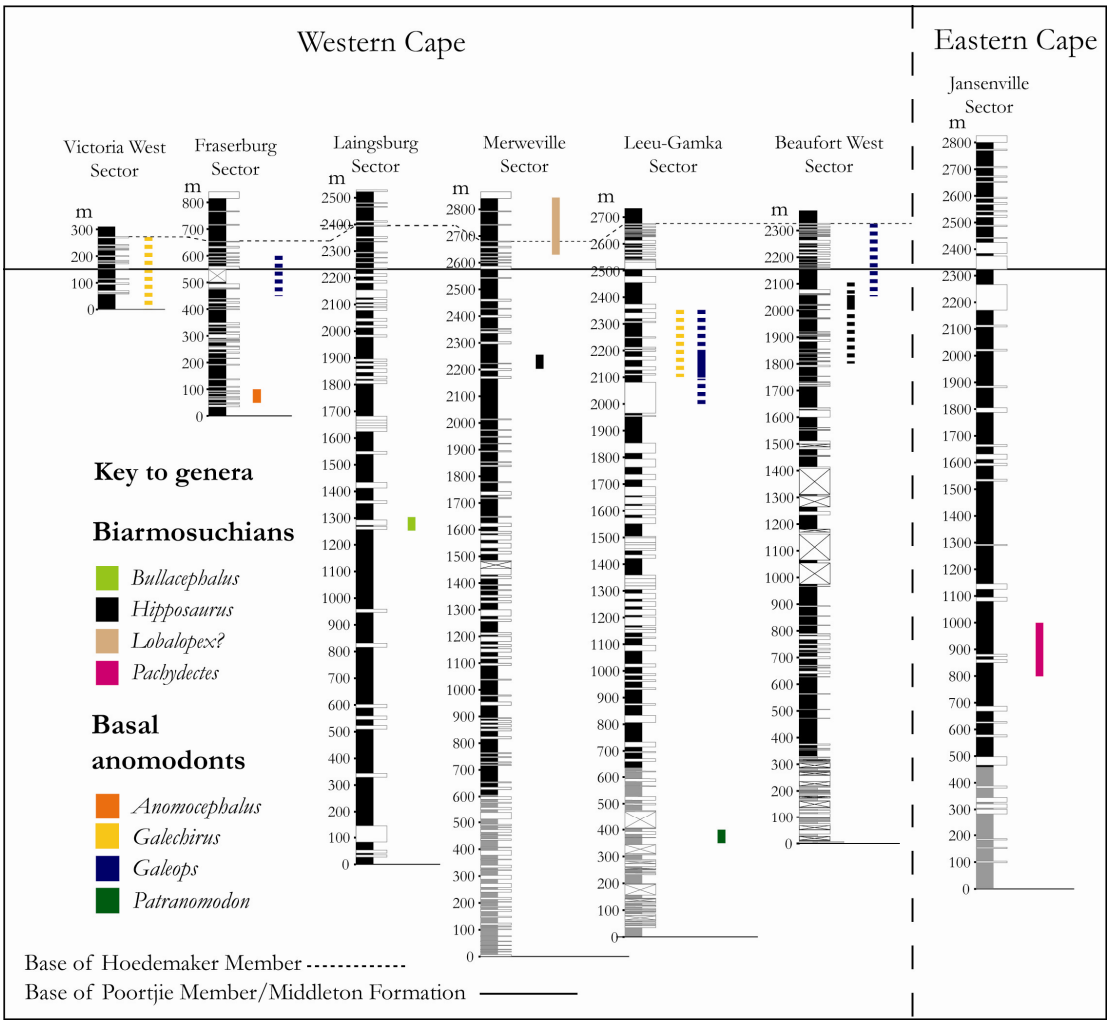


Figure 32. Stratigraphic ranges of biarmosuchian and basal anomodont genera in each of the sectors in which they occur.

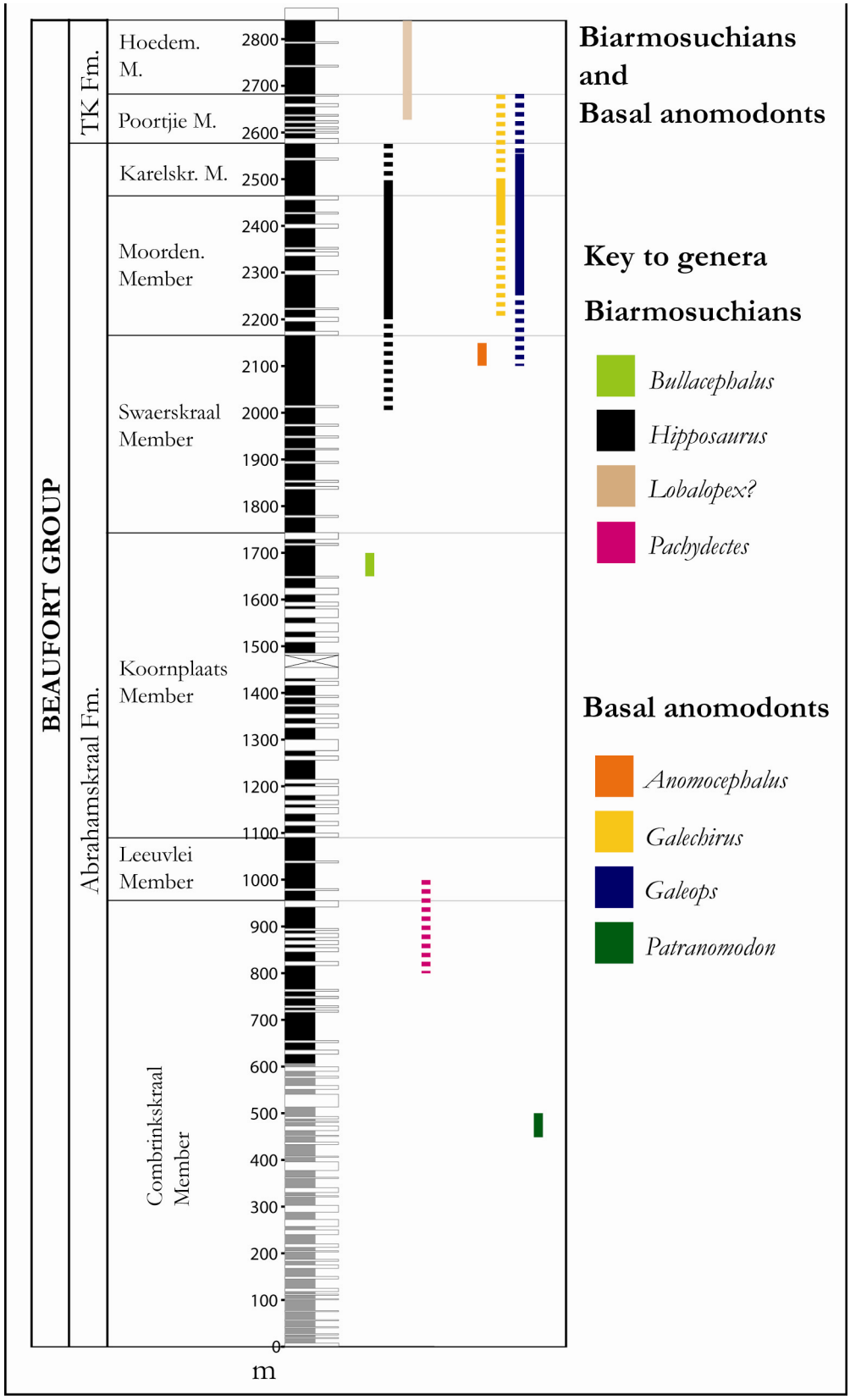


Figure 33. Composite stratigraphic ranges of biarmosuchian and basal anomodont genera in the Middle Permian Beaufort Group.

5.4.4 *Lobalopex*?

Lobalopex mordax was named for a specimen from the Late Permian Hoedemaker Member of the Teekloof Formation, which is curated in the collections of the Council for Geoscience (formerly the Geological Survey) (Sidor *et al.* 2004). Another genus, *Lophorhinus willowdenensis*, was described a few years later from the same horizon (Sidor and Smith 2007) and, while similar to *Lobalopex*, was differentiated from it on the basis of several characters. Initial cladistic analyses have placed *Lobalopex* and later *Lophorhinus* as basal burnetiamorphs.

The addition of a third specimen, collected in 2011, suggests that all three specimens represent a growth series of the same animal (Rubidge pers. comm. 2012). If this is the case, then *Lobalopex* would be the senior synonym. This identification is pertinent as the new specimen, BP/1/7098, was collected from the Poortjie Member of the Teekloof Formation on the farm Springfontein, in the Beaufort West district of the northern Koup (Merweville district). More precisely, it was found approximately 50 m above the base of this unit, which would bring the first occurrence of *Lobalopex* into the Middle Permian (Figure 31).

5.5 Dinocephalians

The dinocephalians are the first terrestrial tetrapods to reach such a large size and, although little is known of their early evolution due to the paucity of suitably aged terrestrial rock sequences, by the late Middle Permian the vast majority of large animals were dinocephalians; only the basal pareiasaurs could compete with them on size.

Dinocephalians are best known from South Africa and Russia (Battail 2000; Rubidge 2005), although they have also been recorded in China (Cheng and Li 1997a, 1997b), Zimbabwe (Munyikwa 2001), Tanzania (Simon *et al.* 2010) and Brazil (Cisneros *et al.* 2012; Langer 2000). Their origins are uncertain, but the earliest forms probably originated in Laurasia in the Early Middle Permian (Kammerer 2010; Liu, Rubidge and Li 2009). Dinocephalians become conspicuously extinct towards the end of the Middle Permian (Lucas 2009; ed. Rubidge 1995) but while later tetrapod assemblages

globally lack dinocephalians, only South Africa preserves a conformable sequence with sufficient outcrop to record the their extinction.

The taxonomic history of the dinocephalian is complex. The clade has mostly maintained its integrity since its inception by Seeley (1894) but the relationships between lower taxa have been fluid (e.g. Boonstra 1972; Broom 1923; King 1988). The most recent cladistic analyses favour the structure of Hopson and Barghusen (1986), concluding that the Anteosauridae are the most basal dinocephalians, while the Titanosuchidae and Tapinocephalidae are united under the umbrella of the Tapinocephalia (Rubidge and Sidor 2001; Sidor 2000). Estemmenosuchids and *Styracocephalus* appear as stem-group tapinocephalians, outside the clade Tapinocephaloidea (Sidor 2000). In recent literature, the tendency is to use this taxonomic scheme (e.g. Simon *et al.* 2010; Cisneros *et al.* 2012) and it is therefore accepted here.

In South Africa, four dinocephalian families are recognised:

The carnivorous **anteosaurids** are currently the best understood dinocephalian family, having recently undergone a comprehensive taxonomic revision that reduced the number of valid genera down to eight (Kammerer 2010). This can be expanded to nine when the recently described *Pampaphoneus* is included (Cisneros *et al.* 2012). Two anteosaurid genera are known from South Africa.

The family Anteosauridae was erected by Boonstra (1954a) for the carnivorous dinocephalians, as formerly the 'anteosaurs' were lumped in the family Titanosuchidae. It is considered to be the most basal of the dinocephalian families (Hopson and Barghusen 1986; Rubidge and Sidor 2001), although this position has been attributed to the Russian estemmenosuchids (King 1988). Within the Anteosauridae, Kammerer (2010) proposes the subfamily Anteosaurinae for all taxa more similar to *Anteosaurus magnificus* than to *Syodon biarmicum* and vice versa for the subfamily Syodontinae. The Anteosauridae are the most widespread dinocephalian family, with representative genera known from South Africa, Brazil, Russia and China (Cisneros *et al.* 2012; Rubidge 2005).

The **titanosuchids**, conversely, have been neglected and the current taxonomy has not changed since the work of Boonstra (1969). After the subdivision of the

dinocephalians by Broom (1923), titanosuchids were considered along with the carnivorous 'anteosaurs' within the 'Titanosuchia.' Boonstra (1954a) erected the family Titanosuchidae for the herbivorous forms but it wasn't until his review of the *Tapinocephalus* AZ (Boonstra 1969) that the numerous titanosuchid genera described up to that point were re-appraised and reduced to two, *Jonkeria* and *Titanosuchus*. The family is known only from South Africa.

The **tapinocephalids** are the most diverse of the dinocephalian families with at least thirteen genera currently considered valid, although they are currently undergoing a taxonomic revision (Güven pers. comm. 2012). They are also the most advanced dinocephalian family (Rubidge and Sidor 2001; Sidor 2000). Tapinocephalids are best known from South Africa and from the Russian genus *Ulemasaurus*, although their distribution across Pangaea is evident from the numerous teeth found in Brazil, Zimbabwe and Tanzania (Rubidge 2005; Simon *et al.* 2010). The family Tapinocephalidae was erected by Owen (1876) but initially contained modern anteosaurid and titanosuchid genera as well; these taxa were removed from the family by Broom (1923). Later, cladistic analyses suggested a close relationship between titanosuchids and tapinocephalids (Hopson and Barghusen 1986), but King (1988) chose to adopt a nomenclature based on Boonstra (1976), reducing the 'tapinocephalids' to sub-familial status. The tapinocephalids are now considered to form a clade exclusive of the titanosuchids, estemmenosuchids and *Styracocephalus* (Rubidge and Sidor 2001; Sidor 2000).

*T*he family **Styracocephalidae** is represented by a single genus, *Styracocephalus platyrhyncus*. The systematic of this genus have been uncertain but it is currently considered to be a basal tapinocephalian (Rubidge and Sidor 2001).

Genera are listed below in taxonomic order, where 5.5.1–5.5.2 are anteosaurids, 5.5.3–5.5.4 are titanosuchids, 5.5.5–5.5.18 are tapinocephalids and 5.5.19 is *Styracocephalus*.

5.5.1 *Australosyodon*

Australosyodon is one of the most recently described dinocephalian genera from the Beaufort Group (Rubidge 1994). It is known from only a single specimen, BP/1/3152, which was collected on the farm Tuinkraal, in the Prince Albert district (Merweville sector). The locality of the specimen constrains it stratigraphically to the SI 400–450 m above the base of the Abrahamskraal Formation, mid-way up the Combrinkskraal Member in this sector, within the *Eodicynodon* AZ (Figure 32; Figure 33).

5.5.2 *Anteosaurus*

Anteosaurus magnificus was described by Watson (1921) for a skull from the farm Tamboersfontein, in the Beaufort West district, to which numerous other species were later added (e. g. Broom 1929; Boonstra 1952d, 1953a, 1954a). Boonstra (1954a) transferred the genera *Dinosuchus* and *Titanognathus* to *Anteosaurus* and, later, synonymised the genera *Micranteosaurus* and *Pseudanteosaurus* with *Anteosaurus* as well (Boonstra 1969). This same publication consolidated all the species of *Anteosaurus* with *A. magnificus*, leaving the genus monospecific.

As Boonstra (1969) had also determined *Eccasaurus* to be a *nomen dubium*, this left *Paranteosaurus* as the only other anteosaurid genus other than *Anteosaurus* in the *Tapinocephalus* AZ (e.g. Smith and Keyser 1995a). Most recently, Kammerer (2010) considered *Paranteosaurus* to be based on un-diagnostic material and therefore to be a junior synonym of *Anteosaurus magnificus*, leaving the latter as the sole representative of the Anteosauridae in the *Tapinocephalus* AZ.

Range in the Beaufort West sector

Six specimens of *Anteosaurus* are known from this sector. Five were collected from the uppermost Abrahamskraal Formation and are reasonably well constrained stratigraphically. The stratigraphically highest specimens are SAM-PK-11485 and SAM-PK-11492, from the farm Mynhardtskraal, in the Beaufort west district. These

can be constrained to the SI 2050–2100 m above the base of the Abrahamskraal Formation in this sector. The stratigraphically lowest specimen is SAM-PK-2752 from the farm Leeukraal, in the Beaufort West district. This specimen can be constrained to a stratigraphic interval 1850–2050 m above the base of the Abrahamskraal Formation in this sector. The certain stratigraphic range of *Anteosaurus* in the eastern Koup therefore extends from 2000–2100 m above the base of the Abrahamskraal Formation in this sector, in the upper Moordenaars Member or lower Karelskraal Member (Figure 32).

Range in the Leeu-Gamka sector

Fourteen specimens of *Anteosaurus* from this sector are recorded on the BFV database (Nicolas 2007). The stratigraphically lowest specimens are SAM-PK-5614 and SAM-PK-7396, which were discovered on the farm Abrahamskraal, in the Prince Albert district. These can be constrained only to a stratigraphic interval 1700–2100 m above the base of the Abrahamskraal Formation in this sector. The stratigraphically highest specimens are SAM-PK-12082 and SAM-PK-12083, from the farm Bushmans kop, in the Beaufort West district. These occur in the uppermost Abrahamskraal Formation, within 50 m of the base of the Teekloof Formation.

The certain range of *Anteosaurus* is constrained to the interval 2050–2468 m above the Ecca-Beaufort boundary, in the upper Abrahamskraal.

Range in the Merweville sector

At twenty-five, there are more specimens of *Anteosaurus* from this sector than any other. All occur in the upper Abrahamskraal Formation but the stratigraphically highest specimen, BP/1/7071, was found immediately below the base of the Poortjie Member on the farm Springfontein, in the Beaufort West district.

The stratigraphically lowest occurrence of the genus is SAM-PK-K284 from the farm Leeuwfontein, which can be constrained stratigraphically to the SI 2150–2200 m above the base of the Abrahamskraal Formation in this sector. This restricts the stratigraphic range of *Anteosaurus* to the Moordenaars and Karelskraal members of the Abrahamskraal Formation in this sector.

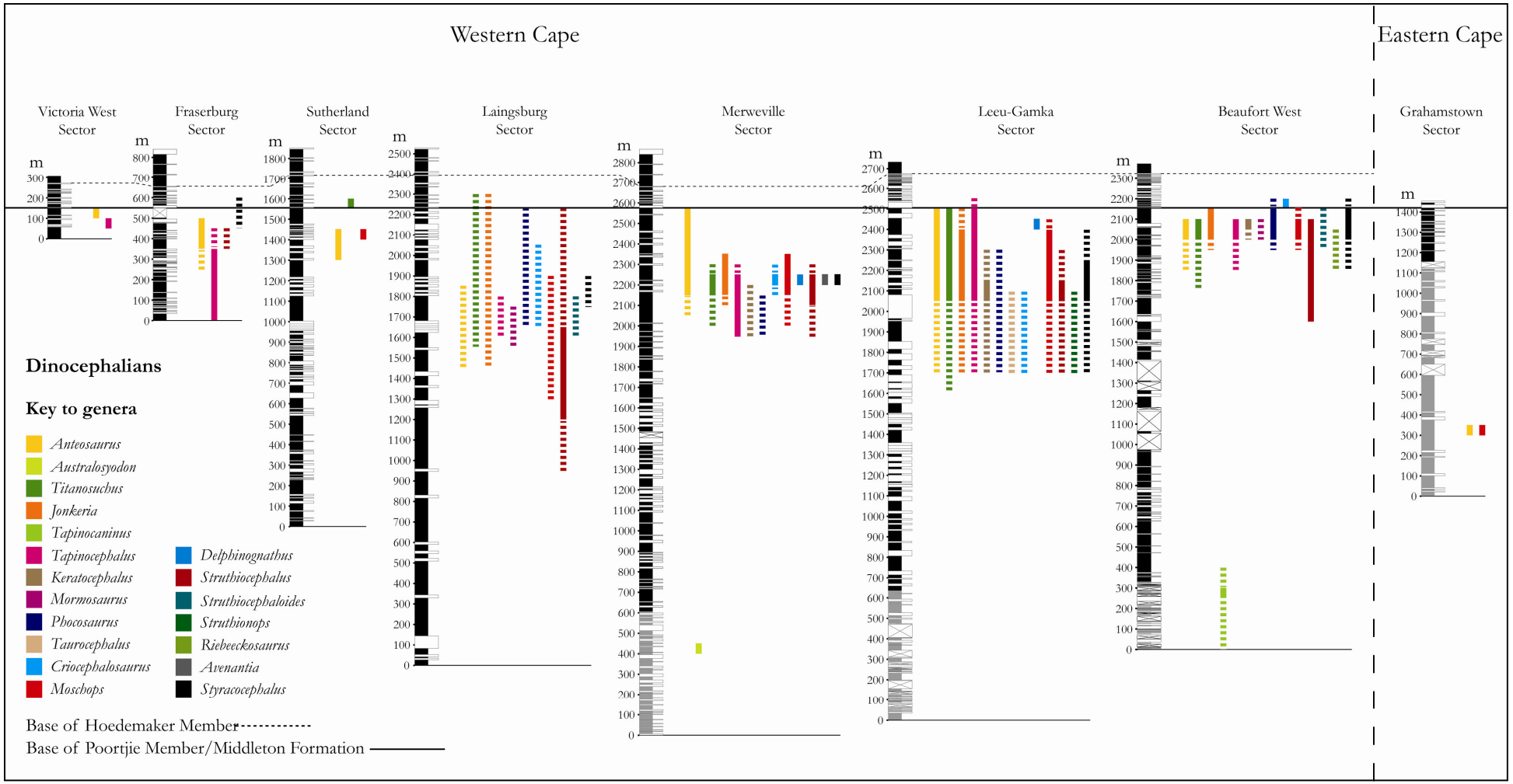


Figure 34. Stratigraphic ranges of dinocephalian genera in each of the sectors in which they occur

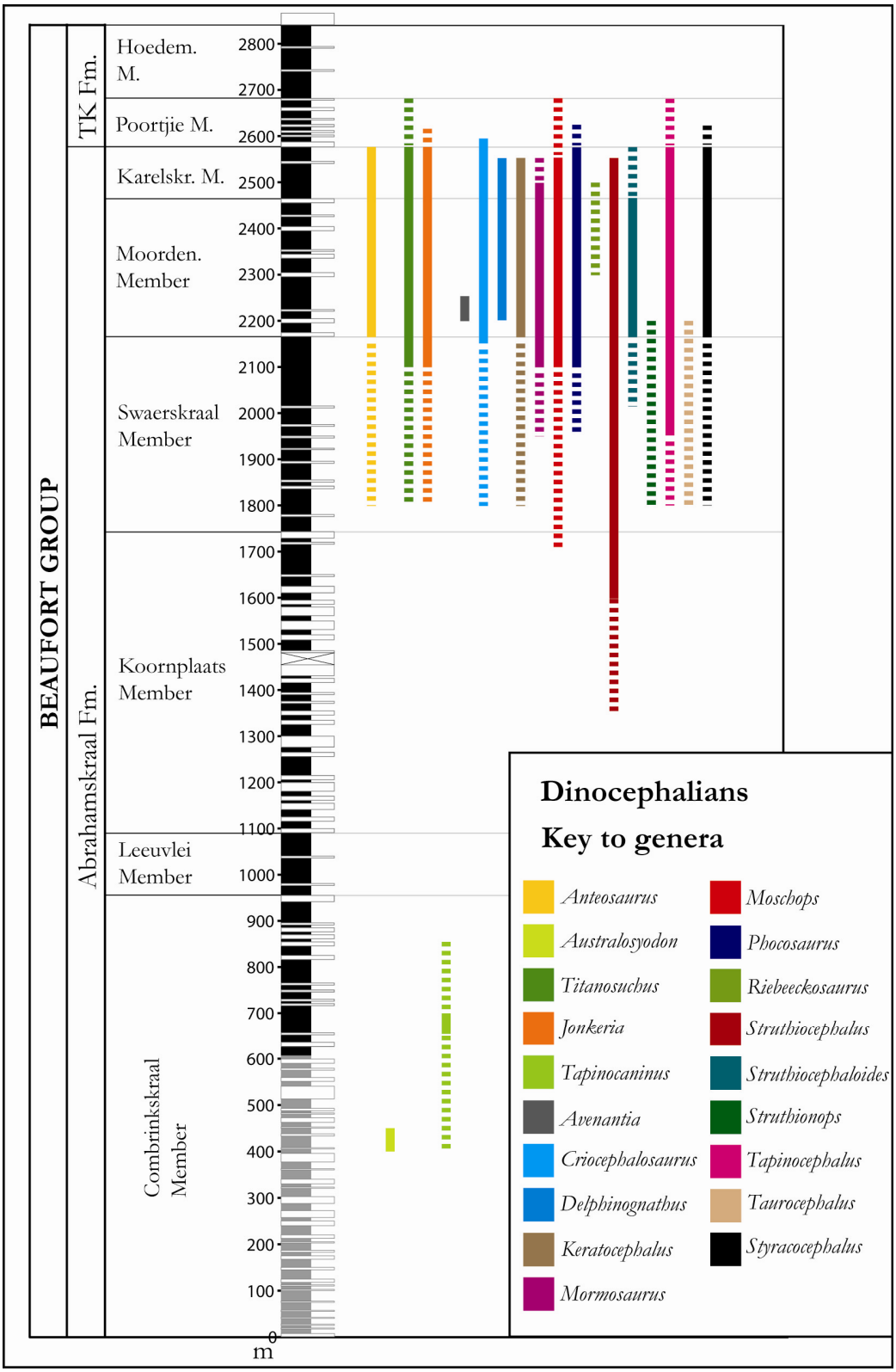


Figure 35. Composite stratigraphic ranges of dinocephalian genera in the Middle Permian Beaufort Group.

Range in the Laingsburg sector

Three well identified specimens of *Anteosaurus* have been collected from this sector. None can be well constrained stratigraphically but the most exclusive interval of occurrence for specimens SAM-PK-11592 and SAM-PK-11592 is 1600–1800 m above the base of the Abrahamskraal Formation in this sector. This equates to the upper Koornplaats member and Swaerskraal Member.

Range in the Sutherland sector

Three specimens of *Anteosaurus* are known from the Sutherland sector, all of which are stratigraphically constrained to an interval 1300–1450 m above the base of the Abrahamskraal Formation.

Range in the Fraserburg sector

The two specimens of *Anteosaurus* from this sector, SAM-PK-11949 and BP/1/7141, constrain the certain stratigraphic range for the genus to an interval 350–500 m above the base of the Abrahamskraal Formation. This corresponds to the Davidskolk and Moordenaars members in this sector.

Range in the Victoria West sector

The single specimen of *Anteosaurus* from this sector, SAM-PK-K360, was collected on the farm Nuwelande, in the Fraserburg district, can be constrained to the upper 50 m of the Abrahamskraal Formation.

Range in the Grahamstown sector

One specimen of this genus, BP/1/7061, has been found the Grahamstown district on the farm Peninsular, Albany district. The specimen is stratigraphically well

constrained to the SI 300–350 m above the base of the Koonap Formation in this sector.

Overall stratigraphic range

The many specimens of *Anteosaurus* that have been collected in South Africa have all been found in the upper Abrahamskraal Formation. Within the southwest of the basin, from where most material originates, the stratigraphically lowest specimens are SAM-PK-5614 and SAM-PK-7396 from the Leeu-Gamka sector, SAM-PK-284 from the Merweville sector, and SAM-PK-11592 and SAM-PK-11694 from the Laingsburg sector. These five specimens have their highest potential occurrence 400–450 m below the base of the Poortjie Member, at the boundary of the Swaerskraal and Moordenaars member when correlated with the Abrahamskraal Formation at its thickest point.

The highest known specimen is, BP/1/7071, which was found less than 30 m below the base of the Poortjie Member in the Merweville sector. The certain stratigraphic range of *Anteosaurus* therefore corresponds to the Moordenaars and Karelskraal members of the Abrahamskraal Formation at its thickest point, between about 2150 m and 2500 m above its base (Figure 33). The genus has its greatest abundance in the lower Moordenaars Member, with an even distribution of specimens in the upper part of its range (Figure 34).

5.5.3 *Titanosuchus*

Along with *Jonkeria*, *Titanosuchus* comprises the family Titanosuchidae (Boonstra 1954a). The genus was first described by Owen (1879) as *T. ferox*, for some poorly preserved tooth roots and postcranial material in the collections of the Natural History Museum in London. A few more species were described but Boonstra (1969) found them to be *nomina dubia*, indicating the monospecificity of *Titanosuchus*.

Stratigraphically, the range of *Titanosuchus* is considered to encompass the *Tapinocephalus* AZ (Smith and Keyser 1995a).

Range in the Beaufort West sector

Most of the twenty-two specimens of *Titanosuchus* from this sector are poorly constrained stratigraphically, having been discovered on farms on the southern margin of the basin, and seven are not included in the analysis for this reason. The stratigraphically lowest specimen is SAM-PK-9106 from the farm Veldmansrivier, in the Prince Albert district, which can be constrained to a stratigraphic interval 1850–2050 m above the base of the Abrahamskraal Formation in this sector. Four specimens provide an upper limit to the certain stratigraphic range of *Titanosuchus*, but the two best constrained specimens are SAM-PK-11488 and SAM-PK-11491 from the farm Mynhardtskraal, in the Beaufort West district. These occur in the SI 2050–2100 m above the base of the Abrahamskraal Formation in this sector.

The certain range of *Titanosuchus* is therefore between 2000–2100 m above the base of the Abrahamskraal Formation in this sector, equivalent to the upper Moordenaars Member and lower Karelskraal Member (Figure 32).

Range in the Leeu-Gamka sector

The stratigraphic constraints on specimens of *Titanosuchus* from the Leeu-Gamka sector are also quite low but the specimen with the stratigraphically lowest position is SAM-PK-731 from the farm Abrahamskraal, in the Prince Albert district. This specimen occurs no higher than the SI 2050–2100 m above the base of the Abrahamskraal Formation. The stratigraphically highest specimen is SAM-PK-12081from the farm Bushmans kop, in the Beaufort West district, which occurs in the upper 50 m of the Abrahamskraal Formation. The certain range of *Titanosuchus* in the Leeu-Gamka is therefore constrained to a stratigraphic interval 2100–2468 m above the base of the Abrahamskraal Formation in this sector, equivalent to its upper 400m.

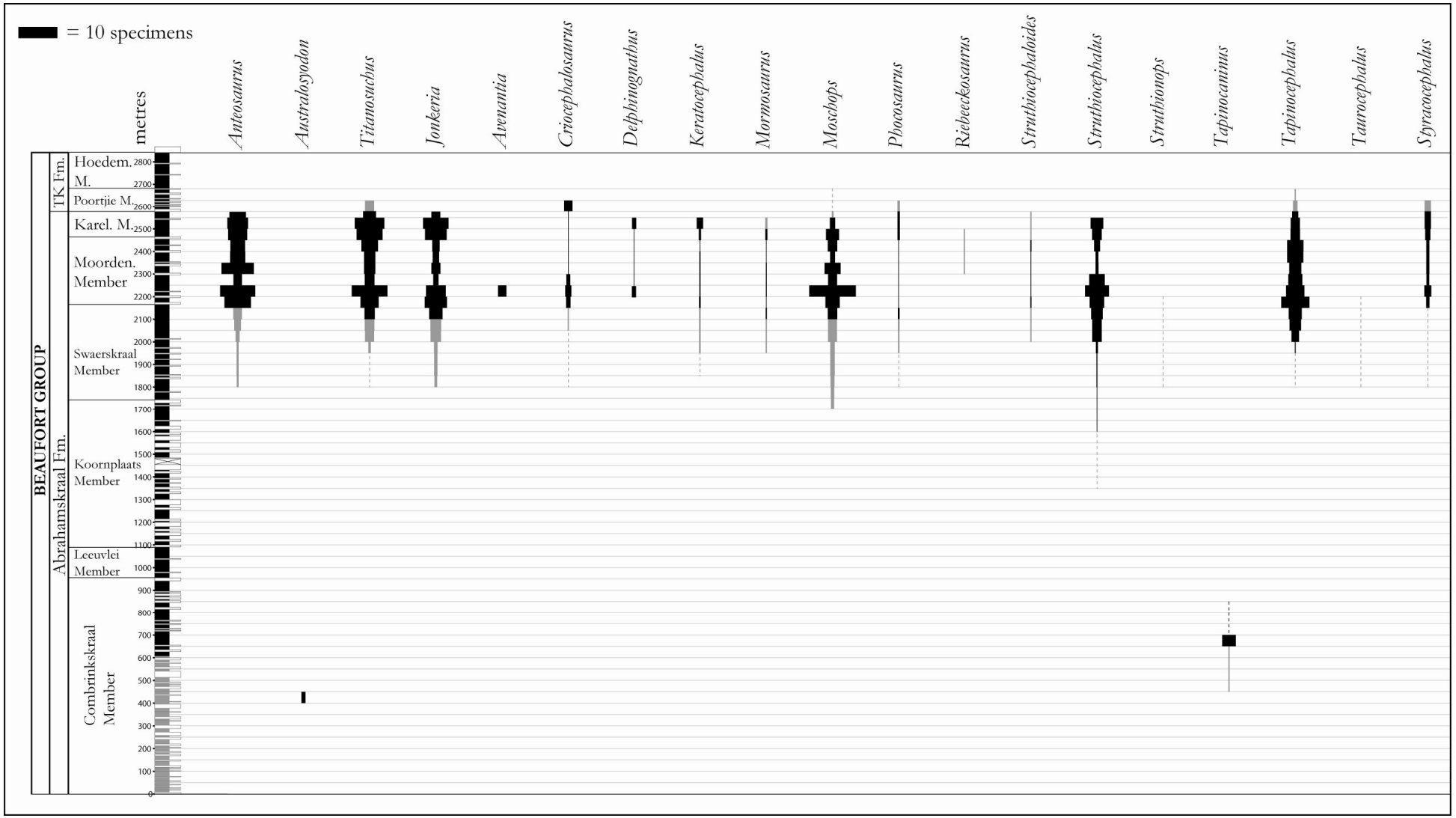


Figure 36. Abundance of dinocephalian genera through the Middle Permian Beaufort Group. Black = abundance within the certain stratigraphic range of the genus, Grey = abundance values outside of certain stratigraphic range.

Range in the Merweville sector

Titanosuchus material from this sector is much better constrained stratigraphically compared to the others and occur in a narrower stratigraphic interval. Of the stratigraphically lowest specimens, the best constrained are SAM-PK-9162 and SAM-PK-9163 from the farm Moordenaarskraal nord, in the Beaufort West district. These occur within the SI 2150–2200 m above the base of the Abrahamskraal Formation. Five specimens can be constrained to the SI 2200–2250 m above the base of the Formation and represent the stratigraphically highest occurrence of *Titanosuchus* in this sector.

Titanosuchus therefore has a definite range of 2150–2250 m above the base of the Abrahamskraal Formation in this sector, which corresponds to the uppermost Swaerskraal Member and the lowest Moordenaars Member.

Range in the Laingsburg sector

Seven specimens of *Titanosuchus* are known from this sector, five of which have relatively well constrained stratigraphic ranges. The potential stratigraphic ranges of all overlap 1650–1750 m above the base of the Abrahamskraal Formation in this sector but, because of this overlap, no certain range can be calculated.

Range in the Sutherland sector

Only a single titanosuchid specimen, BP/1/7168, is known from the Sutherland sector but it is a particularly important one. Although insufficient postcranial material was recovered to determine its genus, the specimen was collected from an horizon 18 m above the base of the Poortjie Member on the farm Ou Tuin, Sutherland district. This represents the stratigraphically highest titanosuchid.

Range in the Fraserburg sector

One specimen of *Titanosuchus* (SAM-PK-K365) is recorded from the Fraserburg sector, from an horizon close to the boundary of the Abrahamskraal and Teekloof formations on the farm Leeukraal, Fraserburg district. However, this can only be identified as an indeterminate titanosuchid (Güven pers. comm.).

Overall stratigraphic range

The genus *Titanosuchus* is in need of taxonomic review and the identities of specimens currently assigned to it are likely to change. However, based on current data, *Titanosuchus* has a stratigraphic range that is constrained to the Abrahamskraal Formation. The stratigraphically lowest specimens are five specimens from the Moordenaarskaroo sector (SAM-PK-011938, SAM-PK-012219, SAM-PK-012218, SAM-PK-012248 and SAM-PK-012221), which occur no higher than the SI 1700–1750 m above the base of the Abrahamskraal Formation in this sector.

The stratigraphically highest specimen identified as *Titanosuchus* is SAM-PK-12081 from the Leeu-Gamka sector, which is constrained to occur in the upper 50 m of the Abrahamskraal Formation. This indicates a certain stratigraphic range for *Titanosuchus* between 2100 m and 2575 m above the base of the Abrahamskraal Formation at its thickest point, equivalent to the upper Swaerskraal Member, the Moordenaars Member and the Karelskraal Member (Figure 33). *Titanosuchus* has two peaks in abundance, in the lower Moordenaars Member and then in the Karelskraal Member (Figure 34).

Specimen BP/1/7168 represents the presence of the Titanosuchidae in the lower Poortjie Member of the Teekloof Formation, if not the genus *Titanosuchus*.

5.5.4 *Jonkeria*

Jonkeria is the second genus of the family Titanosuchidae. It was erected by Van Hoepen (1916) as *J. truclenta* for what Boonstra (1969:36) describes as a 'good holotype,' TM 212, from the farm Abrahamskraal in the Prince Albert district of the

Western Cape. Several additional species were later described (Boonstra 1955; Broom 1929; Janensch 1959) but, as with *Titanosuchus*, the most recent review of the genus was by Boonstra (1969), where eight species were recognised: *J. boonstrai*, *J. haughtoni* (formerly *Dinosphageus*), *J. ingens* (formerly *Dinophoneus*), *J. koupensis*, *J. parva*, *J. rossouwi*, *J. truculenta* and *J. vanderbyli*. As with other genera, all species of *Jonkeria* are here considered together.

The only study to directly address the stratigraphic range of *Jonkeria* has been identified to occur throughout the *Tapinocephalus* AZ (Smith and Keyser 1995a).

Range in the Beaufort West sector

The stratigraphic range of *Jonkeria* in the eastern Koup is well constrained to the uppermost Abrahamskraal Formation. The stratigraphically lowest specimen is SAM-PK-1240 from the farm Bushmans River, in the Beaufort West district, which can be constrained to occur in a stratigraphic interval 1950–2050 m above the base of the Abrahamskraal Formation in this sector. The stratigraphically highest specimens, SAM-PK-9348a and SAM-PK-9348, were collected from the upper 50 m of Abrahamskraal Formation on the farm Mierfontein, in the Beaufort West district. *Jonkeria* therefore occurs in the upper 200 m of the Abrahamskraal Formation in the eastern Koup, within the upper Moordenaars and Karelskraal members (Figure 32).

Range in the Leeu-Gamka sector

The stratigraphically lowest specimens of *Jonkeria* from the Leeu-Gamka sector were collected on the farm Abrahamskraal, in the Prince Albert district and can be constrained to a stratigraphic interval 1700–2100 m above the base of the Abrahamskraal Formation. The stratigraphically highest specimen is SAM-PK-4342 from the farm Rietfontein, Beaufort West district, which was collected from strata 2350–2450 m above the base of the Abrahamskraal Formation. The certain stratigraphic range of *Jonkeria* in this sector therefore corresponds to the interval 2050–2450 m above the base of the Abrahamskraal Formation.

Range in the Merweville sector

In this sector the stratigraphically lowest specimens of *Jonkeria* can be constrained to an interval 2100–2200 m above the base of the Abrahamskraal Formation. The stratigraphically highest specimen is SAM-PK-K08669, which was found on the farm Bullekraal, in the Beaufort West district, and was found in strata 2300–2350 m above the base of the Abrahamskraal Formation. As such, the certain range of *Jonkeria* in the Merweville sector corresponds to the stratigraphic interval 2150–2350 m above the base of the Abrahamskraal Formation, in the lower Moordenaars Member.

Range in the Laingsburg sector

Five of the seven specimens of *Jonkeria* from the Laingsburg sector can be stratigraphically constrained only to an interval 1600–1750 m above the base of the Abrahamskraal Formation in this sector. The two others have broader potential ranges but all overlap in the stratigraphic interval 1650–1750 m above the base of the Abrahamskraal Formation. Because of this overlap, like in *Titanosuchus*, a certain range for *Jonkeria* in this sector cannot be calculated.

Range in the Sutherland sector

Specimen BP/1/7184 from the farm Ou Tuin, in the Sutherland district, was discovered in the lowest Poortjie Member but can only be identified as an indeterminate titanosuchid (see 5.5.3). This potentially extends the range of *Jonkeria* into the lowest Teekloof Formation.

Overall stratigraphic range

Jonkeria has a very similar stratigraphic range to its sister genus, *Titanosuchus,* although this may be due to the similarity between the two genera; the Titanosuchidae are in need of a taxonomic review and therefore generic identifications for specimens assigned to the taxon are likely to change. Based on current data, the stratigraphically

lowest specimens of *Jonkeria* are found in the Laingsburg sector, no higher than the SI 1700–1750 m above the base of the Abrahamskraal Formation. This correlates with the SI 2100–2150 m above the base of the Abrahamskraal Formation at its thickest point.

The stratigraphically highest specimens are SAM-PK-9348 and SAM-PK-9348a from the Beaufort West sector, which were collected from strata in the upper 50 m of the Abrahamskraal Formation. A titanosuchid, BP/1/7168, does occur within the Poortjie Member in the Sutherland sector, but its generic identity cannot be determined. The certain stratigraphic range of *Jonkeria* is therefore constrained to an interval 2100–2575 m above the base of the Abrahamskraal Formation at its thickest point, equivalent to the upper Swaerskraal Member, the Moordenaars Member and the Karelskraal Member (Figure 33). The genus also mirrors *Titanosuchus* in its distribution throughout its range, with two peaks in abundance in both the lower Moordenaars Member and in the Karelskraal Member (Figure 34).

5.5.5 *Avenantia*

Avenantia was first described by Boonstra (1952b) for a skull, SAM-PK-9166, collected on the farm Kruisvallei, in the Beaufort West district north of Merweville (Merweville sector). Some postcranial material allegedly found in association with the holotype, SAM-PK-9167, has been referred to *Avenantia* and has caused some confusion in the literature (e.g. King 1988, Van den Heever and Grine 1981) but this is probably part of the same individual as the holotype (Güven pers. comm.). The holotype is stratigraphically well constrained to the SI 2200–2250 m above the base of the Abrahamskraal Formation, in the lower Moordenaars Member (Figure 33).

5.5.6 *Criocephalosaurus*

Criocephalosaurus was first described as *Criocephalus vanderbyli* (Broom 1928) for the posterior part of a large skull found on the farm Abrahamskraal, in the Prince Albert district (MMK 5138). Further specimens were assigned to this genus before Boonstra's (1969) review of the *Tapinocephalus* AZ. Kammerer and Sidor (2002) later

proposed the revised name *Criocephalosaurus*, as the generic name *Criocephalus* had already been occupied by a beetle, *Criocephalus rusticus* (Mulsant 1839).

In 2010, the posterior part of a dinocephalian skull was discovered in a stream bed on the Beaufort West Common, which probably represents *Criocephalosaurus vanderbyli* (Güven *et al.* in prep). This specimen, SAM-PK-K10888, is important as it was recovered from rocks of the *Pristerognathus* AZ. A second, nearly identical specimen, BP/1/7214, has subsequently been found from the same stratigraphic level.

Range in the Beaufort West sector

The two specimens of *Criocephalosaurus* from the eastern Koup are the two most recently discovered. The first, SAM-PK-K10888, was found on the Beaufort West Common and the second, BP/1/7214, was collected on the farm Putfontein, in the Beaufort West district, about 40km south of Beaufort West. Both can be constrained stratigraphically to the lower 50 m of Poortjie Member of the Teekloof Formation (Figure 32).

Range in the Leeu-Gamka sector

The only specimen of *Criocephalosaurus* known from this sector is the holotype, KM5138, which was found on the farm Abrahamskraal, in the Prince Albert district. Its stratigraphic provenance can therefore be constrained only to an interval 1700–2100 m above the base of the Abrahamskraal Formation in this sector.

Range in the Merweville sector

The three specimens of *Criocephalosaurus* recorded from this sector originate in a similar stratigraphic horizon. The broadest potential stratigraphic range is that of specimen BP/1/1582, which can be constrained to occur 2150–2300 m above the base of the Abrahamskraal Formation. The most accurately stratigraphic position can be calculated for specimen SAM-PK-11794, which was collected on the farm

Kruisvallei, in the Beaufort West district. This specimen can be stratigraphically constrained to the SI 2200–2250 m above the base of the Abrahamskraal Formation but is only tentatively assigned to *Criocephalosaurus* (Güven pers. comm. 2012). The stratigraphic range of the genus in this sector can therefore be constrained to the lower Moordenaars Member.

Range in the Laingsburg sector

The single specimen of *Criocephalosaurus* from the Moordenaarskaroo is SAM-PK-K269 from the farm Tygerhoek, Laingsburg district. This is rather poorly constrained to an interval between 1650–2050 m above the base of the Abrahamskraal Formation, corresponding to the upper Koornplaats Member, Swaerskraal Member and lower Moordenaars Member.

Overall stratigraphic range

The stratigraphically lowest specimen of *Criocephalosaurus* is the holotype from the Leeu-Gamka sector, which occurs no higher than the SI 2050–2100 m above the base of the Abrahamskraal Formation in this sector, or 2150–2200 m above the base of the Abrahamskraal Formation at its thickest point. The stratigraphically highest specimens are the two small individuals from the Beaufort West sector, which were collected from the lower 50 m of the Poortjie member of the Teekloof Formation. The certain stratigraphic range of *Criocephalosaurus* therefore corresponds to a stratigraphic interval between 2100 m above the base of the Abrahamskraal Formation at its thickest point to the lower Teekloof Formation (Figure 33). This equates to the upper Swaerskraal Member, Moordenaars Member and Karelskraal Member of the Abrahamskraal Formation and the lower Poortjie Member of the Teekloof Formation.

Although an unidentified titanosuchid has been found just above the base of the Teekloof Formation in the Sutherland district (see 5.5.3, 5.5.4), *Criocephalosaurus* is the only genus of dinocephalian known to occur in the Poortjie Member.

5.5.7 *Delphinognathus*

Three specimens have been attributed to *Delphinognathus*, including the holotype, SAM-PK-713, which was described by Seeley (1892c). The provenance of this skull is poorly constrained to somewhere near Beaufort West, so not stratigraphically useful. The genus was considered a moschopine by Boonstra (1969), and placed in the tapinocephalini by King (1988). Boonstra (1969) had in fact observed that the holotype of the genus may represent a juvenile *Moschops* and the most recent work suggests that this is true (Güven 2012).

The two referred specimens both originate in the northern Koup. The stratigraphically lowest is SAM-PK-11971, which was collected on the farm Kruisvallei, north of Merweville in the Beaufort West district (Merweville sector), and can be stratigraphically constrained to the SI 2200–2250 m above the base of the Abrahamskraal Formation. The second specimen, SAM-PK-9080, was found on the farm Rietkuil, in the Beaufort West district (Leeu-Gamka sector), and can be constrained to the SI 2400–2450 m above the base of the Abrahamskraal Formation in this sector. When correlated with the Abrahamskraal Formation at its thickest point, the certain stratigraphic range of *Criocephalosaurus* corresponds to an interval 2200–2550 m above the base of the Formation. This range extends from the lower Moordenaars Member to the upper Karelskraal Member of the Abrahamskraal Formation.

5.5.8 *Keratocephalus*

Keratocephalus moloch is one of the poorer known tapinocephalid dinocephalians. It was first decribed by Von Huene (1931) for an individual in the collections of the University of Tübingen, UT Huene 1931 T.167 F4, F8–10. Boonstra (1969) concluded that, along with *Tapinocephalus*, *Mormosaurus* and *Phocosaurus*, this genus comprised the subfamily Tapinocephalinae. Several further specimens have since been attributed to it, with King (1988) listing seven in addition to the holotype. However, the Beaufort Vertebrate Database (Nicolas 2007) only lists four. This study uses those specimens mentioned in King (1988). Most recently, it has been suggested that *Keratocephalus* is junior synonymous of *Struthiocephalus whaitsi* (Güven 2012).

The range of *Keratocephalus* has not yet been attributed to any more exclusive interval than the *Tapinocephalus* AZ (Smith and Keyser 1995a).

Range in the Beaufort West sector

Three specimens of *Keratocephalus* have been found in the eastern Koup, of which two can be well constrained stratigraphically. The first specimen,SAM-8946, was collected on the farm Mynhardskraal, in the Beaufort West district, and was found in strata 2050–2100 m above the base of the Abrahamskraal Formation. The second specimen is SAM-PK-11294, which was found nearby on the farm Boesmansrivier and can be constrained stratigraphically to an interval 2000–2100 m above the base of the Abrahamskraal Formation (Figure 32). *Keratocephalus* therefore occurs with certainty only between 2050 m and 2100 m above the base of the Abrahamskraal Formation in this sector, equivalent to the upper Moordenaars Member or lowest Karelskraal Member.

Range in the Leeu-Gamka sector

Of the four specimens of *Keratocephalus* from the Leeu-Gamka sector, the stratigraphically lowest is the holotype, UT Huene 1931 T.167 F4, F8–10, which was collected on the farm Abrahamskraal, in the Prince Albert district. This specimen can be constrained only to a stratigraphic interval 1700–2100 m above the base of the Abrahamskraal Formation in this sector. The remaining three were found in the vicinity of Leeu-Gamka on the farms Welgemoed (SAM-PK-10557) and Kalkkraal (SAM-PK-12093 and SAM-PK-12094), and can all be stratigraphically constrained to an interval 2100–2300 m above the base of the Abrahamskraal Formation. The certain stratigraphic range of *Keratocephalus* in this sector therefore corresponds only to the interval 2050–2150 m above the base of the Abrahamskraal Formation.

Range in the Merweville sector

Specimen SAM-PK-11937, from the farm Buffelsvlei in the Beaufort West district, was collected from strata 1950–2200 m above the base of the Abrahamskraal Formation and cannot be constrained to any more exclusive stratigraphic interval than the upper Swaerskraal Member or lowest Moordenaars Member.

Overall stratigraphic range

The stratigraphically lowest specimens of *Keratocephalus* are the holotype, from the Leeu-Gamka sector, and SAM-PK-11937, from the Merweville sector. When correlated with the Abrahamskraal Formation at its thickest point, both these specimens were found no higher than the SI 2150–2200 m above the base of the Formation. The stratigraphically highest specimen is SAM-PK-8946, from the Beaufort West district, which is well constrained to occur 50–100 m below the base of the Teekloof Formation.

Keratocephalus therefore has a certain stratigraphic range that extends between 2150 m and 2550 m above the base of the Abrahamskraal Formation at its thickest point and which corresponds to the Moordenaars Member and lower Karelskraal Member (Figure 33).

5.5.9 *Mormosaurus*

Mormosaurus seeleyi was first described by Watson (1914e) for a skull known only to have come from the Koup, South Africa. Further specimens were described, which led Boonstra (1969) to comment that the genus was highly variable in its morphology but King (1988) only noted two referred specimens. One of these specimens, SAM-PK-12060, which was initially referred to *Mormosaurus* by Boonstra (1968), is now recorded on the catalogue of the South African Museum as *Tapinocephalus*. The latter identification is accepted here, so only three specimens, including the type, are currently referable to *Mormosaurus seeleyi*.

Range in the Beaufort West sector

SAM-PK-9082, from the farm Klein Koedoeskop in the Beaufort West district, can be stratigraphically constrained to an interval 2000–2100 m above the base of the Abrahamskraal Formation in this sector (Figure 32). This corresponds to the uppermost Moordenaars Member.

Range in the Laingsburg sector

One specimen of *Mormosaurus*, SAM-PK-11932, is known from the farm Schoppelmaaikraal in the western Koup portion of the Laingsburg district. This specimen can be constrained to a stratigraphic interval 1550–1750 m above the base of the Abrahamskraal Formation in this sector, within the upper Koornplaats Member or Swaerskraal Member.

Overall stratigraphic range

The two referred specimens of *Mormosaurus* indicate a certain stratigraphic range for the genus extending from 2100 m to 2500 m above the base of the Abrahamskraal Formation at its thickest point. This corresponds to the uppermost Swaerskraal Member, Moordenaars Member and lower Karelskraal Member (Figure 33).

5.5.10 *Moschops*

The genus *Moschops* is the most common tapinocephalid, after *Tapinocephalus* and *Struthiocephalus*. The name was first proposed by Broom (1911) for a specimen collected on the farm Spitzkop in the Moordenaarskaroo, which was subsequently transferred to the collections of the American Museum of Natural History with number AMNH 5550. Several other specimens, also at the American Museum, were collected simultaneously from the same locality and were later deemed to be 'topotypes' of *Moschops capensis* (Boonstra 1957).

A second species of *Moschops* was named by Boonstra (1957), *M. koupensis*, for specimen SAM-PK-11582 and several more species of *Moschops* were designated due to the synonymisation of previously described genera with this taxon. *Moschops whaitsi*, represented by specimen AMNH 5602, had formerly been assigned to *Moschognathus whaitsi* by (Broom 1914), while a British Museum specimen, NHMUK R3596, had first been described by Watson (1914e) as *Pnigalion oweni*. Both these genera were synonymised with *Moschops* by Boonstra (1969) and although he retained the species, he believed both *M. whaitsi* and *M. oweni* to be of doubtful validity. Boonstra (1969) also considered the genera *Moschoides* (FMNH UR 367) and *Agnosaurus* (SAM-PK-11832) to be synonymous with *Moschops*. Only *M. capensis* is represented by more than one specimen.

Range in the Beaufort West sector

There are four specimens of *Moschops* that have been found in the eastern Koup. All are found high in the Abrahamskraal Formation but the stratigraphically highest specimen is SAM-PK-3015, from the farm La-de-da in the Beaufort West district. This specimen can be constrained to occur in the upper 100 m of the Abrahamskraal Formation or the Poortjie Member of the Teekloof Formation.

The stratigraphically lowest specimen in this sector is SAM-PK-1057, from the farm Letjesbos, in the Beaufort West district. This specimen is constrained to a stratigraphic interval 1950-2050 m above the base of the Abrahamskraal Formation, which indicates the certain stratigraphic range of *Moschops* in this sector corresponds to the upper Moordenaars Member and lower Karelskraal Member (Figure 32).

Range in the Leeu-Gamka Member

Seven specimens of *Moschops* are known from the Leeu-Gamka sector. The stratigraphically highest specimen is FMNH UR 367 from the farm Hottentotsrivier, in the Beaufort West sector, which is constrained to a stratigraphic interval 2350–2450 m above the base of the Abrahamskraal Formation in this sector. The stratigraphically lowest specimen is SAM-PK-11981 from the farm Abrahamskraal, in

the Prince Albert district, which is constrained to a stratigraphic interval 1700–2100 m above the base of the Abrahamskraal Formation. The certain stratigraphic range of *Moschops* in the Leeu-Gamka sector therefore corresponds to an interval 2050–2400 m above the base of the Abrahamskraal Formation.

Range in the Merweville sector

The Merweville sector has produced the greatest amount of *Moschops* material, with nineteen identified specimens. Most were found on the government farm Van der Byls Kraal, just north of Merweville in the Beaufort West district and all specimens originate in the upper part of the Abrahamskraal Formation. The stratigraphically lowest specimens come from different localities but were found in strata 2150–2200 m above the base of the Abrahamskraal Formation. The stratigraphically highest specimens were all collected on the farm Bullekraal, near the Nuweveld Escarpment north of Merweville. These three specimens, including two adults (BP/1/6987 and BP/1/6993) and a juvenile (BP/1/6986), were recovered from a stratigraphic horizon 2300–2350 m above the base of the Abrahamskraal Formation. The certain stratigraphic range of *Moschops* in this sector extends between 2150 m to 2350 m above the base of the Abrahamskraal Formation, in an interval that corresponds to the lower Moordenaars Member.

Range in the Laingsburg sector

Eleven specimens of *Moschops* are known from the Laingsburg sector, of which eight constitute the type series (AMNH 5550–5557). None of the specimens from this sector are well constrained stratigraphically and the type series, from the farm Spitzkop in the Laingsburg district, can be constrained only to a broad stratigraphic interval 1300–1900 m above the base of the Abrahamskraal Formation. The narrowest potential stratigraphic range is that of BP/1/4858, which was found in strata 1600–1750 m above the base of the Abrahamskraal Formation, corresponding to the upper Koornplaats Member or lower Swaerskraal Member. Because the

potential ranges of all specimens from this sector overlap, a certain stratigraphic range of *Moschops* cannot be calculated.

Range in the Sutherland sector

A single specimen of *Moschops*, SAM-PK-11995, is recorded from the Sutherland sector. This specimen, from the farm Kruisrivier in the Sutherland district, is the most northerly occurrence of the genus and can be stratigraphically constrained to the SI 1400–1450 m above the base of the Abrahamskraal Formation, within the upper Moordenaars member in this sector.

Overall stratigraphic range

Many specimens of *Moschops* were collected before the common usage of grid coordinates but its stratigraphic range is constrained to the upper Abrahamskraal Formation. The stratigraphically lowest occurrence of the genus is specimen BP/1/4858 from the Laingsburg sector, which occurs no higher than the SI 1700–1750 m above the base of the Abrahamskraal Formation in that sector, equivalent to the SI 2100–2150 m above the base of the Abrahamskraal Formation at its thickest point (Figure 32). The stratigraphically highest specimen is SAM-PK-3015 from the Beaufort West sector, which occurs no lower than 100 m below the base of the Teekloof Formation. The certain stratigraphic range of *Moschops* can therefore be constrained to an interval 2100–2550 m above the base of the Abrahamskraal Formation at its thickest point, in the upper Swaerskraal Member, Moordenaars Member and Karelskraal Member (Figure 33). Like *Anteosaurus*, Moschops has its greatest abundance in the lower Moordenaars Member, with relatively stable numbers in the rest of its certain stratigraphic range (Figure 34).

5.5.11 *Phocosaurus*

The type specimen of *Phocosaurus,* NHMUK 43525, was first described by Owen (1876) as belonging to *Pareiasaurus*. Although it consisted only of postcranial elements, including a pelvis, it was later re-described by Seeley (1888), who proposed the name *Phocosaurus migischion*. The material was subsequently determined to be indistinguishable from that of *Tapinocephalus atherstonei* (Lydekker 1890) but Watson (1914e) added a description of some palatal remains associated with the type specimen and supported the distinction of *Phocosaurus*. Watson (1914e) also commented on the similarities this palatal fragment had with a new specimen, NHMUK R3594, which was the holotype of his newly erected genus *Mormosaurus*. It is possible that this observation was shrewd and that the two genera are indeed synonymous (Güven 2012).

Boonstra (1956) described the first skull attributed to *Phocosaurus*, which he identified based on its association with an ilium indicative of that genus; however, as King (1988) points out, this relies on a firm association between the ilium and the skull, as well as the ilium being diagnostic of the genus *Phocosaurus*. Nevertheless, she tentatively accepted Boonstra's (1956) identification but *Phocosaurus* remains are poorly defined taxon.

Range in the Beaufort West sector

Two specimens of *Phocosaurus* are known from the eastern Koup. The stratigraphically highest specimen is SAM-PK-11988 from the farm Boeteka, in the Beaufort West district. This farm straddles the boundary of the Abrahamskraal and Teekloof formations, the latter of which is exposed in a series of synclines in the area south of Beaufort West. The specimen stratigraphically constrained to the upper 50 m of the Abrahamskraal Formation or lower 50 m of the Poortjie Member (Figure 32).

The second specimen, SAM-PK-11306, was collected on the farm Boesmansrivier, in the Beaufort West district, and can be constrained to originate in a stratigraphic interval 2000–2100 m above the base of the Abrahamskraal Formation in this sector.

Range in the Leeu-Gamka sector

The only specimen of *Phocosaurus* found in this sector is the holotype, NHMUK 43525, which was collected on the farm Varsfontein, in the Prince Albert district. This is poorly constrained to occur in a stratigraphic interval 1700–2300 m above the base of the Abrahamskraal Formation, in the upper Koornplaats Member or above.

Range in the Merweville sector

A single specimen of *Phocosaurus*, SAMP-PK-9103, has been found in this sector. This fragmentary skull was found on the farm Droogfontein, in the Prince Albert district, and can be constrained to a stratigraphic interval 1950–2150 m above the base of the Abrahamskraal Formation. This is equivalent to the upper Swaerskraal Member in this sector.

Range in the Laingsburg sector

The single specimen of *Phocosaurus* from this sector, SAM-PK-11300, was collected on the farm Deesweezfontein, in the Laingsburg district of the western Koup. This farm is situated on the exposure of a broad stratigraphic interval, which only constrains the specimen to approximately the upper third of the Abrahamskraal Formation in this sector.

Overall stratigraphic range

The stratigraphically lowest specimen of *Phocosaurus* is SAM-PK-9103 from the Merweville sector, which occurs stratigraphically no higher than the SI 2100–2150 m above the base of the Abrahamskraal Formation. The stratigraphically highest specimen is SAM-PK-11988 from the Beaufort West sector and which occur no lower than the upper 50 m of the Abrahamskraal Formation. The certain stratigraphic range of *Phocosaurus* therefore equates an interval 2100–2575 m above

the base of the Abrahamskraal Formation at its thickest point, encompassing the upper Swaerskraal Member, the Moordenaars Member and Karelskraal Member (Figure 33).

5.5.12 *Riebeeckosaurus*

Riebeeckosaurus and was another dinocephalian genus described by Boonstra (1952a), and is represented by only a single skull, SAM-PK-3400. Boonstra (1969) mentions two skulls for *Riebeeckosaurus* but only the holotype is recorded in King (1988) and by the BFV database (Nicolas 2007).

SAM-PK-3400 was found near the Viviers railway siding, in the Beaufort West district (Beaufort West sector), and can be constrained to an interval 1850–2050 m above the base of the Abrahamskraal Formation in this sector (Figure 32). This corresponds to a stratigraphic interval 2300–2500 m above the base of the Abrahamskraal Formation at its thickest point, inclusive of the upper Moordenaars Member and the lower Karelskraal Member (Figure 33).

5.5.13 *Struthiocephaloides*

This genus is represented by only two specimens, both of which are attributed to different species. The first, SAM-PK-5607, is the genotype and was described by Boonstra (1952c) as *Struthiocephaloides cavifrons*. This specimen was collected on the farm Lammerkraal, in the Prince Albert district of the eastern Koup (Beaufort West sector), and can be stratigraphically constrained to the upper 200 m of the Abrahamskraal Formation (Figure 32).

The second specimen of *Struthiocephaloides* was described at the same time (Boonstra 1952c) and was assigned to the species *S. duplessisi* on the basis of being wider across the tabulars; however, while Boonstra (1969) and King (1988) both retained the distinct species, *S. duplessisi* has recently been suggested to be a junior synonym of *S. cavifrons* (Güven pers. comm. 2012). This holotype of *S. duplessisi*, SAM-PK-11693, comes from the farm Dikbome, in the Laingsburg district (Laingsburg sector), and is

stratigraphically constrained to an interval 1600–1800 m above the base of the Abrahamskraal Formation in the Laingsburg sector.

The certain stratigraphic range of the *Struthiocephaloides* can therefore be constrained to an interval 2150–2450 m above the base of the Abrahamskraal Formation at its thickest point, equivalent to the Moordenaars Member (Figure 33).

5.5.14 *Struthiocephalus*

The species *Struthiocephalus whaitsi* was erected for a skull, SAM-PK-2678, which was collected from near the Viviers railway siding on the farm Leeuwkraal, Beaufort West district (Haughton 1915a). It was diagnosed partly on the basis of having a long snout, unlike other known tapinocephalids at that time. Over the succeeding decades, several more species of *Struthiocephalus* were described (e.g. Boonstra 1952f; Broom 1937; Brink 1957; Olsen and Broom 1937) but Boonstra (1969) considered *Struthiocephalus* to be monspecific; in this work, Boonstra suggested that all existing species of *Struthiocephalus,* along with the genera *Moschosaurus* and *Struthiocephalellus*, represented different growth series of the type species, *S. whaitsi*. This was maintained by King (1988) but, most recently, it has been suggested that *Keratocephalus moloch* is a junior synonym of *Struthiocephalus whaitsi* (Güven 2012).

Stratigraphically, *Struthiocephalus* was assumed, like most dinocephalians, to occur throughout the *Tapinocephalus* AZ (Smith and Keyser 1995a).

Range in the Beaufort West sector

In the eastern Koup, seven specimens of *Struthiocephalus* have been recovered. The stratigraphically lowest specimen SAM-PK-11880 from the farm Arthurskraal, in the Beaufort West district, which is poorly constrained to the lower two thirds of the Abrahamskraal Formation but occurs no higher than the SI 1600–1650 m above its base. The stratigraphically highest specimens are SAM-PK-8947 and SAM-PK-11493 from the farm Mynhardtskraal, in the Beaufort West district, which are well constrained to occur in the SI 2050–2100 m above the base of the Abrahamskraal

Formation in this sector. This corresponds to a stratigraphic range for *Struthiocephalus* in the eastern Koup between 1600 m and 2100 m above the base of the Abrahamskraal Formation, from the uppermost Koornplaats Member to the lower Karelskraal Member (Figure 32).

Range in the Leeu-Gamka sector

Three specimens of *Struthiocephalus* are known from this sector. Two were collected on the farm Abrahamskraal, in the Prince Albert district (SAM-PK-3012 and SAM-PK-3719), where they can be constrained stratigraphically to an interval 1700–2100 m above the base of the Abrahamskraal Formation. The third specimen, SAM-PK-12091, was found in the vicinity of Leeu-Gamka on the farm Kalkkraal, Prince Albert district, where its stratigraphic provenance can be constrained to an interval 2100–2300 m above the base of the Abrahamskraal Formation. The certain stratigraphic range of *Struthiocephalus* in this sector therefore corresponds to a narrow interval 2050–2150 m above the base of the Abrahamskraal Formation.

Range in the Merweville sector

At sixteen, more *Struthiocephalus* specimens have been found in the Merweville sector than any other. Its stratigraphically lowest occurrence is specimen SAM-PK-11941 from the farm Droogfontein, in the Laingsburg district, which can be constrained to a stratigraphic interval 1950–2150 m above the base of the Abrahamskraal Formation. Six specimens were found in a similar stratigraphic horizon but in different localities and represent the stratigraphically highest specimens; these constrained to occur in a stratigraphic interval 2200–2300 m above the base of the Abrahamskraal Formation. The certain stratigraphic range of *Struthiocephalus* in the Merweville sector extends 2100 m to 2250 m above the base of the Abrahamskraal Formation, from the upper Swaerskraal Member to the lower Moordenaars Member.

Range in the Laingsburg sector

Seven specimens of *Struthiocephalus* are known from the Moordenaarskaroo, including its stratigraphically lowest occurrence. This specimen, SAM-PK-12039, was found on the farm Leeuvlei, Laingsburg district, 27 km north of Laingsburg and can be constrained to the upper 300 m of the Leeuvlei Member, 950–1250 m above the base of the Abrahamskraal Formation. The other specimens all have a similar lowest potential occurrence, but the stratigraphically highest specimen is SAM-PK-12050 from the farm Modderfontein, in the Lainsburg district near the Komsberg escarpment. This farm exposes a thick stratigraphic interval from 1600 m above the base of the Abrahamskraal Formation up to the base of the Teekloof Formation, corresponding to an interval from the upper Koornplaats Member in the south to the lowest part of the Poortjie Member in the north-west. The certain stratigraphic range of *Struthiocephalus* in this sector therefore corresponds to an interval 1200–1650 m above the base of the Abrahamskraal Formation, equivalent the upper Leeuvlei Member of Koornplaats Member.

Range in the Fraserburg sector

Two potential specimens of *Struthiocephalus* were recovered from the upper Moordenaars Member on the farm Tontelbosch, Sutherland district, 100–200 m below the base of the Poortjie Member. These specimens have yet to be properly identified.

Overall stratigraphic range

The stratigraphically lowest occurrence of *Struthiocephalus* is specimen SAM-PK-12039 from the Laingsburg sector, which occurs no higher than the SI 1200–1250 m above the base of the Abrahamskraal Formation in that sector, which corresponds to the SI 1600–1650 m above the base of the Abrahamskraal Formation at its thickest point (Figure 32). The stratigraphically highest specimens are SAM-PK-8947 and SAM-PK-11493 from the Beaufort West sector and which are constrained to occur 50–100 m below the base of the Teekloof Formation. The certain stratigraphic range

of the genus therefore extends from 1600 m to 2550 m above the base of the Abrahamskraal Formation at its thickest point, equivalent to a stratigraphic interval from the upper Koornplaats Member to the upper Karelskraal Member (Figure 33). *Struthiocephalus* reaches its maximum abundance in the lower Moordenaars Member like most other dinocephalians (Figure 34).

5.5.15 *Struthionops*

Only a single specimen, SAM-PK-11947, has been described for the genus *Struthionops* (Boonstra 1952e). This is a skull, which was collected on the farm Abrahamskraal, in the Prince Albert district (Leeu-Gamka sector), and that can be stratigraphically constrained only to an interval 1700–2100 m above the base of the Abrahamskraal Formation in this sector (Figure 32). This corresponds to a stratigraphic interval 1800–2200 m above the base of the Abrahamskraal Formation at its thickest point, from the lower Swaerskraal Member to the lowest Moordenaars Member (Figure 33).

5.5.16 *Tapinocaninus*

Tapinocaninus is the most recently described dinocephalian genus from South Africa, for which five specimens are known; all appeared in the original description (Rubidge 1991). The genus was immediately recognised to be a basal tapinocephalid and this has been supported by the most recent cladistic analyses (Rubidge and Sidor 2001; Sidor 2000).

All material was found in the lowest Beaufort Group in the southwest of the basin, within the *Eodicynodon* AZ. Four specimens were collected on the farm Botterkraal, in the Prince Albert district (Beaufort West sector), on the southern margin of the Koup. Three of these specimens, NMQR 2985, NMQR 2986 and NMQR 2987, were found in the same horizon within the SI 250–300 m above the base of the Abrahamskraal Formation. ROZ K95 can be stratigraphically constrained to the lower 300 m of the Abrahamskraal Formation on that farm. The fifth specimen, NMQR 3097, was found on the farm Swartgrond, in the Rietbron district (Beaufort

West sector), and can be stratigraphically constrained to the lower 400 m of the Abrahamskraal Formation (Figure 32).

When correlated with the Abrahamskraal Formation at its thickest point, the certain stratigraphic range of *Tapinocaninus* can only be determined for the SI 650–750 m above the base of the Formation (Figure 33). Its potential range is greater, but this is based on few specimens.

5.5.17 *Tapinocephalus*

Tapinocephalus is the oldest dinocephalian generic name, having been described by Owen (1876a) for a specimen from near Jan Willems fontein, in the Prince Albert district. Unlike many tapinocephalids, *Tapinocephalus* has remained monospecific as *T. atherstoni* and the only addition to the genus through synonymisation was that of *Taurops* (Boonstra 1969).

Around forty-two specimens are currently recorded in South African collections (Nicolas 2007), and all recorded to occur in the *Tapinocephalus* AZ (Smith and Keyser 1995a; Smith *et al.* 2012).

Range in the Beaufort West sector

Only three specimens of *Tapinocephalus* are recorded from this sector. SAM-PK-K203 and SAM-PK-K204 were collected on the farms Vetkoekraal and Meyerspoort, respectively, and were found stratigraphically no lower the SI 2050–2100 m above the base of the Abrahamskraal Formation. The third specimen is SAM-PK-2753 from the farm Leeuwkraal Beaufort West district, which can be constrained to the interval 1850–2050 m above the base of the Abrahamskraal Formation. The certain stratigraphic range of *Tapinocephalus* in this sector is therefore between 2000 m and 2100 m above the base of the Abrahamskraal Formation (Figure 32).

Range in the Leeu-Gamka sector

This sector contains more *Tapinocephalus* material than any other, with eighteen referred specimens, of which most are found throughout the upper 500 m of the Abrahamskraal Formation. The stratigraphically lowest specimen is TM 1060 from the farm Abrahamskraal, Prince Albert district, which is constrained to an interval 1700–2100 m above the base of the Abrahamskraal Formation. The stratigraphically highest specimen is SAM-PK-11998 from the farm Sandrivier, in the Beaufort West district. This specimen was found on the boundary of the Abrahamskraal and Teekloof formations, but probably in the former. The certain stratigraphic range of *Tapinocephalus* in this sector extends from 2050 m to 2468 m above the base of the Abrahamskraal Formation, equivalent to its upper 418 m.

Range in the Merweville sector

Fourteen specimens of *Tapinocephalus* are recorded in this sector and all but one come from a similar stratigraphic interval. The specimen with the highest stratigraphic position is SAM-PK-308 from the farm Bulwater, in the Beaufort West district. This specimen can be constrained to the interval 2200–2300 m above the base of the Abrahamskraal Formation, in the lower Moordenaars Member.

The stratigraphically lowest specimen is SAM-PK-11991 from the farm Tuinkraal, in the Prince Albert district. Because it occurs along the southern margin of the basin where folding is prevalent, the Abrahamskraal Formation outcrop on the farm Tuinkraal corresponds to its lower 2000 m (Jirah 2013). This fossil therefore has a very broad potential range but occurs no higher stratigraphically than the SI 1950–2000 m above the base of the Abrahamskraal Formation. The stratigraphic range of *Tapinocephalus* in this sector therefore corresponds to an interval from 1950–2250 m above the base of the Abrahamskraal Formation, in the upper Swaerskraal and lower Moordenaars members.

Range in the Laingsburg sector

The three specimens of *Tapinocephalus* known from this sector come from farms in the westernmost part of the Koup. The potential stratigraphic ranges of each specimen overlap in the interval 1600–1750 m above the base of the Abrahamskraal Formation, in the upper Koornplaats or Swaerskraal Member. For this reason a certain stratigraphic range for the genus in this sector cannot be calculated.

Range in the Fraserburg district

Three specimens of *Tapinocephalus* are also known from the Fraserburg sector. SAM-PK-1198, which was collected on the farm Vleikraal in the Fraserburg district, is the stratigraphically lowest. It was found close to the Ecca-Beaufort boundary, within the Kopjesfontein Member of the Abrahamskraal Formation. The two other specimens, SAM-PK-11701a and SAM-PK-11702, were collected on the farm Elandsberg, Sutherland district, and can be stratigraphically constrained to an interval 300–450 m above the base of the Abrahamskraal Formation. *Tapinocephalus* therefore certainly occurs in the lower 350 m of the Abrahamskraal Formation in this sector.

Range in the Victoria West sector

A single specimen of *Tapinocephalus*, SAM-PK-11992, comes from this sector and was collected on the farm Vanwegensfontein, in the Carnavon district. This locality is stratigraphically constrained to the central part of the Abrahamskraal Formation in this sector, 50–100 m above its base.

Overall stratigraphic range

All specimens of *Tapinocephalus* are restricted to the upper part of the Abrahamskraal Formation. The stratigraphically lowest specimen is SAM-PK-11991 from the Merweville sector, which was found no higher than the SI 1950–2000 m above the base of the Abrahamskraal Formation. The stratigraphically highest specimen is

SAM-PK-11998 from the Leeu-Gamka sector, which was found on the boundary of the Abrahamskraal and Teekloof formations. The certain range of the genus therefore extends from 1950 m above the base of the Abrahamskraal Formation at its thickest point up to the base of the Teekloof Formation (Figure 33).

Within its certain range, *Tapinocephalus* has its greatest abundance in the lower Moordenaars Member, with a steady decrease above the top of the Moordenaars Member (Figure 34).

5.5.18 *Taurocephalus*

Taurocephalus is represented by a single specimen from the farm Abrahamskraal, in the Prince Albert district (Leeu-Gamka sector). This skull, AMNH 5655, was described by Broom (1928) as *Taurocephalus lerouxi* and was differentiated from *Struthiocephalus* on the basis of having a narrower frontal region and more robust snout. It is retained by both Boonstra (1969) and King (1988). The stratigraphic range of the genus is constrained to an interval 1700–2100 m above the base of the Abrahamskraal Formation in the Leeu-Gamka sector, or 1800–2200 m above the base of the Abrahamskraal Formation at its thickest point.

5.5.19 *Styracocephalus*

Styracocephalus platyrhyncus was described by Haughton (1929) for a specimen collected on the farm Boesmansrivier, in the Beaufort West district (SAM-PK-8936). The systematic position of the genus has been variable and it was recognised as a dinocephalian only in the second half of the 20th Century (Boonstra 1969; King 1988); it is now considered a stem group tapinocephalian, more related to the herbivorous tapinocephalids and titanosuchids than to the Anteosauridae (Rubidge and Sidor 2001; Rubidge and Van den Heever 1997; Sidor 2000). The genus has remained monospecific and twelve specimens are currently known.

Range in the Beaufort West sector

Four specimens of *Styracocephalus* are known from the eastern Koup. The stratigraphically highest specimen is BP/1/5485 from the farm Stellenboschvlei, in the Murraysburg district. This specimen was found close to the boundary of the Abrahamskraal and Teekloof formations but the stratigraphy here is hard to interpret. The geological map of the farm shows the outcrop in this area to be of Teekloof Formation (map sheet: Republic of South Africa 3222, Beaufort West, 1:250 000 Geological Series 1979), which is supported by associated fossils in the area and suggests that this specimen was found in the lower Poortjie Member.

The stratigraphically lowest specimen is SAM-PK-12181 from the farm Dale Ajalon, in the Beaufort West district, which can be constrained to an interval 1850–2050 m above the base of the Abrahamskraal Formation in this sector, within the upper Moordenaars Member. The certain stratigraphic range of *Styracocephalus* in this sector therefore extends from 2000 m above the base of the Abrahamskraal Formation up to the base of the Teekloof Formation, although it may well continue into the lower Poortjie Member.

Range in the Leeu-Gamka sector

Three specimens of *Styracocephalus* have been found in this sector but none are well constrained stratigraphically. SAM-PK-12201 and SAM-PK-12215, from the farms Flagfontein and Leeuwkraal, respectively, both in the Beaufort West district, can be constrained to occur in a stratigraphic interval 2200–2400 m above the base of the Abrahamskraal Formation in this sector. The third specimen, SAM-PK-9346, was found on the farm Abrahamskraal, Prince Albert district, and is stratigraphically constrained to an interval 1700-2100 m above the base of the Abrahamskraal Formation. In this sector, the certain stratigraphic range of *Styracocephalus* extends from 2050–2250 m above the base of the Abrahamskraal Formation.

Range in the Merweville sector

A single specimen of *Styracocephalus* was recently discovered on the farm Rietfontein, in the Beaufort West district, south of Merweville. BP/1/6883 was collected from a stratigraphic horizon 2200–2250 m above the base of Abrahamskraal Formation, in the lower Moordenaars Member.

Range in the Laingsburg sector

The two specimens of *Styracocephalus* from the Laingsburg sector, BP/1/5428 and BP/1/5433, were both collected on the farm Rietfontein, in the Laingsburg district. They were recovered from an interval straddling the boundary of the Swaerskraal and Moordenaars members and can be stratigraphically constrained to an interval 1750–1900 m above the base of the Abrahamskraal Formation in this sector.

Range in the Fraserburg sector

Two specimens of *Styracocephalus* also originate in the Fraserburg sector and were also both found in the same stratigraphic interval. SAM-PK-K364, from the farm Leokraal in the Fraserburg district, and BP/1/7139, from the farm Celeryfontein in the same district, can be stratigraphically constrained to occur in the upper 100 m of the Abrahamskraal Formation or the lowest Poortjie Member in this sector.

Overall stratigraphic range

The stratigraphically lowest occurrence of *Styracocephalus* is SAM-PK-9346 from the Leeu-Gamka sector, which has a broad potential stratigraphic provenance but occurs no higher than the SI 2050–2100 m above the base of the Abrahamskraal Formation. This corresponds to the SI 2150–2200 m above the base of the Abrahamskraal Formation at its thickest point (Figure 32). The stratigraphically highest occurrence of the genus is BP/1/5485 from the Beaufort West sector, which was probably collected from the lower Poortjie Member; however, due to uncertainty in the

stratigraphy of this area and the fact *Styracocephalus* cannot be placed unequivocally in the Poortjie Member elsewhere, the specimen is considered to be constrained to the upper 50 m of the Abrahamskraal Formation or lower 50 m of the Poortjie Member.

The certain stratigraphic range of *Styracocephalus* therefore corresponds to an interval 2150–2575 m above the base of the Abrahamskraal Formation at its thickest point, equivalent to the Moordenaars and Karelskraal members. Its presence in the lower Teekloof Formation is probable but not beyond doubt.

5.6 Non-dicynodont Anomodonts

The Dicynodonts were a highly successful and diverse group of therapsids during the Middle Permian and, as such, they are discussed above. However, several basal genera are included along with the dicynodonts in the taxon Anomodontia. These basal anomodonts were once split between the South African dromasaurs and the Russian venyukovioideans (Watson and Romer 1956), each of which was considered monophyletic (e.g. Hopson and Barghusen 1986) but, after the discovery of *Patranomodon*, Rubidge and Hopson (1990) found both taxa to be paraphyletic. Conversely, Modesto and Rybczynski (2000) concluded that the Venyukovioidea were indeed monophyletic, a conclusion supported by Modesto *et al.* (1999) and all recent phylogenetic analyses (Angielczyk 2004; Fröbisch 2007; Kammerer *et al.* 2011; Modesto and Rubidge 2000).

Several genera of non-dicynodont anomodonts have been described from South Africa, mostly, and potentially all, from the Middle Permian. Given their rarity at higher stratigraphic levels and the number of genera present there, the Middle Permian part of the Beaufort Group provides crucial evidence for understanding the early evolution of anomodonts.

5.6.1 *Anomocephalus*

Anomocephalus is most recently described basal anomodont from South Africa and was considered to be the most primitive representative of the taxon (Modesto *et al.*

1999) until the re-description of the Chinese genus Biseridens as the most basal anomodont (Liu *et al.* 2010). This genus is only known from a single specimen, BP/1/5582, from the farm Vleikraal in the Fraserburg district (Fraserburg sector). The specimen was found approximately 90 m above the base of the Abrahamskraal Formation, 'on the upper surface of a laterally extensive sandstone package' (Modesto and Rubidge 2000:515) that probably represents the Kopjiesfontein Member (Figure 30). Based on the presence of *Diictodon* in the Kopjesfontein Member and the distance below the Poortjie Member of this same unit, this horizon is most likely at the lower end of *Diictodon*'s stratigraphic range. This would suggest the equivalence of this horizon with either the upper Swaerskraal Member or lower Moordenaars Member in the southern part of the basin, within the *Tapinocephalus* AZ (Figure 31).

5.6.2 *Galechirus*

Galechirus was described by Broom (1907) on the basis of two skulls from the Victoria West district and was placed taxonomically within 'Dromasauria'. It is now considered to represent a basal anomodont, after the 'Dromasauria' was found to be paraphyletic (Rubidge and Hopson 1990). The holotype, specimen SAM-PK-1068, is reasonably complete but until very recently most papers discussing anomodont phylogeny have ignored *Galechirus* on the basis that the preservation of the skull is poor (e.g. Modesto and Rubidge 2000; Liu *et al.* 2010). When *Galechirus* was included in cladistic analyses, it was placed as a stem group anomodont basal to *Galeops* and the Dicynodontia (Fröbisch and Reisz 2011). A third specimen has been referred to *Galechirus* and, in the absence of any definite opinion on the validity of the genus, the genus is considered valid here.

All that can be determined for the provenance of the original two specimens is that they was found somewhere 'in the neighbourhood of Victoria West' (Broom 1907:31). Kitching (1977) ascribed *Galechirus* to his *Cistecephalus* AZ, a diagnosis that was subsequently adopted by Rubidge and Hopson (1996) and Modesto and Rubidge (2000). In fact, they were probably collected in either the Abrahamskraal Formation or the Poortjie Member of the Teekloof Formation because the vast majority of the

Beaufort Group exposure in the vicinity of Victoria West is of these units. They are therefore almost certainly of Middle Permian age.

The third specimen, SAM-PK-11896, was found on the farm Welgemoed, close to Leeu-Gamka in the Beaufort West district (Leeu-Gamka sector). This constrains the stratigraphic position of this specimen to between 2100–2350 m above the base of the Abrahamskraal Formation in this sector (Figure 30). The genus is therefore certainly present in the *Tapinocephalus* AZ and possibly higher (Figure 31).

5.6.3 *Galeops*

Galeops whaitsi was erected by Broom (1912) for a partial skeleton from the farm La-de-da, west of Beaufort West. He assigned *Galeops* to the 'Dromasauria' and his description suggests he considered it to most resemble a therocephalian; in fact, he goes as far to state 'certainly the palate is not the least like that of an anomodont' (Broom 1912:861). According to the BFV database, the genus *Galeops* is now represented by more specimens than any other basal anomodont from South Africa (Nicolas 2007).

Of the former dromasaurs, *Galeops* is the only genus that has well defined cranial features and is considered to be a sister-taxon to the dicynodonts within the Anomodontia (Rubidge and Hopson 1990, 1996; Modesto and Rubidge 2000; Liu *et al.* 2010). The genus is monospecific and is represented by five specimens, the lowest three of which all come from Prince Albert district of the southern Koup (Leeu-Gamka sector). NMQR 3065 is the best constrained of these, occurring between 2100–2200 m above the base of the Abrahamskraal Formation on the farm Bloukrans (Figure 30). This interval is within the upper part of the Abrahamskraal Formation and corresponds to the mid-Moordenaars Member of the Formation at its thickest point (Figure 16). SAM-PK-K7630 was also found on Bloukrans but, not having exact coordinates, it can only be constrained to the upper third of the Abrahamskraal Formation, between 1600 m above its base and the base of the overlying Poortjie Member. The third of these specimens is SAM-PK-4005, erroneously written as SAM-PK4000 in Modesto and Rubidge (2000), which was

collected on the farm Jan Willemsfontein. This can be constrained to between 2000–2350 m above the base of the Abrahamskraal Formation, within the upper Swaerskraal Member or Moordenaars Member when correlated with the Formation at its thickest point.

SAM-PK-12261 was found on the farm Alfresco, in the Fraserburg district (Fraserburg sector). This must have been collected in the uppermost Abrahamskraal Formation or the lowest Poortjie Member because the farm straddles the boundary of the Abrahamskraal and Teekloof formations and the strata in this part of the basin are very flat. The holotype was collected on the farm La-de-da, on which is exposed approximately the upper 100 m of the Abrahamskraal Formation and the Poortjie Member of the Teekloof Formation. The definite range of *Galeops* is therefore restricted to the upper Moordenaars Member and the Karelskraal Member of the Abrahamskraal Formation, within the *Tapinocephalus* AZ (Figure 31).

5.6.4 *Galepus*

Galepus jouberti is not usually associated with the Middle Permian. It was described by Broom (1910) for a specimen discovered near Merriman railway siding in the Richmond district of the Northern Cape Province, which now resides in the collections of the American Museum of Natural History, AMNH 5541. This remains the only specimen referred to the genus. Phylogenetically it has been neglected in many analyses but the most recent work suggests it is basal to *Galeops* and the Dicynodontia, along with the genus *Galechirus* (Fröbisch and Reisz 2011).

The Merriman locality (previously Richmond Road) was assigned to the *Cistecephalus* Zone by Kitching (1977) and this designation has been followed by subsequent authors (e.g. Brinkman 1981; Fröbisch 2009; Rubidge and Hopson 1990, 1996); however, the *Cistecephalus* Zone of Kitching (1977) was stratigraphically more extensive than the *Cistecephalus* AZ as used today (Keyser and Smith 1977; Smith and Keyser 1995d; see 2.2). More importantly, the presence of the *Pristerognathus* AZ as far north as Philippolis indicates that it must present in the lowest Beaufort Group strata to the south-west of the Orange River, including to the north of Richmond (Figure 1). Although the area immediately surrounding Richmond has produced a

clearly *Cistecephalus* AZ fauna (Kitching 1977), the surface extent of the biozones to the north of Richmond is uncertain due to a lack of fossil material collected there. Therefore, it is likely that *Galepus* was recovered of rocks older than *Cistecephalus* AZ age and possible that it occurs in the *Pristerognathus* AZ.

5.6.5 *Patranomodon*

Patranomodon is known from a single specimen that was discovered in 1986, on the farm Combrinkskraal in the Prince Albert district (Leeu-Gamka sector). The holotype, NMQR 3000, was first described by Rubidge and Hopson (1990) with a more thorough description following a few years later (Rubidge and Hopson 1996). The former publication found *Patranomodon* to be the most basal anomodont at the time, inclusive of the Russian Venyukovioidea, but this was a short lived status due to the later discovery of the even more primitive *Anomocephalus* (Modesto *et al.* 1999) and later reconsideration of Biseridens (Liu *et al.* 2010).

This specimen was collected around 400 m above the base of the Abrahamskraal Formation and is therefore present in the middle Combrinkskraal Member in this sector (Figure 30). This is comfortably within the *Eodicynodon* AZ.

5.7 Dicynodonts

During the Middle Permian, dicynodonts were one of the most common groups of therapsids in South Africa. The taxonomy of dicynodonts from the *Tapinocephalus* AZ has undergone several revisions throughout the last century but initially a significant number of genera and species were described, especially species of *Dicynodon* (e.g. Boonstra 1948; Broili and Schroeder 1937; Broom 1948; Olson 1937; Owen 1876a). The widespread use of the generic name *Dicynodon* for specimens from the *Tapinocephalus* AZ was challenged by Cluver and Hotton (1981), who transferred many former species of *Dicynodon* to the genus *Diictodon*. The number of taxa was further reduced by King (1988), King and Rubidge (1993) and most recently Kammerer *et al.* (2011). King and Rubidge (1993) recognised only four clearly valid

genera of toothed dicynodonts from the lower three biozones; a fifth, *Brachyprosopus*, was tentatively considered valid despite the type specimen not being seen by the authors (King and Rubidge 1993).

Along with the genus *Diictodon*, which was reduced to a single species by King (1993), the taxonomic diversity of dicynodonts in the *Tapinocephalus* AZ was no more than six genera. More recently, taxonomic reviews have resurrected some genera and collecting has identified new ones (Modesto *et al.* 2002, 2003; Angielczyk *et al.* 2009; Angielczyk and Rubidge 2010, 2012), so the generic diversity of the *Tapinocephalus* AZ now stands at around ten, while the *Pristerognathus* AZ contains at least five genera (Table 3).

Apart from their taxonomic diversity, dicynodonts are relatively abundant in the Middle Permian part of the Beaufort Group, which makes them an important taxon in biostratigraphic studies. As early as 1960s, Boonstra (1969) had divided the *Tapinocephalus* AZ based at least partially on the abundance distribution of dicynodonts. Later, the *Eodicynodon* AZ was subsequently separated from the *Tapinocephalus* AZ based primarily on the presence there of the dicynodont genus *Eodicynodon* (Rubidge 1987, 1988). However, it has only recently been possible to propose that individual dicynodont genera can be used to subdivide the *Tapinocephalus* AZ (e.g. Angielczyk 2001, Rubidge and Angielczyk 2009). This is because, of all the therapsid taxa, the dicynodonts are probably the best understood thanks to the many recent publications on their taxonomy (e.g. King and Rubidge, 1993; Angielczyk and Sullivan, 2008; Kammerer, Angielczyk and Fröbisch, 2011; Angielczyk and Rubidge, 2012). Dicynodonts are therefore one of the most important components of the Middle Permian Beaufort fauna.

5.7.1 *Brachyprosopus*

Brachyprosopus broomi is the only species described for this genus, which was until recently represented by only a single specimen (FMNH 1561) in the collections of the Field Museum of Natural History, Chicago (Olson 1937). Little attention has been paid to this genus, although King and Rubidge (1993) recorded that the

holotype displayed features consistent with the genus *Robertia*. They also admit that it exhibited a potentially unique palatine morphology but they did not see the type specimen themselves. The validity of the genus was therefore uncertain. Most recently, two additional specimens of *Brachyprosopus* have been identified and the possibility has arisen that *Chelydontops* is a junior synonym of *Brachyprosopus* (Angielczyk in prep).

The holotype is reported as coming from the farm Hottentots Rivier, in the Beaufort West district of the Leeu-Gamka sector, which constrains its range only broadly to between the upper Abrahamskraal Formation and the Hoedemaker Member of the Teekloof Formation. However, the majority of the farm is on the low lying, flat ground of the northern Koup, where the upper Abrahamskraal Formation is exposed. It is therefore most likely that the specimen was recovered from a stratigraphic interval 2350–2450 m above the base of Abrahamskraal Formation in this sector, within the upper *Tapinocephalus* AZ (Figure 35).

A second specimen, SAM-PK-K7607, from the farm Rietfontein in the Beaufort West district, is tentatively identified as *Brachyprosopus* (Angielczyk pers. comm. 2012). This specimen is constrained to a similar stratigraphic interval to the holotype, 2350–2450 m above the base of the Abrahamskraal Formation in the Leeu-Gamka sector. This is less than 150 m the base of the overlying Teekloof Formation and is also within the upper *Tapinocephalus* AZ.

The third specimen identified as *Brachyprosopus* is BP/1/6071, from the farm Van Rooyenskraal in the Aberdeen district of the Eastern Cape (Angielczyk pers. comm. 2012). This specimen was found immediately above the first maroon mudstone in that part of the basin, between 450–500 m above the base of the Koonap Formation (Rubidge pers. comm. 2012). Because the locality is situated to the east of Willowmore, the stratigraphy at this locality is assumed to most resemble that recorded in the stratigraphic succession at Klipplaat (4.1.3.1). This brings the stratigraphic range of *Brachyprosopus* down into the lower Koonap Formation, which may correspond to a similar stratigraphic horizon in the Abrahamskraal Formation to the west (see 6.2).

The overall stratigraphic range of *Brachyprosopus* extends from the lower Abrahamskraal Formation, perhaps within the *Eodicynodon* AZ, up to the Karelskraal Member of the Abrahamskraal Formation at its thickest point (Figure 36).

5.7.2 *Chelydontops*

This rare genus was erected by Cluver (1975) for two specimens in the collections of the South African Museum. The genus was accepted by King (1988) but not mentioned by King and Rubidge (1993). It is possible that *Chelydontops* is in fact a junior synonym of the equally rare genus *Brachyprosopus* (Angielczyk in prep) but, currently, three specimens have been securely attributed to *Chelydontops*.

The holotype, SAM-PK-11558, was found on the farm Die Cyfer in the Beaufort West district, Leeu-Gamka sector, exposed on which are strata between 2250 m and 2400 m above the base of the Abrahamskraal Formation. This interval is 100–250 m below the base of the Teekloof Formation in this sector and constrains the SAM-PK-11558 to the upper *Tapinocephalus* AZ (Figure 35). A referred specimen, SAM-PK-12259, was collected on the farm Beukesplaas, in the Fraserburg district, and is therefore constrained to either the uppermost Abrahamskraal Formation or the lowest Poortjie Member. A third specimen, SAM-PK-K7604, from the farm Mynhartskraal near Beaufort West, has been tentatively re-identified as *Chelydontops* (Angielczyk pers. comm. 2012). The stratigraphic interval exposed on this farm is between 50–150 m below the base of the Teekloof Formation and therefore SAM-PK-K7604 also occurs in the upper *Tapinocephalus* AZ. The certain stratigraphic range of *Chelydontops* corresponds to an interval of the Abrahamskraal Formation, 50–150 m below the base of the Teekloof Formation (Figure 36).

5.7.3 *Colobodectes*

The genus *Colobodectes* was described in 2003 for a specimen collected in the Northern Cape Province, near the town of Williston (Modesto *et al.* 2003). Its only species, *E. cluveri*, is now represented by five securely identified specimens, all from

the west and north-western part study area where its stratigraphic range remained uncertain (Angielczyk and Rubidge 2009).

Range in the Sutherland sector

A single securely identified specimen, BP/1/5580, comes from the farm Keerom, at the top of Ouberg Pass, Northern Cape Province. This is the stratigraphically lowest occurrence of *Colobodectes*, as the top of the escarpment here is correlated with the basal Koornplaats Member (Cole and Wipplinger 2001) and is situated 560 m above base of the Abrahamskraal Formation (Figure 35).

Range in the Fraserburg sector

The two specimens of *Colobodectes* recovered from this sector are NMQR 3329 from the farm Vleikraal and BP/1/5584 from the farm Kruidfontein, both in the Fraserburg district. Both specimens were found close to the base of the Abrahamskraal Formation, occurring within the Kopjesfontein Member of Cole and Wipplinger (2001).

Range in the Victoria West sector

Two specimens of *Colobodectes* occur in the eastern Nuweveld and were also found close to the Ecca-Beaufort boundary. BP/1/5737 was collected on the farm Bastersfontein, in what is probably strata of the upper Davidskolk Member or those just above it. Further east, the second specimen of *Colobodectes*, NMQR 3627, is the easternmost *Tapinocephalus* AZ fossil retrieved in the Northern Cape Province. It was collected on the farm Allemansdam in the Richmond district, also close to the Ecca-Beaufort contact. The presence of the Abrahamskraal Formation this far east is uncertain, as the Formation is very thin in this region (see 4.1.1.2) but this specimen certainly occurs close to the base of the Teekloof Formation.

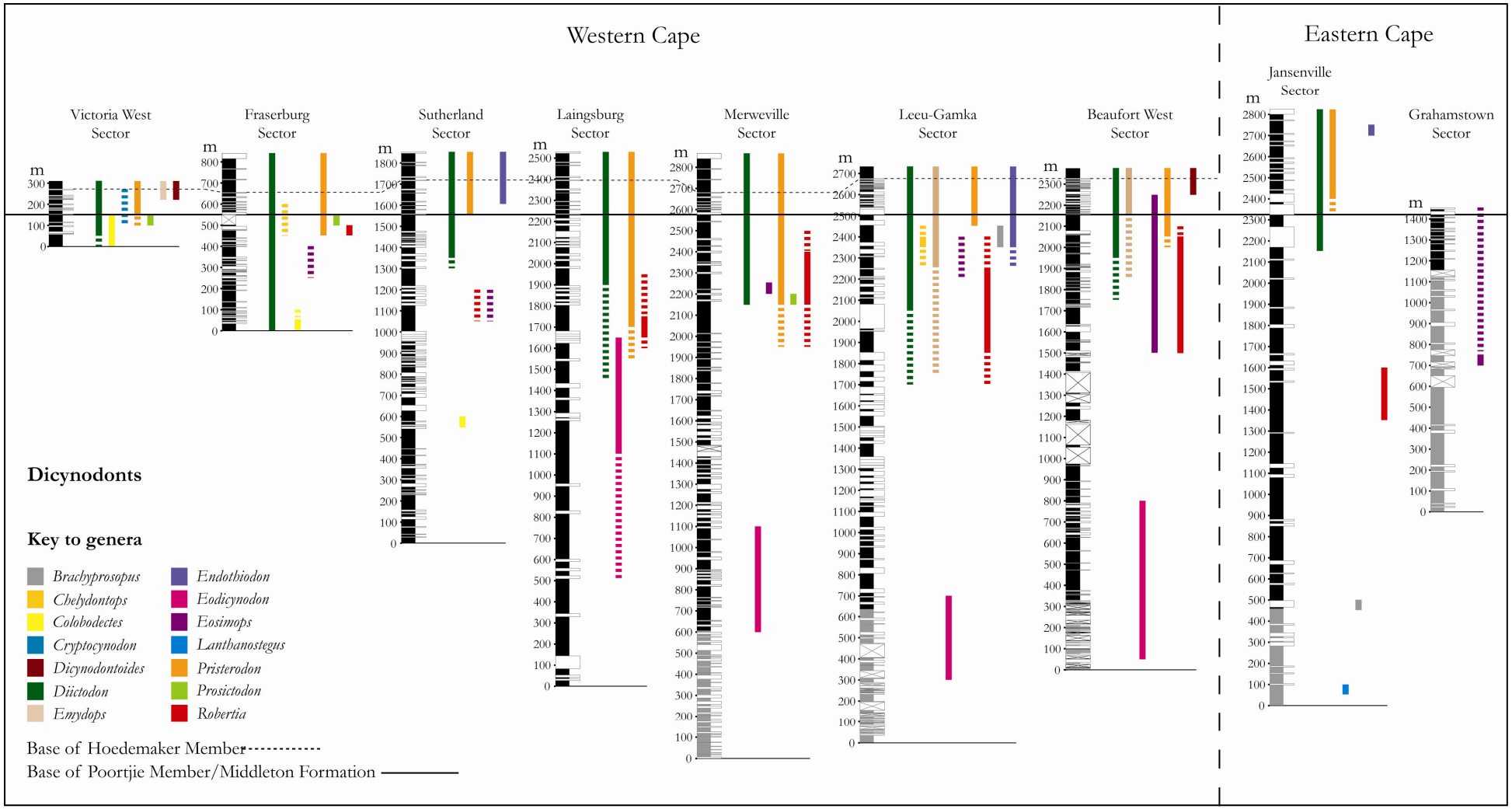


Figure 37. Stratigraphic ranges of dicynodont genera in each of the sectors in which they occur.

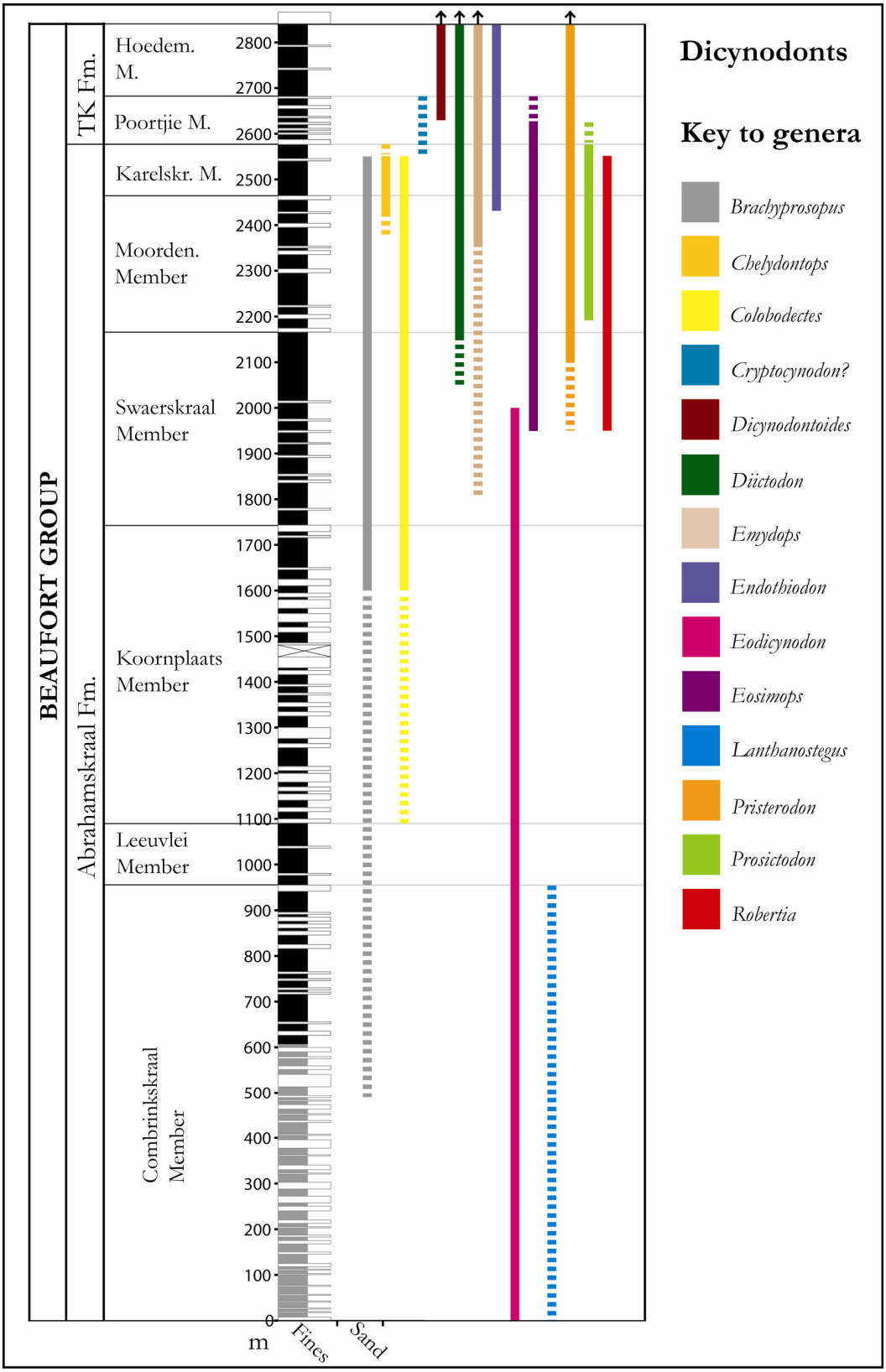


Figure 38. Composite stratigraphic ranges of dicynodont genera in the Middle Permian Beaufort Group.

Overall stratigraphic range

As noted by Angielczyk and Rubidge (2009), all the material of *Colobodectes* is restricted to the west and north-west of the Karoo Basin. The stratigraphically lowest occurrence is BP/1/5580 from Ouberg Pass in the Sutherland sector, which can be constrained to the lateral equivalent of the Koornplaats Member of the Abrahamskraal Formation, 560 m above its base in this sector. However, the distance below the base of the Teekloof Formation at which this specimen occurs equates with an upper Koornplaats Member horizon in Abrahamskraal Formation at its thickest point.

Colobodectes has also been found in the Kopjesfontein Member in the Fraserburg sector, just above the base of the Abrahamskraal Formation. Because *Diictodon* occurs in the same horizon in this area (see 5.1.3), this specimen can be constrained to within the stratigraphic range of *Diictodon* and is probably equivalent to the lower Moordenaars Member in the south of the basin.

The stratigraphically highest specimen is NMQR 3627 from the farm Allemansdam, which was most likely collected from the uppermost Abrahamskraal Formation. The composite stratigraphic range of *Colobodectes* is therefore tentatively restricted to the upper half of the Abrahamskraal Formation, between the base of the Koornplaats Member and the base of the Teekloof Formation (Figure 36).

5.7.4 *Cryptocynodon*

This genus is was first described as *Cryptocynodon simus* by Seeley (1895) for a specimen in the collections of the Natural History Museum in London, NHMUK R2582, which was collected at Molteno Pass near Beaufort West. Two further species, *C. parringtoni* (Von Huene 1942) and *C. schroederi* (Janensch 1952), were later described but the validity of the genus was questioned by King (1988), who referred *C. parringtoni* to the genus *Pristerodon*. King (1988) had tentatively agreed with Broom (1905) that the holotype of *Cryptocynodon* was in fact a juvenile *Endothiodon*; however, it was only later that *Cryptocynodon* was formally recognised as a junior synonym of *E.*

uniseries, with the exception that the species *C. schroederi* was subsumed into *Pristerodon* (King and Rubidge 1993).

Cryptocynodon is therefore currently considered invalid; however, specimen SAM-PK-K4534, previously referred to *Pristerodon*, may share some similarities with the holotype of *Cryptocynodon simus* (Angielczyk pers. comm. 2012). This specimen was recovered from Skietkop on the farm Meltonwold, Victoria West district, and straddles the boundary of the Abrahamskraal and Teekloof formations. Pending the re-evaluation of this genus, *Cryptocynodon* may have its first appearance in the Middle Permian (Figure 36).

5.7.5 *Dicynodontoides*

Dicynodontoides is another genus that has received recent attention (Angielczyk *et al.* 2009). It was first described as the species *D. parringtoni* for specimen RC 45, collected from near Bethesda Road in the Graaff-Reinet district, Eastern Cape Province (Broom 1940). This remained the only specimen of the genus for many years, although Cluver and Hotton (1981) and Cluver and King (1983) observed the similarities between the holotypes of *Dicynodontoides* and *Kingoria*. King (1988) refrained synonymising the two genera on the basis that RC 45 was insufficiently prepared but stated that a review of the two genera was needed.

Meanwhile, seven species of *Kingoria* had been recognised, based on the genotype from Tanzania, *K. nowacki* (Cox 1959). One of these species was represented by a specimen that had originally been described by Owen (1876a) as *Dicynodon recurvidens* and had subsequently been transferred to *Daptocephalus* by Van Hoepen (1934) before being recognised as a species of *Kingoria* (Cluver and Hotten 1981).

Angielczyk *et al.* (2009), taking the advice of King (1988), reviewed both *Kingoria* and *Dicynodontoides*; this led them to propose that all South African material represented a single species, *Dicynodontoides recurvidens*, with all previously named species being either junior synonyms of this, *nomina dubia*, or referable to other existing genera.

In their review, Angielczyk *et al.* (2009) went on to record the first appearance of *Dicynodontoides* in the upper *Pristerognathus* AZ. This was based on specimen SAM-PK-

K7641, which was collected from the Teekloof Formation on the farm La-de-da, just west of Beaufort West. Another specimen, CGS M600, from the farm Snydersfontein in the Beaufort West district, Victoria West sector, is tentatively identified as *Dicynodontoides* on the BFV database and was collected from the upper Poortjie Member. This may represent a second specimen of this genus in the latest Middle Permian.

5.7.6 *Diictodon*

One of the most successful and long ranging dicynodonts of the Permian, *Diictodon* has its first appearance in the Middle Permian *Tapinocephalus* AZ and survives until the end of the Permian where it was a victim of the Permo-Triassic Mass Extinction (Kitching 1995; Smith and Keyser 1995a; Smith and Ward 2001). Of all *Tapinocephalus* AZ dicynodonts, more specimens have been attributed to *Diictodon* than any other.

The first description of the genus *Diictodon* was that of *Diictodon galeops* (Broom 1913). Over the subsequent decades numerous other species of dicynodonts, especially of *Dicynodon*, were erected for small toothless forms that occurred throughout the lower Beaufort Group (e.g. Broom 1912, 1913, 1935; Broili and Schroeder 1937; Von Huene 1931; Boonstra 1948). Subsequently, when Cluver and Hotton (1981) reviewed the genus *Dicynodon*, they found that the majority of these small species were in fact referable to the genus *Diictodon*. One of these species was the former *Dicynodon* (now *Diictodon*) *feliceps*, which had originally been described by Owen (1876a) for a specimen in the collections of the British Museum. As Cluver and Hotton (1981) had retained most of the species that had been referred to *Diictodon*, the genus was considered to be speciose for the next decade (e.g. King 1988) but, more recently, the various species of *Diictodon* have all been synonymised with *Diictodon feliceps* (King, 1993; Sullivan and Reisz 2003; Angielczyk and Sullivan 2008).

Stratigraphically, *Diictodon* is best known from the *Pristerognathus*, *Tropidostoma* and *Cistecephalus* Assemblage Zones, but it is in the *Pristerognathus* AZ that it is the most dominant, representing up to 80 % of fossils recovered (Smith *et al.* 2012). Like *Robertia* and *Eodicynodon*, *Diictodon* has been considered as an important

biostratigraphic indicator species due to its abundance and first appearance in the upper *Tapinocephalus* AZ, approximately 1900 m above the base of the Abrahamskraal Formation (Rubidge and Angielczyk 2009). Because *Diictodon* occurs in the late Permian, only its stratigraphically lowest occurrences are of significance here.

Range in the Beaufort West sector

The eastern Koup has provided a large number of *Diictodon* specimens, second in number only to the Victoria West sector; over 100 specimens have been recovered in the Beaufort West sector, mostly confined to the very top of the Abrahamskraal Formation. Most of these specimens are now in the collections of the South African Museum, Cape Town, and were not given precise provenance information. Many can be constrained only to 200 m intervals or more. However, this is sufficient to identify a first appearance in the upper part of the Abrahamskraal Formation.

The stratigraphically lowest specimens are SAM-PK-K7638 and SAM-PK-K7898, constrained to occur 1750–2000 m above the base of the Abrahamskraal Formation, followed by SAM-PK-11850, SAM-PK-11851, SAM-PK-11852, SAM-PK-11855 and SAM-PK-11865 that are constrained to 1850–2050 m. The lowest occurrence of *Diictodon* in the Beaufort West sector is therefore 1950–2000 m above the base of the Abrahamskraal Formation, within the upper part of the Moordenaars Member (Figure 35).

Range in the Leeu-Gamka sector

In the Leeu-Gamka sector, the first appearance of *Diictodon* is lower in the Abrahamskraal Formation than to the east. Eighty-seven specimens were recorded from this sector, of which three (SAM-PK-2755, TM 361 and TM 1549) are constrained to the SI 1700–2100 m above the base of the Abrahamskraal Formation. This is broad enough to be uncertain but the stratigraphically lowest occurrence of *Diictodon* is constrained to 2050–2100 m above the base of the Abrahamskraal Formation.

Range in the Merweville sector

In this sector, the stratigraphically lowest specimens with narrow potential ranges occur 2150–2200 m above the base of the Abrahamskraal Formation and at least ten specimens can be constrained to this interval. This would suggest the first appearance of *Diictodon* at the base of the Moordenaars Member or within the uppermost Swaerksraal Member in this sector.

Range in Laingsburg sector

There is relatively little *Diictodon* material in the Laingsburg sector when compared to further east. The stratigraphically lowest specimens that are tentatively referred to *Diictodon* are SAM-PK-12035 and BP/1/4852 from Schoppelmaaikraal, Laingsburg district, which occurs no higher than the SI 1700–1750 m above the base of the Abrahamskraal Formation. Another specimen, BP/1/5410, has a similar range stratigraphic provenance but is also only tentatively identified as *Diictodon*. Although no specimens from this sector have had their identifications confirmed recently, the next stratigraphically lowest specimens occur no lower than 1900–1950 m above the base of the Abrahamskraal Formation, in the lower Moordenaars Member.

Range in the Sutherland sector

Half the *Diictodon* material in this sector was collected during one fieldtrip in the same stratigraphic interval. This extends between 1300 m and 1400 m above the base of the Abrahamskraal Formation in this sector, being within the Moordenaars Member, as extrapolated from the Laingsburg sector.

Range in the Fraserburg sector

The numerous specimens of *Diictodon* that have been collected in this sector are mostly distributed throughout the uppermost Abrahamskraal Formation and lower Teekloof Formation, but one specimen is conspicuously low. SAM-PK-K5838 was

recovered from near the Ecca-Beaufort boundary in the north-west of the sector, therefore being within or below the Kopjesfontein Member of Cole and Wipplinger (2001; Figure 25). This specimen is of particular significance for biostratigraphic correlation with the south of the basin.

Range in the Victoria West sector

The Abrahamskraal Formation becomes very thin this far northeast so, of the vast number of *Diictodon* specimens collected in this sector, most were collected from the lower Teekloof Formation. However, the lowest specimen is BP/1/4167 from the farm Booyskraal, Victoria West district, which occurs only up to 100 m above the Ecca-Beaufort boundary in the northwest of the sector. This places it between the Davidskolk Member and Loxton Member.

Range in the Jansenville sector

In the east, specimens of *Diictodon* are found in the upper Koonap Formation, with the majority collected in a single area, at the very top of the Formation. The stratigraphically lowest specimen is BP/1/7066, which can be constrained to the SI 2250–2300 m above the base of the Koonap Formation.

Overall stratigraphic range

In the south of the basin, *Diictodon* has its stratigraphically lowest appearance in the lower Moordenaars Member in the Merweville sector and at a similar level in the Leeu-Gamka sector. It may potentially appear lower, in the Swaerskraal or upper Koornplaats Member, if specimens SAM-PK-12035 and BP/1/4852 from the Laingsburg sector do in fact represent the genus. In the Fraserburg sector, *Diictodon* is found immediately above the base of the Abrahamskraal Formation, which is also potentially its lowest occurrence (Figure 35). In the Eastern Cape, few specimens of *Diictodon* have been recovered from the Middle Permian but the stratigraphically lowest are constrained to the uppermost Koonap Formation. At this time, first

certain appearance of *Diictodon* can placed only at the base of the Moordenaars Member, in the SI 2150–2200 m above the base of the Abrahamskraal Formation at its thickest point (Figure 36).

Throughout the Moordenaars Member, *Diictodon* is the most common dicynodont but is relatively less abundant relative to the vast numbers of specimens recorded in Poortjie Member. It is only in the upper Karelskraal Member that its numbers increase exponentially (Figure 37).

5.7.7 *Emydops*

The genus *Emydops minor* was erected by Broom (1912) for a specimen that now resides in the collections of the American Museum of Natural History. Several further species of *Emydops* were described over the succeeding fifty years (Broom 1913, 1921; Broom and Haughton 1917; Toerien 1953) so that King (1988), in her review of the dicynodonts, recognised at least eleven species of *Emydops*. Keyser (1993) conducted a review of small 'endothiodontid' dicynodonts, including the genus *Emydops*, in which he declared several species to be junior synonyms of *Pristerodon mackayi* and erecting the genus *Emydoses* for others; only *Emydops platyceps* and a new taxon, *E. tener*, were considered valid. This conclusion has been disputed (Angielczyk and Kurkin 2003b; Angielczyk *et al.* 2005; Ray 2001) and, most recently, Fröbisch and Reisz (2008) recognised two valid species of *Emydops*, *E. arctatus* and the new species *E. oweni*. *E. arctatus* is the senior specific name for the genus (Owen 1876a; Broom 1913) and comprises the majority of *Emydops* specimens, while a new species, *E. oweni*, was erected for specimen SAM-PK-3721.

Seventeen specimens of *Emydops* are currently known from the Middle Permian and are therefore pertinent to this project (Nicolas 2007). Recent work has securely identified two of these specimens as *Emydops* (Angielczyk *et al.* 2005; Kammerer *et al.* 2011) and seven specimens overall are now confirmed from these strata (Angielczyk pers. comm. 2012). Stratigraphically, *Emydops* was considered to have its first appearance in the *Tropidostoma* AZ (Smith and Keyser 1995c) and, more recently, in the *Pristerognathus* AZ (Angielczyk *et al.* 2005; Smith *et al.* 2012); however, the

potential presence of *Emydops* in the *Tapinocephalus* AZ has been suggested (Angielczyk *et al.* 2005; Kammerer *et al.* 2011).

Range in the Beaufort West sector

Two of the *Emydops* specimens constrained to the Middle Permian were certainly recovered in the eastern Koup. Both of these, SAM-PK-K6515 and SAM-PK-K6522, were collected on the farm Putfontein, which sits astride the boundary of the Abrahamskraal and Teekloof formations. Both specimens were allegedly found within the upper Poortjie Member (Smith pers. comm. 2012; Figure 35).

A third specimen, SAM-PK-708, is recorded only as coming from the 'Gouph' in the magisterial district of Beaufort West. Its potential collection locality has been suggested to encompass an area within the Beaufort West sector and therefore its stratigraphic provenance was constrained to the upper Abrahamskraal Formation or to the Poortjie Member of the Teekloof Formation (Angielczyk *et al.* 2005). This deduction is accepted here.

Range in the Merweville sector

In the Merweville sector, one specimen, SAM-PK-640, was recently identified to represent the genus *Emydops* (Kammerer *et al.* 2011). SAM-PK-640 was collected on the farm Goeiemoed, Prince Albert district, which lies close to the southern boundary of the basin where the steep northward dip exposes older strata. The specimen can therefore be constrained only to a broad stratigraphic interval extending from 1750 m to 2300 m above the base of the Abrahamskraal Formation in this sector. This would indicate that SAM-PK-640 occurs no higher stratigraphically than the mid-Moordenaars Member. This position is uncertain as the Poortjie Member is mapped on the nearby Elandsberg, but the fossil is certainly restricted to the Abrahamskraal Formation.

Range in the Victoria West sector

Thirteen specimens of *Emydops* that are potentially of Middle Permian age have been collected from the Victoria West sector. All occur, either certainly or potentially, in the upper Poortjie Member of the Teekloof Formation.

Overall stratigraphic range

The presence of *Emydops* within the *Tapinocephalus* AZ is confirmed by SAM-PK-640 from the farm Goeiemoed in the Merweville sector, which represents its stratigraphically lowest occurrence. This may be supported by SAM-PK-708 from the Beaufort West sector but the first appearance of *Emydops* cannot be precisely delineated; it can only be calculated to be no higher than the mid-Moordenaars Member of the Abrahamskraal Formation (Figure 36).

Emydops is certainly present in the upper Poortjie Member, as evidenced by specimens SAM-PK-K6515 and SAM-PK-K6522 from the Beaufort West sector and several specimens from the Victoria West sector. Below the upper Poortjie Member, *Emydops* is a rare constituent of the Middle Permian fauna.

5.7.8 *Endothiodon*

Endothiodon was one of the first described dicynodont genera and today is best known from the *Tropidostoma* AZ (Smith and Keyser 1995c; Smith *et al.* 2012). Its taxonomy is in need of review but three South African species are currently recognised. The genotype, specimen NHMUK R1646, was described by Owen (1876a) as *E. bathystoma* and two further species were later described, *E. whaitsi* (Broom 1912) and *E. uniseries* (Cox 1964). Both Cox (1964) and King (1988) considered that all three species were valid, although the former recorded that the differentiation between them was based on size alone. More recently, Fröbisch (2009) has suggested that the differences in size reflect an ontogenetic series and that only one species, *E. bathystoma*, is valid; however, in the absence of a thorough review of the genus, Fröbisch tentatively retained all three genera. He illustrated *E. uniseries* to extend from

the *Pristerognathus* AZ to the *Cistecephalus* AZ, probably after Rubidge (ed. 1995), while restricting the other two species to the *Tropidostoma* AZ. The Middle Permian representatives of *Endothiodon* are therefore considered to be *E. uniseries*, although future work may lead to the recognition of a monospecific *Endothiodon bathystoma*.

Smith and Keyser (1995b) suggest the presence of *Endothiodon* in the Middle Permian upper *Pristerognathus* AZ. Several specimens identified as *Endothiodon* in the collections of the Council for Geoscience, namely CGS M407, M408 and M409, were collected on the farm Driekop, Beaufort West district, Victoria West sector, and can be constrained to occur in the Poortjie Member or lowest Hoedemaker Member. Another two, as yet un-catalogued specimens (field numbers 12/2/A3 and 12/2/C1) are held at the BPI and were found within the middle Poortjie Member on the farm Uitvlug, Sutherland district, Northern Cape Province (Figure 35).

Two specimens of *Endothiodon* are in fact recorded from the *Tapinocephalus* AZ. SAM-PK-628 and SAM-PK-629 were both found on the farm Spes Bona in the northern Koup, Leeu-Gamka sector, and the latter specimen has recently been confirmed as *Endothiodon* (Angielczyk pers. comm. 2012). This brings the first appearance of *Endothiodon* down much lower stratigraphically than previously acknowledged, into the upper Abrahamskraal Formation, although the genus certainly remains rare until the upper *Pristerognathus* AZ (Figure 36; Figure 37).

5.5.20 *Eodicynodon*

Eodicynodon is the most basal dicynodont in the Beaufort Group and is one of the most useful biostratigraphically as it is the most common taxon in the relatively unfossiliferous *Eodicynodon* AZ. It was first described by Barry (1974) and at the time was thought to occur in the upper Ecca Group. When it was later revealed that these rocks belonged to a sub-aerial facies association, and therefore to the Beaufort Group, *Eodicynodon* became the index taxon for the *Eodicynodon* AZ (Rubidge 1987, 1988).

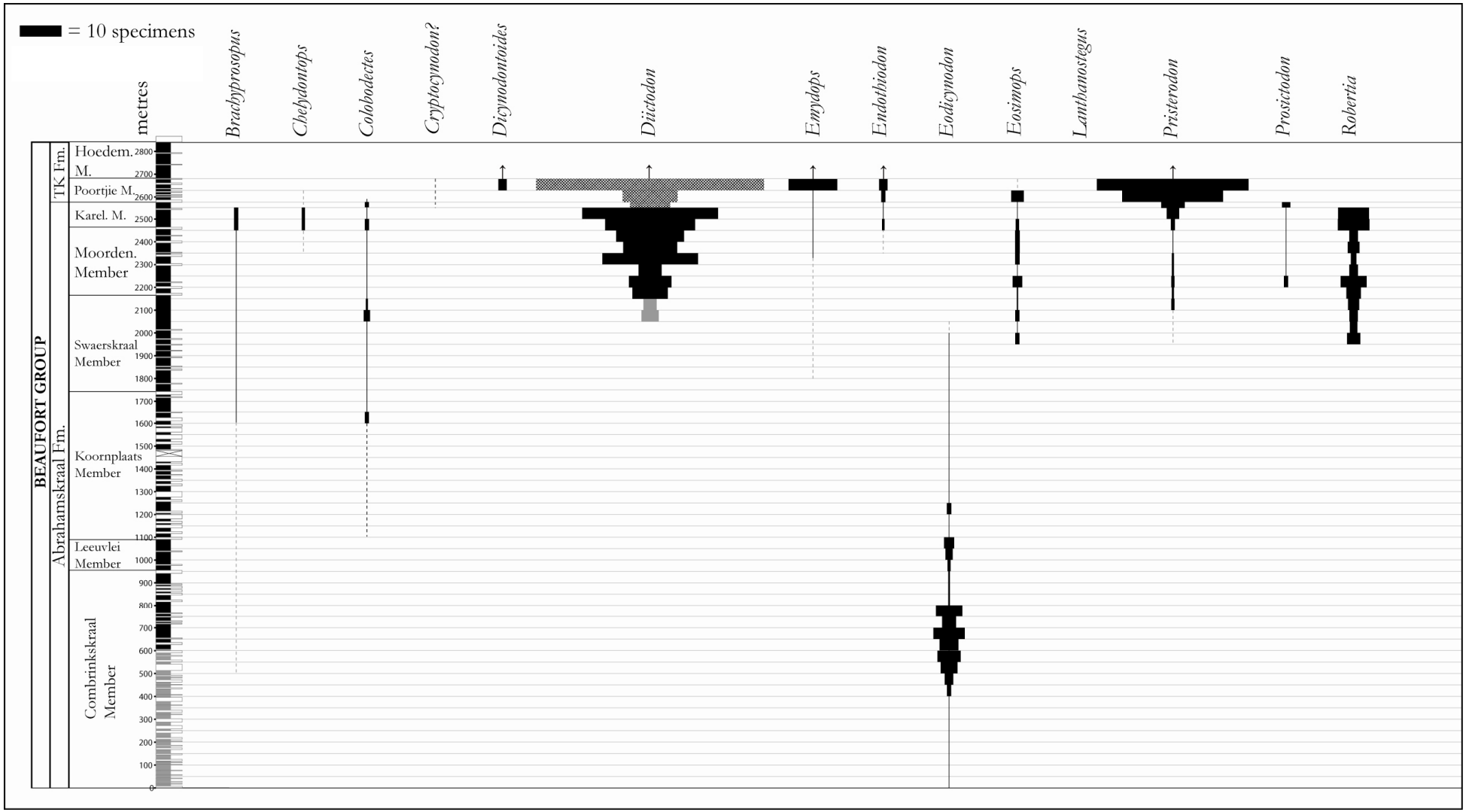


Figure 39. Abundance of dicynodont genera through the Middle Permian Beaufort Group. Black = abundance within the certain stratigraphic range of the genus, Grey = abundance values outside of certain stratigraphic range. The abundance of *Diictodon* in the upper three SIs is reduced by a factor of 10 due to the great number of specimens in these horizons.

The genus currently comprises two species, *Eodicynodon oosthuizeni* (Barry 1974) and *E. oelofseni* (Rubidge 1990b), both of which are found only in the lowest Beaufort Group in the south-west of the Karoo Basin; however, the second species, *E. oelofseni,* may represent a new, as yet undescribed genus, as the two species do not form a monophylum (Modesto *et al.* 2003). Accordingly, and because *E. oelofseni* is represented by only a single specimen, all references to *Eodicynodon* without species modifier henceforth refer exclusively to the species *E. oosthuizeni*.

Eodicynodon is currently considered to be restricted to the *Eodicynodon* AZ, in the lower 1100 m of the Abrahamskraal Formation, and have a stratigraphic range exclusive of advanced dinocephalians (Jinnah and Rubidge 2007; Rubidge and Angielczyk 2008; ed. Rubidge 1995).

Range in the Beaufort West Sector

Thirty two specimens of *Eodicynodon* are listed on the BFV database (Nicolas 2007) whose localities fall within this sector, excluding NMQR 2913 (the holotype of *E. oelofseni*). All occur in the lower 800 m of the Abrahamskraal Formation, with the highest well constrained specimen (NMQR 3026) being approximately 800m above its base (Figure 35). Most specimens are clustered between 100–350 m above the base of the Abrahamskraal Formation but this may well be due to collecting bias as Rubidge, who collected most of the specimens, was primarily concerned with strata below the first purple mudstone (Figure 36). The stratigraphically lowest specimens occur within 100 m of the boundary between the Beaufort and Ecca Groups, which indicates that *Eodicynodon* is restricted to the Combrinkskraal Member in this sector but occurs throughout it. Specimen NMQR 2913, and hence all known material of *E. oelofseni*, was found in the lowest 100 m of the Abrahamskraal Formation in this sector.

Range in the Leeu-Gamka Sector

Six specimens of *Eodicynodon* were recorded on the BFV database within this sector, but only five were of stratigraphic value. They occur between 300–700 m above the

base of the Abrahamskraal Formation: NMQR 3157 is the lowest and is constrained to 300–350 m, while NMQR 2998 and BP/1/5577 are the highest, constrained to occur in the SI 650–700 m above the base of the Formation. All specimens are therefore found within the upper half of the Combrinkskraal Member in this sector.

Range in the Merweville Sector

Three specimens of *Eodicynodon* occur in this sector and they have well documented stratigraphic positions: NMQR 2992 is the lowest between 600–650 m and BP/1/6230 the highest, between 1050–1100 m above the Ecca-Beaufort boundary (Jinnah and Rubidge 2007). Though the specimen number is low, the range clearly corresponds to the upper Combrinkskraal Member and the Leeuvlei Member.

Range in the Laingsburg sector

In the Laingsburg sector, only two specimens of *Eodicynodon* are known. The stratigraphic provenance of the first, BP/1/5575, is not well constrained but is restricted to the Combrinkskraal Member or perhaps the Leeuvlei Member. The second specimen is SAM-PK-11879, which can be constrained to between 1600–1700 m above the base of the Abrahamskraal Formation, corresponding to the upper Koornplaats Member. This makes SAM-PK-11879 the highest known specimen of *Eodicynodon*.

Overall stratigraphic range

Eodicynodon is most prevalent in the Combrinkskraal Member of the Abrahamskraal Formation (Figure 37). In the Beaufort West sector, where specimens of *Eodicynodon* are most numerous, the genus is only known from this unit. However, two specimens confirm its occurrence higher in the stratigraphy: BP1/6230, from the farm Bloukrantz, Prince Albert district, which occurs between 1050–1100 m above the base of the Abrahamskraal Formation and SAM-PK-11879 from the farm Dikbome, Laingsburg district, which occurs 1600–1700 m above the base of the

Formation within the upper Koornplaats Member. The stratigraphic range of *Eodicynodon* therefore extends at least as high as the SI 1950–2000 m above the base of the Abrahamskraal Formation at its thickest point (Figure 36).

The stratigraphically lowest specimens of *Eodicynodon* are found within 100 m of the Ecca-Beaufort boundary in the Beaufort West sector but, when the overall thickness of the Abrahamskraal Formation is taken into account, the lowest specimen may be NMQR 3157 from the farm Combrinkskraal, Prince Albert district. This specimen occurs in the SI 300–350 m above the base of the Formation (Figure 36).

In the composite section for the Abrahamskraal Formation at its thickest point, *E. oelofseni* (NMQR 2913) can be correlated with the mid-Combrinkskraal Member.

5.7.10 *Eosimops*

Eosimops newtoni was first described by Broom (1921) for a specimen found near Victoria West, Northern Cape Province. It remained monospecific and was represented by only a single specimen until the recent work of Angielczyk and Rubidge (2012), who recognised that several specimens attributed to *Robertia* in fact bore the characteristic feature of *Eosimops*. Several further specimens of *Eosimops* have since been collected or identified in existing South African collections.

The stratigraphically lowest appearance of *Eosimops* was reported by Angielczyk and Rubidge (2012) to occur in the mid-*Tapinocephalus* AZ, 1565 m above the base of the Abrahamskraal Formation in the Beaufort West sector, based on specimens from the farm Seekoegat, Prince Albert district. The stratigraphically highest specimens were reported as from the *Pristerognathus* AZ as exposed near Philippolis, Free State Province.

Range in the Beaufort West sector

Two specimens of *Eosimops* with good provenance data have been recovered from this sector. NMQR 3145 and NMQR 3139 were both collected on the farm Seekoegat and can be constrained to 1550–1600 m and 1650–1700 m above the base

of the Abrahamskraal Formation, respectively. The stratigraphic position of the lower specimen, NMQR 3145, corresponds to the uppermost Koornplaats Member and that of NMQR 3139 to the Swaerskraal Member in this sector (Figure 35). In the western Karoo, this is the stratigraphically lowest specimen of *Eosimops*, as already noted by Angielczyk and Rubidge (2012).

A further potential specimen of *Eosimops* resides in collections of the South African Museum and was found within the upper Poortjie Member on the farm Putfontein, Beaufort West district (Angielczyk, pers. comm. 2012). This specimen, SAM-PK-K10105, was previously described as *Diictodon* but displays the wide postorbital bar indicative of *Eosimops*. If this revised identification proves true, then it represents the first occurrence of *Eosimops* within the *Pristerognathus* AZ in the southwest of the basin.

Range in the Leeu-Gamka sector

The three *Eosimops* specimens recovered from this sector occur slightly higher stratigraphically than those at Seekoegat. All three (SAM-PK-K296 from the farm Vlakkraal and BP/1/1779 and BP/1/1780 from the farm Stinkfontein) occur in the Abrahamskraal Formation and can be constrained to an interval 2200–2400 m above its base.

Range in the Merweville sector

The two specimens of *Eosimops* from this sector, BP/1/7039 and BP/1/7041, were found on the farm Ongeluksfontein 261, Beaufort West district, within an horizon 2200–2250 m above the base of the Abrahamskraal Formation. This is securely within the lower Moordenaars Member in this sector.

Range in the Fraserburg Member

One specimen, BP/1/6989, has been found in the north of the escarpment in the southwest of the basin. It was discovered on the farm Baviaansdrif, Sutherland district, and occurs within the mid-Abrahamskraal Formation in this sector, either within the Davidskolk Member or slightly above.

Range in the Grahamstown sector

Two potential specimens of *Eosimops* have been found in the far eastern sector of the basin. The first, BP/1/7059, is tentatively assigned to *Eosimops* and was collected on the farm Peninsular, Albany district, in the mid-Koonap Formation. It can be constrained to the SI 700–750 m above the base of the Koonap Formation. The second specimen, BP/1/6688, was found on the farm Windsor, Albany district, between 150 m and 250 m above the base of the Middleton Formation. This latter specimen is poorly preserved, however, and can at best be identified as either *Eosimops* or *Robertia* (Angielczyk pers. comm. 2011).

Range in the Philippolis sector

Several specimens of *Eosimops* were retrieved from immediately above the Ecca-Beaufort boundary in the Philippolis district, Free State Province. These include one of the best preserved specimens, BP/1/6674, from which the postcranial skeleton of *Eosimops* is known (Angielczyk and Rubidge 2012). The lithostratigraphic provenance of these specimens is uncertain but is within the *Pristerognathus* AZ (Welman *et al.* 2001).

Overall stratigraphic range

Eight securely identified specimens of *Eosimops* are known from the south-western part of the basin, with a further three in east. Of the western specimens, all are confined to the upper Abrahamskraal Formation. The stratigraphically lowest is

NMQR 3145, which occurs within the upper Koornplaats Member in the Beaufort West sector. This is equivalent to the mid-Swaerskraal Member of the Abrahamskraal Formation at its thickest point, in the SI 1950–2000 m above its base (Figure 36). The stratigraphically highest securely identified specimens in the southwest of the basin are those from the Leeu-Gamka sector. They occur no lower than the SI 2200–2250 m above the base of the Abrahamskraal Formation, equivalent to the 2300–2350 m above the base of the Formation at its thickest point.

However, the stratigraphic range of *Eosimops* does extend up into the *Pristerognathus* AZ. In the eastern part of the basin, three securely identified specimens (NMQR 2505, BP/1/6673 and BP/1/6674) have been found in the *Pristerognathus* AZ at Philippolis and a fourth potential specimen has been recovered from the lower Middleton Formation in the Grahamstown sector. In addition, a potential specimen of *Eosimops*, SAM-PK-K10105, was found in the Poortjie Member in the Beaufort West sector.

Although fossils of *Eosimops* are geographically disparate, a composite range can be calculated. *Eosimops* therefore has a stratigraphic range that extends from mid-Swaerskraal Member of the Abrahamskraal Formation at its thickest point up to at least the lower Poortjie Member of the Teekloof Formation (Figure 36).

5.7.11 *Lanthanostegus*

Lanthanostegus mohoii was described only in 2002 and is unique among Middle Permian dicynodonts in that it is known exclusively from the eastern part of the Karoo Basin (Modesto *et al.* 2002). It is represented by only two specimens, NMQR 3396 and NMQR 3398, both of which were found in the lower 100 m of the Koonap Formation on the farm Mandalay, Jansenville district (Figure 35).

Because of the paucity of fossil material in this part of the basin, biostratigraphic correlations are uncertain, especially for base of the Koonap Formation. Further east, the *Eodicynodon* AZ is absent (Modesto *et al.* 2001b) but, in the Jansenville sector, its absence is uncertain. The occurrence of potentially advanced tapinocephalid dinocephalians in the lowest Koonap Formation and the lack of any *Eodicynodon*

material suggest that the *Tapinocephalus* AZ lies immediately above the Ecca group rocks in the Jansenville sector (Rubidge pers. comm. 2011). However, if the Koonap Formation is equivalent to the Abrahamskraal Formation and the base of the overlying Middleton Formation is roughly coeval with the base of the Poortjie Member (Day *et al.* 2013; Hill 1993), then the thickness of sediment in the Jansenville sector would suggest that either 1) the *Eodicynodon* AZ is present at Jansenville or 2) sedimentation was far more rapid in the eastern part of the basin (Figure 16).

The thickness of the Koonap Formation in the Jansenville sector is considered here to represent the stronger line of evidence and therefore an *Eodicynodon* AZ age tentatively accepted for *Lanthanostegus* (Figure 36).

5.7.12 *Pristerodon*

Pristerodon is one of the oldest described genera of Middle Permian dicynodont, having been originally erected by Huxley (1868) as the species *P. mackayi* for a specimen found near East London. King (1988) recognised several additional species for the genus, although all these were for '*Cistecephalus* Zone' specimens. It was later admitted that the majority of these species were based on insufficient characteristics and that the genus was probably monospecific (King and Rubidge 1993). Most recently, the monospecific *Pristerodon* has been upheld (Fröbisch 2009).

Smith and Keyser (1995a) refer to the presence of *Pristerodon* throughout the *Tapinocephalus* AZ as the species *P. brachyops* and in the *Pristerognathus* AZ as *P. mackayi*. However, the one specimen bearing this name *P. brachyops*, from an unknown locality in the upper *Tapinocephalus* or *Pristerognathus* AZ, has now been identified as *Emydops*. Several specimens referable to *Pristerodon* have been recovered from the Abrahamskraal Formation and these are considered to represent *P. mackayi*. Stratigraphically, Fröbisch (2008) shows the range of *Pristerodon mackayi* to extend down to the lower *Tapinocephalus* AZ.

Range in the Beaufort West sector

There is only one specimen of *Pristerodon* that is certainly occurs within the Abrahamskraal Formation in the eastern Koup. SAM-PK-K6537, from the farm Klein Koedoes Kop, can be constrained to 2000–2100 m above the base of the Abrahamskraal Formation. This interval corresponds to the upper Moordenaars Member (Figure 35). SAM-PK-K9997 occurs on the farm La-de-da near Beaufort West and can only constrained to the uppermost Abrahamskraal Formation the lower Poortjie Member of the Teekloof Formation.

Range in the Leeu-Gamka sector

Five specimens recovered from this sector have been identified as *Pristerodon*. The lower three were found on the farm Klipplaatsfontein 210, west of Beaufort West, and straddle the boundary between the Abrahamskraal and Teekloof formations. CGS RS423 can be constrained to the upper 50 m of the Abrahamskraal Formation, while CGS RS416 and CGS RS417 occur in the lowest Poortjie Member.

Range in Merweville sector

In the Merweville sector, three specimens can be confidently constrained to occur within the Abrahamskraal Formation, two of which are securely identified as *Pristerodon*. The lowest is BP/1/346, from Buffelsvlei, near Merweville, which occurs 1950–2200 m above the Ecca-Beaufort boundary in this sector. This specimen, now lost, was originally described as the holotype of *Brachyuraniscus merwevillensis* but was later transferred to *Pristerodon* (King and Rubidge 1993). The other securely identified specimen, BP/1/7091, was found on the farm Rondom, Beaufort West district, and is constrained to 2400–2450 m above the base of the Abrahamskraal Formation. If specimen BP/1/346 is acknowledged, *Pristerodon* is therefore present throughout the Moordenaars Member and potentially within the upper part of the Swaerskraal Member in the Merweville sector.

A further specimen, which is co numbered BP/1/1580 along with a specimen of *Anteosaurus*, is tentatively identified as *Pristerodon* (Angielczyk pers. comm. 2012) and was discovered on the farm Die Bad in the Beaufort West district. It can be constrained to 2150–2300 m above the base of the Abrahamskraal Formation, within the lower Moordenaars Member.

Range in the Laingsburg sector

There are only two specimens of *Pristerodon* that have been collected from the Laingsburg sector. SAM-PK-11933 from Schoppelmaaikraal in the Laingsburg district is securely identified and is constrained only to the interval 1550–1750 m above the base of the Abrahamskraal Formation as the locality encompasses a significant anticline (map sheet: Republic of South Africa 3220, Sutherland, 1:250 000 Geological Series 1983). Skoppelmaaikraal is also closer to the Wilgerbos stratigraphic section so this interval probably corresponds to the Koornplaats Member (Figure 17).

Specimen BP/1/5425 is tentatively assigned to *Pristerodon* and occurs slightly higher in the Abrahamskraal Formation, between 1650 m and 1950 m above the base of the Formation.

Range in the Sutherland sector

The four *Pristerodon* specimens from this sector occur on the farm Ou Tuin in the Sutherland district and are all constrained to the lower 50 m of the Poortjie Member of the Teekloof Formation.

Range in the Fraserburg sector

In the Fraserburg sector, six specimens of *Pristerodon* have been recorded. The lowest two are specimen BP/1/7148, from the farm Prinshof in the Sutherland district, and BP/1/7203, from the farm Baviaansdrif in the same district. Both occur between 50

m and 100 m below the base of the Poortjie Member and therefore no higher than the top of the Moordenaars Member in this sector.

Range in the Victoria West sector

While this sector has produced the greatest number of specimens attributed to *Pristerodon*, none can be placed unequivocally in the Abrahamskraal Formation. Several South African Museum specimens from the farm Meltonwold, Victoria West district (SAM-PK-K4510, SAM-PK-K5203, SAM-PK-K10003, SAM-PK-K10004), can be constrained only to the uppermost Abrahamskraal Formation or the lower Poortjie Member. Another South African Museum specimen from Meltonwold, SAM-PK-K4534, only tentatively represents *Pristerodon* and is constrained to either the upper Abrahamskraal Formation or Poortjie Member. Most specimens in the sector occur in the Teekloof Formation.

Range in the Jansenville sector

In the Jansenville sector, three specimens of *Pristerodon* have been recovered from Middle Permian strata, all of which occur within the Middleton Formation. BP/1/7126 from the farm Hilary in the Jansenville district is the stratigraphically lowest, and is constrained to the lower 100 m of the Middleton Formation. The other specimens, GCS JP8 and CGS JP10, are found several hundred metres higher.

Overall stratigraphic range

Pristerodon, like *Diictodon*, reaches its greatest abundance in the Late Permian (Smith *et al.* 2012) but it also has its origins in the Middle Permian. The stratigraphically lowest occurrence of *Pristerodon* is of SAM-PK-11933, within the upper Koornplaats Member in the eastern Laingsburg sector and no higher than the IS 1700–1750 m above the base of the Abrahamskraal Formation in this sector. This is equivalent to the uppermost Swaerskraal Member of the Abrahamskraal Formation at its thickest point, 2100–2150 m above its base (Figure 36). Several other securely identified

specimens of *Pristerodon* occur in the upper Abrahamskraal Formation in the southwest of the basin but the abundance of the genus remains low (Figure 37). Only in the Karelskraal Member do its numbers start to increase and only in the Poortjie Member does it become common.

5.7.13 *Prosictodon*

This genus is the most recently described Middle Permian dicynodont of the Beaufort Group (Angielczyk and Rubidge 2010). Until recently the only securely identified specimen of *P. dubeii* was BP/1/5589, from the farm Kliphokjes to the northeast of Victoria West. This specimen was found within 50 m of the Ecca-Beaufort contact but the Abrahamskraal Formation is very thin in this area (see 4.1.1.2). As such, BP/1/5589 can be constrained to the Abrahamskraal Formation immediately below the base of the Teekloof Formation (Figure 35).

Two further specimens of *Prosictodon* have recently been identified. BP/1/7096 was found on the farm Celeryfontein in the Fraserburg district, in an horizon immediately below the base of the Poortjie Member. It therefore occurs within the same stratigraphic interval as the holotype. The third specimen, BP/1/7190, was collected on the farm Goeiemoed, near Prince Albert Road in the Merweville sector, and can be constrained to the SI 2150–2200 m above the base of the Abrahamskraal Formation in this sector. This represents the stratigraphically lowest specimen and, together with BP/1/5589 and BP/1/7096, indicates that *Prosictodon* occurs between the base of the Moordenaars Member of the Abrahamskraal Formation and the base of the Poortjie Member (Figure 36).

5.7.14 *Robertia*

Robertia was first described by Boonstra (1948), although at this time the holotype was still partially encased in an 'intractable matrix' (King 1988:120) that obscured some of its features. The genus was maintained by Cluver and King (1983) and King (1988) but the holotype was not fully prepared until the review of King and Rubidge

(1993), when it was fully described and considered valid. It is represented by a single species, *R. broomiana*.

Robertia is one of the most common dicynodonts from the *Tapinocephalus* AZ. It is most easily distinguished from the other common genus, *Diictodon,* by its possession of a broad intertemporal region of the skull; many specimens have in fact been arbitrarily assigned to the genus on account of this one feature. However, recent taxonomic studies and associated re-identification, i.e. Angielczyk and Rubidge (2012), have greatly reduced the number of dubious specimens. As such, *Robertia* is a useful biostratigraphic indicator taxon and its stratigraphic range was used by Rubidge and Angielczyk (2009) in their dicynodont-based subdivision of the *Tapinocephalus* AZ.

The last holistic biostratigraphic review of the Beaufort Group had illustrated the range of *Robertia* to correspond to the majority of the *Tapinocephalus* AZ (Smith and Keyser 1995a). Angielczyk and Rubidge (2009) extended the stratigraphic range of *Robertia* up into the *Pristeroganthus* AZ based on specimens from Philippolis but are vague about its first appearance.

Range in the Beaufort West sector

In the eastern Koup, the stratigraphically lowest secure specimen of *Robertia* is NMQR 3135 from the farm Seekoegat, Prince Albert district. This defines the first appearance of *Robertia* in this sector at around 1500 m above the base of the Abrahamskraal Formation, in what is potentially the Koornplaats Member (Figure 35). The stratigraphically highest, securely identified specimens in this sector are SAM-PK-11756 and SAM-PK-11761 from Klein Koedoeskop in the Beaufort West district. These occur between 50–150 m below the base of the Teekloof Formation.

Range in the Leeu-Gamka sector

In this central Koup, two stratigraphically secure *Robertia* specimens have been recovered: BP/1/5576 from the farm Combrinkskraal in the Prince Albert district

and BP/1/6967 from the farm Bloukrans in the same district. The former occurs 1850–1900 m above the base of the Abrahamskraal Formation, while the latter is constrained to the SI 2200–2250 m. This corresponds to strata above the Koornplaats Member in this sector.

Two other specimens, SAM-PK-3354 and BP/1/5578, may have been found as low as 1700 m above the base of the Abrahamskraal Formation, within the Koornplaats Member. At the other extreme, BP/1/1778, from the farm Stinkfontein, may have originated as high as 2400 m above the base of the formation, close to the base of the overlying Teekloof Formation. The range of *Robertia* in this sector is therefore restricted to the upper third of the Abrahamskraal Formation.

Range in the Merweville sector

In this sector, north of Prince Albert Road, ten potential *Robertia* specimens have been discovered. The lowest two are SAM-PK-11461 and SAM-PK-K7982, which may occur as low as 1950 m above the base of the Abrahamskraal Formation on the farm Buffelsvlei, Beaufort West district. The stratigraphically highest specimen is SAM-PK-11855 from Mechaus Request, Beaufort West district, which is constrained only to between 2350–2500 m above the base of the formation. This specimen may therefore occur only 75 m below the base of the Teekloof Formation. The genus certainly occurs between 2150–2350 m above the base of the Abrahamskraal Formation in this sector, within the lower Moordenaars Member.

Range in the Laingsburg sector

The Laingsburg sector contains only four specimens of *Robertia*. All occur in a relatively narrow stratigraphic interval, which is likely the result of the limited collecting conducted in this area. SAM-PK-11878 and SAM-PK-11890 can be constrained to between 1600 m and 1750 m above the base of the Abrahamskraal Formation in this sector, while SAM-PK-11595 from Dikbome in the Laingsburg district is constrained to 1600–1800 m above the base of the formation. BP/1/5423, from Swaerskraal in the Moordenaarskaroo, has a wider potential range. All

specimens are restricted to an interval between the upper Koornplaats Member and the lower Moordenaars Member.

Range in the Sutherland sector

Specimens BP/1/7163 and BP/1/7164 can be constrained to between 1050–1200 m above the base of the Abrahamskraal Formation but both specimens are poorly preserved. As such, their stratigraphic utility is limited.

Range in Fraserburg sector

The four specimens of *Robertia* recorded on the BFV database from this sector have also proved problematic. BP/1/5585 has now been identified as an indeterminate pylaecephalid (Angielczyk pers. comm. 2011), leaving two CGS specimens, GM69 and GM70, that have not been recently identified. A further specimen, BP/1/7188, from the farm Palmietfontein in the Sutherland district, is securely identified as *Robertia* and can be constrained to between 450–500 m above the base of the Abrahamskraal Formation in this sector. Robertia therefore occurs securely in the Moordenaars Member and perhaps in the upper Davidskolk Member.

Range in the Jansenville sector

In the Jansenville sector, *Robertia* is known from three securely identified specimens: BP/1/5852, BP/1/5855 and BP/1/6682. All were recovered on the farm Uintjies Vlakte between 1350–1600 m above the base of the Koonap Formation. A dicynodont from the farm Hilary, BP/1/6687, has been identified as either *Robertia* or *Eosimops* (Angielczyk pers. comm. 2012) and was found in the lowest Middleton Formation. A further specimen, NMQR 3392, is recorded as being found on the farm Swart Rivier, Klipplaat district, but the specimen was not located in the collections of the National Museum. These last two specimens are therefore not considered further in this study.

Overall stratigraphic range

Robertia has a stratigraphic range that is limited to the upper half of the Abrahamskraal Formation. The lowest occurrences are within the upper Koornplaats Member in the Beaufort West and Leeu-Gamka sectors and, as these are based on specimens that are well constrained, this is relatively secure (Figure 35). The highest specimen is BP/1/7188 from the Fraserburg sector, which occurs 50–100 m below the base of the Poortjie Member. This means the certain stratigraphic range of *Robertia* extends between 1950–2550 m above the base of the Abrahamskraal Formation, encompassing the Karelskraal, Moordenaars and upper Swaerskraal Members of the Abrahamskraal Formation at its thickest point (Figure 36). The majority of specimens, however, are found in the upper Swaerskraal Member and Moordenaars Member (Figure 37). Contrary to Rubidge and Angielczyk (2009), *Robertia* is therefore restricted to the *Tapinocephalus* AZ.

5.8 Gorgonopsians

The gorgonopsians from the Middle Permian part of the Beaufort Group are poorly understood. While some taxonomic reviews of the Gorgonopsia have been conducted (e.g. Gebauer 2007; Haughton and Brink 1954; Sigogneau 1970; Signogneau-Russell 1989), no consensus has been reached. Signoneau-Russell (1989) considered five genera of gorgonopsians from the *Tapinocephalus* AZ to be valid, while Gebauer (2007) only acknowledged one, *Eoarctops*. Smith *et al.* (2012) record five genera from the *Tapinocephalus* AZ and two from the *Pristerognathus* AZ. Most recently, it has been suggested that the previously dismissed genus, *Eriphostoma microdon,* may be potentially valid (Kammerer pers. comm. 2013).

As Gorgonopsian taxonomy is so poorly understood, and the genera from the Middle Permian are likely to be revised in the near future (Kammerer pers. comm. 2013), they are not included here by genus. They do, however, occur throughout the Middle Permian of the Beaufort Group (ed. Rubidge 1995; Figure 29).

5.9 Therocephalians

Until the middle of the 20th Century, there was a lot of disagreement over the relationships within the Theriodontia and even now the taxonomy of the Therocephalia is a matter of dispute. The basal therocephalians have been particularly neglected and the only comprehensive taxonomic revision of the Middle Permian genera was conducted only in the 1980s by Van den Heever (1987).

The first *Tapinocephalus* AZ therocephalian to be described was *Pristerognathus polyodon* (Seeley 1894); although the genus *Hyorhyncus platyceps* was described earlier (Seeley 1889) and has been considered to be a pristerognathid therocephalian (Boonstra 1934, 1969), the holotype is too poor to be placed within even the Theriodontia (King 1988). The taxon Therocephalia was introduced by Broom (1903a), who also erected the family Scylacosauridae for the most primitive therocephalians. Haughton (1924) preferred a family based on the earliest valid genus, *Pristerognathus*, and replaced the name Scylacosauridae with the Pristerognathidae. This preference was to become ubiquitous in the mid-20th Century, with the exception of Williston (1925); this author also proposed the family Lycosuchidae for genera more closely related to the genus *Lycosuchus*, which had been described by Broom (1903b), than to *Scylacosaurus*.

Boonstra (1953b, 1954c) recognised both the Pristerognathidae and the Scylacosauridae as separate families, in addition to the Lycosuchidae but the family Pristerognathidae was subsequently used to refer to all basal forms that were not lycosuchids (e.g. Haughton and Brink 1955). Boonstra (1969), in his review of the *Tapinocephalus* Zone fauna (now the *Tapinocephalus* and *Pristerognathus* assemblage zones), accepted the therocephalian families Pristerognathidae, Lycosuchidae, Alopecodontidae and Scaloposauridae to be present in these horizons.

Van den Heever (1987) maintained the validity of only two families: the Lycosuchidae for the two species of *Lycosuchus* and the Scylacosauridae for all other basal therocephalian genera. In this review, Van den Heever reduced the number of valid scylacosaurid genera to six. Abdala *et al.* (2008) accepted Van den Heever's (1987) taxonomic structure but acknowledged three further genera of unknown family, although the validity of these genera remains tenuous (Abdala pers. comm.).

Because the generic definitions for basal therocephalian genera are poor, only the families are regarded here as well-substantiated. However, a re-evaluation of the basal therocephalians is ongoing, including the present description of a new genus of lycosuchid (Abdala *et al.* in prep). The genera listed below are currently valid as recorded by Abdala *et al.* (2008).

5.9.1 *Lycosuchus*

The Lycosuchidae is one of the two families of basal therocephalians and is considerably less diverse than its sister taxon, the Scylacosauridae. The family was proposed by Williston (1925) and was based upon the genus *Lycosuchus*, which had been described by Broom (1903b) for a specimen now in the collections of the Field Museum of Natural History, FMNH US D173.

The Lycosuchidae is comprised only of the genus *Lycosuchus*. Van den Heever (1987) recognised twelve specimens of the type species, *L. vanderrieti*, and about as many again that were referable to the only to Lycosuchidae. This author also proposed the species *L. keyseri* for a previously undescribed specimen in the collections of the Geological Survey (now the Council for Geoscience), CGS C60; however, Van den Heever (1994) considered it to be identifiable only as lycosuchid and the species was not accepted by Abdala *et al.* (2008). Most recently, a new genus of lycosuchid is being described based on a single individual (Abdala *et al.* in prep), but this is not considered here.

The total number of specimens currently identified as lycosuchid is thirty-two but the genus *Lycosuchus* is represented by only six individuals, of which five have workable provenance data. The holotype was reported to have come only from the Groot Vlakte, to east of Beaufort West (Broom 1903a; see 1.4; Figure 2), and is therefore not stratigraphically useful, although it was probably recovered from the *Pristerognathus* AZ. Van den Heever (1987) mentions that this specimen was included in the Fraserburg Road (Leeu-Gamka) locality by Kitching (1977) but this author did not provide specimen numbers and recorded *Lycosuchus* to occur at the Groot Vlakte locality, indicating Van den Heever was mistaken.

Until recently, *Lycosuchus* was considered to be restricted to the *Tapinocephalus* AZ (Abdala *et al.* 2008; Smith and Keyser 1995a; Smith *et al.* 2012); however, *Lycosuchus* is now recognised to occur within both the *Tapinocephalus* and *Pristerognathus* assemblage zones (Abdala *et al.* in prep).

Of the five specimens securely identified as *Lycosuchus* and that have acceptable provenance data, the stratigraphically lowest is SAM-PK-1079, from the farm Rietfontein in the Prince Albert district (Leeu-Gamka sector). This specimen is not well constrained stratigraphically but was found in a horizon within the Abrahamskraal Formation, 1850–2400 m above its base in the Leeu-Gamka sector (Figure 38). The stratigraphically highest specimen is CGS M793, from the farm Drie Kop in the Beaufort West district (Beaufort West sector). This specimen is stratigraphically constrained to the uppermost Poortjie Member of the Teekloof Formation. The certain stratigraphic range of *Lycosuchus* therefore extends from a horizon 2450 m above the base of the Abrahamskraal Formation at its thickest point, in the uppermost Moordenaars Member, to the top of the Poortjie Member of the Teekloof Formation (Figure 39). This corresponds to the upper *Tapinocephalus* AZ and *Pristerognathus* AZ.

Two lycosuchid specimens of indeterminate genus, TM 275 and SAM-PK-2756, have been collected on the farm Abrahamskraal in the Prince Albert district (Leeu-Gamka sector). These are constrained to an interval between 1700–2100 m above the base of the Abrahamskraal Formation in the Leeu-Gamka sector and, as a result, extend the certain stratigraphic range of the Lycosuchidae down to the lower Moordenaars Member of the Abrahamskraal Formation at its thickest point. The family reaches its highest abundance in the uppermost Abrahamskraal Formation.

5.9.2 *Alopecodon*

Alopecodon priscus was first described by Broom (1908b) and although it has had a couple of specimens referred to it, only the holotype was deemed to be diagnostic by Van den Heever (1987). The genus briefly formed the basis of the Alopecodontidae (Broom 1932) but was returned to the Pristerognathidae by Boonstra (1934), who considered it to be monospecific. Both Van den Heever (1987) and Abdala *et al.*

(2008) regard *Alopecodon* as valid, although only two specimens are currently assigned to it (SAM-PK-920 and AMNH 5569).

According to Van den Heever (1987), the holotype of *Alopecodon* (SAM-920) was allegedly collected 14 km northwest of the farm Seekoegat, in the Prince Albert district of the Western Cape Province (Beaufort West sector). The BFV database records the specimen to occur on the farm Seekoegat itself (Nicolas 2007) but 14 km northwest of the farmstead would place the locality of the specimen on the farm Smal Deel. The provenance of the specimen is therefore uncertain and it is possible that it was collected from almost anywhere within the Abrahamskraal Formation, given the folded nature of the rocks on the southern margin of the basin. If it was collected on Smal Deel, it can only be constrained stratigraphically to the upper half of the Abrahamskraal Formation.

The referred specimen AMNH 5569 was recovered from the vicinity of Fraserburg Road (now Leeu-Gamka station), which constrains the stratigraphic provenance of the specimen to an interval 2100–2350 m above the base of the Abrahamskraal Formation in the Leeu-Gamka sector (Figure 38). When correlated with the Abrahamskraal Formation at its thickest point, this indicates that *Alopecodon* occurs in the Moordenaars Member of the Abrahamskraal Formation (Figure 39).

A third specimen, BP/1/1771, is attributed to either *Alopecodon* or *Pardosuchus* (Abdala pers. comm.) and was found on the farm Stinkfontein, in the Beaufort West district (Leeu-Gamka Sector). This specimen can be constrained to the interval 2200–2400 m above the base of the Abrahamskraal Formation in this sector.

5.9.3 *Glanosuchus*

Glanosuchus is the most common therocephalian genus from the Middle Permian of South Africa (Van den Heever 1987). It was described as the species *G. macrops* by Broom (1904) on the basis of dental characters but this was later elaborated by Boonstra (1954c), who also referred several more specimens to the genus. With the work of Van den Heever (1987), *Glanosuchus* became the most common basal therocephalian genus through the re-identification of existing therocephalian

specimens. Almost all scylacosaurid specimens that have been scrutinised recently represent *Glanosuchus* and it is likely that many remaining specimens attributed to *Pristerognathus* are in fact individuals of *Glanosuchus* (Abdala pers. comm. 2011).

Range in the Beaufort West sector

Fourteen specimens of *Glanosuchus* are known from the eastern Koup. The stratigraphically lowest specimen is NMQR 2908 from the farm Modderdrift, in the Prince Albert district. This was first described by Rubidge (1983) as coming from the *Eodicynodon* AZ, and can be constrained to occur in an interval 200–250 m above the base of the Abrahamskraal Formation in this sector, within the lower Combrinkskraal Member.

The stratigraphically highest occurrence of *Glanosuchus* is specimen SAM-PK-3415, which was collected on the farm Klipbanksfontein, near Beaufort West. This can be stratigraphically constrained to an interval straddling the boundary of the Abrahamskraal and Teekloof formations, within the upper 50 m of the Abrahamskraal Formation or the lower 50 m of the Poortjie Member. The certain stratigraphic range of *Glanosuchus* in this sector extends from the lower Combrinkskraal Member to the base of the Poortjie Member, equivalent to the upper 1950 m of the Abrahamskraal Formation (Figure 38).

Range in the Leeu-Gamka sector

Glanosuchus is represented in the Leeu-Gamka sector by eight specimens. The stratigraphically lowest of these is MM 5139, which was collected on the farm Abrahamskraal, in the Prince Albert district. This farm exposes a stratigraphic interval of the Abrahamskraal Formation 1700-2100 m above its base in this sector. The stratigraphically highest specimen is AMNH 5559 from the farm Grootfontein, in the Beaufort West district to the west of that town. This farm straddles the boundary between the Abrahamskraal and Teekloof formations and the specimen can be constrained to an horizon within the upper 50 m of the Abrahamskraal Formation or the lower 50 m of the Teekloof Formation. The certain stratigraphic

range of *Glanosuchus* in this sector therefore corresponds to an interval 2050–2468 m above the base of the Abrahamskraal Formation.

Range in the Merweville sector

Five specimens of *Glanosuchus* are known from this sector. The stratigraphically lowest specimens are SAM-PK-11456 and SAM-PK-11460, which were collected on the farm Buffelsvlei, in the Beaufort West district southwest of Merweville and are stratigraphically constrained to an interval 1950–2200 m above the base of the Abrahamskraal Formation. The stratigraphically highest specimen is BP/1/1100 from the farm Elandsfontein, also in the Beaufort West district, which was found in within a stratigraphic interval 2200–2300 m above the base of the Abrahamskraal Formation. The certain stratigraphic range of *Glanosuchus* in this sector corresponds to a narrow interval 2150–2250 m above the base of the Abrahamskraal Formation, equivalent to the uppermost Swaerskraal Member and the lower Moordenaars Member.

Range in the Laingsburg sector

Outside the Koup, there are only a few identified specimens of *Glanosuchus*. A single specimen, SAM-PK-11963, is known from the Moordenaarskaroo sector, which was collected on the farm Dikbome, in the Laingsburg district. This specimen is stratigraphically constrained to an interval 1600–1800 m above the base of the Abrahamskraal Formation in this sector, equivalent to the uppermost Koornplaats Member and or the Swaerskraal Member.

Range in the Sutherland sector

A single specimen of *Glanosuchus* has been recovered from this sector. SAM-PK-9356a was collected on the farm Roggenkloof, in the Sutherland district south of Sutherland, can be stratigraphically constrained to an interval 1050–1200 m above

the base of the Abrahamskraal Formation. This equates to the upper Swaerskraal Member or lower Moordenaars Member in this sector.

Range in the Fraserburg sector

A single specimen from the Fraserburg sector, CGS RD116, is tentatively assigned to *Glanosuchus* (Abdala pers. comm.). This specimen was recovered from the farm Kalkfontein, in the Fraserburg district, in a horizon that is stratigraphically constrained to the lower 50 m of the Poortjie Member.

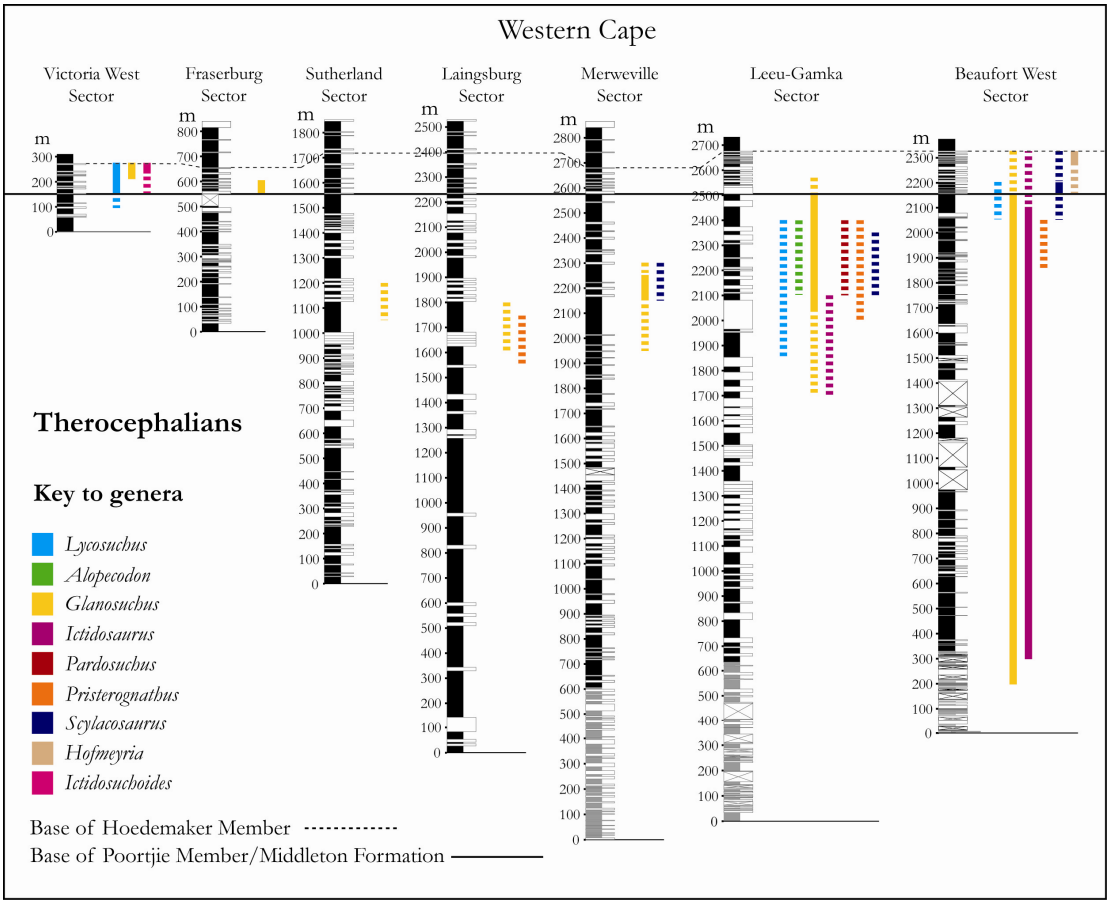


Figure 40. Stratigraphic ranges of therocephalian genera in each of the sectors in which they occur.

Range in the Victoria West sector

One securely identified specimen of *Glanosuchus* is known in the Victoria West sector (CGS M796), which was found on the farm Drie Kop in the Beaufort West district. This specimen was collected from strata of the uppermost Poortjie Member of the Teekloof Formation. A second specimen that is tentatively assigned to *Glanosuchus* by the author, SAM-PK-10544, was found in the same stratigraphic horizon on the farm Brakfontein, Victoria West district.

Overall stratigraphic range

Glanosuchus has the longest stratigraphic range of any tetrapod genus that is restricted to the Middle Permian of the Beaufort Group. The stratigraphically lowest occurrence of the genus is NMQR 2908 from the Beaufort West sector and which occurs in the SI 200–250 m above the base of the Abrahamskraal Formation in this sector. This correlates to the SI 650–700 m above the base of the Abrahamskraal Formation at its thickest point. The stratigraphically highest specimen is CGS M796 from the Vitoria West sector, which is constrained to occur in the uppermost Poortjie Member. The certain stratigraphic range of *Glanosuchus* therefore extends from the upper Combrinkskraal Member of the Abrahamskraal Formation at its thickest point to the top of the Poortjie Member of the Teekloof Formation, corresponding to nearly the entire Middle Permian part of the Beaufort Group (Figure 39). *Glanosuchus* is also quite geographically widespread, occurring in seven of the ten sectors.

Glanosuchus reaches its highest abundance in the upper 50 m of the Abrahamskraal Formation but is more common in the upper Moordenaars Member, Karelskraal Member and Poortjie Member than in stratigraphically lower horizons. A large number of specimens referred to *Pristerognathus* have not yet been re-assessed since the revisions of Van den Heever (1987) many of them probably represent *Glanosuchus* (Abdala pers. comm.). In this case, this genus would be most abundant in the Poortjie Member, as most *Pristerognathus* material has been collected from this unit.

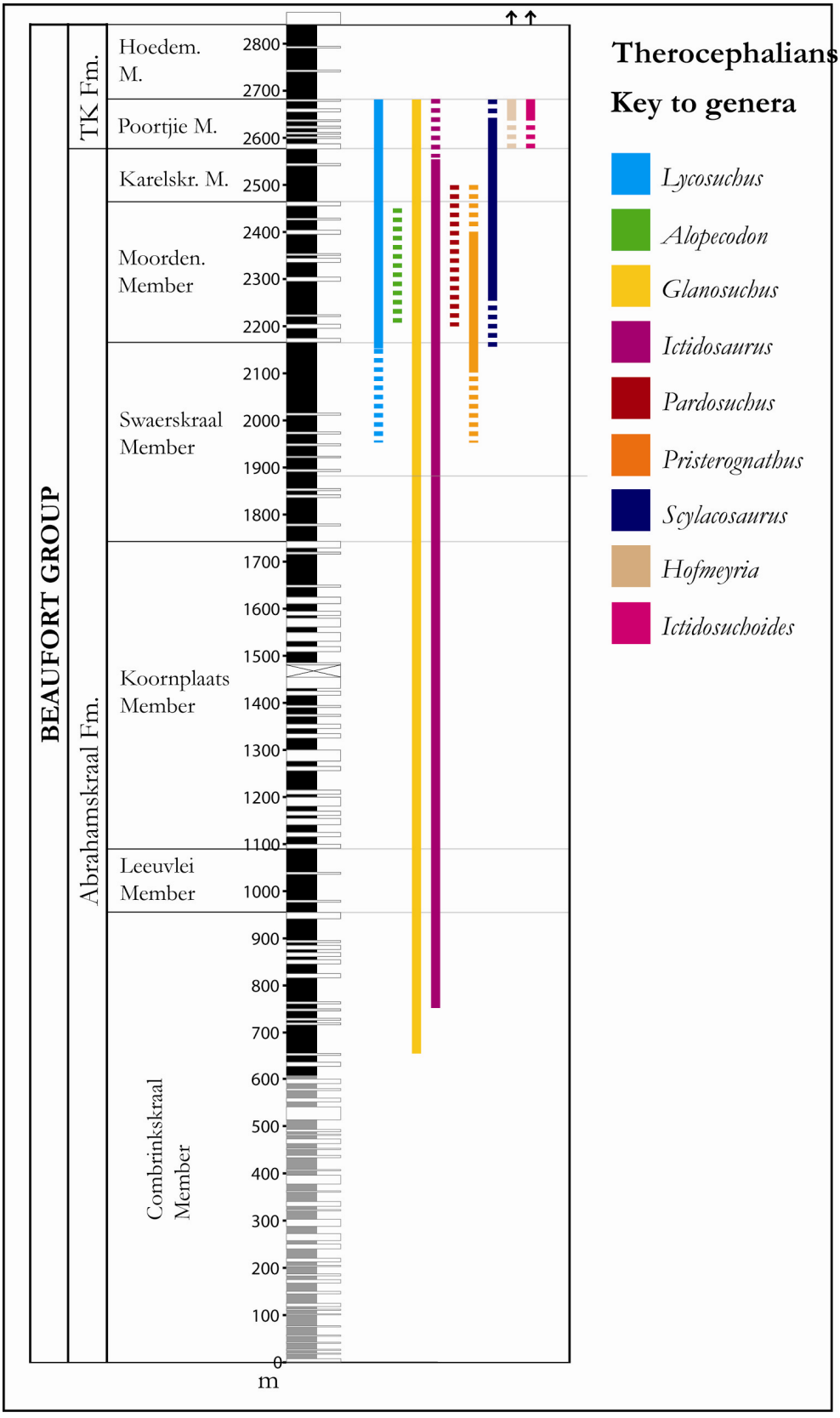


Figure 41. Composite stratigraphic ranges of therocephalian genera in the Middle Permian Beaufort Group.

5.9.4 *Ictidosaurus*

Ictidosaurus is a less well known therocephalian genera from the Middle Permian. It was described by Broom (1903c) as the species *I. angusticeps* for specimen SAM-PK-630, which Van den Heever (1987:301) later described as a 'very badly weathered anterior portion of a scylacosaurid snout with anterior portions of both lower jaw rami.' Although the genus has been taxonomically unstable, most authors have considered it to be a pristerognathid (e.g. Haughton 1924; Kitching 1977) and, most recently, a scylacosaurid (Van den Heever 1987). Apart from the holotype, only two specimens have been referred to the genus (SAM-PK-11957 and NMQR 2910).

The stratigraphically lowest specimen is NMQR 2910, which was identified as *Ictidosaurus* only recently (Abdala *et al.* 2008). It was collected on the farm Modderdrift, in the Prince Albert district (Beaufort West sector), in a stratigraphic horizon 300–350 m above the base of the Abrahamskraal Formation in this sector, within the *Eodicynodon* AZ. The stratigraphically highest specimen is the holotype, SAM-PK-630, which was collected in the vicinity of Beaufort West and can therefore be stratigraphically constrained to originate in the upper 100 m of the Abrahamskraal Formation or the lower Teekloof Formation. The certain stratigraphic range of *Ictidosaurus* therefore extends from the upper Combrinkskraal Member of the Abrahamskraal Formation at its thickest point, 750–800 m above its base, to the upper Karelskraal Member (Figure 39).

5.9.5 *Pardosuchus*

This genus was described by Broom (1908b) as *Pardosuchus whaitsi* and has been considered as pristerognathid, a scylacosaurid and an alopecodontid (e.g. Haughton 1924; Williston 1925; Broom 1932). The genus was represented only by the holotype, SAM-PK-1077, until a second specimen formerly assigned to *Pristerognathus*, SAM-PK-9111, was referred to *Pardosuchus* by Van den Heever (1987). Most recently, a specimen in the collections of the Bernard Price Institute in Johannesburg, BP/1/1768, has been identified as *Pardosuchus* (Abdala pers. comm. 2012), while a fourth, BP/1/1771, can be attributed to either *Pardosuchus* or *Alopecodon*.

All specimens come from the same stratigraphic interval in the Leeu-Gamka sector but the stratigraphically lowest is the holotype, which was found on the farm Welgemoed, Prince Albert district, and can be constrained to a stratigraphic interval 2100–2350 m above the base of the Abrahamskraal Formation in this sector. The stratigraphically highest specimen is SAM-PK-9084a from the farm Rietkuil, in the Beaufort West district, which was found in strata 2250–2400 m above the base of the Abrahamskraal Formation. Because the ranges of these two specimens overlap, a certain stratigraphic range for *Pardosuchus* cannot be calculated, although it occurs within the Moordenaars Member of the Abrahamskraal Formation at its thickest point (Figure 39).

5.9.6 *Pristerognathus*

Pristerognathus polyodon is the best known early therocephalian species and, of those that are currently valid, was the first to be described (Seeley 1894). Although there had been concern over the validity of the name *Pristerognathus* by several early authors (e.g. Broom 1932; Boonstra 1969), it is now considered accepted as valid (Abdala et al. 2008; Van den Heever 1987).

The type specimen, NHMUK R2518, was initially thought to have six incisors until a later re-description recognized seven (Mendrez 1972), a fact which has caused some confusion with the genus *Glanosuchus*; Van den Heever (1987) found that only two of the specimens referred to *Pristerognathus* that he examined, SAM-PK-631 and SAM-PK-11848, were correctly diagnosed, and that only one additional specimen in existing collections, SAM-PK-11942, could be identified as *Pristerognathus*.

A fifth specimen of *Pristerognathu*s, SAM-PK-12122, was tentatively recognised by the author in the collections of the South African Museum but, until such time as they are re-examined, all other material referred to *Pristerognathus* is considered here to be Scylacosauridae indet. Therefore, only the five specimens mentioned above are considered here. Because the *Pristerognathus* AZ had been defined on the presence of this genus, the dubious identity of most specimens referred to *Pristerognathus* has considerable implications for the biostratigraphy of the late Middle Permian.

Of the five securely identified specimens, the stratigraphically lowest is SAM-PK-11942, which was collected on the farm Schoppelmaaikraal, in the Laingsburg district (Laingsburg sector). This specimen can be stratigraphically constrained to an interval 1550–1750 m above the base of the Abrahamskraal Formation in this sector, within the upper Koornplaats Member or Swaerskraal Member (Figure 38). The stratigraphically highest specimen is the holotype, NHMUK R2581, which was discovered on the farm De Cyfer in the Beaufort West district (Leeu-Gamka sector). The horizon from which this specimen was collected is stratigraphically constrained to occur 2250–2400 m above the base of the Abrahamskraal Formation in the Leeu-Gamka sector.

The certain stratigraphic range of *Pristerognathus* therefore corresponds to an interval 2100–2400 m above the base of the Abrahamskraal Formation at its thickest point, from the uppermost Swaerskraal Member to the upper Moordenaars Member (Figure 39). Ironically, no securely identified specimens of the genus *Pristerognathus* are found in the assemblage zone that bears its name.

5.9.7 *Scylacosaurus*

The name *Scylacosaurus sclateri* first mentioned by Broom (1903a) but the holotype was only described in two subsequent papers (Broom 1903b, 1903c). Broom considered the genus to form the basis of the family Scylacosauridae, as well as the type genus of the Therocephalia (Broom 1903a). Van den Heever (1987) accepted the validity of the genus *Scylacosaurus* and mentioned four specimens that could be definitively assigned to it, while one other, SAM-PK-K10530, is listed on the BFV database (Nicolas 2007). The diagnosis of this latter specimen is probably correct given its more recent collection date and so five specimens are acknowledged in this study.

Of the five specimens accepted to belong to *Scylacosaurus*, only four have reliable provenance data. The holotype of *Scylacosaurus*, SAM-PK-634, was recorded to have been 'obtained at Colesberg' by Broom (1903c:343) but Kitching (1977) described the locality as unreliable. Because no other basal therocephalians were known from the biozones that outcrop in the Colesberg area, Van den Heever (1987) suggested

the specimen may have been collected in the *Tapinocephalus* AZ and brought to Colesberg, effectively considering its locality unknown.

The stratigraphically lowest specimen is SAM-PK-11888, from the farm Vindragersfontein in the Beaufort West district (Merweville sector). This specimen is stratigraphically constrained to an interval 2150–2300 m above the base of the Abrahamskraal Formation, in the upper Swaerskraal or lower Moordenaars Member (Figure 38). The stratigraphically highest specimen is SAM-PK-K10530 from the farm Lombardskraal, in the Beaufort West district (Beaufort West sector), which was collected from the lower Poortjie Member. The certain stratigraphic range of *Scylacosaurus* therefore extends from 2250 m above the base of the Abrahamskraal Formation at its thickest point, in the lower Moordenaars Member, up to the mid-Poortjie Member of the Teekloof Formation (Figure 39).

5.9.8 *Ictidosuchoides*

Ictidosuchoides is one of the stratigraphically longest ranging therocephalian genera in the Beaufort Group. The genus was first described by Broom (1931) as the species *I. longiceps* and is now considered a basal baurioid in the family Ictidosuchidae (e.g. Huttenlocker 2009). Stratigraphically, Rubidge (ed. 1995) records its range to extend from the *Pristerognathus* AZ to the top of the *Dicynodon* AZ, where it succumbs to the end-Permian mass extinction. Later, Smith and Botha (2005) referred to the occurrence of *Ictidosuchoides* in the earliest Triassic Palingkloof Member of the Balfour Formation but provide no details as to the specimens involved. Abdala *et al.* (2008) list its occurrence from the *Pristerognathus* AZ to the *Lystrosaurus* AZ.

One specimen can be stratigraphically constrained to occur in the Middle Permian. This specimen, CGS M765, was collected on the farm Quaggasfontein, in the Victoria West district, at a locality that is situated on outcrop of the uppermost Poortjie Member (Nicolas 2007; map sheet: Republic of South Africa 3122, Victoria West, 1:250 000 Geological Series 1992; Figure 38). Three others were found either in the upper Poortjie Member or the lower Hoedemaker Member. The certain stratigraphic range of *Ictidosuchoides* therefore extends down to the upper Poortjie Member, within the *Pristerognathus* AZ (Figure 39).

5.9.9 *Ictidosuchus*

The genus *Ictidosuchus primaevus* is not usually associated with the Middle Permian; Abdala *et al.* (2008) recognise the genus to occur only in the *Tropidostoma* AZ. One specimen, SAM-PK-K8305, was listed on the BFV database as occurring in the *Pristerognathus* AZ (Nicolas 2007) but this is now identified as the varanopid synapsid *Heleosaurus scholtzi* and is only mentioned here for the sake of completeness.

5.9.10 *Hofmeyria*

Hofmeyria atavus was described by Broom (1935) and is now considered a basal eutherocephalian that forms the basis of the family Hofmeyriidae (see Huttenlocker 2009). This genus is also not usually associated with the Middle Permian; Abdala *et al.* (2008) consider it to be present in the *Tropidostoma* and *Cistecephalus* assemblage zones only. However, there are two certain occurrences of *Hofmeyria* in the *Pristerognathus* AZ.

Specimen SAM-PK-K10525 was found on the farm Lombardskraal, in the Beaufort West district (Beaufort West sector). This farm exposes outcrop of the Poortjie Member and, in the absence of more precise data, can be stratigraphically constrained to that unit (Figure 38). The second specimen, TM 254, was collected on the farm Kookfontein in the Victoria West district (Victoria West sector) and is stratigraphically constrained to occur in the upper Poortjie Member. This specimen is, however, identified only as an indeterminate hofmeyriid (Van den Heever 1987).

A third specimen, BP/1/4401, is securely identified as *Hofmeyria* (Abdala pers. comm.) and was collected on the farm Highlands, in the Victoria West district (Victoria West sector). The geological maps here indicates the exposure of upper Poortjie Member on the low ground and Hoedemaker Member on the slopes of the surrounding hills (map sheet: Republic of South Africa 3122, Victoria West, 1:250 000 Geological Series 1989), so the specimen may have come from either member.

The certain stratigraphic range of *Hofmeyria* therefore extends down as low as the upper Poortjie Member of the Teekloof Formation (Figure 39).

5.9.11 *Blattoidealestes, Crapartinella* and *Simorhinella*

These three genera, of which *Blattoidealestes* was described by Boonstra (1954b) and the other two by Mendrez (1975), are all known from singular, poorly preserved specimens. All occur within the *Tapinocephalus* AZ as currently defined (Abdala *et al.* 2008) but their validity is dubious and they are not considered in this study.

5.10 Stratigraphic patterns of higher taxa in the Middle Permian

This section aims to summarise the stratigraphic ranges of the higher taxa, based on the occurrences of their individual genera.

5.10.1 Temnospondyl amphibians

The Middle Permian temnospondyls from South Africa are very poorly understood, but the taxon is present in the *Tapinocephalus* and *Eodicynodon* assemblage zones (ed. Rubidge 1995). All belong to the family Rhinesuchidae.

5.10.2 Parareptiles

Middle Permian parareptiles are not a diverse taxon. Only two genera, *Broomia* and *Eunotosaurus*, are not pareiasaurs. This pareiasaurs themselves are also not particularly diverse but they are the third most common taxon in the upper Abrahamskraal Formation, after the dinocephalians and the dicynodonts (Figure 29). Unlike these two taxa, pareiasaurs have not yet been found in the lower two-thirds of the Abrahamskraal Formation. Although many specimens attributed to *Embrithosaurus* were considered only as indeterminate pareiasaurs for the purposes of this study (see 5.2.2), they are included in the abundance calculations for pareiasaurs as a whole.

The stratigraphically lowest occurrence of a pareiasaur is of *Bradysaurus*, in the upper Swaerskraal Member (see 5.2.1), while the other two genera (*Embrithosaurus* and *Nochelosaurus*) are first recorded at the base of the Moordenaars Member (Figure 28).

The stratigraphic range of all three pareiasaur genera extends into the Karelskraal Member of the Abrahamskraal Formation but none are found in the Poortjie Member of the Teekloof Formation. There is a steady increase in pareiasaur abundance from the first appearance of *Bradysaurus*, with a distinct peak in the lower Moordenaars Member, 2200–2300 m above the base of the Abrahamskraal Formation, where the taxon reaches its greatest numbers (Figure 29). Above the lower Moordenaars Member, pareiasaur abundance is relatively stable until the middle of the Karelskraal Member, after which there is a steady decline in numbers.

The millerettid *Broomia* is poorly constrained to occur in the Moordenaars Member and upper Koonap Formation, based on two specimens (see 4.2.4). *Eunotosaurus*, conversely, is better represented and has its first appearance in the lower Moordenaars Member. This stratigraphic range of this genus extends up to the top of the Poortjie Member, where it reaches its greatest abundance (Figure 29).

5.10.3 Basal synapsids

The two genera of basal synapsids known from the Middle Permian of South Africa, *Elliotsmithia* and *Heleosaurus*, are both represented by only two specimens. *Elliotsmithia* is stratigraphically constrained to occur with certainty in the Moordenaars Member of the Abrahamskraal Formation, but *Heleosaurus* has an uncertain occurrence in either the upper Abrahamskraal Formation or the Poortjie Member of the Teekloof Formation (Figure 31).

5.10.4 Biarmosuchians

Biarmosuchians are very rare in the Middle Permian Beaufort Group, with three of the four genera (*Bullacephalus*, *Lobalopex*? and *Pachydectes*) being represented by only a single specimen. *Hipposaurus*, the most common genus, has five specimens attributed to it. Biarmosuchians are found throughout the Middle Permian of South Africa, with the stratigraphically lowest genus being *Pachydectes*. This genus occurs in the lower Koonap Formation in the Jansenville sector, which is correlated with the upper Combrinkskraal Member of the Abrahamskraal Formation at its thickest point (see

5.4.3). *Bullacephalus* and *Hipposaurus* are found in the upper Abrahamskraal Formation and *Lobalopex*? is found in the Poortjie Member and overlying Hoedemaker Member of the Teekloof Formation (Figure 28). *Bullacephalus*, *Hipposaurus* and *Pachydectes* are therefore only found in the Middle Permian, while *Lobalopex*? is found in the Late Permian as well.

5.10.5 Dinocephalians

Dinocephalians are the second most abundant therapsid taxon in the Middle Permian of South Africa. They are present in the lower Abrahamskraal Formation but are represented by only six specimens in the mid-Combrinkskraal Member, five of which belong to the basal tapinocephalid genus *Tapinocaninus*; the sixth specimen is of the anteosaurid *Australosyodon*. Very little dinocephalian material has yet been discovered in the Leeuvlei or Koornplaats members of the Abrahamskraal Formation at its thickest point but the tapinocephalid *Struthiocephalus* is present in the upper Koornplaats Member (Figure 33). In the upper Abrahamskraal Formation there are two peaks in dinocephalian abundance: one between 2150–2250 m above the base of the Abrahamskraal Formation, in the lower Moordenaars Member, and another in the uppermost Moordenaars Member and lower Karelskraal Member (Figure 29). Throughout the Swaerskraal Member and lower Moordenaars Member, dinocephalians are the most common tetrapod taxon.

The stratigraphic ranges of dinocephalian genera are relatively homogeneous when compared to other taxa, with most having ranges that extend from the upper Swaerskraal Member or lower Moordenaars Member to the upper Karelskraal Member of the Abrahamskraal Formation (Figure 33). Currently, seventeen of the nineteen recognised dinocephalian genera are found in this stratigraphic interval. Of these, *Struthiocephalus* has its first appearance in the Koornplaats Member, eight genera (*Jonkeria*, *Titanosuchus*, *Mormosaurus*, *Moschops*, *Phocosaurus*, *Struthionops*, *Tapinocephalus* and *Taurocephalus*) have their first appearances in the upper Swaerskraal Member, while the remaining eight genera (*Anteosaurus*, *Avenantia*, *Criocephalosaurus*, *Delphinognathus*, *Keratocephalus*, *Riebeeckosaurus*, *Struthiocephaloides*, and *Styracocephalus*) first appear in the lower Moordenaars Member.

A phenomenon that creates an apparent lumping first appearance in many dinocephalian genera is the provenance of many holotype specimens on the farm Abrahamskraal, in the Prince Albert district (Leeu-Gamka sector), which exposes a stratigraphic interval 1700–2100 m above the base of the Abrahamskraal Formation; when correlated with the Abrahamskraal Formation at its thickest point, this corresponds to a stratigraphic interval 1800–2200 m above the base of the Formation. As so many dinocephalian holotypes have been found at this locality, it creates the illusion that many genera have similar first appearances that correspond to the stratigraphic interval that outcrops on this farm, either at the stratigraphically lower horizon 1800 m above the base of the Abrahamskraal Formation, or the upper horizon at 2200 m. The first appearances of dinocephalian genera in the upper Abrahamskraal Formation is therefore probably more variable than illustrated in this study (Figure 33).

The highest occurring genera are *Criocephalosaurus*, *Styracocephalus* and an unnamed titanosuchid. Two specimens of *Criocephalosaurus* (SAM-PK-K10888 and BP/1/7214) and one of a titanosuchid (BP/1/7168) have been recovered from the lowest Poortjie Member, while one specimen of *Styracocephalus* (BP/1/5485) was most likely found in this horizon (see 5.5.19).

The stratigraphic resolution across the Karelskraal Member and Poortjie Member may not yet be high enough to truly elucidate the differential reactions of dinocephalian genera during the extinction of the taxon. Another caveat is, as always, that some genera are represented by so few specimens; *Struthionops*, *Taurocephalus*, *Avenantia* and *Riebeeckosaurus* have very poorly defined ranges and are only given a tentative range from which their specimen or specimens may have originated. However, the Dinocephalia achieves its highest taxonomic diversity in the Moordenaars Member of the Abrahamskraal Formation, where at least fifteen genera are present. Although at least twelve genera are also present in the Karelskraal Member of the uppermost Abrahamskraal Formation, only one genus, *Criocephalosaurus*, can unequivocally be placed in the lower Poortjie Member.

5.10.6 Non-dicynodont anomodonts

Non-dicynodont anomodonts are also very rare elements of the Middle Permian. All four genera are known from the Abrahamskraal Formation but the stratigraphically lowest is *Patranomodon*, which is present in the Combrinkskraal Member (Figure 31). The other three genera, *Anomocephalus*, *Galechirus* and *Galeops*, are found in the upper Abrahamskraal Formation: *Anomocephalus* was found in the northwest of the basin but the horizon it was collected from probably correlates with the Swaerskraal Member of the Abrahamskraal Formation at its thickest point (see 5.6.1). *Galechirus* and *Galeops* are certainly present in the Moordenaars Member and in the case of the latter, the lower Karelskraal Member, but the stratigraphic constraints on some of their specimens are poor (see 5.6.2 and 5.6.3).

5.10.7 Dicynodonts

Dicynodonts are the most abundant group of tetrapods in the Middle Permian overall but their distribution is quite uneven (Figure 36). They are the most common tetrapods in the lower two-thirds of the Abrahamskraal Formation, although only a single genus, *Eodicynodon*, is present there (Figure 29). The number of *Eodicynodon* specimens in this interval relatively low and the majority are clustered between 400–800 m above the base of the Abrahamskraal Formation at its thickest point, within the Combrinkskraal Member.

Few dicynodont specimens have yet been found in the Leeuvlei or Koornplaats Member of the central Abrahamskraal Formation but the taxon becomes common above the top of the Koornplaats Member, approximately 1950 m above the base of the Abrahamskraal Formation at its thickest point (Figure 29). There are two peaks in dicynodont abundance in the Moordenaars Member, one in the lower part and another in the middle of the member, between 2300–2350 m above the base of the Abrahamskraal Formation. At the top of the Moordenaars Member dicynodont abundances begin to increase and become exponential above the mid-Karelskraal Member, although latter development is primarily due to the increase in abundance of the genus *Diictodon* (Figure 37).

Of the fourteen dicynodont genera from the Middle Permian of South Africa, ten have their first certain appearance in the upper Abrahamskraal Formation. Of those that do not, *Eodicynodon* is the only genus known from the *Eodicynodon* AZ and by definition does not extend above it, while *Dicynodontoides* and *Cryptocynodon* only appear in the *Pristerognathus* AZ. *Lanthanostegus* is only known from two specimens that were collected from the lowest Koonap Formation in the Jansenville sector, which can probably be correlated with the lower Abrahamskraal Formation in the southwest of the basin and thus the *Eodicynodon* AZ (see 5.7.10).

Ten genera are present in the upper Abrahamskraal Formation, of which five are also certainly present in the overlying Teekloof Formation (*Diictodon*, *Emydops*, *Endothiodon*, *Eosimops* and *Pristerodon*). Only two genera of significant abundance (*Robertia* and *Colobodectes*) disappear near the top of the Abrahamskraal Formation (Figure 36).

Four of the five dicynodont genera that are present in both the upper Abrahamskraal Formation and Teekloof Formation (*Diictodon*, *Emydops*, *Endothiodon* and *Pristerodon*) are relatively rare in the Abrahamskraal Formation portion of their stratigraphic range (Figure 36); *Pristerodon* and *Diictodon* in particular are far more common in the Poortjie Member of the Teekloof Formation than in the Karelskraal Member of the Abrahamskraal Formation.

Overall, the certain stratigraphic ranges of dicynodont genera in the Middle Permian of South Africa are relatively heterogeneous. The taxon achieves its highest abundance in the Karelskraal Member of the Abrahamskraal Formation, but its highest abundance in the Poortjie Member of the Teekloof Formation.

5.10.8 Gorgonopsians

The taxonomy of gorgonopsians from the Middle Permian of South Africa is currently in a state of confusion and therefore the genera described from this period are of dubious validity. Combined with the often fragmentary nature of gorgonopsian specimens, generic identifications are unreliable and, as such, individual gorgonopsian genera are not considered in this study. However, specimens

can be identified as gorgonopsian and the taxon is represented by a significant number of specimens.

The stratigraphically lowest gorgonopsian was found in the Combrinkskraal Member, in the lower Abrahamskraal Formation (Rubidge 1995). Gorgonopsians are rare throughout the Abrahamskraal Formation and only increase in significantly in numbers in the Poortjie Member of the Teekloof Formation, reaching their maximum abundance of the Middle Permian in the upper Poortjie Member (Figure 29).

5.10.9 Therocephalians

The therocephalians from the Middle Permian Beaufort Group have their stratigraphically lowest occurrence in the upper Combrinkskraal Member of the Abrahamskraal Formation, from which two genera, *Glanosuchus* and *Ictidosaurus*, are recorded (Abdala *et al.* 2008). These are represented by only two specimens but, unlike other taxa, the genera found in the lower Abrahamskraal Formation are also found in the upper part of the Formation. No therocephalian fossils have been collected from the Leeuvlei Member or Koornplaats Member. Above the mid-Swaerskraal Member, therocephalian abundance steadily increases until the base of the Teekloof Formation, after which their abundance increases at a greater rate throughout the Poortjie Member (Figure 29). Although many specimens attributed to *Pristerognathus* have been considered only as indeterminate scylacosaurids for the purposes of this study (see 5.9.6), they are included in the abundance calculations for the Therocephalia and Scylacosauridae.

Of the two basal families, the Scylacosauridae have their highest overall abundance in the Poortjie Member, while the Lycosuchidae are at their most common in the uppermost Abrahamskraal Formation. Both families are present in the upper Abrahamskraal Formation and Poortjie Member of the Teekloof Formation but only the Scylacosauridae are found in the lower Abrahamskraal Formation (Figure 39). The more derived ictidosuchids and hofmeyriids are only found in the upper Poortjie Member. Overall, therocephalians in the Middle Permian of South Africa have their greatest taxonomic diversity in the Karelskraal Member of the Abrahamskraal

Formation but their greatest abundance in the Poortjie Member of the Teekloof Formation.

5.11. Summary

The stratigraphic distribution of taxa within the Middle Permian strata of the Beaufort Group is rather more complex than previous studies have been able to recognise (e.g. Keyser and Smith 1977; ed. Rubidge 1995). Most individual genera have unique stratigraphic ranges and are not evenly distributed throughout the Abrahamskraal Formation, although there are many more genera that occur only in the upper Abrahamskraal Formation, particularly in the Moordenaars and Karelskraal members (Figure 40). Many taxa have their stratigraphically highest occurrences in the uppermost Abrahamskraal Formation or the lowest Poortjie Member, which strongly implies an extinction event at the top of the *Tapinocephalus* AZ. This will be discussed in more detail in chapter 6.

This more precise understanding of the stratigraphic occurrences of each genus also provides the means to critically examine the existing biostratigraphic paradigm for the lower Beaufort Group, although only dicynodonts, dinocephalians, pareiasaurs and scylacosaurid therocephalians are present in sufficient numbers to be of practical biostratigraphic use. It also allows fossil genera to be better utilised for intra-basinal correlation. Thirdly, the data can be analysed to reveal biodiversity changes through the Middle Permian at a higher resolution than has been possible before. These points will be discussed in the next chapter.

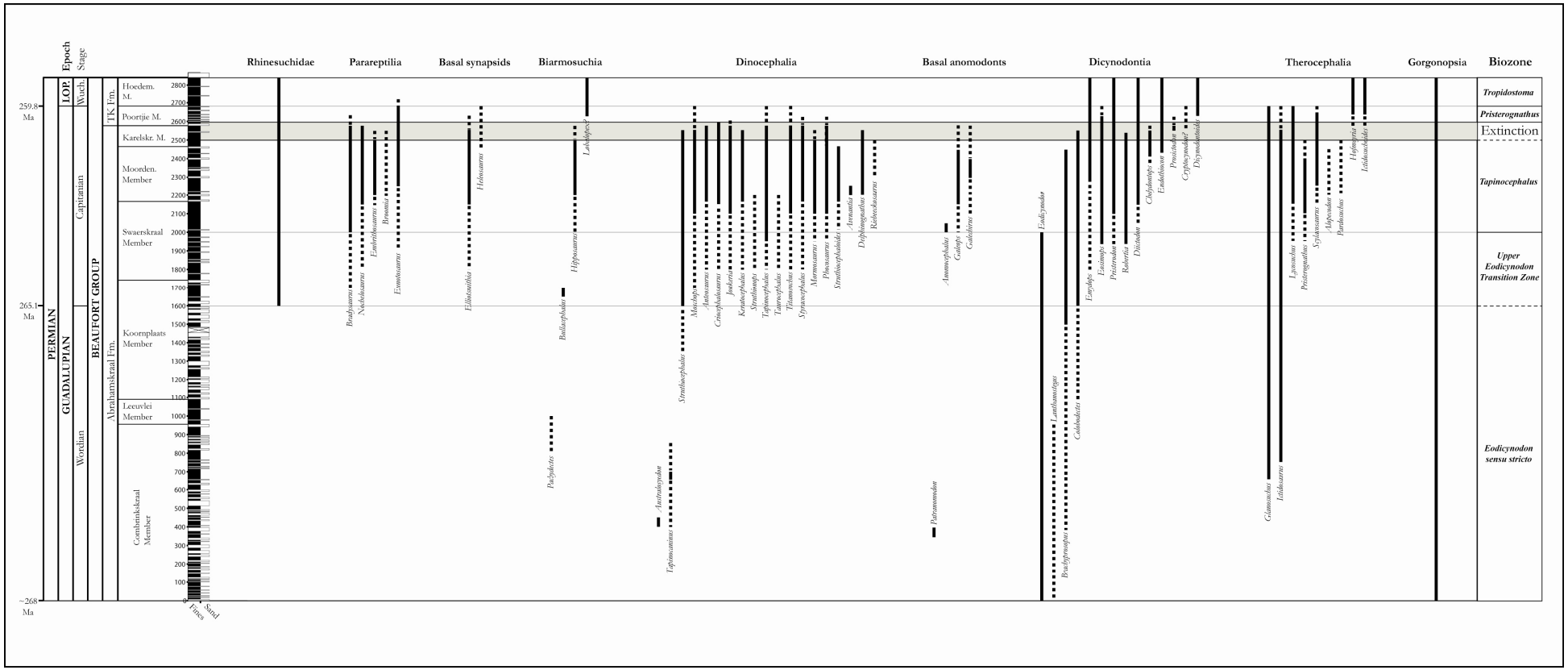


Figure 42. Stratigraphic ranges of all tetrapod genera from the Middle Permian Beaufort Group, inclusive of temnospondyl amphibians and gorgonopsians. LOP. = Lopingian, Wuch. = Wuchiapingian, Hoedem. = Hoedemaker, Karelskr. = Karelskraal.

CHAPTER 6: DISCUSSION

This chapter aims to explore the implications of the data collected during the course of this study. All elements are considered, beginning with the interpretations of the lithostratigraphy of the Abrahamskraal Formation (6.1). This leads on to an analysis of intra-basinal correlations and an evaluation of the Middle Permian tetrapod biostratigraphy of the Beaufort Group based on the occurrences of fossil taxa as detailed in chapter 5 (6.2). The geological aspect of this study is then tied together with an interpretation of Karoo Basin development (6.3).

The biological aspect of this study is first addressed with a review of tetrapod biodiversity change within the Karoo Basin and a description of the end-*Tapinocephalus* AZ extinction (6.4). The chapter is then concluded with a review of global tetrapod diversity change in the Middle Permian and a discussion of the Capitanian mass extinction in light of the new data obtained from the terrestrial Karoo Basin (6.5).

6.1 Lithostratigraphy

6.1.1 Thicknesses

Within the southwest of the Karoo Basin, borehole cores from the Nuweveld highlands and the Koup (SOEKOR cores AB11/65, KW1/67, QU1/65 and SA1/66) have already provided evidence that the Abrahamskraal Formation is thinner north of the Nuweveld Mountains than to the south (borehole localities shown in Figure 5). Along with the additional stratigraphic sections measured around the periphery of the basin, including those measured for this study, the differential thickness of the Abrahamskraal Formation can now be elaborated upon.

At the southern edge of the basin, between 33° 2.0' S and 33° 5.0' S, the Abrahamskraal Formation has a thickness that varies between 2575 m at its thickest, south of Merweville, and 2150 m at its thinnest, south of Beaufort West (Figure 16). This is similar to the thickness of approximately 2500 m interpreted for the Abrahamskraal Formation at the Klein Waterval syncline based on core KW1/67

(LeRoux 1985), although this is only an approximation as the definition of the Ecca-Beaufort contact has changed since this interpretation was made (Rubidge 1987, 1988). These are the thickest occurrences of the Abrahamskraal Formation.

At the latitude of Merweville, around 32° 40.0' S, the Abrahamskraal Formation is thinner. Core SA1/66, which was drilled at a locality near Merweville, records a thickness of approximately 1100 m for Beaufort Group rocks in the subsurface (Le Roux 1985). According to Jirah (2013), the locality of this core (on the farm Hamelkraal) is stratigraphically positioned within the upper part of his 'Mudstone B,' which forms the upper 165 m of the Swaerskraal Member of the Abrahamskraal Formation (see 4.2.4). When extrapolated from the stratigraphic section measured through this area (see 4.1.2.5), approximately 400 m of Abrahamskraal Formation strata have been eroded from the Hamelkraal locality (Figure 19). This suggests a total thickness for the Abrahamskraal Formation near Merweville of over 1500 m, which is similar to the estimated thickness of 1534 m for the Abrahamskraal Formation at Verlatenkloof (Figure 5; Figure 8). Because both localities occur at similar latitudes, this supports a northward thinning of the Abrahamskraal Formation that is already evident 50 km north of the southern margin of the basin.

To the north of the escarpment, there is less opportunity to compare stratigraphic sections measured on the surface to those measured from borehole cores. The majority of stratigraphic information for this area is derived from cores QU1/65 and AB1/65, which are situated at similar latitudes between 31° 47.0' S and 31° 49.0' S. At Fraserburg, QU1/65 records 500 m of subsurface Abrahamskraal Formation rocks with around another 50 m of missing rock below the base of the Poortjie Member, providing a total thickness for the Abrahamskraal Formation at this locality of approximately 550 m (see 4.1.1.3**;** Figure 8). Core AB1/65, situated on the farm Abrams Kraal in the Victoria West district, records a thickness of only 390 m for the Abrahamskraal Formation at this locality (Figure 8). This further supports the northward thinning of the Abrahamskraal Formation when compared to thicknesses measured further south. It also indicates that the Abrahamskraal Formation is thinner in the east than in the west at this latitude.

This appears to be the result of progradation mediated by the east-south-east fluvial transport system of Cole and Wipplinger (2001). Because this fluvial transport system

has been shown to have deposited the lower parts of the Abrahamskraal Formation at both of these localities (Cole and Wipplinger 2001), terrestrial sedimentation would have entered the basin from the northwest and so the more proximal areas would have experienced greater deposition. The Abrahamskraal Formation is therefore thicker in the northwest.

The northernmost stratigraphic section in the south-western Karoo Basin was measured on the farm Spuitpoort, north of Victoria West, between the Ecca-Beaufort contact at latitude 31° 4.0' S and the base of the Poortjie Member of the Teekloof Formation at latitude 31° 10.0' S (Figure 8**;** Figure 9). At this locality, the Abrahamskraal Formation is perhaps only 45 m thick or less, which is its thinnest occurrence of any locality at which it has been measured. This indicates that the Abrahamskraal Formation pinches out not far to the northeast of Victoria West.

In the east, the Koonap Formation experiences a considerable drop in thickness between Klipplaat and the localities along the Great Fish River (Figure 16). This is not due to a great variance in latitude but rather to the more distal position of the latter localities. The Koonap Formation at both The Grant (4.1.3.2) and Bucklands (4.1.3.3) is similar in thickness and is approximately 900 m thinner than the Koonap Formation at Klipplaat. Because of the paucity of stratigraphic sections in the Eastern Cape Province, it is difficult to identify at which point the Koonap Formation reduces in thickness; however, at Klipplaat it is more comparable in thickness with the Abrahamskraal Formation to the west and this suggests that Koonap Formation experiences a relatively rapid reduction in thickness to the east of Klipplaat but to the west of the great Fish River, where it is between 1420 m and 1445 m thick.

All lithostratigraphic units are established to become thinner in a north-western, distal direction. This is important in reconstructing basin development.

6.1.2 Distribution of Members in the Abrahamskraal Formation

Along the southern margin of the basin, where the Abrahamskraal Formation is at its most complete, six stratigraphic sections have been measured or collated in the course of this study (see 4.1.2.1, 4.1.2.2, 4.1.2.4, 4.1.2.5, 4.1.2.7, 4.1.2.8; Figure 5). From these stratigraphic sections, up to five fining-upwards megacycles have been recognised in the Abrahamskraal Formation, comprising six members (the Combrinkskraal, Leeuvlei, Koornplaats, Swaerskraal, Moordenaars and Karelskraal members). The distribution of sandstone packages and hence of individual members is not identical across the southern margin of the basin but a pattern is clear. In particular, the similarity between the stratigraphy at the Wilgerbos locality at the southwest corner of the Koup (4.1.2.2), the Merweville locality in the central Koup (4.1.2.5) and the Jansens kraal locality in the south-eastern Koup (4.1.2.8), indicates some common regulatory factor in their deposition.

The similarities are greatest between the stratigraphy of the Abrahamskraal Formation at the Wilgerbos locality and the Jansens kraal locality at opposite ends of the southern Koup region, although at the latter locality it is more argillaceous; the thickness of Abrahamskraal Formation at these two localities is also less than at either the Prince Albert Road/Merweville or Combrinkskraal localities in the central Koup (Figure 16). Furthermore, at Dwyka River (4.1.2.4), Prince Albert Road (4.1.2.5) and Combrinkskraal (4.1.2.7), the Abrahamskraal Formation is relatively arenaceous in its lower two thirds, and the sandstone-rich Koornplaats Member is far more pronounced than at localities at the eastern and western boundaries of the Koup. There is therefore a vague symmetry within the Koup region, with the Abrahamskraal Formation being thicker and more arenaceous in the central part of that region than to either the east or west.

This demonstrates the deposition of a greater amount of coarse material in the lower two thirds of the Abrahamskraal Formation in the central Koup, which may indicate the presence in this area of a major distributory system or megafan, originating in the higher ground to the south (Figure 41 – Time 2). Such structures have been described from the modern Himalayan (deCelles and Cavazza 1999) and Andean (Horton and deCelles 2001) foreland basins. Above the Koornplaats Member of the Abrahamskraal Formation, the position of a megafan is less distinct, as the

Swaerskraal, Moordenaars and Karelskraal Members of the Abrahamskraal are less heterogeneous (Figure 16).

Despite the similarities in the lithostratigraphy in the south-western part of the basin and the apparent symmetry about the central Koup region, the surface expression of the members of the Abrahamskraal Formation does not reflect this; more specifically, the members exposed in the western Koup are older than those exposed in the west. This is due to a gentle but steady eastwards dip in the Beaufort Group strata in the south-western Karoo Basin, as first recognised by Stear (1980). The western Koup exposes the upper Koornplaats Member and the Swaerskraal Member, which dip under the Moordenaars Member just to the west of Merweville (Figure 25). The Moordenaars Member is exposed over most of the central and eastern Koup, before it in turn dips below the Karelskraal Member and then the Poortjie Member of the Teekloof Formation. However, because the stratigraphy is rather argillaceous in the eastern Koup, the Karelskraal Member is difficult to identify in outcrop. The altitude of the base of the Teekloof Formation corroborates this phenomenon: this horizon is ~1622 m above sea level on the eastern Komsberg Mountains, 1190 m above sea level north of Merweville and 851 m above sea level at the eastern border of the Koup, 35 km south of Beaufort West.

6.1.3 Changes to existing geological maps

Two potential alterations to the existing geological maps of the study area are suggested by the stratigraphic data now available. Firstly, the stratigraphic section measured at Spuitpoort, in the Victoria West district, has identified the Poortjie Member at this locality (see 4.1.1.2; Figure 5). The sandstone package that is exposed on the lower part of the hill at Spuitpoort is currently mapped as Abrahamskraal Formation, but a volcanic ash horizon near its upper boundary has yielded a Ur/Pb date of 260.9 Ma (Rubidge pers. comm. 2012), which indicates a *Pristerognathus* AZ age for this unit (Rubidge *et al.* 2013). Consequently, this sandstone package is recognised as the Poortjie Member of the Teekloof Formation and can be updated on the 1:250 000 geological map of the area (map sheet: Republic of South Africa 3122, Victoria West, 1:250 000 Geological Series 1992).

The second potential alteration concerns the presence of the Poortjie Member at Elandsberg, just east of Prince Albert Road, as currently mapped (map sheet: Republic of South Africa 3220, Sutherland, 1:250 000 Geological Series 1983). The thickness found by Jirah (2009) to the base of the Poortjie Member as mapped on Elandsberg was 1860 m from the first purple mudstone, plus 606 m which was subsequently measured from the Ecca–Beaufort contact to the first purple mudstone (Jirah 2013). This provides a total thickness of 2466 m for the Abrahamskraal Formation below Elandsberg, which is 109 m less than when the Abrahamskraal Formation is measured up to the base of the Poortjie Member as exposed on the Nuweveld Escarpment (Figure 19). Although the great thickness allows for some variation in result, it can be assumed that if the Abrahamskraal Formation becomes thinner towards the north, then its total thickness should be greater at Prince Albert Road than further north, not less. Despite this reasoning, the strata that cap Elandsberg do contain a great abundance of sandstone and so the presence of the Poortjie Member is only deemed to be uncertain.

6.2 Middle Permian Beaufort Group Biostratigraphy and Intra-basinal Correlation

Although sandstone packages can be recognised in stratigraphic sections throughout the south-western part of the Karoo Basin, they cannot currently be distinguished through lithological characteristics and therefore cannot be easily identified in outcrop at ground level. The Abrahamskraal Formation contains no other geographically widespread lithological marker horizons that could be used to easily correlate geographically disparate localities. Furthermore, the Abrahamskraal Formation represents fluvial sedimentation where sandstone packages are not necessarily coeval throughout the basin; this can only be determined through biostratigraphy, as with the base of the Poortjie Member (Keyser and Smith 1977; ed. Rubidge 1995).

6.2.1 Indicator taxa

For biostratigraphic correlation, dicynodont fossils are the most useful as they are abundant and the most likely to be identifiable, which prompted Rubidge and Angielczyk (2009) and Angielczyk and Rubidge (2012) to propose a biostratigraphic divisions of the Abrahamskraal Formation based primarily on the first appearance of dicynodont genera. Not all genera of dicynodonts fulfil these criteria but six genera are of particular biostratigraphic use.

Eodicynodon has been found primarily in the Combrinkskraal Member along the southern margin of the basin between Laingsburg and Rietbron (5.7.9). It is therefore a good indicator for the oldest Beaufort rocks and, as it has been found as high as the upper Koornplaats Member in the Laingsburg sector, has a stratigraphic range corresponding to the lower 2000 m of the Abrahamskraal Formation at its thickest point (Figure 35**;** Figure 36). The lower Koonap Formation is expected to be of *Eodicynodon* AZ age on the basis of thickness (see 5.4.3) but only the discovery of an *Eodicynodon* AZ fauna there would confirm this.

Robertia is restricted to the *Tapinocephalus* AZ as currently defined (5.7.14). This genus occurs mostly in the Swaerskraal and Moordenaars Members of the Abrahamskraal Formation, although in several sectors in the south-western part of the basin it occurs as low as the uppermost Koornplaats Member (Figure 36). As its stratigraphic range extends from 1950m to 2550 m above the base of the Abrahamskraal Formation at its thickest point and overlaps only slightly with the stratigraphic range of *Eodicynodon*, the genus is therefore a good indicator taxon for the uppermost part of the Abrahamskraal Formation. The related genus *Eosimops* has a similar stratigraphic range to *Robertia*, having its stratigraphically lowest occurrence at the same horizon in the upper Koornplaats Member, although in the Beaufort West sector (5.7.10). However, *Eosimops* is also present in the *Pristerognathus* AZ, so the presence of *Eosimops* in the absence of *Robertia* and dinocephalians would therefore be indicative of a *Pristerognathus* AZ fauna.

Pristerodon has less biostratigraphic use than the other dicynodont taxa. Its stratigraphically lowest occurrence is in the Swaerskraal Member in the Laingsburg sector (5.7.12), which corresponds to a horizon 2100 m above the base of the

Abrahamskraal Formation at its thickest point (Figure 37). This means that the stratigraphic range of *Pristerodon* does not overlap with that of *Eodicynodon* and its first appearance is also slightly higher stratigraphically than that of *Robertia* or *Eosimops*. The greatest utility of *Pristerodon* lies in its relative rarity in the Abrahamskraal Formation compared to its abundance in the Poortjie Member of the Teekloof Formation.

The most common dicynodont genus is *Diictodon*. Its first appearance is at the base of the Moordenaars Member in the Merweville sector, approximately 2150 m above the base of the Abrahamskraal Formation at its thickest point (5.7.6), which is slightly later than *Pristerodon* (Figure 37). One instance where this genus has proved useful is in the north-west, where the genus is found just above the Ecca-Beaufort boundary north of Fraserburg. This locality is stratigraphically within the Kopjesfontein Member, the stratigraphically lowest unit in the northwest of the basin, and therefore indicates that the first terrestrial sedimentation began in the northwest of the basin after the first appearance of *Diictodon*. As a distal part of the Moordenaars Member occurs in the Fraserburg sector stratigraphically above the Kopjesfontein Member, and *Diictodon* first appears at the base of the Moordenaars Member along the southern margin of the basin, the Kopjesfontein Member must correlate with the lower Moordenaars Member of the Abrahamskraal Formation in the south of the basin. *Diictodon* also becomes considerably more abundant into the *Pristerognathus* AZ.

The last biostratigraphically useful dicynodont is *Colobodectes*, which has its first appearance at the base of the Koornplaats Member in the Sutherland sector and occurs up to the top of the Abrahamskraal Formation (5.7.3). *Colobodectes* has not yet been found in the south of the basin, but five specimens are known from north of the Great Escarpment. It is therefore potentially restricted to this part of the basin. If the genus does occur in the south of the basin, correlation of the Ouberg Pass locality suggests that its stratigraphically lowest occurrence should be in the Koornplaats Member.

Dinocephalians remain useful biostratigraphic indicators but, due to the often fragmentary nature of their fossils, they are most useful as a taxon rather than at genus level. Dinocephalians are most abundant in the upper Abrahamskraal

Formation, particularly within the Moordenaars Member, although they are found throughout the Abrahamskraal Formation and in the lowermost Poortjie member of the Teekloof Formation (Figure 29). Of the derived tapinocephalid genera present in the Beaufort Group of South Africa (all tapinocephalids excluding *Tapinocaninus*), no genus is known to occur below the Swaerskraal Member except *Struthiocephalus*, which first appears in the uppermost Leeuvlei member in the Laingsburg sector, equivalent to the upper Koornplaats Member of the Abrahamskraal Formation at its thickest point. Within the Abrahamskraal Formation, therefore, advanced tapinocephalids are indicative of the upper half of the Formation only.

Pareiasaurs also remain useful biostratigraphic indicators within the Middle Permian, as they are securely restricted to the upper Abrahamskraal Formation. The absence of dinocephalians and pareiasaurs in the Philippolis area, along with the presence of other Middle Permian genera such as *Eunotosaurus* and scylacosaurid therocephalians, therefore suggests an upper *Pristerognathus* AZ age for this locality.

In the southwest of the basin, the parareptile *Eunotosaurus* occurs within the upper Abrahamskraal Formation, from the lower Moordenaars Member, up to the top of the Poortjie Member of the Teekloof Formation (Figure 28). This corresponds to the majority of the *Tapinocephalus* AZ and the *Pristerognathus* AZ. In the southeast of the basin it occurs in the upper 700 m of the Koonap Formation and in the basal Middleton Formation (Figure 27). The distribution of *Eunotosaurus* thereby supports the temporal equivalence of the base of the Teekloof and Middleton Formations and thus the lithological equivalence of the Abrahamskraal and Koonap formations (Day *et al.* 2013; Hill 1993).

Scylacosaurid therocephalians are present throughout the Middle Permian but can be used as biostratigraphic indicator in that they are considerably more common in the *Pristerognathus* AZ than in the Abrahamskraal Formation (Figure 29).

6.2.2 Biostratigraphic nomenclature

From the data generated for this thesis, it is clear that the biostratigraphy of the Middle Permian Beaufort sequence has been, up until now, very generalised. Due to

the size of the basin and the difficulty in subdividing the homogeneous fluvial sequence, ranges assigned to taxa of this age have varied greatly between publications on the subject, often being assumed cover entire biozones (e.g. Fröbisch 2009; Keyser and Smith 1977; Nicolas and Rubidge 2009; ed. Rubidge 1995). However, collecting work conducted in South Africa over recent decades, along with the advent of new technologies, has allowed a far more refined interpretation of the biostratigraphy.

When the stratigraphic ranges of existing indicator taxa for the *Eodicynodon* (*Eodicynodon*) and *Tapinocephalus* (*Tapinocephalus* and *Bradysaurus*) AZs are considered, both biozones are supported (see ed. Rubidge 1995). This is because the last occurrence of *Eodicynodon* at 2000 m above the base of the Abrahamskraal Formation coincides closely with the first certain appearance of *Tapinocephalus* (at 1950 m) and *Bradysaurus* (at 2000 m). The first appearance of *Robertia* at 1950 m and its disappearance in the uppermost Abrahamskraal Formation makes it an additional indicator taxon for the *Tapinocephalus* AZ.

The boundary between the *Eodicynodon* and *Tapinocephalus* AZs is less clear then in the past. Although *Tapinocephalus* and *Bradysaurus* only appear at a similar horizon to the last occurrence of *Eodicynodon*, the advanced tapinocephalid genus *Struthiocephalus* and the dicynodont *Colobodectes* are both present from 1600 m above the base of the Abrahamskraal Formation. Furthermore, eighteen *Tapinocephalus* AZ genera have potential first appearances between 1600 m and 2000 m. This indicates that at least some and possibly more typically *Tapinocephalus* AZ forms appear within the range of *Eodicynodon*. A transition zone is therefore recognised between the *Eodicynodon* and *Tapinocephalus* AZs, corresponding to the upper 400 m of the *Eodicynodon* AZ.

The *Pristerognathus* AZ cannot be better defined than it already is (Smith and Keyser 1995b), but its stratigraphic extent is reduced based on the presence of dinocephalians in the lowest Poortjie Member.

It is proposed here that the existing biozones of the Middle Permian Beaufort Group are upheld, excepting alterations in their extent and the recognition of a transition zone between the *Eodicynodon* and *Tapinocephalus* AZs. These are:

1) *Eodicynodon* AZ *sensu stricto*, 0–1600 m

This unit is defined on the presence of the dicynodont *Eodicynodon* in the absence of derived tapinocephalid dinocephalians. This unit occupies the lower 1600 m of the Abrahamskraal Formation at its thickest point, corresponding to lithostratigraphic units below the upper Koornplaats Member, and is bounded below by the Ecca-Beaufort contact and above by the first appearance of the tapinocephalid dinocephalian *Struthiocephalus*. This unit contains all previously described *Eodicynodon* AZ taxa.

2) Upper *Eodicynodon* AZ transition zone, 1600–2000 m

This unit is defined on the presence of both *Eodicynodon* and *Struthiocephalus* and corresponds to the uppermost Koornplaats Member and lower Swaerskraal member of the Abrahamskraal Formation at its thickest point, 1600–2000 m above its base. It is bounded below by the first appearance of *Struthiocephalus* and above by the last appearance of *Eodicynodon* and the first appearance of *Bradysaurus*, *Tapinocephalus, Moschops* and *Robertia*. This unit is poorly fossiliferous but the stratigraphic ranges of the dicynodonts *Brachyprosopus* and *Colobodectes* range throughout it. It represents the transition period between the underlying *Eodicynodon* AZ *sensu stricto* and overlying *Tapinocephalus* AZ faunas.

3) *Tapinocephalus* AZ, 2000 m (Abrahamskraal Formation)–50 m (Teekloof Formation)

This unit is defined on the presence of *Tapinocephalus* and *Bradysaurus* in the absence of *Eodicynodon* and corresponds to the uppermost Swaerskraal Member, Moordenaars Member and Karelskraal Member of the Abrahamskraal Formation, from 2000m above its base up to the lower Poortjie Member of the overlying Teekloof Formation. It is bounded below by the first appearance of *Bradysaurus* and the last appearance of *Eodicynodon* and above by the last appearance of basal pareiasaurs and dinocephalians. The stratigraphic ranges of basal pareiasaurs and the dicynodont *Robertia* are restricted to this interval, as are many rarer forms, and it is where dinocephalians are most abundant. The top of this unit are still poorly defined, based as it is on the disappearance of dinocephalians, but it coincides with point of lowest generic diversity associated with the end-*Tapinocephalus* AZ extinction.

4) *Pristerognathus* AZ

This unit is defined by the dominance of scylacosaurid therocephalians and the abundance of the dicynodont *Diictodon* in the absence of dinocephalians. The base of this biozone is hard to pin-point, but it occurs above the base of the Poortjie Member where dinocephalians are now recorded. In the field, it is primarily evident by the abundance of *Diictodon* and *Pristerodon* and the presence of *Eosimops*, *Eunotosaurus* and basal therocephalians, in combination with a conspicuous lack of large animals. The top of the biozone coincides with the first appearance of the dicynodont *Tropidostoma*, the last occurrences of scylacosaurid and lycosuchid therocephalians and the last occurrence of *Eunotosaurus*.

6.2.3 Collecting Bias

Collecting bias is a real concern in large-scale diversity studies involving geographically wide areas. While this debate continues, recent studies that have discussed the Karoo Basin have concluded that although collecting at the basin level has been relatively even (Nicolas and Rubidge 2009), outcrop area has a positive correlation with the number of genera recorded from any particular stratigraphic unit (e.g. Fröbisch 2013). The reason for the paucity of fossil occurrences in the central part of the Abrahamskraal Formation is at least partly a result of collection biases related to the area of outcrop for each stratigraphic level, rather than a genuine paucity of tetrapod life. The Moordenaars Member is exposed over a greater area than any other and so it is logical that most specimens were found in this interval (Figure 25). Furthermore, most collecting efforts have been concentrated in the Koup region due to the relatively flat topography and the exposure of near horizontal beds, which yield the greatest number of fossils, if not the greatest number of those *in situ*; this area covers exposure almost exclusively of the Moordenaars and Karelskraal members, which has exacerbated the bias.

Even when outcrop is uniformly exposed (visible), the potential to find fossils is not necessarily the same, as when folding causes beds to dip steeply, the potential to find fossils is significantly reduced. Within the lowest part of the Abrahamskraal Formation, the Combrinkskraal Member has the poorest, most folded and

geographically most restricted outcrop of all the Middle Permian members of the Beaufort Group. Fossils have only been found here due to intensive targeted collecting conducted over the last 30 years (e.g. Rubidge 1988). Conversely, the middle part of the Abrahamskraal Formation, inclusive of the Leeuvlei, Koornplaats and lower Swaerskraal members, has not been specifically collected and therefore, although it has better outcrop and is exposed over a greater area than the underlying Combrinkskraal Member, has yielded practically no fossil material. This interval covers the upper part of the *Eodicynodon* AZ and the mid-Abrahamskraal Formation Transition Zone, which frustrates any study of the *Eodicynodon-Tapinocephalus* AZ transition at present.

The Poortjie Member has been well collected, which lends greater confidence to the results of diversity change across the *Tapinocephalus-Pristerognathus* AZ transition.

6.3 Karoo Basin Development

With the lithostratigraphy of the Middle Permian part of the Beaufort Group better understood and with the recognition of biostratigraphically useful taxa identified, it is now possible to use this information to reconstruct the formation of the Karoo Basin during the late Middle Permian. The number of lithostratigraphic sections used in this study is greater than in any previous study and therefore allows a higher resolution depiction of terrestrial deposition in the basin during this time.

6.3.1 The Karoo Basin: flexural retroarc foreland basin or Ramp syncline

Two major possibilities exist for the formation of the Karoo Basin: 1) the flexural model, whereby the Karoo Basin formed as a retroarc foreland basin directly linked to orogenic loading in the Cape Fold Belt (e.g. Catuneanu *et al.* 1998; Cole 1992), and 2) the ramp syncline model, whereby differential subsidence of basement blocks occurred in response to crustal tension (Tankard *et al.* 2009). Both models posit subduction along the southern margin of Gondwanaland as the underlying cause but they differ in the nature of the stress experienced by the crust, at least during lower

Beaufort Group deposition, and, consequently, in the timing of the onset of orogenic activity in the Cape Fold Belt.

The flexural model accepts the dates of Hälbich (1983) as a basis for when orogenic activity began (Catuneanu *et al.* 1998). This suggests that crustal compression was occurring from at least the Early Permian, with the termination of the first 'paroxysm,' or compression event, at approximately 278 million years ago (Hälbich 1983). Le Roux *et al.* (1994) described monoclinal folds in south of the Karoo Basin that were associated with channel sandstones, which he claimed was evidence that the folding was syndepositional. Such a phenomenon is potentially responsible for the greater east-west orientation of palaeocurrent directions recorded along the southern margin of the basin (Cole and Wipplinger 2001; Le Roux *et al.* 1994; Theron 1973).

Alternatively, the ramp syncline model disputes this on the basis that bedding orientation of the Ecca and Beaufort groups in the south of the basin runs parallel to the top of a tectonic wedge, as evidenced by seismic reflection graphs; this is used to imply that sedimentation occurred before the tectonic folding of the Beaufort rocks in the south of the basin (Tankard *et al.* 2009). The absence of syndepositional deformation of the Lower Beaufort Group strata has also been supported by deep-burial diagenetics, which indicate that tectonic induced cleavage planes of mineral grains deposited in the basin post-date the formation of early diagenetic minerals (de Swardt and Rowsell 1974). While this does not categorically disprove the occurrence of tectonic activity before diagenesis, the first evidence for Cape Supergroup-derived rocks in the Karoo Supergroup is in the Katberg Formation, which would seem to corroborate a lack of significant uplift in the Cape Fold Belt prior to the Triassic (Andersson 2004; Johnson 1991).

6.3.1.1 Sediment source

The absence in the Lower Beaufort rocks of lithic fragments derived from the Cape Supergroup is hard to explain if the Cape Fold Belt existed near the southern margin of the basin, where its primary source area was situated (Cole and Wipplinger 2001; Johnson 1991; Theron 1975). Several studies have demonstrated that orogenic thrust

belts provide the primary sediment source for associated foreland basins (e.g. DeCelles & Hertel 1989; Schwab 1986), which would indicate the absence of such an orogen during deposition of the Lower Beaufort Group. In addition, the fine grain size of the lower Beaufort rocks suggests a distant source area (Johnson 1976; Stear 1980), but the transport of sediment to the basin from the south would have been prevented by the Cape Fold Mountains if they had existed at that time. The ramp syncline model fails to provide an alternative sediment source, although Johnson (1976) calculated the source area to consist primarily of felsic volcanic rocks.

Hälbich (1983) provide a possible alternative sediment source for the Lower Beaufort Group. Within lower Beaufort Group rocks, they recognised minerals in lithic fragments that had been subjected to tectonic compression, which they dated to approximately 292 Ma. This pre-dated Beaufort sedimentation and provided a clue to the age of the sediment source rock. They subsequently found evidence of metamorphic minerals formed at this time within Gezwinds Kraal phyllite, which forms part of the Kango Formation and which is exposed on the southern side of the Swartberg. It was also posited that the exposure of granite basement in the George Anticlinorium became a more significant source during deposition of the Abrahamskraal Formation (Hälbich 1983).

Yet even if older granite basement or Kango Group sediments formed the source for the lower Beaufort Group (Hälbich 1983), rocks of the overlying Cape Supergroup would have to have been eroded first and so evidence of Cape Supergroup derived lithics should therefore be represented in the Ecca Group. It has been proposed that coarse, quartzite derived sediments typical of the Witteberg Group may have been captured in the proximal regions of the basin if rate of subsidence was high (Flemings and Jordan 1989) but today the most proximal regions of the Karoo Basin have been removed by erosion and this is impossible to test.

Scott (1997; In Andersson *et al.* 2004) found heavy mineral suites within the middle and upper Ecca Group that consistent with a high-grade metamorphic source terrane, which could probably be found between the subduction-related magmatic arc far to the south and an incipient, still submerged Cape Fold Belt. Andersson *et al.* (2004) described an increasingly igneous source in the Skoorsteenberg Formation of the upper Ecca Group and, along with the other data for igneous and metamorphic

sediment provenance, used this to suggest the exposure of Saldanian (Pan-African) basement during incipient Ecca Group deposition. More specifically, they suggest that compression and uplift of the mountain belt began to the south of the existing remnant, beyond the extent of the Cape Supergroup. Such a theory agrees with the suggestion of Cole (1992) that the Cape Fold Mountains had not yet risen above sea level during deposition of the lower Ecca Group, and that the mountain belt extended further to the south. In this case, the southern part of the mountain belt would have been actively uplifted, while sediment derived from there bypassed much of the still low-lying Cape Supergroup.

Alternatively, axial flow along the southern margin of the basin, a suggested by palaeocurrent directions there (Cole and Wipplinger 2001; Theron 1975), may indicate that lower Beaufort Group sediment was not necessarily derived from the orogen at all times (Clevis *et al.* 2004). In this case, sediment could have originated in areas to the south-west and south-east of the basin, from the syntaxis of the southern and western branches of the Cape Fold Mountains (for the south-western Karoo) or from Antarctica (for the south-eastern Karoo). This could explain the lack of Cape Supergroup-derived material in the Lower Beaufort Group, but does not provide any better suggestions for potential source areas. In order to pursue this line of enquiry, it is necessary to conduct more specific petrographic work on the lower Beaufort Group in the south-west of the basin, as well as further investigate potential source rocks in South America, the Falkland Islands and Antarctica.

6.3.1.2 Timing of Cape Fold Belt initiation

In terms of timing, while Tankard *et al.* (2009) claim that no compression had occurred in the Cape Fold Belt in the Permian, Hälbich (1983) and Hälbich (1992) found that several stages of compression could be dated by the formation age of metamorphic minerals along cleavage planes in rocks of the Cape Fold Mountains. This evidence suggests a multiple event orogen, with the first 'paroxysm' ending around 278 Ma, and Hälbich (1983) state that the Dwyka Group was the youngest unit to have been affected by this paroxysm and that the lower Ecca Group was being deposited at the time. A radiometric date of 274.8 ± 1.5 Ma has been obtained

for the lower Collingham Formation (Fildani *et al.* 2007), which supports the deposition of the upper Ecca Group at the termination of 'paroxysm' 1. This suggests the formation of the Cape Fold Mountains closest to the basin well within the Permian, contrary to Andersson *et al.* (2004) Cole (1992).

6.3.1.3 Tectonics

DeCelles and Giles (1996) describe the morphology of foreland basins as being separated into four regions: the wedge-top, foredeep, forebulge and backbulge. Catuneanu *et al.* (1998) considered the south and south-western part of the exposed Karoo Basin to form the foredeep and the north-east of the basin to form the forebulge, with a hinge-line that was mobile through time. However, rocks of the Ecca and lowest Beaufort Group strata in the south of the basin are heavily folded and dip steeply to the north, indicating that the basin previously extended further south than it does today, having been truncated by the development of the Cape Fold Mountains. The orogen was therefore situated further to the south than its existing remnant.

Dynamic subsidence has been cited as the reason for subsidence across this area of southern Gondwanaland (Cole 1992; Lock 1980; Pysklywec and Mitrovica 1999). This helps explain the great extent of Karoo sedimentation, but not the great distances over which flexural dynamics are proposed to occur (Catuneanu *et al.* 1998). The maximum width of described, extant foredeep regions is around 300 km (DeCelles and Giles 1996), a distance far exceeded by the Karoo Basin if the orogenic belt was south of the current position of the Swartberg Mountains. More specifically, simulations suggest that beyond 400 km from the maximum foredeep subsidence, flexural subsidence does not contribute anything to the observed level subsidence (Pysklywec and Mitrovica 1999). The model of Catuneanu *et al.* (1998) also conflicts with claims that the basin existed in an under-filled state during early Ecca deposition and an over-filled state during Beaufort deposition, because if deposition beyond the foreland system defines an overfilled state, then the presence of both Ecca and Dwyka Group rocks in the north of the main basin indicates and overfilled state during early Karoo deposition as well.

Biostratigraphically, the most northerly occurrence of the *Tapinocephalus* AZ is in the vicinity of Victoria West and further north, as far as Philippolis, the *Pristerognathus* AZ is present above the Waterford Formation of the Ecca Group (Welman *et al.* 2001). Further north, to the southeast of Jagersfontein, the *Dicynodon* AZ is present immediately above the Ecca-Beaufort contact (ed. Rubidge 1995). In the 55 km between Philippolis and Jagersfontein, the *Tropidostoma* and *Cistecepahalus* assemblage zones should directly overlie the Ecca Group but this has not yet been identified due to the poor outcrop and must be very limited if (Van der Walt *et al.* 2010). This may be explained as a result of localized faulting along the Doringberg fault described by Tankard *et al.* (2009). A short period of fault activity, whereby the Namaqua-Natal basement block descended against the Kaapvaal Craton, could have created enough accommodation space to arrest the progradation of the shoreline into the Ecca Sea for the duration of the *Tropidostoma* and *Cistecephalus* assemblage zones. The geographically extensive presence of the *Dicynodon* AZ immediately above the Ecca Group to the north of Jagersfontein indicates the onset of progradation. Alternatively, the arrest of shoreline progradation during the *Tropidostoma* and *Cistecephalus* assemblage zones could be explained by a reduction in sediment input due to source area denudation.

Faulting is the primary cause of subsidence in the ramp syncline model but is not incompatible with the flexural foreland basin model. On the contrary, both Hälbich (1992) and Cole (1992) ascribe the earliest subsidence of the Karoo Basin to faulting along a zone of weakness corresponding to the suture between the Namaqua-Natal and Saldanian basement blocks. This faulting was responsible for creating the accommodation space in which the Dwyka Group was deposited, before the onset of Cape Fold Belt compression during deposition of the Ecca Group. Once the Cape Fold Mountains were established, it is agreed by most authors that subsidence related to orogenic loading predominated, at least in the foredeep (Cole 1992; Hälbich 1992; Pysklywec and Mitrovica 1999). Once orogenic activity became the primary influence of the Karoo Basin, flexural responses to periods of loading or unloading would have determined the location and magnitude of sedimentation (Catuneanu *et al.* 1998). Another factor potentially affecting accommodation space during this time was dynamic loading, caused by the behaviour of the subducting plate beneath the Karoo Basin (Catuneanu *et al.* 2002; Pysklywec and Mitrovica 1999). In this updated model,

the sedimentary base level within the basin would therefore be controlled by a combination of these two factors, with flexural subsidence leading to localised deposition and dynamic subsidence to basin-wide deposition.

The flexural model of Catuneanu *et al.* (1998) dictates that when flexural processes predominate, deposition in the proximal and distal parts of the Karoo Basin is reciprocal, i.e. deposition in one area is coeval with non-deposition or erosion in the other. This model therefore proposes that the deep water upper Volksrust Formation was deposited in the distal part of the basin concurrently with deposition of the lower Beaufort Group in the proximal part of the basin. However, it seems unlikely that the lower Beaufort Group was deposited during a period of proximal uplift, as attested by the thick rock sequence in the proximal part of the basin and the far thinner sequence in distal area; indeed, the Abrahamskraal Formation is over 2000 m thick along most of the southern margin of the Karoo and less the 50 m thick north of Victoria West.

Within the southwest of the basin, the Ecca-Beaufort contact is diachronous and the *Eodicynodon* AZ is present only along the southern margin of the basin between Laingsburg and Rietbron (Figure 1; ed. Rubidge 1995; Rubidge *et al.* 1999; Van der Walt *et al.* 2010). The *Tapinocephalus* AZ then occurs immediately above the Ecca Group from a point north of Laingsburg to the vicinity of Victoria West, a distance of 300 km, while the *Pristerognathus* AZ occurs immediately above the contact from Victoria West as far as Philippolis, a distance of 250 km (ed. Rubidge 1995; Van der Walt *et al.* 2010; Welman *et al.* 2001). The distance of contact between each biozone and the Ecca Group is approximately linked to the distance that the shoreline prograded during that biozone. The *Eodicynodon* AZ is the thickest of these biozones and the *Pristerognathus* AZ is by far the thinnest (Figure 40), yet the geographical area of the *Eodicynodon* AZ is most restricted and the *Pristerognathus* AZ most widespread when including the rock that has now been eroded. This inverse relationship between biozone thickness and area suggests that subsidence was high during the *Eodicynodon* AZ, where most sediment was caught in the proximal southern part of the basin, but was waned throughout the late Middle Permian leading to reduced sedimentation in proximal areas during the *Pristerognathus* AZ but a greater transport of sediment to more distal parts of the basin.

6.3.1.4 Sandstone Packages

Only the flexural model attempts to explain finer-scale stratigraphic phenomena. Catuneanu and Bowker (2001) and Catuneanu and Elango (2001) supported a tectonic control of sandstone packages within the Lower Beaufort group in the Eastern Cape Province, related to third-order sequence stratigraphic cyclicity. This process could presumably be extended to the sandstone packages in the southwest of the basin, within the Abrahamskraal and Teekloof Formations. However, it has also been suggested that the sandstone packages are the result of migration of channelized areas, possibly due to variations on precipitation in the source area (Smith 1981, 1990).

The comparison of these two theories is not clear as each of the studies was conducted in a different part of the basin. Catuneanu and Bowker (2001) and Catuneanu and Elango (2001) worked in the south-eastern part of the basin, where the climate is purported to have been temperate to humid during deposition of the lower Beaufort Group as indicated by petrography (Johnson 1976). Conversely, Smith (1981, 1990) was writing about the Lower Beaufort Group in the southwest of the basin, where the climate was arid and the fluvial discharge was ephemeral and 'flashy' (Smith 1987, 1990; Stear 1980). These differences in climate may have influenced the formation of sandstone packages in these two areas and are potentially the reason for the presence of identifiable, laterally traceable sandstone packages in the southwest of the basin and their absence in the southest of the basin.

6.3.1.5 Summary

Several studies have attempted to reconstruct both the tectonic and sedimentological development of the Karoo Basin (e.g. Catuneanu *et al.* 1998; Catuneanu *et al.* 2002; Cole 1992; Smith 1990; Tankard *et al.* 2009) but all have been quite broad-scale studies and no consensus has been achieved. While the evidence made available in this study cannot resolve the ultimate question of Karoo Basin development, it can help to reconstruct the Karoo basin during the late Middle Permian. Overall, four circumstances can be better understood.

Firstly, the Karoo Basin extended further to the south during deposition of the lower Beaufort Group, as evidenced by the steep dips and extensive folding of the lower Beaufort strata in the south of the basin. The fine-grained nature of all existing lower Beaufort Group rocks also indicates that the most proximal areas are not recorded, further indicating the extension of the basin to the south.

Secondly, while the primary source of sediment to the Karoo Basin during deposition of the lower Beaufort Group has not been unequivocally identified, one potential candidate is Saldanian basement, which would provide an appropriate felsic, recycled orogen provenance area as suggested by petrographic studies (Andersson 2004; Johnson 1976; Scott 1997). This basement could have been exposed during incipient crustal compression to the south of the Cape Supergroup depocentre, after which the sediment was transported northwards to the current position of Karoo basin over a great enough distance that only fine material was deposited there. More proximal deposition of the lower Beaufort Group would have occurred on top of the low-lying Cape Supergroup and the outcrop area of the Cape Supergroup either experienced deposition or non-deposition but not erosion, as evidenced by the lack of Cape Supergroup lithic fragments in the Lower Beaufort Group rocks. Compression and uplift of the Cape Supergroup, to the point where it began to supply sediment to the Karoo Basin, is only evident in the earliest Triassic Katberg Formation (Johnson 1976). While axial flow along the south of the basin may have brought sediment around the Cape Fold Mountains and therefore negate this line of argument, no better alternative source area has yet been identified.

Thirdly, the above evidence suggests that the timing of the onset of crustal compression did occur before deposition of the Lower Beaufort Group but did not lead to uplift of the Cape Supergroup. The age of the onset of compression is still disputed (e.g. Cole 1992; Catuneanu *et al.* 1998; Hälbich 1983; Tankard *et al.* 2009) but the metamorphic mineral grains used as evidence for a paroxysm in the Cape Fold Belt approximately 278 Ma could easily have been derived from far to the south. While this paroxysm did affect Cape Supergroup rocks in the existing remnant of the Cape Fold Mountains, it is not specified whether this compression was sufficient to cause uplift. Petrographic evidence suggests that it wasn't.

Finally, the thickness of the Lower Beaufort Group along the southern margin of the basin indicates significant subsidence in the south of the basin at the onset of Beaufort Group deposition, contrary to Catuneanu *et al.* (1998). However, the reduction in thickness of the Middle Permian biozones combined with their greater geographic extent at the time of deposition suggests a reduction in subsidence rates during the late Middle Permian. Sediment was therefore trapped in the proximal part of the basin during the *Eodicynodon* AZ and transported over a wider area of the basin during the *Tapinocephalus* and *Pristerognathus* assemblage zones. This may be inconsistent with a distant orogen if the basin was a typical retroarc foreland basin.

6.3.2 Deposition of the Lower Beaufort Group

Now that several important aspects of the Karoo Basin have been identified, it is possible to propose a timeline for the deposition for the Beaufort Group during the Middle Permian (Figure 41). Terrestrial deposition initially entered the current extent of the basin from the southwest, as evidenced from the restriction of the oldest vertebrate assemblage zone, the *Eodicynodon* AZ, to that area (ed. Rubidge 1995; Van der Walt *et al.* 2010). At this time, the Ecca Sea covered the entire current extent of the basin. By the end of the Middle Permian, the shoreline has prograded as far north as Philippolis, in the southwest Free State, which is indicated by the presence there of the *Pristerognathus* AZ immediately above the Ecca Group (Welman *et al.* 2001). The intermediate stages are deduced from both lithostratigraphic and biostratigraphic data.

The earliest Beaufort Group strata were deposited in the southwest of the basin, probably during the Wordian (Rubidge 2005). As the *Eodicynodon* AZ is found only in this area (ed. Rubidge 1995; Van der Walt *et al.* 2010) and the *Eodicynodon* AZ *sensu stricto* occupies the lower 1600 m of Abrahamskraal Formation at its thickest point (see 6.2; Figure 40), then it could also be supported that this lithostratigraphic interval, comprising the Combrinkskraal, Leeuvlei and Koornplaats members, is also restricted to the southwest of the basin. The Koornplaats Member has been traced as far north as Ouberg Pass (Cole and Wipplinger 2001), where there is no evidence for

Eodicynodon, but these correlations may imply the presence of the *Eodicynodon* AZ further north than is currently accepted.

The northward extent of Beaufort Group deposition during the *Eodicynodon* AZ is unclear, as the pinching out of the *Eodicynodon* AZ against the Ecca Group will be exposed on the surface only in the southwest extreme of the basin, in the western Moordenaarskaroo and on the Roggeveld Escarpment, where very few fossils have been found. However, lithostratigraphic units associated with the *Eodicynodon* AZ *sensu stricto* are not present north of the Nuweveld Escarpment in borehole cores QU1/65 or AB1/65 (Cole and Wipplinger 2001; Figure 5). The thickness of the lithostratigraphic units in the south of the basin and their northward restriction indicates that progradation of the shoreline during deposition on the lower three members of the Abrahamskraal Formation was slow and that terrestrial deposition was limited to the southern margin of the basin and perhaps to the south-western corner as well (Figure 41 - Time 2).

North of the Nuweveld Escarpment, the geographically restricted Kopjesfontein Member and Davidskolk Member were deposited by the southeast fluvial transport system and were therefore derived from a western provenance that was likely related to the development of the western branch of the Cape Fold Belt (Cole and Wipplinger 2001). Where they are known, these members directly overlie the Ecca Group, which indicates that the southeast fluvial transport system was prograding into the Ecca Sea in this region. The southern extent of the southeast fluvial transport system is not clear, although palaeocurrent measurements suggest it does not extend much further south than Middelpos, at least at the edge of the basin. This point would be useful to know as it would delineate the location of the watershed when the Ecca Sea was last present.

The presence of *Diictodon* in the lowest Kopjesfontein Member (see 5.7.6) means that the first terrestrial sedimentation in the north-west of the basin cannot have been earlier than the first appearance of *Diictodon*, which is situated at the base of the Moordenaars Member of the Abrahamskraal Formation at its thickest point (Figure 36). Because the upper Moordenaars Member is recorded as overlying both the Kopjesfontein and Davidskolk members at Fraserburg (Cole and Wipplinger 2001; Figure 8), the deposition of the Kopjesfontein and Davidskolk members must

therefore have occurred during the deposition of the lower Moordenaars Member in the south of the basin (Figure 41 – Time 3).

If the Davidskolk Member is present immediately above the Ecca Group at Middelpos and Koornplaats Member is still present north of Ouberg Pass, then there is little room for the Swaerskraal Member or lower Moordenaars Member to contact the Ecca Group. This would indicate that little progradation occurred during the deposition of these units, at least at the western extreme of the basin (Figure 41 – Time 2). However, the position of the shoreline under what is now the Nuweveld Mountains cannot be ascertained and therefore the distribution of the Swaerskraal Member and lower Moordenaars Member is impossible to predict. The upper Moordenaars Member is present at Fraserburg (Cole and Wipplinger 2001), which demonstrates that at during deposition of the uppermost Abrahamskraal Formation sediment input from the south relatively high enough to overwhelm that from the northwest. The Abrahamskraal Formation pinches out against the Ecca Group in the vicinity of Victoria West, which indicates that this was the location of the shoreline at the end of Abrahamskraal Formation deposition (Figure 41 – Time 4).

In the south-eastern part of the basin during this time, the Ecca Sea persisted longer than in the west and terrestrial depositional environments were more lacustrine (Smith 1990). The Koonap Formation is a similar thickness to the Abrahamskraal Formation on the southern margin of the basin at Klipplaat (4.1.3.1) but in the vicinity of the Great Fish River it is approximately 900 m thinner (Figure 16). The *Eodicynodon* AZ is also certainly absent in the latter area, which indicates the later occurrence of terrestrial deposition in this part of the basin (Day *et al.* 2013; Modesto *et al.* 2001b). At Klipplaat the lower Koonap Formation is not well-constrained biostratigraphically, but the thickness would suggest the earlier onset of terrestrial deposition in this area than at the Great Fish River.

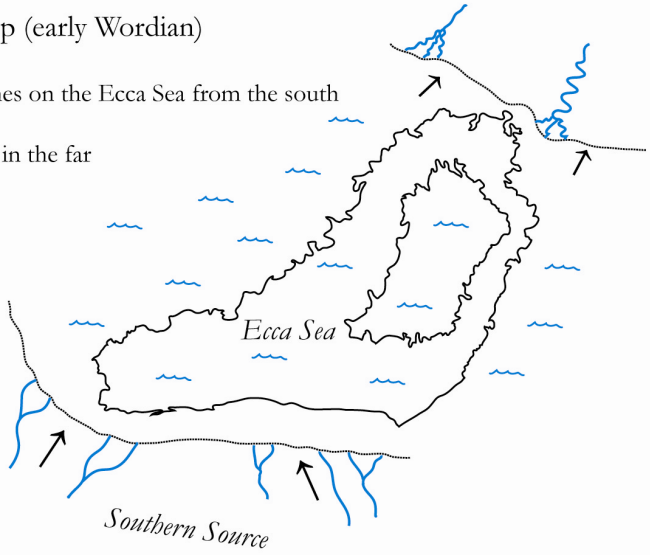
The deposition of the Poortjie Member, which is the most widespread of the Middle Permian members, coincides closely with the *Pristerognathus* AZ, except for its lowest horizons (see 6.2.2). Allen (1978) proposed that a decrease in subsidence rates would lead to the reworking of meanderbelts and stacking of channel sandstones as sedimentation rates dropped and channels cannibilised themselves. This is supported by the reduced thickness and greater geographic extent of the *Pristerognathus* AZ

compared to older biozones, which indicates reduced subsidence. As a result, the terrestrial deposition at the end of the Middle Permian in the Karoo Basin occurred over a wide area and prograded north-eastwards into the Ecca sea at least as far as Philippolis (Figure 41 – Time 5).

Time 1 - Late Ecca Group (early Wordian)

Terrestrial deposition encroaches on the Ecca Sea from the south

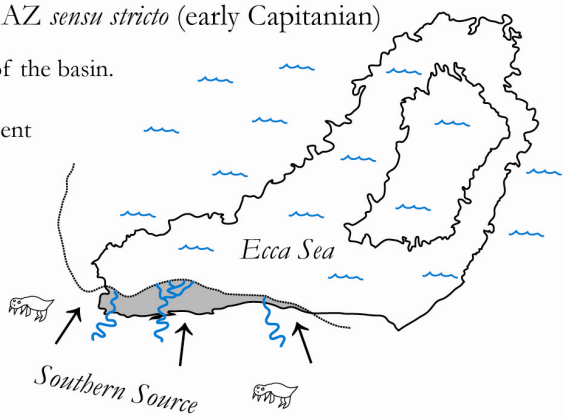
Transgression of the Ecca Sea in the far northeast of the karoo Basin.



Time 2 - End of the *Eodicynodon* AZ *sensu stricto* (early Capitanian)

Deposition restricted to the southwest of the basin.

A major distributory river system is present in what is now the central Koup region.



Time 3 - End of middle Moordenaars Member and Davidskolk Member deposition (Mid-Capitanian)

Deposition occurring simultaneously from the the southwest, northwest and southeast.

Tetrapod biodiversity in the Middle Permian is reaching its zenith.

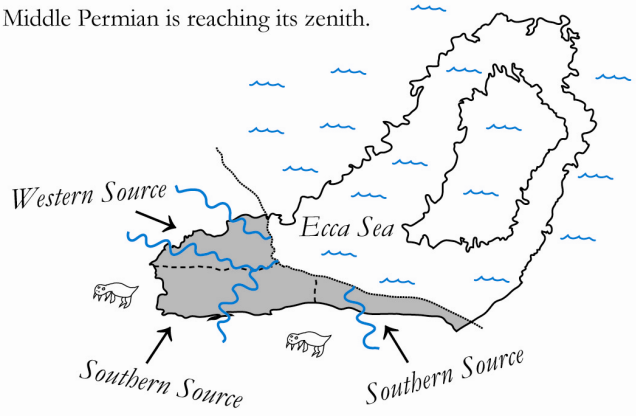


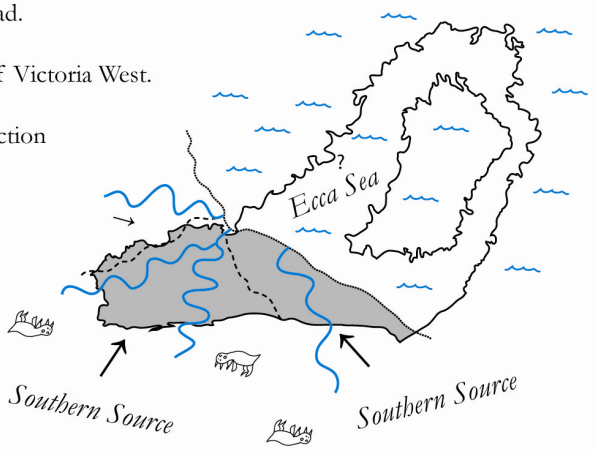
Figure 43a. Stages of Karoo Basin development during the Middle Permian.

Time 4 - End of Abrahamskraal Formation deposition (Late Capitanian)

Sediment input from the south overwhlems that from the northwest and deposition is more widespread.

The shoreline is situated north of Victoria West.

The End-*Tapinocephalus* AZ extinction event takes place.



Time 5 - End of Poortjie Member/lowest Middleton Member deposition (Latest Capitanian)

Shoreline situated near Philippolis and deposition is occurring over a wide area.

Extinction of Scylacosaurid therocephalians and *Eunotosaurus*.

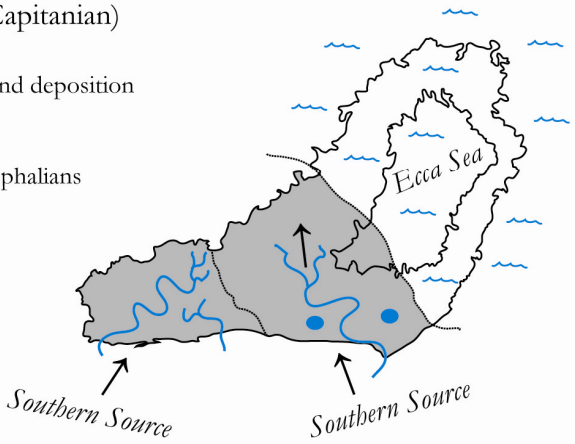


Figure 43b. Stages of Karoo Basin development during the Middle Permian (cont.).

6.4. Middle Permian tetrapod diversity change in South Africa

This section forms the first of the discussion sections concerning the biological aspects of the Middle Permian Beaufort Group. It draws heavily on the data provided in chapter 5 and will therefore general stratigraphic information will not be repeated in detail. As is clear from Chapter 5, only the pareiasaurs, dinocephalians, dicynodonts and therocephalians are present in sufficient numbers to make detailed observations of generic diversity and abundance through time; therefore, only these taxa are considered individually. This is followed by a more complete analysis of Middle Permian biodiversity in the Beaufort Group.

6.4.1 Pareiasaurs

The *Tapinocephalus* AZ contains the most basal pareiasaurs (Lee 1997), which constitute the third most abundant taxon in this biozone after the Dinocephalia and Dicynodontia. Pareiasaurs have a relatively stable record of abundance throughout the upper Abrahamskraal Formation, with the exception of a peak in numbers within the lower Moordenaars Member (Figure 29). Their numbers only begin to decline within the Karelskraal Member and by the base of the Teekloof Formation they are no longer present (Figure 28), although possible pareiasaur remains have been discovered there during fieldwork this study. This indicates that pareiasaurs were one of the primary victims of the end-*Tapinocephalus* AZ extinction.

Pareiasaurs are the only major taxon not found in the *Eodicynodon* AZ but, as mentioned above, were abundant in the *Tapinocephalus* AZ. As dinocephalians were already present in the Karoo Basin, this suggests some difference in the niche-occupation of pareiasaurs, which is supported by the disparity in tooth morphology of the two taxa and starkly different taphonomy of their remains within the *Tapinocephalus* AZ (Boonstra 1969).

The lack of confirmed pareiasaur specimens in the Poortjie Member of the Teekloof Formation and the apparent extinction of all basal genera at the end of the *Tapinocephalus* AZ supports a distinct stratigraphic and temporal 'gap' between the Middle and Late Permian pareiasaur taxa in South Africa (Watson 1914B; Lee 1997).

The next occurrence of a pareiasaur in the Beaufort Group is of the crown-group genus *Pareiasaurus* (Lee 1997), in the earliest Late Permian *Tropidostoma* AZ (Smith and Keyser 1995c, Smith *et al.* 2012). The duration of the pareiasaur 'gap' is equivalent to the *Pristerognathus* AZ and can be approximated from the radiometric dates determined for this biozone (Rubidge *et al.* 2013): because the lower-middle part of the *Pristerognathus* AZ produced a date of 261.24 Ma and the upper part a date of 260.41 Ma, it can be deduced that approximately 1–1.2 Ma separated the extinction of the basal pareiasaurs and the appearance of the Late Permian crown-group genera.

6.4.2 Dinocephalians

Dinocephalians are found throughout the Abrahamskraal Formation in both the *Eodicynodon* and *Tapinocephalus* assemblage zones but only one basal genus, *Tapinocaninus*, occurs in the lower part of the Abrahamskraal Formation. Although the genus *Struthiocephalus* occurs as stratigraphically low as the Koornplaats Member, dinocephalian generic diversity does not begin to increase until the upper Swaerskraal Member of the Abrahamskraal Formation and peaks in the Moordenaars Member (Figure 33). Dinocephalians are the most generically diverse tetrapods through the Swaerskraal and Moordenaars members of the Abrahamskraal Formation, and are the most common.

The dinocephalians diversify quickly from the upper Swaerskraal Member and by the lower Moordenaars Member reach their greatest abundance (Figure 29). They become less common, although still dominant, throughout the Moordenaars Member but dinocephalian abundance again increases in the Karelskraal Member. This latter peak in dinocephalian abundance, which is still associated with relatively high generic diversity, makes the decline and disappearance of the taxon appear rapid, occurring over less than 100 m of the uppermost Abrahamskraal Formation and lowest Teekloof Formation.

In South Africa, the radiation of dinocephalians was rapid, as was their decline, and the taxon was highly successful but only over a short period of time, corresponding to the upper Swaerskraal, Moordenaars and lower Karelskraal Member of the Abrahamskraal Formation (Figure 34). Evidence is emerging that several genera

survived into the lower *Pristerognathus* AZ, but all known fossil occurrences are close to the lower boundary of the Poortjie Member (see 5.5.3 and 5.5.6).

6.4.3 Dicynodonts

Dicynodonts are found throughout the Permian of South Africa. Like with dinocephalians, their taxonomic diversity in the lower Abrahamskraal Formation is low and only *Eodicynodon* is consistently found in this interval. Three other genera, *Brachyprosopus*, *Colobodectes* and *Lanthanostegus*, are present below the Swaerskraal Member of the Abrahamskraal Formation or equivalent part of the Koonap Formation but their stratigraphic ranges are not well constrained. Dicynodont generic diversity does not significantly increase until the first appearance of *Robertia* and *Eosimops*, in the Swaerskraal Member (Figure 36), after which it continues to increase throughout the *Tapinocephalus* AZ before reaching a maximum in the Karelskraal Member of the Abrahamskraal Formation. In the Poortjie Member, dicynodont generic diversity is reduced by about half of that in the upper Abrahamskraal Formation (Figure 36).

Several dicynodont genera that appear in the *Tapinocephalus* AZ were particularly successful, both in the Middle Permian and in the Late Permian. The most successful of these was the genus *Diictodon*, which first appeared in the lower *Tapinocephalus* AZ and rapidly became the most common dicynodont genus in that biozone (Figure 40**;** Figure 37); however, the abundance of *Diictodon* increases exponentially in the Karelskraal Member of the Abrahamskraal Formation and into the Poortjie Member of the Teekloof Formation. *Pristerodon* experiences a similar increase in numbers into the Poortjie Member, although it is less common in the Abrahamskraal Formation. Conversely, *Emydops* and *Endothiodon* were very minor parts of the dicynodont fauna below the Poortjie Member, and did not become successful until the Late Permian (Smith *et al.* 2012).

It is therefore evident that within the *Tapinocephalus* AZ dicynodont generic diversity reached its highest of the Middle Permian but that while this was reduced in the overlying *Pristerognathus* AZ, a few genera became highly successful, constituting the most common taxa of the ecosystem into the early part of the Late Permian.

6.4.4 Therocephalians

The therocephalians of the Middle Permian have a distribution that indicates a gradual increase in abundance throughout the period (Figure 29). There are similarities with dinocephalians and dicynodonts in that, while they do occur in the *Eodicynodon* AZ, therocephalian generic diversity in this biozone is low. Therocephalian abundance does not start to increase until the upper Swaerskraal Member and became relatively stable in the Moordenaars Member. Therocephalian generic diversity reaches its greatest point of the Middle Permian in the Moordenaars Member due to the various genera of the basal family Scylacosauridae (Figure 39).

Therocephalian generic diversity is steadily reduced through the Karelskraal Member and lower Poortjie Member but, like dicynodonts, therocephalians show an initial increase in abundance in response to the dinocephalian extinction at the top of the Abrahamskraal Formation. They increase in abundance slightly into the upper Karelskraal Member and then noticeably more into the Poortjie Member (Figure 29). They reached their greatest abundance of the Middle Permian in the upper Poortjie Member and, although this abundance is primarily the result of scylacosaurids, therocephalian taxonomic diversity is also higher in this horizon due to the appearance of more advanced therocephalian genera.

As is evident from the above, the scylacosaurids are the most successful group of therocephalians in the Middle Permian and are present throughout it. The second major family, the Lycosuchidae, only have their first appearance in the *Tapinocephalus* AZ (Figure 40). Both overall therocephalian generic diversity and abundance in the Middle Permian are influenced almost entirely by these taxa.

Contrary to the abundance pattern for scylacosaurid and lycosuchid therocephalians as a whole, there is a general decline in abundance for individual genera from the upper *Tapinocephalus* AZ to the *Pristerognathus* AZ (see 5.9.1 and 5.9.3). Much of the abundance value for therocephalians is derived from indeterminate scylacosaurid or lycosuchid material and therefore it is impossible to identify which genus is responsible for this. Both families go extinct at the top of the Poortjie Member, after which more derived therocephalians radiate (Abdala *et al.* 2008).

6.4.5 Tetrapod biodiversity in the *Eodicynodon* and *Tapinocephalus* assemblage zones

Within the *Eodicynodon* AZ *sensu stricto*, the major tetrapod groups of the Middle Permian are already present, with the exception of pareiasaurs, but the generic diversity of each is low (Figure 42). The most diverse taxa are the scylacosaurid therocephalians and dinocephalians, with two genera each, and the dicynodonts, of which there are potentially four genera present in the *Eodicynodon* AZ (Figure 40; Figure 36). Because of the paucity of fossils in the lower Abrahamskraal Formation, when considering 50 m SIs the highest overall generic diversity achieved at any one time in the *Eodicynodon* AZ was 4 (Figure 42). If the assemblage zone is considered as one stratigraphic entity, then its generic diversity was between 7 and 10, depending on the presence of the dicynodont genera.

Total generic diversity increased by up to three times during the *Eodicynodon-Tapinocephalus* Transition Zone, when only the certain stratigraphic ranges of individual genera are considered. This zone is where the first 'advanced' tapinocephalid dinocephalians appeared, and contains the first certain occurrence of the dicynodont genus *Colobodectes*. This Zone is also relatively poorly sampled, but demonstrates the first definitive occurrences of typically *Tapinocephalus* AZ genera.

Tetrapod biodiversity is more easily observed within the *Tapinocephalus* AZ, as the number of fossil specimens found there is much higher. It is only in this AZ that the generic richness of all major taxa began to increase significantly, as is evidenced by the increase in originations and in the lower part of the zone (Figure 43). Throughout the lower part of the *Tapinocephalus* AZ, below the Karelskraal Member of the Abrahamskraal Formation, there is a continuous increase in overall generic richness, which reaches its peak in the lower Karelskraal Member (Figure 42).

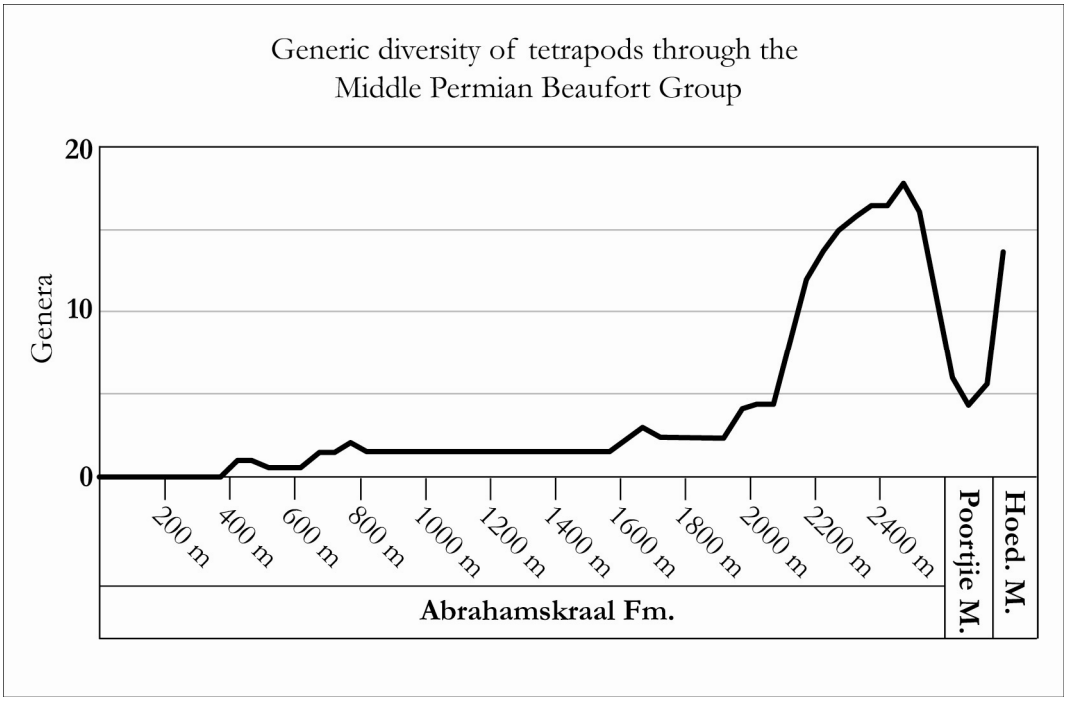


Figure 44. Graph of overall tetrapod generic richness through the Middle Permian Beaufort Group. Generic richness reaches its peak immediately before the extinction interval between the *Tapinocephalus* and *Pristerognathus* assemblage zones.

The increase in generic richness in the lower *Tapinocephalus* AZ, at the base of the Moordenaars Member, is primarily due to rapid radiation of the dinocephalians, given the relative synchronisation in the stratigraphic ranges of dinocephalian genera (Figure 33). In terms of abundance, the four major clades (pareiasaurs, dinocephalians, dicynodonts and therocephalians) are all present in greater numbers, but the data indicate that this is due to the proliferation of particular genera and is therefore not evenly spread across all genera.

The rapidity of the early radiation dinocephalians leads to them having their greatest generic diversity in the lower Moordenaars Member, but this remains high until the upper Karelskraal Member (Figure 33). Basal therocephalians achieve their maximum generic diversity, if not abundance, in the mid-Moordenaars Member, while the generic diversity of dicynodonts is last to peak, in the Karelskraal Member, after steady climb starting at the base of the *Tapinocephalus* AZ.

Overall tetrapod generic richness in the *Tapinocephalus* AZ is also supplemented by the presence of two small parareptiles (*Broomia* and *Eunotosaurus*), the only basal

synapsids known from South Africa (*Elliotsmithia* and *Heleosaurus*), three of the four known basal anomodont genera (*Anomocephalus*, *Galechirus* and *Galeops*) and two biarmosuchians (*Bullacephalus* and *Hipposaurus*). Apart from *Eunotosaurus*, all these genera have certain stratigraphic ranges restricted to the *Tapinocephalus* AZ and are represented by only a small number of specimens. They therefore provide little information on overall generic richness trends beyond the level of the biozone.

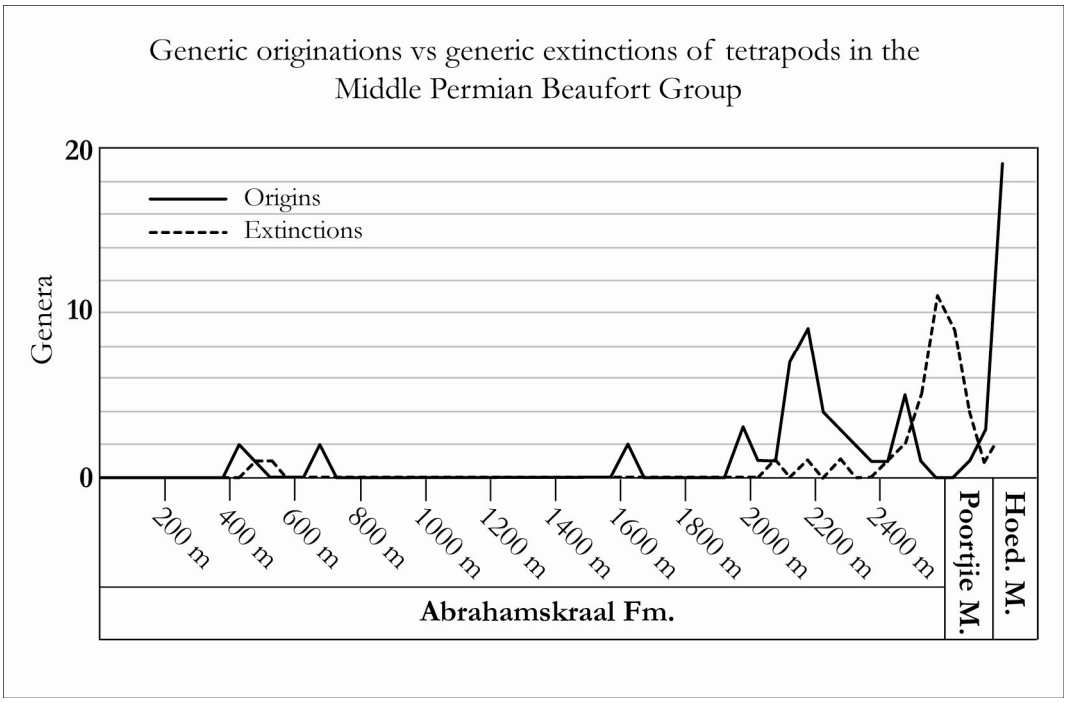


Figure 45. Tetrapod generic originations and extinctions through the Middle Permian Beaufort Group. The increase in extinctions and decrease in originations at the top of the *Tapinocephalus* AZ is evident. The last point represents the condensed *Tropidostoma* AZ using data from Smith *et al.* (2012); the large number of originations here is partly the result of the inclusion of gorgonopsian genera but does demonstrate the recovery stage after the end-*Tapinocephalus* AZ extinction.

6.4.6 The end-*Tapinocephalus* AZ extinction and tetrapod biodiversity in the *Pristerognathus* AZ

Based on all biostratigraphic data from the Middle Permian, an extinction event is evident at the end of the *Tapinocephalus* AZ. Most clades are affected by some loss of generic diversity, while the dinocephalians and basal synapsids are completely extinguished. In previous analyses, the available stratigraphic data allowed the extinction to be considered only at the resolution of the biozones and so it was considered to occur at a single stratigraphic horizon at the boundary of the *Tapinocephalus* and *Pristerognathus* assemblage zones (Fröbisch 2013; ed. Rubidge 1995; Retallack *et al.* 2006; Lucas 2009). In the light of the stratigraphic data provided by this study, which is based on the summation of three decades of stratigraphic investigation, it is now clear that the end-*Tapinocephalus* AZ extinction was rather more complex, and that the loss of taxonomic diversity at the top of the *Pristerognathus* AZ has been understated.

6.4.6.1 Karelskraal Member

The first signs of the extinction event are evident in the lower Karelskraal Member, where the extinction rate rose above 1 genus per 50 m SI for the first time in the Middle Permian (Figure 43). However, this is also the stratigraphic interval where overall generic richness was at its highest of the Middle Permian (Figure 42). In the mid-Karelskraal Member, five genera became extinct and total generic richness began to drop, but the total abundance of each taxon remained high, with dinocephalians and dicynodonts experiencing an increase in numbers of specimens in this interval (Figure 29). The greatest number of generic extinctions occurred in the uppermost Karelskraal Member, immediately below the base of the Teekloof Formation. Eleven genera became extinct in this interval, corresponding to the upper 25 m of the Karelskraal Member, which were spread across all major clades (Figure 40). In spite of this, pareiasaurs and dinocephalians suffered a dramatic drop in abundance, while dicynodont abundance increased at a greater rate than previously.

Within the Karelskraal Member, *Anteosaurus* was relatively common right up until the base of the Poortjie Member, where it suddenly became extinct. This was not the

case for most dinocephalians, although the two titanosuchid genera and *Struthiocephalus* also demonstrate a rapid extinction in the upper Karelskraal Member. The dinocephalian genera that are present immediately below the Teekloof Formation include members of the more basal Anteosauridae and Titanosuchidae but relatively few tapinocephalids (Figure 33). Those tapinocephalids that are present in the upper 25 m of the Abrahamskraal Formation are also relatively rarer than *Anteosaurus*, the two titanosuchids or *Styracocephalus*, which indicates that within the Dinocephalia genera of more basal families took longer to respond to the extinction stress (Figure 34).

Of the dicynodonts, the most remarkable in the Karelskraal Member is *Diictodon*. This genus began to increase exponentially in abundance within the upper 25 m of the Karelskraal Member, while practically no other dicynodont genus experienced such increase in numbers (Figure 37). Only *Pristerodon* has a slightly greater abundance in this interval compared to the mid-Karelskraal Member.

6.4.6.2 Poortjie Member

In the lowest Poortjie Member, the high rate of extinction continued, with nine generic extinctions recorded (Figure 43). The drop in taxonomic diversity across the boundary of the Abrahamskraal and Teekloof formations is compounded by a lack of any originations in either the uppermost Karelskraal Member or the lowest Poortjie Member, so within this latter interval tetrapod generic richness dropped to nearly a third of what it had been in the mid-Karelskraal Member. Unlike in the upper 25 m of the Karelskraal Member, the drop in generic richness in the lowest Poortjie Member was disproportionately the result of the extinction of dinocephalian genera (Figure 40). An indeterminate titanosuchid and the tapinocephalid *Criocephalosaurus* are still present but they do not appear to persist very far into the member and are represented by only a combined three specimens.

All basal pareiasaurs had gone extinct by the lowest Poortjie Member, of which *Bradysaurus* and *Nochelosaurus* were present right up to the base of the Poortjie Member. Two more genera of dicynodonts also became extinct in this interval but the generic diversity of the taxon remained stable after this. Therocephalians

continued to experience a slow decrease in generic diversity into the lowest Poortjie Member, which demonstrates that both the Therocephalia and Dicynodontia suffered in their overall generic diversity across the *Tapinocephalus-Pristerognathus* AZ transition. However, many of the genera that did survive this period were subsequently highly successful, achieving great abundances in the *Pristerognathus* AZ and into the late Permian. The best examples of this are the dicynodonts *Diictodon* and *Pristerodon*.

The middle of the Poortjie Member marks the end of the decline in generic richness associated with the end-*Tapinocephalus* AZ extinction, when generic richness reached its lowest point of the Middle Permian (Figure 42). After this interval, in the upper Poortjie Member, generic originations increase with the appearance of *Dicynodontoides* and two advanced therocephalians, the hofmeyriid *Hofmeyria* and the ictidosuchid *Ictidosuchoides* (Figure 40). Scylacosaurid therocephalian numbers continue to increase up to the top of the member, as do the numbers of the dicynodonts *Diictodon*, *Pristerodon*, *Emydops* and *Endothiodon*. The parareptile *Eunotosaurus* also achieves its highest abundance in the upper Poortjie Member (Figure 29).

At the top of the Poortjie Member or just above (at the boundary of the *Pristerognathus* and *Tropidostoma* assemblage zones) there is a small but significant extinction. This is rather different to the end-*Tapinocephalus* AZ extinctions in that it occurs in an environment of recovery, as generic originations during this transition exceed generic extinctions, based on data for the earliest Late Permian *Tropidostoma* AZ (Figure 43; ed. Rubidge 1995; Smith *et al.* 2012). Very few taxa are affected but the scylacosaurid and lycosuchid therocephalians and the parareptile *Eunotosaurus* became extinct (Figure 40). This is important, as both the family Scylacosauridae and the genus *Eunotosaurus* achieved their greatest abundance in the upper Poortjie Member. Scylacosaurids and lycosuchids are also the sole representatives of the Therocephalia in all but the uppermost Middle Permian Beaufort Group strata. Their sudden disappearance at the end of the Middle Permian coincides with the advent of Late Permian therocephalian genera so competition may therefore be the driving factor the driving factor.

The existence of these extinctions demonstrates a similarity to the Permo-Triassic mass extinction, whereby several genera survive the initial event but disappear shortly

after the appearance of a 'recovery fauna' (Smith and Botha 2005). To borrow the terminology of these authors, scylacosaurid therocephalians and *Eunotosaurus* potentially represent a 'survivor fauna' after the end-*Tapinocephalus* AZ extinction. They disappear at the same time that many new genera indicative of the Late Permian, representing the 'recovery fauna,' first appear. The primary difference between the paradigm described for the Permo-Triassic mass extinction by Smith and Botha (2005) and the end-*Tapinocephalus* AZ extinction is that several genera survive through to constitute a significant proportion of the 'recovery fauna', in this case the dicynodonts *Diictodon*, *Pristerodon*, *Emydops* and *Endothiodon*. The patterns are similar, but it would seem that the end-*Tapinocephalus* AZ extinction was of a lesser magnitude to the Permo-Triassic mass extinction.

Because most scylacosaurid specimens from the upper Poortjie Member are not determined to genus level in this study, the generic diversity of the family clearly cannot be assessed in this interval. The extinction of the Lycosuchidae and the Scylacosauridae mean that, while the Therocephalia continued into the Late Permian, it was not directly through the survivors of the end-*Tapinocephalus* AZ event, but through more derived forms that appeared in the upper *Pristerognathus* AZ.

6.4.7 Magnitude and timing

Lucas (2009) recorded what he termed the 'Dinocephalian extinction event' at the top of his Gamka land-vertebrate faunachron, where he calculated a loss of 73% in generic richness globally, although based to a large degree on the South Africa record. Retallack *et al.* (2006) made the same calculations for the Karoo Basin alone and retrieved a figure of 67% for the loss generic richness at an extinction 'event' at the top of the *Tapinocephalus* AZ, which they state to be conservative. However, both Lucas (2009) and Retallack *et al.* (2006) obtained their datasets from the biostratigraphy described by Rubidge (ed. 1995) which, as is clearly indicated by the range charts provided by this study, was based on insufficient biostratigraphic data (Figure 40).

The data presented in this study shows that the end-*Tapinocephalus* AZ extinction occurs over a more protracted stratigraphic interval than was previously recognised,

extending from the mid-Karelskraal Member to the mid-Poortjie Member. This corresponds to the distance between the highest generic richness of the Middle Permian and the lowest thereafter (Figure 43). Over this stratigraphic interval of approximately 100 m, there was a 75 % drop in generic richness. This figure is conservative, as several described genera are excluded from the analysis.

Although radiometric dates are only available for the latter part of the end-*Tapinocephalus* AZ extinctions (Rubidge *et al.* 2013), temporal constraints on the extinction interval can be estimated. The earliest dates provided by Rubidge *et al.* (2013) are from the lower-middle *Pristerognathus* AZ and indicate an age of 261.28 ± 0.08 Ma for this horizon. The upper *Pristerognathus* AZ was dated at 260.36 ± 0.07 Ma. Because the point of lowest generic richness is in the mid-*Pristerognathus* AZ, the termination of the end-*Tapinocephalus* AZ extinction interval occurred at approximately 261 Ma. From this same data, the *Pristerognathus* AZ has an estimated duration of 1–1.2 Ma, which would indicate that approximately 500–600 Ka are represented in the lower part of the *Pristerognathus* AZ.

The point of highest generic richness is within the lower Karelskraal Member within a stratigraphic interval approximately 75 m below the base of the Poortjie Member. Given the variability in the thickness of the Poortjie Member, this stratigraphic distance can be approximated to the thickness of the lower Poortjie Member and therefore potentially represents a similar period of deposition. In this case, the end-*Tapinocephalus* AZ extinction is estimated to have transpired over a period of 1–1.2 Ma, beginning approximately 262.2–262 Ma and terminating at 261 Ma (Figure 40).

The end-*Pristerognathus* AZ extinctions are better constrained to occur at approximately 259.9 Ma, at the boundary of the *Pristerognathus* and *Tropidostoma* assemblage zones (Rubidge *et al.* 2013).

6.4.8 Selectivity

In the earliest stages of the end-*Tapinocephalus* AZ extinction, within the upper Karelskraal Member, all the major clades experience some loss of generic richness (Figure 40). However, in the uppermost Karelskraal Member pareiasaurs and

dinocephalians experienced a drop in abundance, while therocephalian numbers remained stable and dicynodonts abundance increased (Figure 29). This is exacerbated into the lowest Poortjie Member, when pareiasaurs and dinocephalians experience a disproportionately greater number of generic extinctions.

Overall, from the base of the Karelskraal Member to the mid-Poortjie Member, dicynodont generic diversity drops from 10 to 5, a loss of 50% of genera, while therocephalian generic diversity drops from 5 to 2, equivalent to a 60% loss. Pareiasaur generic diversity drops from 3 to 0, an apparent 100% loss of genera; the clade itself reappears in younger Beaufort Group biozones, albeit with different genera. Varanopid generic diversity drops from 2 to 0, a 100% loss that is also the extinction of the last stem group synapsids. The worst affected group is still the Dinocephalia, the generic diversity of which drops from 12 to 0 over this interval, being also the extinction of the clade. In less common taxa, like in basal anomodonts, it is difficult to make such comparison.

The synchronous decline in the abundance of pareiasaurs and dinocephalians in the upper Karelskraal Member and the complete loss of both taxa by the end of the extinction interval, in the mid-Poortjie Member, strongly supports a common vulnerability for the two taxa. Dinocephalians included both carnivorous and herbivorous genera, while the difference in lifestyle between herbivorous dinocephalians and pareiasaurs is evident from their disparate nature of their tooth morphology and taphonomy (Boonstra 1969). Large size is therefore the most obvious factor that unites these two taxa; it is this, and the many life history characteristics associated with large size, which appear to have increased their susceptibility to extinction (McKinney 1997). This pattern has already been noted for the Permo-Triassic mass extinction (Benton *et al.* 2004; Fröbisch *et al.* 2010).

Throughout the latter phase of the end-*Tapinocephalus* AZ extinction, within the lower Poortjie Member, four genera of dicynodonts (*Diictodon*, *Emydops*, *Endothiodon* and *Pristerodon*) and scylacosaurid therocephalians increase in abundance (Figure 37; Figure 29). The degree of generic richness loss within this interval is also less for both therocephalians and dicynodonts than for dinocephalians. The reason for this is also probably linked to size, as both the scylacosaurid therocephalians and the Middle Permian dicynodonts were either small or medium-sized animals. The dicynodonts

that survived the end-*Tapinocephalus* AZ all occupied a low trophic level and had a small size, with the exception of the medium-sized *Endothiodon*. They may also have undergone relatively rapid growth, at least in the genus *Diictodon* (Ray and Chinsamy 2004).

Dicynodonts and therocephalians in the Middle Permian are probably also linked by a predator-prey relationship, as already suggested by Modesto *et al.* (2011): as all species of therocephalians in the Middle Permian were carnivores, their increase in abundance throughout the *Pristerognathus* AZ implies a similarly abundant food source. Their increased abundance therefore suggests a healthy prey population for which the only viable candidate in the *Pristerognathus* AZ would be the dicynodonts.

6.4.9 The genus *Diictodon*

Diictodon is remarkable among the dicynodonts of the *Tapinocephalus* and *Pristerognathus* assemblage zones. After its first appearance it rapidly becomes the most common dicynodont and from the mid- Karelskraal Member its abundance increases exponentially so that in the succeeding three biozones it comprises between 40-85% of all fossils recovered (Figure 37; Smith *et al.* 2012). The reason for its success may be burrowing, as *Diictodon* is the only dicynodont from the *Tapinocephalus* and *Pristerognathus* assemblage zones to be found in burrows (Smith 1987). It has been suggested that burrowing is advantageous during periods of climatic disruption (Damiani *et al.* 2003; Retallack *et al.* 2003) and the success of burrowing dicynodont genera during both the Permo-Triassic extinction event and during the end-*Tapinocephalus* AZ extinction would appear to support this (Retallack *et al.* 2006).

The reason for relatively modest abundance of *Diictodon* through most of the *Tapinocephalus* AZ is probably due to the constraints of the existing ecosystem (Figure 37). *Diictodon* clearly enjoyed a competitive advantage over other dicynodonts because it became the most common genus right from its first appearance the *Tapinocephalus* AZ, yet its drastic increase in abundance from the mid-Karelskraal Member coincides so closely with the base of the extinction interval that a link is hard to refute. Like *Lystrosaurus* in the earliest Triassic (Retallack *et al.* 2003), *Diictodon* appears to have thrived during the period of ecological disruption at the top of the *Tapinocephalus* AZ;

however, contrary to *Lystrosaurus*, *Diictodon* was highly successful during periods of stability as well and was present in large numbers throughout the Late Permian before its extinction at the end of the Permian (ed. Rubidge 1995; Smith *et al.* 2012).

6.5 Middle Permian tetrapod diversity change globally and the Guadalupian extinctions

The previous section has presented a description of tetrapod biodiversity through the late Middle Permian as recorded in the Beaufort Group of South Africa. Correlation of this stratigraphic sequence with other Middle Permian terrestrial sequences elsewhere in the world is hindered by a lack of continuity in terrestrial fossil records for this time period outside of South Africa. This means that the phenomena observed in South Africa provide a unique insight into the dynamics of the 'dinocephalian extinction event'.

The biostratigraphic correlations already outlined in chapter 2 allow Middle Permian tetrapod diversity change to be summarised in light of the elucidation of end-*Tapinocephalus* AZ extinction. These biostratigraphic correlations are then discussed in order to clarify the timing of the Guadalupian extinction on land, after which the coincidence of the marine and terrestrial extinctions and the implications for a global Guadalupian extinction event are investigated. As an extinction in the late Middle Permian was first recognised in the marine realm and this system is the most applicable to global faunas, the international marine timescale is used throughout this section (Figure 3), as was done by Rubidge (2005).

6.5.1 Global tetrapod diversity in the late Middle Permian

Outside of South Africa, an assessment of tetrapod diversity change in the Capitanian, or across the boundary of the Gamkan and Hoedemakeran LVFs of Lucas (2006), has been attempted only in Russia (Benton *et al.* 2004; Lucas 2009). Using the dataset compiled by Tverdokhlebov *et al.* (2005), Benton *et al.* (2004) found a drop in generic richness from 16 to 6 genera between the Amanakskaya and

Malokinelskaya/Vyakovskaya svitas, which they correlated to the boundary of the *Tapinocephalus* and *Pristerognathus* assemblage zones. This would equate to a 62.5% loss of generic richness.

Conversely, Lucas (2009) found no loss of generic richness between the Ischeevo fauna and the next youngest Kotel'nich assemblage, using the dataset produced by Ivakhnenko *et al.* (1997), though he does admit the presence of a hiatus between the two. Lucas recorded a drop in generic richness between the Ocher and Ischeevo complexes, which, as constituents of the Kapteinskraalian and Gamkan LVFs, respectively, would be equivalent to the *Eodicynodon–Tapinocephalus* AZ transition. This is not evident in South Africa, where generic richness only increases from the base of the *Eodicynodon* AZ up until the uppermost *Tapinocephalus* AZ (Figure 42). As discussed by Lucas (2009), both Russian datasets have significant shortcomings when used in an analysis of overall biodiversity change.

What can be determined from assemblages outside South Africa is that dinocephalians are not found in the Late Permian and that all localities where they do occur can be correlated with either the *Tapinocephalus* or *Eodicynodon* assemblages zone (except for perhaps the early Kazanian fauna reported from Russia, which may be older; see 2.4.1). This led Lucas (2009:495) to describe it as a 'Pangaea-wide event.' Another group that is not found later than the Middle Permian is the basal synapsids. Of these, caseids are reported last from the Mezen complex (Battail 2000). The Varanopidae has been reported from the *Pristerognathus* AZ of South Africa, but this appears to be erroneous (see 5.3, Appendix A2). If this is ignored, varanopids are last recorded at Mezen and in the *Tapinocephalus* AZ of South Africa (Dilkes and Reisz 1996; Battail 2000; Reisz and Modesto 2007**;** Figure 40).

Three taxa are noteworthy for their success after the 'dinocephalian extinction event.' Firstly are the dicynodonts, which in the Capitanian are found only in South Africa, become an integral part of tetrapod faunas throughout Gondwana in the Wuchiapingian (Rubidge 2005). They first appear in Laurasia during the Wuchiapingian but do not become widespread there until the Changhsingian, and never achieve the taxonomic diversity that they do in Gondwana. The radiation of dicynodonts in the Wuchiapingian may well be a result of ecosystem restructuring in response to the Capitanian extinctions.

Pareiasaurs are found outside the Karoo Basin during the Middle Permian, in the Rio do Rasto Formation of Brazil (Araujo 1985; Malabarba *et al.* 2003). The genus that is found there, *Provelosaurus*, was described by Lee (1997) to be intermediate between the large, basal pareiasaurs of the *Tapinocephalus* AZ and the more derived, armoured species of the Late Permian. The intermediate morphology of *Provelosaurus* in Brazil, combined with the observed extinction of all basal pareiasaurs during the end-*Tapinocephalus* AZ extinction, alludes to the possible repopulation of the Karoo by pareiasaur genera from Brazil in the Wuchiapingian. In the Late Permian, pareiasaurs proceed to become a common element of tetrapod fauna, especially in Laurasia (Rubidge 2005).

The third taxon to be successful after the 'dinocephalian extinction event' is the Gorgonopsia, which in the Middle Permian is also only recorded in the Beaufort Group of South Africa. In the Late Permian, gorgonopsians are become widespread across Pangaea (Battail 2000; Rubidge 2005).

6.5.2 Timing of the terrestrial extinction

Until now, the absolute age assignments for global terrestrial tetrapod assemblages from the Middle to Late Permian, and hence the 'dinocephalian extinction event,' have relied heavily on palaeomagnetic correlations in Russia and particularly on the stratigraphic position of the Illawara reversal relative to tetrapod assemblages (Benton 2012; Bond *et al.* 2010a; Lucas 2009). Lucas (2009) determined the Ischeevo fauna to occur below the Illawara reversal, which most recent magnetostratigraphic places in the late Wordian (Menning *et al.* 2005, 2006; Molostovsky *et al.* 2007; Steiner 2006). This led him to conclude that the 'dinocephalian extinction event' occurred in either the Roadian or Wordian stages and was therefore much older than proposed by Rubidge (2005). However, the stratigraphic position of tetrapod assemblages in Russia relative to the magnetostratigraphy is far from clear, and Lucas does not provide evidence for this. Biostratigraphic correlation with the Beaufort Group is much more consistent with a Capitanian age for Ischeevo fauna (Battail 2000; Rubidge 2005; Fröbisch 2009).

Alternatively, (Retallack *et al.* 2006) used carbon isotope chemostratigraphic correlation between the *Tapinocephalus* AZ and the Guadalupian-Lopingian boundary GSSP at Penglaitan to suggest that the 'dinocephalian extinction event' coincided with the end of the Guadalupian, and hence the end of the Capitanian. This was, however, based on very scant evidence and was refuted by Bond *et al.* (2010a) on this basis.

Tetrapod faunas of the late Middle Permian are best constrained using biostratigraphic correlation with the Beaufort Group of South Africa, which now possesses the most reliable absolute dates (Rubidge *et al.* 2013; Figure 3). As a result, the Beaufort Group is likely to form the global standard for terrestrial tetrapod evolution from the Wordian to the end of the Changhsingian and a mid-Capitanian age for the 'dinocephalian extinction event' is suggested by the age of the end-*Tapinocephalus* AZ extinction, which occurred approximately 262–261 Ma (see 6.4.7).

A biodiversity study of terrestrial plant faunas has identified a floral extinction in the middle Upper Shihhotse Formation, dated magnetostratigraphically to the mid-Capitanian (Stevens *et al.* 2011). This is approximately within the same timeframe as the end-*Tapinocephalus* AZ extinction but the upper Upper Shihhotse Formation is currently only poorly constrained temporally.

6.5.3 Age of the marine extinctions and a global Capitanian extinction event

It appears that most evidence for an end-Guadalupian Mass extinction is derived from broad-scale studies, in which time resolution is low and the Capitanian is often considered as a single unit (e.g. Isozaki 2009; Isozaki *et al.* 2004; Stanley and Yang 1994; Wang and Sugiyama 2000). Conversely, detailed studies of stratigraphic sections in southern China, including Penglaitan and Tiequao, have demonstrated that the late Capitanian Maokou Formation contains a distinctly Wuchiapingian fauna and that fusilinacean foraminiferans and brachiopods in fact undergo an extinction event in the mid-Capitanian, around the J. *altudaensis* and *J. xuanhanensis* conodonts zones (Bond *et al.* 2010b; Shen and Shi 1996, 2009; Wignall *et al.* 2009b).

When studied in section at Tiequao, Wang and Sugiyama (2001) identified several rugose coral assemblages in the Guadalupian, with taxonomic diversity becoming very low after the *J. postserrata* conodont zone, in the early Capitanian. Ota and Isozaki (2006) refer to the end-Guadalupian extinction at Kamura in Japan but they record the extinction of fusilinacean foraminiferans at the base of their 'barren zone,' which they attribute to the latest Capitanian. The biostratigraphic correlation for the Kamura section was poorly constrained by foraminiferans but more recent carbon isotope correlation with Penglaitan suggests a mid-Capitanian age for base of the 'barren zone,' within the *J. xuanhanensis* conodont zone (Isozaki *et al.* 2007; Wang *et al.* 2004); alternatively, Bond *et al.* (2010b) correlate the Kamura section to their carbon isotope curve at Xiong Jia Chang and determined it to be older, which would place the base of the 'barren zone' in the early Capitanian *J. shannoni* condont zone.

Extinctions identified at the boundary of the Guadalupian and Lopingian epochs (GLB) therefore appear to be mostly false. An extinction recorded at the GLB at Penglaitan by Kaiho *et al.* (2005) was based on a severe reduction in the abundance of fossil material belonging to seven benthic invertebrate groups. They also found fossil material of foraminiferans to be very scarce in strata above the GLB. However, at Penglaitan and Tiequiao, the GLB is situated at the boundary between the Laibin Limestone Member of the Capitanian Maokou Fomration and the siliceous muds of the Wuchiapingian Heshan Formation. The patterns observed by Kaiho *et al.* (2005) are therefore indicative of a facies shift from shallow carbonate platform to deeper water muds. Indeed, Lai *et al.* (2008) admit that various marine genera disappear in northern Sichuan Province within the Capitanian due to the termination of marine sedimentation, while the same genera continue to be present later in the south where the environment was more stable. At Penglaitan and Tiequao, Wignall *et al.* (2009b) described the foraminiferans in the late Capitanian Laibin Limestone and found them to be representative of the Lopingian.

At Choatian in Sichuan Province is there an apparent extinction recorded at or close to the GLB (Isozaki *et al.* 2004; Lai *et al.* 2008). At this locality, a distinct clay tuff represents the boundary of the Maokou and Wuchiaping formations (Isozaki *et al.* 2004). This clay tuff was later dated using SHRIMP, whereby 16 zircon grains produced an age of 260 ± 4 Ma (He *et al.* 2007). Such a date broadly agrees with a

GLB age but the considerable error margin does not discriminate between a GLB or mid-Capitanian age for this horizon. Conodont biostratigraphy shows the presence of the mid-Capitanian *J. shannoni* conodont zone 3m below the base of the clay tuff, which prompted Lai *et al.* (2008) to postulate a significant hiatus at Chaotian, representing much of the late Capitanian; however, the lack of any conodonts above the last appearance of *J. shannoni* and the error margin for the date on the clay tuff make the age of the Chaotian extinctions unreliable.

The temporal constraints on the Guadalupian conodont zones are poor. As conodont zones are the primary defining units for the International Timescale (ICS 2012), this has implication for the age assignment of any extinction event during this time. Only the base of the Capitanian has been reliably dated to 265 ± 0.2 Ma (Bowring *et al.* 1998), whereas the upper boundary of the Capitanian has only been circumstantially dated to 259.8 ± 0.4 Ma (Shen pers. comm. 2013; Shen *et al.* 2010;).

If the late Guadalupian extinction is constrained by conodont biostratigraphy to within or between the *J. shannoni*, *J. altudaensis* and *J. xuanhanensis* conodont zones, as most evidence suggests (Bond *et al.* 2010a, 2010b; Isozaki *et al.* 2007, Shen and Shi, 2009; Wang and Sugiyama 2009; Wignall *et al.* 2009a), then an age of 262.5–261 Ma can be roughly extrapolated from the most recent Permian timescale (ICS 2012).

A potentially superior method of dating the late Guadalupian extinctions comes from the Emeishan volcanics, which are intercalated with fossiliferous marine rocks at two important sections in southern China, namely Xiong Jia Chang (Wignall *et al.* 2009a) and Chaotian (Isozaki *et al.* 2004; He *et al.* 2007). At Xiong Jia Chang, within the 'outer zone' of the Emeishan Large Igneous Province (ELIP) (He *et al.* 2007), over 70m of basalt and mafic breccia is emplaced between the *J. altudaensis* and *J. prexuanhanensis/xuanhanensis* conodont zones within the Maokou Formation (Wignall *et al.* 2009a). This horizon immediately postdates the extinction interval and is well constrained by conodont biostratigraphy but has not yet been radiometrically dated directly.

At Chaotian, which is situated at least 400 km outside the ELIP, the clay tuff that occurs at the boundary between the Maokou and Wuchiaping formations is now considered to be the result of volcanic ash output from eruptions within the ELIP

(He *et al.* 2007; cf. Isozaki *et al.* 2004). Although this clay tuff has been dated, as discussed above, the high margin of error (4 Ma) and the lack of conodont zone data from the overlying Wuchiaping Formation prevent it from providing any meaningful time constraints.

Despite the lack of data at these localities, some time constraints on the marine extinctions can be imposed using radiometric dates from elsewhere in the ELIP. A date of approximately 260 Ma has been calculated for the final stage of felsic eruptions and in the ELIP (He *et al.* 2007) but the error is sufficient that it may correspond to the end of the Guadalupian at ~259 Ma, as proposed by Shen *et al.* (2010). An estimate of ~263 Ma for the earliest onset of volcanic activity in the ELIP is based on an even distribution of conodont zones within the Capitanian (Sun *et al.* 2010); however, if the conodont zones are more bunched in the later part of that stage, as suggested in the most recent Permian timescale (ICS 2012), then an age of ~262 Ma for the onset of Emeishan volcanism may be more likely.

He *et al.* (2007) observed that the stratigraphically lowest volcanic rocks become younger towards the periphery of the ELIP. This was developed by Sun *et al.* (2010), who determined that initial volcanism occurred during the *J. altudaensis* conodont zone before activity greatly increased in the *J. xuanhanensis* conodont zone. It was at the beginning of this increased activity phase that, exacerbated by regional regression, widespread basalt emplacement and the marine extinctions occurred. Sun *et al.* (2010) therefore concluded that a lag period existed between the onset of volcanism at ~263 Ma and the extinction, which they indicated to occur at ~262 Ma. If the Capitanian conodont zones are bunched in the upper part of the stage as per the Permian timescale (ICS 2012), then the date of the extinction may be closer to 261 Ma.

Based on this data, the age of the marine extinction is therefore most likely constrained to occur at approximately 262–261 Ma, which coincides closely with the approximate duration of the end-*Tapinocephalus* AZ (Figure 44).

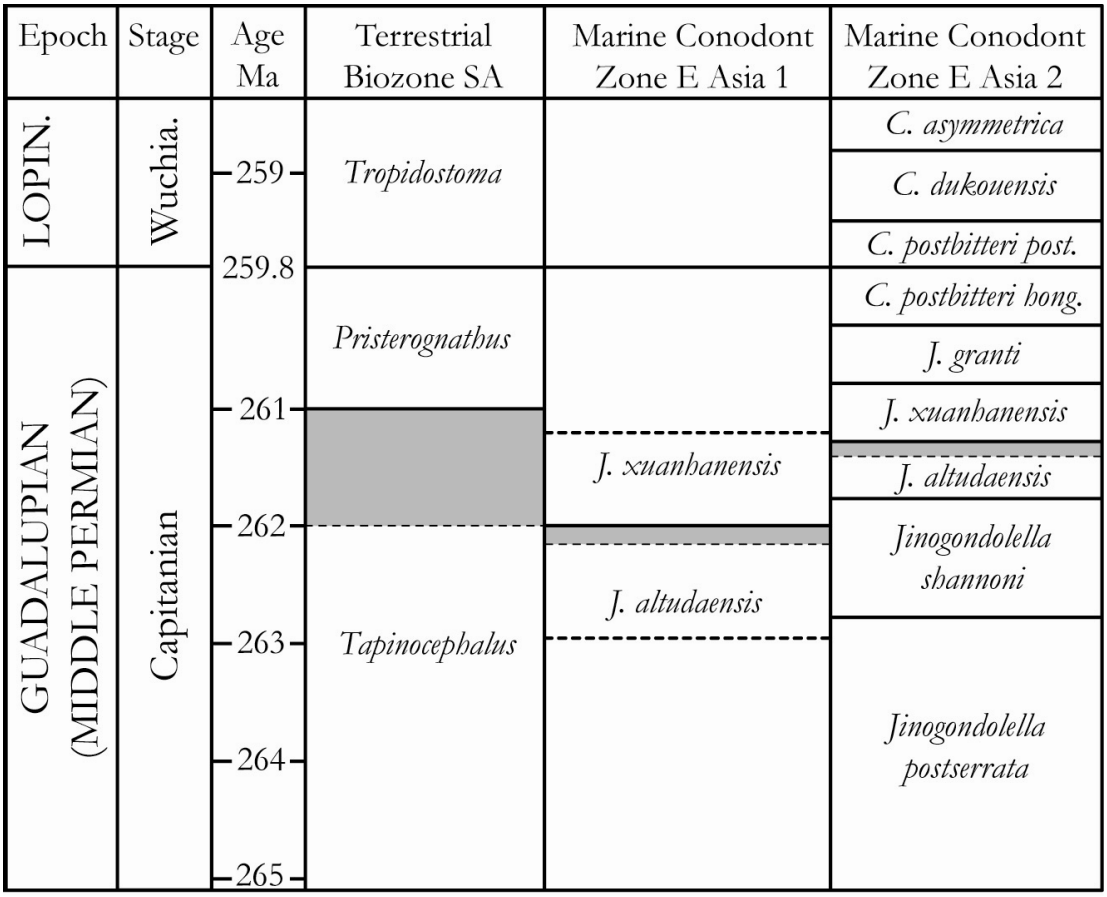


Figure 46. Timing of the extinctions in the terrestrial and marine realms during the late Capitanian. Shaded areas indicate extinction intervals. The age of the boundary between the *J. altudaensis* and *J.xuanhanensis* conodont zones in scenario 1 is based on the occurrence of a basalt horizon in the Xiong Jia Chang section, within the *J. altudaensis* conodont zone, and the association of this with the increase in Emeishan volcanism ~262 Ma (Sun *et al.* 2010). The position of the marine extinction interval is based on Bond *et al.* (2010a) and Wignall *et al.* (2009a). Scenario 2 is based only on the distribution of conodont zones presented in the latest Permian Timescale (ISC 2012). Terrestrial biozone ages extrapolated from Rubidge *et al.* (2013). Abbreviated conodont genera are *Clarkina postbitteri hongshuiensis* and *Clarkina postbitteri postbitteri*. LOPIN. = Lopingian, Wuchia. = Wuchiapingian.

6.5.4 Possible causes

Initially, the causes of the end-Guadalupian marine extinction were posited to be related to global regression (Hallam and Wignall 1997) or the onset of oceanic stratification (Isozaki 1997) but a link to the Emeishan basalt eruptions in south-east China were soon proposed (Courtillot *et al.* 1999**;** Zhou *et al.* 2002). Bond *et al.* (2010a) excluded the 'dinocephalian extinction event' from their discussion on causes of the marine extinctions on the basis it occurred too early, but this was based on the age provided by Lucas (2009). Because both the marine and terrestrial Middle Permian extinctions can now be constrained to occur approximately 262–261 Ma, their timing is consistent with the eruption of the Emeishan volcanics that were active approximately 263–260 Ma (Sun *et al.* 2010).

A correspondence between the marine and terrestrial extinction events suggest that certain marine-specific extinction mechanisms, such as regression and oceanic anoxia, are less likely to be primary causes of the marine extinction. The involvement of terrestrial ecosystems would have required a mechanism that could affect both realms and is therefore consistent with atmospheric disruption, such as could result from volcanism (e.g. Williams-Jones and Rymer 2000). Furthermore, the great distance that separated the Karoo Basin from the Palaeo-Tethys and China would require that this atmospheric disruption be on a global scale. Bond *et al.* (2010a) proposed that volcanism on the scale of the Emeishan eruptions would cause significant climatic disruption due to acidification, cooling and the reduction in photosynthesis due to ash particles in the atmosphere. Isozaki *et al.* (2004) supported a volcanic cause for the marine extinctions as rhyolitic ashes were associated with both the Middle and Late Permian extinction horizons at Chaotian; the same phenomenon was later recorded in south-west Japan, in sediments deposited in mid-Panthalassa (Isozaki *et al.* 2007).

It has been proposed that the climatic affects of greenhouse gases and volcanic ash released directly from the Emeishan eruptions may have been exacerbated by the further release of methane, and associated oxygen depletion, resulting from volcanic intrusion into coals (Retallack and Jahren 2008). This phenomenon was used to explain a negative carbon isotope excursion seen at the base of the Graphite Peak section from Antarctica, which is interpreted to be situated at the Guadalupian-

Lopingian boundary (Retallack *et al.* 2006; Retallack and Jahren 2008). Bond *et al.* (2010b) record a significant negative carbon excursion coinciding with the marine extinction interval at the Xiong Jia Chang locality, so it is possible that methane release from coal combustion was also active during the Capitanian. Bond *et al.* (2010a) objected to this cause for the marine extinctions on the basis that the extinction interval occurs at the very onset of the negative carbon excursion, preferring more proximal extinction mechanisms associated with the early stages of the eruptions (see Ukstins Peate and Bryan 2008; Wignall *et al.* 2009a and references therein). However, it is still possible that while thermogenic methane release was not the underlying cause for the marine extinctions at Xiong Jia Chang, it was important in the terrestrial extinctions.

An alternatively global extinction mechanism is the 'Kamura event,' a period of heavy atmospheric carbon ratios that is potentially linked to global cooling (Isozaki *et al.* 2007). Isozaki *et al.* (2007) record the plateau of high carbon values in the late Capitanian, but the temporal constraints on their sections is poor. According to Bond *et al.* (2010b), chemostratigraphic correlations with Xiong Jia Chang indicate this plateau of high carbon values occurs below the negative carbon excursion in the mid-Capitanian. If this is so, the 'Kamura event' would predate the extinctions.

CHAPTER 7: CONCLUSIONS

The thesis has drawn on various aspects of geology and palaeontology to conduct a multidisciplinary investigation of the terrestrial Middle Permian of South Africa. The primary conclusions that have resulted from this project can be split into five main areas: lithostratigraphy, biostratigraphy, Karoo Basin development, Middle Permian tetrapod biodiversity in South Africa, including the end-*Tapinocephalus* AZ extinction event, and the global Capitanian extinctions. Each of these areas is quite distinct and therefore they are considered separately in this concluding chapter.

Because the range of topics covered in this thesis are so broad, many potential avenues of investigation have not been pursued. It is hoped that this thesis will provide the basis for more exhaustive studies of the Middle Permian of South Africa, and provide a template for similar studies in other stratigraphic levels.

7.1 Lithostratigraphy

Despite extensive research on the stratigraphy of the lower Beaufort Group in the southwest of the Karoo Basin during the uranium exploration of the 1980s, no consensus was reached on a subdivision of the Abrahamskraal Formation (Jordaan 1990; LeRoux 1985; Stear 1980; Turner 1981; Wadley and Hoffman 1986). The six sub-units of the Abrahamskraal Formation defined by LeRoux (1985) and the subsequent used by Loock *et al.* (1994) are found to be the most applicable (Figure 19), with one minor exception. The Wilgerbos Member as defined by LeRoux was incorrectly correlated between its type area in the northern Koup and the Moordenaarskaroo by Loock *et al.* (1994). As such, the distinct argillaceous unit presented as the 'Wilgerbos Member' by Loock *et al.* (1994) is renamed the Swaerskraal Member for its distinct outcrop on that farm in the Moordenaarskaroo.

The member level stratigraphic sub-units of the Abrahamskraal Formation are primarily recognised on the basis of sandstone packages but can also be characterised by number of fining upwards cycles present within them (Figure 5; Figure 16). Across the southern margin of the basin, the Combrinkskraal Member is formed by an entire fining-upwards megacycle and the base of a second, comprising two

sandstone packages, while the Leeuvlei Member is formed by the finer, upper portion of fining-upward cycle 2. The Koornplaats Member is formed by the lower part of fining-upward cycle 3, and is present along the southern margin of the basin and as far north as Ouberg Pass. Above the Koornplaats Member, the Swaerskraal Member corresponds to the argillaceous upper part of fining-upward cycle 3. The Moordenaars Member in most localities comprises two sandstone packages formed by the fourth fining-upward cycle and the lower part of fining-upward cycle 5, but this is less distinct in the eastern Koup region. The sixth and final member of the Abrahamskraal Formation recognised here is the Karelskraal Member, which corresponds to the argillaceous interval between the upper boundary of the Moordenaars Member and base of the Teekloof Formation.

East of 24° E, sub-units of the Koonap Formation cannot yet be determined with confidence. At least two fining-upward cycles appear to exist in the region of the Great Fish River but they are not easily traceable due to the overall argillaceous nature of the Koonap Formation (Figure 40). Although the Koonap and Abrahamskraal Formation may be contemporaneous and stratigraphically equivalent (Day *et al.* 2013; Hill 1993), palaeocurrent studies indicate a different source area for the eastern Karoo (Cole 1992; Cole and Wipplinger 2001; Theron 1975) and therefore the stratigraphic structure of both these formations was not necessarily related. The climate is known to have been more arid in the western Karoo during deposition of the lower Beaufort Group (Johnson 1976; Smith 1987; Smith 1990; Stear 1980), which may have influenced low order, sub-formational cyclicity.

In the lower Abrahamskraal Formation, represented by the Combrinkskraal, Leeuvlei and Koornplaats members, the lithostratigraphy is far more arenaceous in the central Koup region than either to the west, in the Moordenaarskaroo, or to the east, in the eastern Koup region (Figure 16). The Abrahamskraal Formation is also thicker in the central Koup than laterally. The greater abundance of coarse material and greater thickness suggests the presence of a major distributory system in the central Koup region during deposition of the Abrahamskraal Formation, while the areas lateral to this experienced a greater amount of overbank deposition (Figure 41 – Time 2). The upper Abrahamskraal Formation, including the Swaerskraal, Moordenaars and Karelskraal members, is overall more argillaceous across the whole south-western

part of the Karoo Basin, which may indicate that less coarse sediment was entering the basin.

7.2 Biostratigraphy

The most effective biostratigraphic indicator taxa are dicynodonts, as suggested by Rubidge and Angielczyk (2009) and Angielczyk and Rubidge (2012), and the order of appearance for key dicynodont genera can now be elaborated on (Figure 36). The stratigraphically lowest dicynodont indicator genus is *Eodicynodon*, which occurs within the lower 2000 m of the Abrahamskraal Formation at its thickest point. *Colobodectes* has a stratigraphic range that extends from at least 1600 m above the base of Abrahamskraal Formation to near the top of the Formation at 2550 m. The next highest indicator genus is *Robertia*, the stratigraphic range of which extends from 1950 m to 2550 m above the base of the Abrahamskraal Formation; this genus therefore has a stratigraphic range that corresponds to the upper 600 m of the Abrahamskraal Formation, but for the uppermost 25 m, and is almost exclusive of *Eodicynodon*. The genus *Eosimops* has a similar stratigraphic range to *Robertia* but also occurs above the Abrahamskraal Formation, in the temporal equivalent of the Poortjie Member. Lastly, *Pristerodon* and *Diictodon* have their first appearances at 2100 m and 2150 m above the base of the Abrahamskraal Formation, respectively.

Overall, the fauna from the lower Abrahamskraal Formation remains distinct from that of the upper Abrahamskraal Formation and so its bilateral division into a lower *Eodicynodon* AZ and upper *Tapinocephalus* AZ is retained. Contrary to former projections, the *Eodicynodon* AZ is now demonstrated to be the thickest biozone of the Middle Permian and, indeed, of the Beaufort Group, extending over the lower 2000 m of the Abrahamskraal Formation. The *Tapinocephalus* AZ is found in the upper part of the Abrahamskraal Formation and into the lowest part of the Poortjie Member of the Teekloof Formation (Figure 42).

The distinction between the *Eodicynodon* and *Tapinocephalus* assemblage zones would actually appear to be exacerbated in that the central part of the Abrahamskraal Formation has so far yielded very few fossils (Figure 31). However, the stratigraphic

ranges of individual dicynodont and dinocephalian genera presented in this thesis indicate a transitional interval within the upper part of the *Eodicynodon* AZ.

This transition zone occurs between the first appearance of the tapinocephalid dinocephalian *Struthiocephalus*, at 1600 m above the base of the Abrahamskraal Formation at its thickest point, in the upper Koornplaats Member, and the last occurrence of *Eodicynodon* at 2000 m, in the mid-Swaerskraal Member (Figure 40); below 1600 m, *Eodicynodon* is present in the absence of characteristic *Tapinocephalus* AZ genera, while above 2000 m, *Tapinocephalus* and *Bradysaurus* are found together in the absence of *Eodicynodon*. While this part of the Abrahamskraal Formation is still poorly understood, the appearance of advanced tapinocephalid dinocephalians in the upper *Eodicynodon* AZ suggests that there was a more gradual replacement of *Eodicynodon* AZ genera by more derived taxa.

For the purposes of biostratigraphy, the range of *Eodicynodon* exclusive of *Struthiocephalus* is henceforth referred to as the *Eodicynodon* AZ *sensu stricto*, which is separated from the *Tapinocephalus* AZ by a transition zone (Figure 40). The *Pristerognathus* AZ is retained using its existing definition of a low diversity fauna dominated by scylacosaurid therocephalians and the dicynodont *Diictodon*, in the absence of dinocephalians (Smith and Keyser 1995b), and overlies the *Tapinocephalus* AZ. However, its stratigraphic extent is reduced to accommodate the presence of dinocephalians in the basal Poortjie Member.

7.3 Basin Development

The development of the Karoo Basin, for which two primary models have been proposed, remains contentious but certain contextual factors appear likely. Firstly, that during deposition of the Abrahamskraal Formation and Poortjie Member, the Karoo Basin extended further to the south than its current outcrop area, as evidenced by the highly folded but parallel nature if the beds along the southern margin of the basin and the lack of coarse proximal sediments in the preserved portion of the basin.

The further extent of the Karoo Basin to the south of its current exposure is further supported by the second factor, that the source area for the Middle Permian Beaufort rocks was situated far to south, beyond the Cape Supergroup depocentre. The evidence for this comes primarily from petrographic studies of the Lower Beaufort and Ecca groups, which indicate that sediment derived from the Cape Supergroup was unlikely to have contributed to the Karoo Basin fill until the Katberg Formation in the earliest Triassic (Andersson *et al.* 2004; Johnson 1976; Scott 1997 In Andersson *et al.* 2004). The extent of Cape Supergroup exposure during the Middle Permian was therefore still limited to low-lying ground and was experiencing either deposition or non-deposition, but not erosion. Crustal compression associated with the paroxysms of Hälbich (1983) is not ruled out, but uplift appears only to have occurred to the south of the Cape Supergroup depocentre leading to erosion of Saldanian basement, which forms a more suitable source terrane for the Middle Permian Beaufort Group.

Within the existing remnant of the Karoo Basin, the litho- and biostratigraphy of the Beaufort Group provide an important source of information for the pattern of subsidence during the Middle Permian. Initially, in the *Eodicynodon* AZ *sensu stricto*, subsidence rates were high along the southern margin of the basin, where terrestrial sedimentation deposited a thick sequence corresponding to the Combrinkskraal, Leeuvlei and Koornplaats members of the Abrahamskraal Formation. Although no fossils of *Eodicynodon* have yet been found west of Laingsburg or east of Rietbron (Rubidge 1995b), the presence of the Koornplaats Member at Ouberg Pass and the thickness of the Koonap Formation at Klipplaat suggest that the *Eodicynodon* AZ *sensu stricto* may be more extensive than currently recognised (Figure 1).

Subsidence slowed in the *Tapinocephalus* AZ, as is evidenced by the more widespread lithostratigraphic units of the upper Abrahamskraal Formation, and reduced thickness of the *Tapinocephalus* AZ in the south of the basin compared to the underlying *Eodicynodon* AZ (Figure 40). More specifically, the rate at which accommodation space was created along the southern margin of the basin decreased to the point that sediment was not captured there and so was transported to more distal areas. By the end of the Middle Permian, the wide geographical extent of the Poortjie Member and the further reduced thickness of the associated *Pristerognathus*

AZ indicate that subsidence was further reduced, and that sediment was now transported widely across the basin.

As a result, the advance of terrestrial deposition into the Karoo Basin during the Middle Permian can be tacked. By the end of the *Eodicynodon* AZ *sensu stricto*, the shoreline had prograded from the south-western margin of the basin to a position somewhere south of the Nuweveld Escarpment, although it is possible that it extended further north on the western margin of the basin (Figure 41 – Time 2). By the end of the *Tapinocephalus* AZ, the shoreline had prograded as far north as the vicinity of Victoria West (Figure 41 – Time 4). Although sediment being deposited at the northern extent shoreline at this time had been transported from a southern source area, a large area north of the Nuweveld Escarpment had first undergone terrestrial deposition by sediment transported from the northwest before this was overwhelmed (Figure 41 – Time 3). By the end of the *Pristerognathus* AZ, the shoreline was situated to the north of Philippolis, which means that from the onset of Beaufort Group deposition to the end of the Middle Permian, the shoreline had therefore prograded at least 320 km north of the southern margin of the basin (Figure 41 – Time 5).

7.4 The end-*Tapinocephalus* AZ extinction in the Karoo Basin

The tetrapod faunal extinctions of the late Middle Permian in the Karoo Basin can be roughly divided into two phases: the end-*Tapinocephalus* AZ extinction, which occurs lithostratigraphically between the mid-Karelskraal Member of the uppermost Abrahamskraal Formation, and the extinctions of most remaining *Tapinocephalus* AZ genera at the top of the *Pristerognathus* AZ (Figure 40).

The first event is by far the most significant, involving a rapid increase in the extinction rate and the simultaneous reduction of originations to zero (Figure 43). Its onset coincided with the point of maximum tetrapod generic diversity recorded in the Middle Permian and in its initial stage, within the upper Karelskraal Member, all major taxa are equally affected by a loss of generic diversity; only larger taxa suffer in terms of abundance. In its latter stage, within the lowest Poortjie Member, larger taxa

experienced differentially higher rates of loss in both abundance and generic diversity, leading to the reduction of dinocephalian genera to only 2 or 3 and a total loss of pareiasaur genera. By the end of this extinction interval, at the point of lowest generic diversity, all dinocephalian genera had also become extinct and all surviving taxa were relatively species poor. The fauna at this point was dominated by only a few highly successful genera of dicynodonts and therocephalians. Overall, a 75% loss of generic diversity is experienced by terrestrial tetrapods in the end-*Tapinocephalus* AZ extinction, which is reasonably well constrained to have occurred approximately 261–262 Ma.

The extinctions that occur at the top of the *Pristerognathus* AZ coincide with the top of the Poortjie member of the Teekloof Formation. Throughout the upper part of this unit, the rate of generic originations began to increase and rate of extinction to drop, so that overall generic diversity was increasing and continued to rise across the boundary of the *Pristerognathus* and *Tropidostoma* assemblage zones (Figure 43). Therefore, the ecological environment during this biotic turnover was rather different to end-*Tapinocephalus* AZ extinction in that it occurred in a period of recovery. Few taxa became extinct but those that did were survivor taxa from the *Tapinocephalus* AZ and were at in fact at their most abundant in the upper Poortjie Member, which shows similarities with the Permo-Triassic Mass Extinction (Smith and Botha 2005). The timing of the extinctions at the top of the *Pristerognathus* AZ are well constrained to have occurred 260 Ma (Rubidge *et al.* 2013).

7.5 Global Capitanian tetrapod diversity change and the Guadalupian extinction on land

Outside South Africa, the evidence for a terrestrial extinction in the Capitanian comes largely from the absence of dinocephalians in all assemblages bearing typically Wuchiapingian taxa (Rubidge 2005; Lucas 2009). For other tetrapod taxa extinctions appear to have been more localised, as is exemplified by the survival of scylacosaurid therocephalians perhaps as late as the Changhsingian in Russia and the survival of pareiasaurs somewhere beyond the Karoo Basin pareiasaurs, potentially in the Parana Basin of Brazil. Because the fossil record for the Capitanian is not as continuous

anywhere outside South Africa, the effects of the 'dinocephalian extinction event' on generic diversity and the timing of the extinctions can be only poorly understood (Figure 3). However, the global extinction of dinocephalians at the end of the Middle Permian and the radiation of dicynodonts, pareiasaurs and gorgonopsians in the Late Permian are almost certainly linked.

Contrary to Rubidge *et al.* (2013), the temporal coincidence of the end-*Tapinocephalus* AZ extinction with the marine Capitanian extinctions in East Asia is found to be supported on the basis that the latter extinction is best constrained to occur within the Capitanian, rather than at its end (Bond *et al.* 2010a). A contemporaneous extinction in the East Asian marine realm and the geographically disparate terrestrial Karoo Basin would imply a mechanism with the potential for global atmospheric disruption, for which Emeishan volcanism is the most consistent. The proximal mechanisms probably differed geographically, as explosive eruptions and the local effects of aerosol production in the early stages of eruption in the Emeishan LIP have been implicated in the marine extinction in China (Bond *et al.* 2010a; Wignall *et al.* 2009a). Conversely, the extinctions in the terrestrial realm in southern Gondwana would have required large scale climatic change involving acidification and a reduction in primary productivity due to ash in the atmosphere or global warming and a reduction in atmospheric oxygen due to methane released by volcanic intrusion into coal deposits (Retallack and Jahren 2008).

CHAPTER 8: FUTURE DIRECTIONS

The conclusions presented above are based on the available data for the Middle Permian part of the Beaufort Group but several avenues for future research have been identified that would improve their accuracy. In particular, for the investigation of the transition between the *Eodicynodon* AZ and the *Tapinocephalus* AZ, further collecting work needs to be conducted in the Koornplaats and Swaerskraal members of the Abrahamskraal Formation. This is also the case for *Tapinocephalus-Pristeroganthus* AZ transition which, although the interval has been well collected in a general sense, has not yet been subject to dedicated stratigraphic collecting. This would vastly improve the resolution at which the end-*Tapinocephalus* AZ extinction could be described.

Because the recovery fauna after the end-*Tapinocephalus* AZ extinction is not well represented in the Middle Permian, data was used in this study for the earliest Late Permian that was derived from the genus list for the entire *Tropidostoma* AZ (Smith *et al.* 2012). This is quite a broad time bin and, as this study proves, the range of individual genera within the *Tropidostoma* AZ is likely to more complex than currently understood. Therefore, a similar biostratigraphic study to this but focussed on the *Tropidostoma* and *Cistecephalus* assemblages zones would allow the post-extinction recovery to be described far more completely.

At a more fundamental level, the taxonomy of Middle Permian tetrapod groups could also be improved upon. Only dicynodonts and anteosaurid dinocephalians have received decent attention, although work is ongoing with tapinocephalid dinocephalians and lycosuchid therocephalians. Revision of the scylacosaurid therocephalians, pareiasaurs, temnospondyls and in particular the gorgonopsians would provide important refinement of these findings and could easily build upon the stratigraphic database for individual specimens the now exists for the Middle Permian Beaufort Group.

Lastly, the marine and terrestrial extinctions can be approximately constrained in time to occur 262–261 Ma but more direct evidence required to confirm this. The most influential means to this end is the acquisition of accurate radiometric dates from two particular horizons: 1) the basalt horizon at Xiong Jia Chang within the *J.*

altudaensis conodont zone, in order to constrain the marine extinctions and 2) tuffs within the *Tapinocephalus* AZ, in order to provide a lower constraint for the dinocephalian extinction.

REFERENCES

Abdala, F., Hancox, P. J. & Neveling, J. 2005. Cynodonts from the Uppermost Burgersdorp Formation, South Africa, and Their Bearing on the Biostratigraphy and Correlation of the Triassic *Cynognathus* Assemblage Zone. *Journal of Vertebrate Paleontology,* 25**,** 192-199.

Abdala, F., Rubidge, B. S. & Van Den Heever, J. 2008. The oldest therocephalians (Therapsida, Eutheriodontia) and the early diversification of Therapsida. *Palaeontology,* 51**,** 1011-1024.

Allen, J. R. L. 1978. Studies in fluviatile sedimentation: an exploratory quantitative model for the architecture of avulsion-controlled alluvial suites. *Sedimentary Geology,* 21**,** 129-147.

Anderson, J. M. 1977. The biostratigraphy of the Permian and the Triassic. Part 3. A review of Gondwana Permian palynology with particular reference to the northern Karoo Basin, South Africa. *Memoir Botanical Survey South Africa,* 41**,** 1-188.

Anderson, J. & Cruickshank, A. 1978. The biostratigraphy of the Permian and the Triassic. Part 5. A review of the classification and distribution of Permo-Triassic tetrapods. *Palaeontologia Africana,* 21**,** 15-44.

Anderson, J. S. & Reisz, R. R. 2004. *Pyozia mesenensis*, a new, small varanopid (Synapsida, Eupelycosauria) from Russia: "pelycosaur" diversity in the Middle Permian. *Journal of Vertebrate Paleontology,* 24**,** 173-179.

Andersson, P. O. D., Worden, R. H., Hodgson, D. M. & Flint, S. 2004. Provenance evolution and chemostratigraphy of a Palaeozoic submarine fan-complex: Tanqua Karoo Basin, South Africa. *Marine and Petroleum Geology,* 21**,** 555-577.

Angielczyk, K. 2001. Preliminary phylogenetic analysis and stratigraphic congruence of the dicynodont anomodonts (Synapsida: Therapsida). *Palaeontologia Africana,* 37**,** 53-79.

Angielczyk, K. D. 2004. Phylogenetic evidence for and implications of a dual origin of propaliny in anomodont therapsids (Synapsida). *Paleobiology,* 30**,** 268-296.

Angielczyk, K., Fröbisch, J. & Smith, R. 2005. On the stratigraphic range of the dicynodont taxon *Emydops* (Therapsida: Anomodontia) in the Karoo Basin, South Africa. *Palaeontologia Africana,* 41**,** 23-33.

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 Pangaean biogeography. *Zoological Journal of the Linnean Society,* 139**,** 157-212.

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. 2012. 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***,** 1-41.

Angielczyk, K. D., Sidor, C. A., Nesbitt, S. J., Smith, R. M. & Tsuji, L. A. 2009. Taxonomic revision and new observations on the postcranial skeleton, biogeography, and biostratigraphy of the dicynodont genus *Dicynodontoides*, the senior subjective synonym of *Kingoria* (Therapsida, Anomodontia). *Journal of Vertebrate Paleontology,* 29**,** 1174-1187.

Angielczyk, K. D. & Sullivan, C. 2008. *Diictodon feliceps* (Owen, 1876), a dicynodont (Therapsida, Anomodontia) species with a Pangaean distribution. *Journal of Vertebrate Paleontology,* 28**,** 788-802.

Araujo, D. C. 1985. Sobre *Pareiasaurus americanus* sp. nov., do Permiano Superior do Rio Grande do Sul, Brasil. I Diagnose específica. *Anais da Academia Brasileira de Ciências,* 57**,** 63–66.

Attridge, J., Ball, H. W., Charig, A. J. & Cox, C. B. 1964. The British Museum (Natural History)–University of London joint palaeontological expedition to Northern Rhodesia and Tanganyika, 1963. *Nature***,** 445–449.

Bain, A. 1856. On the Geology of Southern Africa. *Transactions of the Geological Society of London,* 7**,** 175-192.

Barberena, M., Araújo, D. & Lavina, E. 1985. Late Permian and Triassic tetrapods of southern Brazil. *National Geographic Research,* 1**,** 5-20.

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*, Cape Town and Johannseburg: C.S.I.R. Pretoria, 653–656.

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

Battail, B. 2000. A comparison of Late Permian Gondwanan and Laurasian amniote faunas. *Journal of African Earth Sciences,* 31**,** 165-174.

Battail, B. & Surkov, M. V. 2000. Mammal-like reptiles from Russia. *In:* Benton, M. J., Shishkin, M. A. & Unwin, D. M. (eds.) *The Age of Dinosaurs in Russia and Mongolia*, 86–119. Cambridge: Cambridge University Press.

Baud, A., Atudorei, V. & Sharp, Z. 1996. Late Permian and Early Triassic evolution of the Northern Indian margin: carbon isotope and sequence stratigraphy. *Geodinamica Acta,* 9**,** 57–77.

Benton, M. J. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society,* 84**,** 97-164.

Benton, M. J. 2012. No gap in the Middle Permian record of terrestrial vertebrates. *Geology,* 40**,** 339-342.

Benton, M. J., Tverdokhlebov, V. P. & Surkov, M. V. 2004. Ecosystem remodelling among vertebrates at the Permian-Triassic boundary in Russia. *Nature,* 432**,** 97-100.

Blignaut, J. J. G., Rossouw, P. J., De Villiers, J. & Russell, H. D. 1950. The Geology of the Schoorsteenberg Area, Cape Province: An Explanation of Sheet No. 166 (Schoorsteenberg). 80. Geological Survey of South Africa, Pretoria.

Bond, D. P. G., Hilton, J., Wignall, P. B., Ali, J. R., Stevens, L. G., Sun, Y. & Lai, X. 2010a. The Middle Permian (Capitanian) mass extinction on land and in the oceans. *Earth-Science Reviews,* 102**,** 100-116.

Bond, D. P. G., Wignall, P. B., Wang, W., Izon, G., Jiang, H. S., Lai, X. L., Sun, Y. D., Newton, R. J., Shao, L. Y., Védrine, S. & Cope, H. 2010b. The mid-Capitanian (Middle Permian) mass extinction and carbon isotope record of South China. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 292**,** 282-294.

Boonstra, L. D. 1934. A contribution to the morphology of the mammal-like reptiles of the sub-order Therocephalia. *Annals of the South African Museum,* 31**,** 215–267.

Boonstra, L. D. 1940. Twee nuwe ragitome Labirintodontiers. *Oorgedruk uit Tydskrif vir Wetenskap en Kuns,* 1**,** 195–198.

Boonstra, L. D. 1946. Report on some reptilian fossils from Gunyankaskraal, Busi Valley. *Proceedings and Transactions of the Rhodesian Science Association,* 41**,** 46–49.

Boonstra, L. D. 1948. Anomodont reptiles from the *Tapinocephalus* zone of the Karroo System. *In:* Du Toit, A. L. (ed.) *Special Publications of the Royal Society of South Africa. Robert Broom Commemorative Volume.*, 57-64. Cape Town: The Royal Society.

Boonstra, L. D. 1952a. 'n Nuwe tapinocephalide, *Riebeeckosaurus longirostris* ge. et sp. nov. *Tydskruif Wet. Kuns,* 12**,** 246–249.

Boonstra, L. D. 1952b. ‘n Uiters interessante nuwe deinocephaliër, *Avenantia kruisvleiensis* gen. Et. Sp. nov. *Tydskruif Wet. Kuns*, 12, 250–255.

Boonstra, L. D. 1952c. *Struthiocephaloides*: 'n Nuwe genus van mormosauride tapinocephaliers. *Tydskruif Wet. Kuns,* 12**,** 237–241.

Boonstra, L. D. 1952d. 'n Nuwe Titanosuchiersoort (*Anteosaurus abeli*) *Tydskruif Wet. Kuns,* 12**,** 150–151.

Boonstra, L. D. 1952e. A new deinocephalian from the Karoo. *Annals of the Magazine of Natural History,* 5**,** 988–989.

Boonstra, L. D. 1952f. 'n Nuwe soort van tapinocephalide deinocephaliër *Struthiocephalus akraalensis* sp. nov. *South African Journal of Science,* 48**,** 247–248.

Boonstra, L. D. 1953a. A suggested clarification of the taxonomic status of the South African titanosuchians. *Annals of the South African Museum,* 42**,** 19–28.

Boonstra, L. D. 1953b. A new scaloposaurian genus. *Annals and Magazine of Natural History,* 6**,** 601–605.

Boonstra, L. D. 1954a. The cranial structure of the titanosuchian: *Anteosaurus*. *Annals of the South Africa Museum,* 42**,** 108–148.

Boonstra, L. D. 1954b. A scaloposaurid from the *Tapinocephalus* Zone. *Annals and Magazine of Natural History,* 7**,** 153–157.

Boonstra, L. D. 1954c. The pristerognathid therocephalians from the *Tapinocephalus* zone in the South African Museum. *Annals of the South African Museum,* 42**,** 65–107.

Boonstra, L. D. 1955. The girdles and limbs of the South African Deinocephalia. *Annals of the South Africa Museum,* 42**,** 185–326.

Boonstra, L. D. 1956. The skull of *Tapinocephalus* and its near relatives. *Annals of the South Africa Museum,* 43**,** 137–169.

Boonstra, L. D. 1957. The moschopd skulls in the South African Museum. *Annals of the South Africa Museum,* 44**,** 15–38.

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

Boonstra, L. D. 1972. Discard the names Theriodontia and Anomodontia: a new classification of the therapsida. *Annals of the South Africa Museum,* 59**,** 315-338.

Botha-Brink, J. & Modesto, S. P. 2007. A mixed-age classed 'pelycosaur'aggregation from South Africa: earliest evidence of parental care in amniotes? *Proceedings of the Royal Society B: Biological Sciences,* 274**,** 2829-2834.

Bowring, S. A., Erwin, D., Jin, Y., Martin, M., Davidek, K. & Wang, W. 1998. U/Pb zircon geochronology and tempo of the end-Permian mass extinction. *Science,* 280**,** 1039-1045.

Brink, A. S. 1957. *Struthiocephalus kitchingi* sp. nov. *Palaeontologia Africana,* 5**,** 39–56.

Brinkman, D. 1981. The structure and relationships of the dromasaurs. *Breviora,* 465**,** 1–34.

Broom, R. 1903a. II.—On the Structure of the Palate in the Primitive Theriodonts. *Geological Magazine (Decade IV),* 10**,** 343-345.

Broom, R. 1903b. On the classification of the theriodonts and their allies. *Report of the South African Association for the Advancement of Science,* 1**,** 286–294.

Broom, R. 1903c. On an almost perfect skull of a new primitive theriodont (*Lycosuchus vanderrieti*). *Transactions of the South African Philosophical Society,* 14**,** 197–205.

Broom, R. 1903d. On some new primitive theriodonts in the South African Museum. *Annals of the South African Museum,* 4**,** 147–158.

Broom, R. 1904. On two new therocephalian reptiles (*Glanosuchus macrops* and *Pristerognathus baini*). *Transactions of the South African Philosophical Society,* 15**,** 85–88.

Broom, R. 1905. On the structure and affinities of the endothiodont reptiles. *Transactions of the South African Philosophical Society,* 15**,** 259–282.

Broom, R. 1906a. The Classification of the Karoo Beds of South Africa. *Geological Magazine,* 5**,** 36.

Broom, R. 1906b. On the Permian and triassic faunas of South Africa. *Geological Magazine,* 5**,** 29-30.

Broom, R. 1907. On some new fossil reptiles from the Karroo Beds of Victoria West, South Africa. *Transactions of the South African Philosophical Society,* 18**,** 31-42.

Broom, R. 1908a. On a new labyrinthodont *Rhinesuchus whaitsi*, from the Permian beds of South Africa. *Annals of the South Africa Museum,* 4**,** 373-377.

Broom, R. 1908b. On some new therocephalian reptiles. *Annals of the South African Museum,* 4**,** 361–367.

Broom, R. 1910. A comparison of the Permian reptiles of North America with that of South Africa. *Bulletin of the American Museum of Natural History,* 28**,** 197–234.

Broom, R. 1911. On some new South African Permian reptiles. *Proceedings of the Zoological Society of London,* 1911**,** 1073–1082.

Broom, R. 1912. On some fossil reptiles from the Permian and Triassic beds of South Africa. *Proceedings of the Zoological Society of London,* 1912**,** 859-876.

Broom, R. 1913. On some new genera and species of dicynodont reptiles, with notes on a few others. *Bulletin of the American Museum of Natural History,* 32**,** 441-457.

Broom, R. 1914. A further comparison of the South African dinocephalians with the American pelycosaurs. *Bulletin of the American Museum of Natural History,* 33**,** 135–141.

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.

Broom, R. & Haughton, S. H. 1917. New species of Anomodontia (Reptilia). *Annals of the South African Museum,* 12**,** 119–125.

Broom, R. 1921. On some new genera and species of anomodont reptiles from the Karroo Beds of South Africa. *Proceedings of the Zoological Society of London,* 1921**,** 647–674.

Broom, R. 1923. On the structure of the skull in the carnivorous dinocephalian reptiles. *Proceedings of the Zoological Society of London,* 1923**,** 661–684.

Broom, R. 1927. On a New Type of Mammal-like Reptile from the South African Karroo Beds (Anningia megalops). *Proceedings of the Zoological Society of London,* 97**,** 227-232.

Broom, R. 1928. On *Tapinocephalus* and two other dinocephalians. *Annals of the South Africa Museum,* 22**,** 427–428.

Broom, R. 1929. On the carnivorous mammal-like reptiles of the family Titanosuchidae. *Annals of the Transvaal Museum,* 13**,** 9–36.

Broom, R. 1931. Notices of some new genera and species of Karroo fossil reptiles. *Record of the Albany Museum,* 4**,** 161–166.

Broom, R. 1932. *The mammal-like reptiles of South Africa*. London, Whitherby.

Broom, R. 1935. On some new genera and species of Karroo fossil reptiles. *Annals of the Transvaal Museum,* 18**,** 55–72.

Broom, R. 1937. A further contribution to our knowledge of the fossil reptiles of the Karroo. *Proceedings of the Zoological Society of London B***,** 299–318.

Broom, R. 1940. On some new genera and species of fossil reptiles from the Karroo Beds of Graaff-Reinet. *Annals of the Transvaal Museum,* 20**,** 157–192.

Broom, R. 1948. A contribution to our knowledge of the vertebrates of the Karroo Beds of South Africa. *Transactions of the Royal Society of Edinburgh,* 61**,** 577–629.

Carroll, R. L. 1976. Eosuchians and the origin of archosaurs. *Essays on Palaeontology in Honour of Loris Shano Russell. Royal Ontario Museum, Toronto***,** 58-79.

Catuneanu, O. 2004. Basement control on flexural profiles and the distribution of foreland facies: The Dwyka Group of the Karoo Basin, South Africa. *Geology,* 32**,** 517-520.

Catuneanu, O. & Bowker, D. 2001. Sequence stratigraphy of the Koonap and Middleton fluvial formations in the Karoo foredeep South Africa. *Journal of African Earth Sciences,* 33**,** 579-595.

Catuneanu, O. & Elango, H. N. 2001. Tectonic control on fluvial styles: the Balfour Formation of the Karoo Basin, South Africa. *Sedimentary Geology,* 140**,** 291-313.

Catuneanu, O., Hancox, P., Cairncross, B. & Rubidge, B. 2002. Foredeep submarine fans and forebulge deltas: orogenic off-loading in the underfilled Karoo Basin. *Journal of African Earth Sciences,* 35**,** 489-502.

Catuneanu, O., Hancox, P. J. & Rubidge, B. S. 1998. Reciprocal flexural behaviour and contrasting stratigraphies: a new basin development model for the Karoo retroarc foreland system, South Africa. *Basin Research,* 10**,** 417-439.

Cheng, Z. & Li, J. 1997a. First record of a primitive anteosaurid dinocephalian from the Upper Permian of Gansu, China. *Vertebrata Palasiatica,* 34**,** 123-134.

Cheng, Z. & Li, J. 1997b. A new genus of primitive dinocephalian - the third report on Late Permian Dashankou lower tetrapod fauna. *Vertebrata Palasiatica,* 35**,** 35-43.

Chudinov, P. K. 1969. [On the stratigraphic distribution of Permian vertebrates in eastern European parts of the USSR.]. *[Questions on the Geology of the South Urals and Povolga Region]*, 96–105. Saratov: Izdatel'stvo Saratovskogo Universiteta.

Chudinov, P. K. 1983. [early therapsids]. *Trudy paleontologischeskogo Instituta,* 202**,** 1–230.

Cisneros, J. C., Abdala, F., Atayman-Güven, S., Rubidge, B. S., Şengör, A. M. C. & Schultz, C. L. 2012. Carnivorous dinocephalian from the Middle Permian of Brazil and tetrapod dispersal in Pangaea. *Proceedings of the National Academy of Sciences,* 109**,** 1584-1588.

Cisneros, J. C., Abdala, F., Rubidge, B. S., Dentzien-Dias, P. C. & Bueno, A. D. O. 2011. Dental Occlusion in a 260-Million-Year-Old Therapsid with Saber Canines from the Permian of Brazil. *Science,* 331**,** 1603-1605.

Cisneros, J. C., Rubidge, B. S., Mason, 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. *Journal of Systematic Palaeontology,* 6**,** 453-462.

Clapham, M. E., Shen, S. & Bottjer, D. J. 2009. The double mass extinction revisited: reassessing the severity, selectivity, and causes of the end-Guadalupian biotic crisis (Late Permian). *Paleobiology,* 35**,** 32-50.

Clevis, Q., De Boer, P. L. & Nijman, W. 2004. Differentiating the effect of episodic tectonism and eustatic sea-level fluctuations in foreland basins filled by alluvial fans and axial deltaic systems: insights from a three-dimensional stratigraphic forward model. *Sedimentology,* 51**,** 809-835.

Cluver, M. A. 1975. A new dicynodont reptile from the Tapinocephalus Zone (Karoo System, Beaufort series) of South Africa, with evidence of the jaw adductor musculature. *Annals of the South Africa Museum,* 67**,** 7–23.

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.

Cluver, M. A. & King, G. M. 1983. A reassessment of the relationships of Permian Dicynodontia (Reptilia, Therapsida) and a new classification of dicynodonts. *Annals of the South African Museum,* 91**,** 195–273.

Cole, D. I. 1992. Evolution and development of the Karoo Basin. *In:* De Wit, M. J. & Ransome, I. G. D. (eds.) *Inversion Tectonics of the Cape Fold Belt, Karoo and Creataceous basins of Southern Africa*, 87–99. Rotterdam: Balkema.

Cole, D. I. & Wipplinger, P. E. 2001. Sedimentology and molybdenum potential of the Beaufort Group in the main Karoo basin, South Africa. *Council for Geoscience Memoirs,* 80**,** 1–225.

Courtillot, V., Jaupart, C., Manighetti, I., Tapponnier, P. & Besse, J. 1999. On causal links between flood basalts and continental breakup. *Earth and Planetary Science Letters,* 166**,** 177-195.

Cox, C. B. 1959. On the anatomy of a new dicynodont genus with evidence of the position of the tympanum. *Proceedings of the Zoological Society of London,* 132**,** 321–367.

Cox, C. B. 1964. On the palate, dentition, and classification of the fossil reptile Endothiodon and related genera. *American Museum Novitates,* 2171**,** 1–25.

Damiani, R. & Rubidge, B. 2003. A review of the South African temnospondyl amphibian record. *Palaeontologia Africana,* 39**,** 21-36.

Damiani, R. J. 2004. Temnospondyls from the Beaufort Group (Karoo Basin) of South Africa and their biostratigraphy. *Gondwana Research,* 7**,** 165-173.

Day, M. O., Rubidge, B. S. R., Almond, J. & Jirah, S. 2013. Biostratigraphic correlation in the Karoo: The case of the Middle Permian parareptile *Eunotosaurus*. *Journal of African Earth Sciences,* (In Press).

De Swardt, A. & Rowsell, D. 1974. Note on the relationship between diagenesis and deformation in the Cape Fold Belt. *Transactions of the Geological Society of South Africa,* 77**,** 53-58.

De Wit, M. J. & Ransome, G. D. 1992. Regional inversion tectonics along the southern margin of Gondwana. *In:* De Wit, M. J. R., G. D. (ed.) *Inversion Tectonics of the Cape Fold Belt, Karoo and Cretaceous Basins of Southern Africa*, 15-22. Rotterdam: Balkema.

DeCelles, P. & Cavazza, W. 1999. A comparison of fluvial megafans in the Cordilleran (Upper Cretaceous) and modern Himalayan foreland basin systems. *Geological Society of America Bulletin,* 111**,** 1315-1334.

DeCelles, P. G. & Giles, K. A. 1996. Foreland basin systems. *Basin Research,* 8**,** 105-123.

DeCelles, P. G. & Hertel, F. 1989. Petrology of fluvial sands from the Amazonian foreland basin, Peru and Bolivia. *Geological Society of America Bulletin,* 101**,** 1552-1562.

Dilkes, D. W. & Reisz, R. R. 1996. First record of a basal synapsid ('mammal-like reptile') in Gondwana. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 263**,** 1165-1170.

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*, 71–181.

Du Toit, A. L. 1929. The geology of the major portion of East Griqualand: Explanation of Cape Sheet 35 (Matatiele). 31. Geological Survey of South Africa, Pretoria.

Du Toit, A. L. 1937. *Our Wandering Continents: an hypothesis of continental drifting.* London, Oliver and Boyd.

Du Toit, A. L. 1954. *The Geology of South Africa (3rd Edition),* 325. London, Oliver and Boyd.

Dunn, E. J. 1873. *Geological sketch map of Cape Colony; I inch=24 miles.* London: Sandford's Geographical Establishment.

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

Efremov, I. A. 1940. Kurze Ubersicht uber die Formen der Perm- und Trias-Tetrapoden-Fauna der USSR. *Centralblatt fur Mineralogie, Geologie, und Palaontologie,* Abtheilung B**,** 372–383.

Efremov, I. A. 1954. [Fauna of terrestrial vertebrates from the Copper Sandstones of the western Cis-Urals]. *Trudy paleontologischeskogo Instituta,* 54**,** 1–416.

Efremov, I. A. & V'yushkov, B. P. 1955. [Catalogue of the localities of Permian and Triassic vertebrates in the territories of the USSR]. *Trudy paleontologischeskogo Instituta,* 236**,** 1–147.

Fildani, A., Drinkwater, N. J., Weislogel, A., Mchargue, T., Hodgson, D. M. & Flint, S. S. 2007. Age controls on the Tanqua and Laingsburg deep-water systems: new insights on the evolution and sedimentary fill of the Karoo basin, South Africa. *Journal of Sedimentary Research,* 77**,** 901-908.

Fleming, P. B. & Jordan, T. E. 1989. A synthetic stratigraphic model of foreland basin development. *Journal of Geophysical Research,* 94:B4**,** 3851-3866.

Fröbisch, J. 2007. The cranial anatomy of *Kombuisia frerensis* Hotton (Synapsida, Dicynodontia) and a new phylogeny of anomodont therapsids. *Zoological Journal of the Linnean Society,* 150**,** 117-144.

Fröbisch, J. 2008. Global taxonomic diversity of anomodonts (tetrapoda, therapsida) and the terrestrial rock record across the Permian-Triassic boundary. *PloS one,* 3**,** e3733.

Fröbisch, J. 2009. Composition and similarity of global anomodont-bearing tetrapod faunas. *Earth-Science Reviews,* 95**,** 119-157.

Fröbisch, J. 2013. Vertebrate diversity across the end-Permian mass extinction — Separating biological and geological signals. *Palaeogeography Palaeolimatology Palaeoecology,* 372**,** 50–61.

Fröbisch, J., Angielczyk, K. & Sidor, C. 2010. The Triassic dicynodont *Kombuisia* (Synapsida, Anomodontia) from Antarctica, a refuge from the terrestrial Permian-Triassic mass extinction. *Naturwissenschaften,* 97**,** 187-196.

Fröbisch, J. & Reisz, R. R. 2008. A new species of *Emydops* (Synapsida, Anomodontia) and a discussion of dental variability and pathology in dicynodonts. *Journal of Vertebrate Paleontology,* 28**,** 770-787.

Fröbisch, J. & Reisz, R. R. 2011. The postcranial anatomy of *Suminia getmanovi* (Synapsida: Anomodontia), the earliest known arboreal tetrapod. *Zoological Journal of the Linnean Society,* 162**,** 661-698.

Gebauer, E. 2007. *Phylogeny and Evolution of the Gorgonopsia with a Special Reference to the Skull and Skeleton of GPIT/RE/7113 ('Aelurognathus?' parringtoni).* Unpublished PhD thesis, Universität Tübingen.

Gialanella, P. R., Heller, F., Haag, M., Nurgaliev, D., Borisov, A., Burov, B., Jasonov, P., Khasanov, D., Ibragimov, S. & Zharkov, I. 1997. Late Permian magnetostratigraphy on the eastern Russian platform. *Geologie en Mijnbouw,* 76**,** 145-154.

Glenister, B. F., Wardlaw, B. R., Lambert, L. L., Spinosa, C., Bowring, S. A., Erwin, D. H., Menning, M. & Wilde, G. L. 1999. Proposal of Guadalupian and component Roadian, Wordian, and Capitanian stages as international standards for the Middle Permian Series. *Permophiles,* 34**,** 3–11.

Golubev, V. K. 2005. Permian tetrapod stratigraphy. *New Mexico Museum of Natural History and Science Bulletin,* 30**,** 95-99.

Gow, C. E. & De Klerk, W. 1997. First record of *Eunotosaurus* (Amniota: Parareptilia) from the Eastern Cape. *Palaeontologia Africana,* 34**,** 37–31.

Gradstein, F. M., Ogg, J. G. & Smith, A. G. 2004. *A geologic time scale 2004*. Cambridge, UK, Cambridge University Press.

Green, A. H. 1888. A Contribution to the Geology and Physical Geography of the Cape Colony. *Quarterly Journal of the Geological Society,* 44**,** 239–270.

Güven, S. 2012. Taxonomy of tapinocephalid dinocephalia from the South African Karoo Basin. *In:* 16th Biennial Conference of the Palaeontological Association of Southern Africa, Cape Town. Palaeontologia Africana, 37.

Hälbich, I. 1992. The Cape Fold Belt Orogeny: State of the art 1970s-1980s. *Inversion tectonics of the Cape Fold Belt, Karoo and Cretaceous Basins of Southern Africa,* AA Balkema, Rotterdam, The Netherlands**,** 141-158.

Hälbich, I. W. 1983. A tectonogenesis of the Cape Fold Belt (CFB). *In:* Sohnge, A. P. & Hälbich, I. W. (eds.) *Geodynamics of the CapeFold Belt. Geological Society of South Africa*, 165-175.

Hallam, A. & Wignall, P. B. 1997. *Mass extinctions and their aftermath*. Oxford University Press, USA.

Hancox, P. 1998. *A stratigraphic, sedimentological and palaeoenvironmental synthesis of the Beaufort-Molteno contact in the Karoo Basin.* Unpublished PhD thesis, University of the Witwatersrand, Johannesburg.

Hancox, P. J., Shishkin, M. A., Rubidge, B. S. & Kitching, J. W. 1995. A threefold subdivision of the Cynognathus Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographical implications. *South African Journal of Science,* 91**,** 143–144.

Harland, W. B., Armstrong, R. L., Cox, A. V., Craig, L. E., Smith, A. G. & Smith, D. G. 1990. *A geologic time scale 1989,* 262. Cambridge University Press.

Hatch, F. H. & Corstorphine, G. S. 1905. *The Geology of South Africa (1st Edition),* 348. London, Macmillan.

Hatch, F. H. & Corstorphine, G. S. 1909. *The Geology of South Africa (2nd Edition),* 389. London, Macmillan.

Haughton, S. H. 1915. On a new dinocephalian from the Gouph. *Annals of the South Africa Museum,* 12**,** 52–54.

Haughton, S. H. 1924. A bibliographical list of pre-Stormberg Karroo Reptilia, with a table of horizons. *Transactions of the Royal Society of South Africa,* 12**,** 51–104.

Haughton, S. 1929. On some new therapsid genera. *Annals of the South African Museum,* 28**,** 55-78.

Haughton, S. H. 1932. On a collection of Karroo vertebrates from Tanganyika Territory. *Quarterly Journal of the Geological Society,* 88**,** 634-671.

Haughton, S. H. & Boonstra, L. D. 1929. Pareiasaurian studies Part I. An attempt at a classification of the Pareiasauria based on skull features. *Annals of the South Africa Museum,* 28**,** 79–87.

Haughton, S. H. & Brink, A. S. 1954. A bibliographic list of Reptilia from the Karroo beds of Africa. *Palaeontologia Africana,* 2**,** 1–187.

He, B., Xu, Y.-G., Huang, X.-L., Luo, Z.-Y., Shi, Y.-R., Yang, Q.-J. & Yu, S.-Y. 2007. Age and duration of the Emeishan flood volcanism, SW China: Geochemistry and SHRIMP zircon U–Pb dating of silicic ignimbrites, post-volcanic Xuanwei Formation and clay tuff at the Chaotian section. *Earth and Planetary Science Letters,* 255**,** 306-323.

Helber, J. & Gebauer, E. 2001. Geologische Karierung: Westlich von Jansenville, Great Karoo/Sudafrika. *Unpublished report.* Eberhard-Karls-Universitat, Tubingen.

Henderson, C. M., Mei, S. & Wardlaw, B. R. 2002. New Conodont Definitions at the Guadalupian-Lopingian Boundary. *In:* Hills, L. V., Henderson, C. M. & Bamber, E. W. (eds.) *Carboniferous and Permian of the World*, 725-735. Canadian Society of Petroleum Geologists Memoir 19.

Hill, R. S. 1993. Explanation to geological map sheet 3224 (Graaff-Reinet). 31. Council for Geoscience, Pretoria.

Hopson, J. & Barghusen, H. 1986. An analysis of therapsid relationships. *In:* Hotton, N. (ed.) *The Ecology and Biology of the Mammal-like Reptiles*, 83-106. Washington: Smithsonian Institution Press.

Hopson, J. & Kitching, J. W. 1972. A revised classification of cynodonts (Reptilia; Therapsida). *Palaeontologia Africana,* 14**,** 71-85.

Horton, B. & Decelles, P. 2002. Modern and ancient fluvial megafans in the foreland basin system of the central Andes, southern Bolivia: implications for drainage network evolution in fold-thrust belts. *Basin Research,* 13**,** 43-63.

Hotton, N. & Kitching, J. W. 1963. Speculations on Upper Beaufort deposition. *South African Journal of Science,* 59**,** 254-258.

Huttenlocker, A. 2009. An investigation into the cladistic relationships and monophyly of therocephalian therapsids (Amniota: Synapsida). *Zoological Journal of the Linnean Society,* 157**,** 865-891.

Huxley, T. H. 1868. On Saurosternon bainii and Pristerodon mcKayi, two new fossil lacertilian reptiles from South Africa. *Geological Magazine,* 5**,** 201-205.

ICS. 2012. *International Stratigraphic Chart* [Online]. Available: http://www.stratigraphy.org/column.php?id=Chart/Time%20Scale [Accessed 24 January 2013].

Isozaki, Y. 1997. Permo-Triassic boundary superanoxia and stratified superocean: records from lost deep sea. *Science,* 276**,** 235-238.

Isozaki, Y. 2009. Illawarra Reversal: the fingerprint of a superplume that triggered Pangean breakup and the end-Guadalupian (Permian) mass extinction. *Gondwana Research,* 15**,** 421-432.

Isozaki, Y., Kawahata, H. & Minoshima, K. 2007. The Capitanian (Permian) Kamura cooling event: the beginning of the Paleozoic–Mesozoic transition. *Palaeoworld,* 16**,** 16-30.

Isozaki, Y., Yao, J., Matsuda, T., Sakai, H., Ji, Z., Shimizu, N., Kobayashi, N., Kawahata, H., Nishi, H. & Takano, M. 2004. Stratigraphy of the Middle-Upper Permian and Lowermost Triassic at Chaotian, Sichuan, China Record of Late Permian double mass extinction event. *Proceedings of the Japan Academy, Series B,* 80**,** 10-16.

ISSC 1976. *International Stratigraphic Guide (1st Edition), Hedberg, H. D.* (ed.)*,* 200. New York, John Wiley and sons Inc.

ISSC 1994. *International Stratigraphic Guide (2nd Edition), Salvador, A.* (ed.)*,* 214. Boulder, Geological Society of America.

Ivakhnenko, M. F. 1991a. Elements of the Early Permian tetrapod faunal assemblages of Eastern Europe. *Paleontological Journal,* 24**,** 104–112.

Ivakhnenko, M. F. 1991b. Late palaeozoic tetrapod faunal assemblage from the Mezen' River Basin. *Paleontological Journal,* 24**,** 76–84.

Ivakhnenko, M. F. 1995. Primitive Late Permian dinocephalian-titanosuchids of Eastern Europe. *Paleontological Journal,* 29**,** 120-129.

Ivakhnenko, M. F., Golubyev, V. K., Gubin, Y. M., Kalandadze, N. N., Novikov, I. V., Sennikov, A. G. & Rautian, A. S. 1997. *Permian and Triassic tetrapods of Eastern Europe,* 216. Moscow, GEOS.

Janensch, W. 1952. Zwei neue Anomodontier mit Molaren und Crista masseterica aus der Karoo-Schicten Südafrikas. *Paläontologische Zeitschrift,* 26**,** 218–228.

Janensch, W. 1959. Eine *Jonkeria* aus der Karru-Formation des Kaplandes. *Paläontologische Zeitschrift,* 33**,** 22–49.

Jin, Y., Shen, S., Henderson, C. M., Wang, X., Wang, W., Wang, Y., Cao, C. & Shang, Q. 2006. The Global Stratotype Section and Point (GSSP) for the boundary between the Capitanian and Wuchiapingian stage (Permian). *Episodes,* 29**,** 253.

Jin, Y. G., Zhang, J. & Shang, Q. 1994. Two phases of the end-Permian mass extinction. *CSPG Special Publications, Pangea: Global Environments and Resources, Memoir 17***,** 813-822.

Jinnah, Z. & Rubidge, B. 2007. A double tusked dicynodont and its biostratigraphic significance. *South African Journal of Science,* 103**,** 51–53.

Jirah, S. 2009. *Sedimentological, palaeontological & stratigraphic analysis of the Abrahamskraal Formation (Beaufort Group) in an area south of Merweville, South Africa.* Unpublished Bsc Honours Dissertation, University of the Witwatersrand, Johannesburg.

Jirah, S. 2013. *Stratigraphy and sedimentology of the Middle Permian Abrahamskraal Formation (Tapinocephalus Assemblage Zone) in the Southern Karoo around Merweville, South Africa.* Unpublished Msc Thesis, University of the Witwatersrand, Johannesburg.

Johnson, M. R. 1966. *The Stratigraphy of the Cape and Karoo Systems in the Eastern Cape Province.* Unpublished PhD Thesis, Rhodes University, Grahamstown.

Johnson, M. R. 1976. *Stratigraphy and Sedimentology of the Cape and Karoo Sequences in the Eastern Cape Province.* Unpublished PhD thesis, Rhodes University, Grahamstown.

Johnson, M. R. 1991. Sandstone petrography, provenance and plate tectonic setting in Gondwana context of the southeastern Cape-Karoo Basin. *South African Journal of Geology,* 94**,** 137-154.

Johnson, M. R., Botha, B. J. V., Engelbrecht, L. N. J., Hugo, P. J., Keyser, A. W., Turner, B. R. & Winter, H. 1975. Preliminary report on lithostratigraphic nomenclature in the Karoo Sequence. *Unpublished report of the South African Committee for Stratigraphy (Karoo Working Group).*

Johnson, M. R. & Keyser, A. W. 1979. The Geology of the Beaufort West area: An Explanation of sheet 3222. 14. Geological Survey of South Africa, Pretoria.

Johnson, M. R. & Le Roux, F. G. 1994. Explanation of geological map sheet 3326 (Grahamstown). 41. Council for Geoscience, Pretoria.

Jordaan, M. J. 1990. *Basin analysis of the Beaufort Group in the western part of the Karoo Basin.* Unpublished PhD thesis, University of the Orange Free State, Bloemfontein.

Kaiho, K., Chen, Z.-Q., Ohashi, T., Arinobu, T., Sawada, K. & Cramer, B. S. 2005. A negative carbon isotope anomaly associated with the earliest Lopingian (Late Permian) mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 223**,** 172-180.

Kammerer, C. & Sidor, C. 2002. Replacement names for the therapsid genera Criocephalus Broom 1928 and Olivieria Brink 1965. *Palaeontologia Africana,* 38**,** 71-72.

Kammerer, C. F. 2010. Systematics of the Anteosauria (Therapsida: Dinocephalia). *Journal of Systematic Palaeontology,* 9**,** 261-304.

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. *Journal of Vertebrate Paleontology,* 31**,** 1-158.

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*, 13–29. Johannesburg: Geological Society of South Africa.

Keyser, A. W. 1993. A re-evaluation of the smaller endothiodontidae. *Geological Survey of South Africa Memoir* 82**,** 1-53.

Keyser, A. W. & Gow, C. E. 1981. First complete skull of the Permian reptile *Eunotosaurus africanus* Seeley. *South African Journal of Science,* 77**,** 417–420.

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

Keyser, A. W. & Smith, R. H. M. 1979. Vertebrate biozonation of the Beaufort Group with special reference to the Western Karoo Basin. *Annals Geological Survey South Africa,* 12**,** 1-36.

Khramov, A. N. 1963. Palaeomagnetic investigations of Upper Permian and Lower Triassic sections on the northern and eastern Russian Platform. *trudy VNIGRI, Nedra, Leningrad,* 204**,** 145–174.

King, G. 1988. Anomodontia, 17C. *In:* Wellnhofer, P. (ed.) *Handbuch der Palaoherpetologie*, 174. Stuttgart: Gustav Fischer Verlag.

King, G. & Rubidge, B. S. 1993. A taxonomic revision of small dicynodonts with postcanine teeth. *Zoological Journal of the Linnean Society,* 107**,** 131-154.

King, G. M. 1993. How many species of Diictodon were there? *Annals of the South Africa Museum,* 102**,** 303–325.

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 Johannseburg: C.S.I.R. Pretoria.

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 PhD 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*, 1–131. Johannesburg: Bernard Price Institute for Palaeontological research, University of the Witwatersrand.

Kitching, J. W. 1995. Biostratigraphy of the *Dicynodon* Assemblage Zone. *In:* Rubidge, B. S. (ed.) *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy Biostratigraphic Series, 1: Council for Geoscience, 29-34.

Kubler, M. 1977. *The sedimentology and uranium mineralisation of the Beaufort Group in the Beaufort West-Fraserburg-Merweville area, Cape Province.* Unpublished Msc thesis, University of the Witwatersrand, Johannesburg.

Kurkin, A. 2000. New dicynodonts from the Upper Permian of the Vyatka Basin. *Paleontological Journal,* 34**,** S203-S210.

Kutorga, S. S. 1838. *Beitrag zur Kenntnis der organischen Ueberreste Kupfersandsteins am westlichen Abhange des Urals,* 38. St. Petersburg, N. Gretsch.

Lai, X., Wang, W., Wignall, P., Bond, D., Jiang, H., Ali, J., John, E. & Sun, Y. 2008. Palaeoenvironmental change during the end-Guadalupian (Permian) mass extinction in Sichuan, China. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 269**,** 78-93.

Langer, M. C. 2000. The first record of dinocephalians in South America: Late Permian (Rio do Rasto Formation) of the Paraná Basin, Brazil. *Neues Jahrbuch fur Geologie und Palaontologie,* 215**,** 69–95.

Laurin, M. & Reisz, R. R. 1995. A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society,* 113**,** 165-223.

Le Roux, P. J. 1985. *Palaeochannels and uranium mineralisation in the main Karoo Basin of South Africa.* Unpublished PhD thesis, University of Port Elizabeth, Port Elizabeth.

Le Roux, J., Grobler, L. & Smit, P. 1994. Monoclines and palaeochannels: evidence for syntectonic sedimentation in the Beaufort Group of the Karoo basin, South Africa. *Journal of African Earth Sciences,* 18**,** 219-226.

Lee, M. S. Y. 1993. *Eunotosaurus* reinterpreted as an aberrant synapsid. *In:* Abstracts of the Second World Congress of Herpetology. 150.

Lee, M. S. Y. 1995. Historical Burden In Systematics And The Interrelationships Of 'Parareptiles'. *Biological Reviews,* 70**,** 459-547.

Lee, M. S. Y. 1997. A taxonomic revision of pareiasaurian reptiles: implications for Permian terrestrial palaeoecology. *Modern Geology,* 21**,** 231–298.

Lee, M. S. Y. 2000. The Russian Pareiasaurs. *In:* Benton, M. J., Shishkin, M. A. & Unwin, D. M. (eds.) *The Age of Dinosaurs in Russia and Mongolia*, 71–85. Cambridge: Cambridge University Press.

Leonova, T. B. 2007. Correlation of the Kazanian of the Volga–Urals with the Roadian of the global Permian scale. *Palaeoworld,* 16**,** 246-253.

Lepper, J., Raath, M. A. & Rubidge, B. S. 2000. A diverse dinocephalian fauna from Zimbabwe. *South African Journal of Science,* 96**,** 403.

Leven, E. & Bogoslovskaya, M. 2006. The Roadian Stage of the Permian and problems of its global correlation. *Stratigraphy and Geological Correlation,* 14**,** 164-173.

Li, J. 2001. The most primitive lower tetrapod fauna in China. *Science in China Series D: Earth Sciences,* 44**,** 47-51.

Li, J. & Cheng, Z. 1997. First discovery of eotitanosuchian (Therapsida, Synapsida) of China. *Vertebrata Palasiatica,* 35**,** 268-282.

Liu, J., Rubidge, B. & Li, J. 2009. New Basal Synapsid Supports Laurasian Origin for Therapsids. *Acta Palaeontologica Polonica,* 54**,** 393-400.

Liu, J., Rubidge, B. & Li, J. 2010. A new specimen of *Biseridens qilianicus* indicates its phylogenetic position as the most basal anomodont. *Proceedings of the Royal Society B: Biological Sciences,* 277**,** 285-292.

Lock, B. E. 1978. The Cape Fold Belt of SouthAfrica; tectonic control of sedimentation. *Proceedings of the Geological Association of London,* 89**,** 263–281.

Lock, B. E. 1980. Flat-plate subduction and the Cape Fold Belt of South Africa. *Geology,* 8**,** 35–39.

Loock, J. C. 1993. The Stratigraphy of the Beaufort Group in the Moordenaarskaroo. Unpublished report for the Atomic Energy Corporation of South Africa.

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.

Lozovsky, V. 2005. Olson's gap or Olson's bridge, that is the question. *New Mexico Museum of Natural History and Science Bulletin,* 30**,** 179-184.

Lozovsky, V., Minikh, M., Grunt, T., Kukhtinov, D., Ponomarenko, A. & Sukacheva, I. 2009. The Ufimian Stage of the East European scale: Status, validity, and correlation potential. *Stratigraphy and Geological Correlation,* 17**,** 602-614.

Lucas, S. G. 2001. A Global Hiatus in the Middle Permian Tetrapod Fossil Record. *Permophiles,* 38**,** 24–27.

Lucas, S. G. 2002. Discussion and reply: The reptile *Macroleter*: First vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia. *Geological Society of America Bulletin,* 114**,** 1174–1177.

Lucas, S. G. 2005a. *Dicynodon* (Reptilia:Therapsida) from the Upper Permian of Russia: Biochronologic significance. *New Mexico Museum of Natural History and Science Bulletin,* 30**,** 192–196.

Lucas, S. G. 2005b. Permian tetrapod faunachrons. *New Mexico Museum of Natural History and Science Bulletin,* 30**,** 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*, 65-93. London: Geological Society, Special Publication 265, 65–93.

Lucas, S. G. 2009. Timing and magnitude of tetrapod extinctions across the Permo-Triassic boundary. *Journal of Asian Earth Sciences,* 36**,** 491-502.

Lucas, S. G. & Heckert, A. B. 2001. Olson's Gap: A Global Hiatus in the Record of Middle Permian Tetrapods. *Journal of Vertebrate Palaeontology*, 75A. 21:3. Supplement. Abstracts of Papers, Sixty-First Annual Meeting, Society of Vertebrate Paleontology, 75A.

Lydekker, R. 1890. *Catalogue of the fossil Reptilia and Amphibia in the British Museum. part IV. Containing the orders Anomodontia, Ecaudata, Caudata and Labyrinthodontia; and supplement*. London.

Lyson, T. R., Bever, G. S., Bhullar, B.-a. S., Joyce, W. G. & Gauthier, J. A. 2010. Transitional fossils and the origin of turtles. *Biology Letters,* 6**,** 830-833.

Malabarba, M. C., Abdala, F., Weiss, F. E. & Perez, P. A. 2003. New data on the late Permian vertebrate fauna of Posto Queimado, Rio do Rasto Formation, southern Brazil. *Revista Brasileira de Paleontologia,* 6**,** 49-54.

Martini, J. E. J. 1974. The presence of ash bands and volcanic fragments in the greywackes of the Karoo System in the Southern Cape Province. *Transactions of the Geological Society of South Africa,* 77**,** 11–116.

Mason, R. 2007. *A bio- and litho-stratigraphic study of the Ecca-Beaufort contact in the southeatern Karoo Basin (Albany district, Eastern Cape Province).* Unpublished Msc thesis, University of the Witwatersrand, Johannesburg.

Mckinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics***,** 495-516.

Mendrez, C. H. 1972. Premièrs ébauches d'un palais secondaire osseux chez les Reptiles mammaliens. *Compte Rendu Hebtomadaire des Séances de l'Académie des Sciences, Paris,* 274**,** 2960–2961.

Mendrez, C. H. 1975. Principales variations du palais chez les thérocéphales Sud-Africains (Pristerosauria et Scaloposauria) au cours du Permien Supérieur et du Trias Inférieur. *Problèmes actuels de paléontologie-évolution des Vertébrés*. Colloque International CNRS, 218, 379–408.

Menning, M., Alekseev, A. S., Chuvashov, B. I., Davydov, V. I., Devuyst, F. X., Forke, H. C., Grunt, T. A., Hance, L., Heckel, P. H., Izokh, N. G., Jin, Y. G., Jones, P. J., Kotlyar, G. V., Kozur, H. W., Nemyrovska, T. I., Schneider, J. W., Wang, X. D., Weddige, K., Weyer, D. & Work, D. M. 2006. Global time scale and regional stratigraphic reference scales of Central and West Europe, East Europe, Tethys, South China, and North America as used in the Devonian–Carboniferous–Permian Correlation Chart 2003 (DCP 2003). *Palaeogeography, Palaeoclimatology, Palaeoecology,* 240**,** 318-372.

Menning, M. & Jin, Y. 1998. Comment on 'Permo-Triassic magnetostratigraphy in China: the type section near Taiyuan, Shanxi Province, North China' by Embleton, B. J. J., McElhinny, M. W., Ma, X., Zhang, X. and Li, Z. X. *Geophysical Journal International,* 133**,** 213-216.

Meyer, H. V. 1857. Reptilien aus der Steinkohlen-Formation in Deutschland. *Palaeontographica (1846-1933),* 6**,** 59-106.

Modesto, S. 2000. Eunotosaurus africanus and the Gondwanan ancestry of anapsid reptiles. *Palaeontologia Africana,* 36**,** 15-20.

Modesto, S. & Rubidge, B. 2000. A basal anomodont therapsid from the lower Beaufort Group, Upper Permian of South Africa. *Journal of Vertebrate Paleontology,* 20**,** 515-521.

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., Rubidge, B. & Welman, J. 1999. The most basal anomodont therapsid and the primacy of Gondwana in the evolution of the anomodonts. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 266**,** 331-337.

Modesto, S., Sidor, C. A., Rubidge, B. S. & Welman, J. 2001a. A second varanopseid skull from the Upper Permian of South Africa: implications for Late Permian 'pelycosaur'evolution. *Lethaia,* 34**,** 249-259.

Modesto, S. P., Rubidge, B. S., De Klerk, W. J. & Welman, J. 2001b. A dinocephalian therapsid fauna on the Ecca–Beaufort contact in Eastern Cape Province, South Africa.

Modesto, S. P., Rubidge, B. S. & Welman, J. 2002. A new dicynodont therapsid from the lowermost Beaufort Group, Upper Permian of South Africa. *Canadian Jouranl of Earth Science,* 39**,** 1755-1765.

Modesto, S. P. & Rybczynski, N. 2000. The amniote faunas of the Russian Permian: implications for Late Permian terrestrial vertebrate biogeography. *In:* Benton, M. J., Shishkin, M. A. & Unwin, D. M. (eds.) *The Age of Dinosaurs in Russia and Mongolia*. Cambridge, UK: Cambridge University Press.

Modesto, S., Smith, R. H., Campione, N. & Reisz, R. 2011. The last "pelycosaur": a varanopid synapsid from the *Pristerognathus* Assemblage Zone, Middle Permian of South Africa. *Naturwissenschaften,* 98**,** 1027-1034.

Molostovsky, E., Pechersky, D. & Frolov, I. Y. 2007. The Phanerozoic magnetostratigraphic scale and its model on thebasis of the cumulative distribution function. *Izv. RAN., Fizika Zemli,* 43**,** 811-818.

Mountain, E. D. 1946. The Geology of an Area East of Grahamstown: An Explanation of Sheet No. 136 (Grahamstown). 56. Geolological Survey of South Africa, Pretoria.

Müller, J. & Tsuji, L. A. 2007. Impedance-matching hearing in Paleozoic reptiles: evidence of advanced sensory perception at an early stage of amniote evolution. *PloS one,* 2**,** e889.

Munyikwa, D. 2001. *Cranial morphology of a primitive dinocephalian (Amniota: Therapsida) from the Madumabisa Mudstone Formation, Zimbabwe.* Unpulished Msc Thesis, University of the Witwatersrand, Johannesburg.

Nechaev, A. V. 1915. Kazanian and Ufimian stages of the Permian. *Geol. Vestnik,* 1**,** 20–31 [In Russian].

Neveling, J., Rubidge, B. S. & Hancox, P. J. 1999. A lower Cynognathus Assemblage Zone fossil from the Katberg Formation (Beaufort Group, South Africa). *South African Journal of Science,* 95**,** 555-556.

Nicolas, M. 2007. *Tetrapod biodiversity through the Permotriassic Beaufort Group (Karoo Supergroup) of South Africa.* Unpublished PhD thesis, University of the Witwatersrand, Johannesburg.

Nicolas, M. & Rubidge, B. S. 2009. Assessing content and bias in South African Permo-Triassic Karoo tetrapod fossil collections. *Palaeontologia Africana,* 44**,** 13–20.

Olson, E. C. 1965. New Permian vertebrates from the Chickasha Formation in Oklahoma. *Oklahoma Geological Survey Circular,* 70**,** 1–70.

Olson, E. C. 1937. The skull structure of a new anomodont. *Journal of Geology,* 45**,** 851–958.

Olson, E. C. & Broom, R. 1937. New genera and species of tetrapods from the Karroo beds of South Africa. *Journal of Paleontology,* 11**,** 613-619.

Ota, A. & Isozaki, Y. 2006. Fusuline biotic turnover across the Guadalupian–Lopingian (Middle–Upper Permian) boundary in mid-oceanic carbonate buildups: Biostratigraphy of accreted limestone in Japan. *Journal of Asian Earth Sciences,* 26**,** 353-368.

Owen, R. 1876a. Descriptive illustrated catalogue of the fossil Reptilia of South Africain the collections of the British Museum. London: British Museum.

Owen, R. 1876b. Evidences of theriodonts in Permian deposits elsewhere than in South Africa. *Quarterly Journal of the Geological Society,* 32**,** 352–363.

Owen, R. 1879. Description of fragmentary indications of a huge kind of theriodont reptile (*Titanosuchus ferox* Ow.) from Beaufort West, Gouph Tract, Cape of Good Hope. *Quarterly Journal of the Geological Society of London,* 35**,** 189-198.

Partridge, T. C. 1998. Of diamonds, dinosaurs and diastrophism; 150 million years of landscape evolution in southern Africa. *South African Journal of Geology,* 101**,** 167-184.

Partridge, T. C. & Maud, R. R. 1987. Geomorphic evolution of southern Africa since the Mesozoic. *South African Journal of Geology,* 90**,** 179–208.

Peate, I. U. & Bryan, S. E. 2008. Re-evaluating plume-induced uplift in the Emeishan large igneous province. *Nature Geoscience,* 1**,** 625-629.

Pysklywec, R. N. & Mitrovica, J. X. 1999. The Role of Subduction-Induced Subsidence in the Evolution of the Karoo Basin. *The Journal of Geology,* 107**,** 155-164.

Ray, S. 2001. Small Permian dicynodonts from India. *Paleontological Research,* 5**,** 177-191.

Ray, S. & Chinsamy, A. 2004. *Diictodon feliceps* (Therapsida, Dicynodontia): bone histology, growth, and biomechanics. *Journal of Vertebrate Paleontology,* 24**,** 180-194.

Reisz, R. R. 1986. Pelycosauria, 17. *In:* Wellenhofer, P. (ed.) *Handbuch der Palaoherpetologie*, 102. Stuttgart, New York: Gustav Fischer Verlag.

Reisz, R. R. & Berman, D. S. 2001. The skull of *Mesenosaurus romeri*, a small varanopseid (Synapsida: Eupelycosauria) from the Upper Permian of the Mezen River Basin, northern Russia. *Annals of the Carnegie Museum,* 70**,** 113-132.

Reisz, R. R., Dilkes, D. W. & Berman, D. S. 1998. Anatomy and relationships of *Elliotsmithia longiceps* Broom, a small synapsid (Eupelycosauria: Varanopseidae) from the Late Permian of South Africa. *Journal of Vertebrate Paleontology,* 18**,** 602-611.

Reisz, R. R. & Laurin, M. 2001. The reptile *Macroleter*: First vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia. *Geological Society of America Bulletin,* 113**,** 1229-1233.

Reisz, R. R. & Laurin, M. 2002. Reply. *Geological Society of America Bulletin,* 114**,** 1176-1177.

Reisz, R. R. & Modesto, S. P. 2007. *Heleosaurus scholtzi* from the Permian of South Africa: a varanopid synapsid, not a diapsid reptile. *Journal of Vertebrate Paleontology,* 27**,** 734-739.

Resolutions of the All-Russia Conference on Structure and Status of the East European Stratigraphic Scale for the Permian, Improved Stage Division of the Upper Permian Series of the Standard Stratigraphic Scale. 2006. Kazan: Kazan University (In Russian].Retallack, G. J. & Jahren, A. H. 2008. Methane release from igneous intrusion of coal during Late Permian extinction events. *The Journal of Geology,* 116**,** 1-20.

Retallack, G. J., Metzger, C. A., Greaver, T., Jahren, A. H., Smith, R. M. H. & Sheldon, N. D. 2006. Middle-Late Permian mass extinction on land. *Geological Society of America Bulletin,* 118**,** 1398-1411.

Retallack, G. J., Smith, R. M. & Ward, P. D. 2003. Vertebrate extinction across Permian–Triassic boundary in Karoo Basin, South Africa. *Geological Society of America Bulletin,* 115**,** 1133-1152.

Rieppel, O. & Reisz, R. R. 1999. The origin and early evolution of turtles. *Annual Review of Ecology and Systematics,* 30**,** 1-22.

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 Edition),* 463. London, Longmans Green and Co.

Rogers, A. W. 1925. The Geology of the country near Laingsburg: An Explanation of Cape sheet No. 5 (Laingsburg). Geological Survey of the Union of South Africa.

Rogers, A. W. & Du Toit, A. L. 1909. *An Introduction to the Geology of the Cape Colony (2nd Edition),* 491. 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.

Romer, A. S. 1970. Tetrapod vertebrates and Gondwanaland. *In:* Haughton, S. H., ed. Proceedings of the 2nd Gondwana Symposium, Pretoria, South Africa. 111-124.

Romer, A. S. & Price, L. I. 1940. Review of the Pelycosauria. *Geological Society of America, Special Paper 28*, 1-538.

Rossouw, P. J. & De Villiers, J. 1953. The Geology of the Merweville area, Cape Province: An Explanation of sheet 198 (Merweville). 80. Geological Survey of South Africa, Pretoria.

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 PhD 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. 1990b. The cranial morphology of a new species of the genus *Eodicynodon* (Therapsida, Dicynodontia). *Navorsinge van die Nasionale Museum, Bloemfontein,* 7**,** 29–41.

Rubidge, B. S. 1991. A new primitive dinocephalian mammal-like reptile from the Permian of southern Africa. *Palaeontology,* 34**,** 547-559.

Rubidge, B. S. 1994. *Australosyodon*, the first primitive anteosaurid dinocephalian from the Upper Permian of Gondwana. *Palaeontology,* 37**,** 579-594.

Rubidge, B. 1995a. Biostratigraphy of the *Eodicynodon* Assemblage Zone. *In:* Rubidge, B. S. (ed.) *Biostratigraphy of the Beaufort Group (Karoo Supergroup).* South African Committee for Stratigraphy Biostratigraphic Series, 1: Council for Geoscience, 3–7.

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

Rubidge, B. S. 2005. 27th Du Toit Memorial Lecture: Re-uniting lost continents - Fossil reptiles from the ancient Karoo and their wanderlust. *South African Journal of Geology,* 108**,** 135-172.

Rubidge, B. S., Kitching, J. W. & Van Den Heever, J. 1983. First record of a therocephalian (Therapsida: Pristerognathidae) from the Ecca of South Africa. *Navorsinge van die Nasionale Museum, Bloemfontein,* 4**,** 229–235.

Rubidge, B. & Hopson, J. 1990. A new anomodont therapsid from South Africa and its bearing on the ancestry of Dicynodontia. *South African Journal of Science,* 86**,** 43-45.

Rubidge, B. S. & Hopson, J. A. 1996. A primitive anomodont therapsid from the base of the Beaufort Group (Upper Permian) of South Africa. *Zoological Journal of the Linnean Society,* 117**,** 115–139.

Rubidge, B. S. & Heever, J. A. 1997. Morphology and systematic position of the dinocephalian *Styracocephalus platyrhynchus*. *Lethaia,* 30**,** 157-168.

Rubidge, B. S., Modesto, S. P. & Sidor, C. P. 1999. Eunotosaurus africanus from the Ecca–Beaufort contact in Northern Cape Province, South Africa — implications for Karoo Basin development. *South African Journal of Science,* 95**,** 553–555.

Rubidge, B., Hancox, P. & Catuneanu, O. 2000. Sequence analysis of the Ecca—Beaufort contact in the southern Karoo of South Africa. *South African Journal of Geology,* 103**,** 81-96.

Rubidge, B. S. & Sidor, C. A. 2001. Evolutionary patterns among Permo-Triassic therapsids. *Annual Review of Ecology and Systematics***,** 449-480.

Rubidge, B. S. & Kitching, J. W. 2003. A new burnetiamorph (Therapsida: Biarmosuchia) from the Lower Beaufort Group of South Africa. *Palaeontology,* 46**,** 199-210.

Rubidge, B. S., Sidor, C. A. & Modesto, S. P. 2006. A New Burnetiamorph (Therapsida: Biarmosuchia) from the Middle Permian of South Africa. *Journal of Paleontology,* 80**,** 740-749.

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., Hancox, P. J. & Mason, R. 2011. Waterford Formation in the south-eastern Karoo: Implications for basin development. *South African Journal of Science,* 108**,** 1–5.

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, (In Press) doi:10.1130/G33622.1.* *http://dx.doi.org/10.2113/103.1.81*.

Ruzhencev, V. E. 1962. Superorder Ammonoidea. *In:* Orlov, Y. A. (ed.) *Osnovy Paleontologii [Principles of Paleontology]. Mollusca-Cephalopoda I*, 243–438. Moscow: Izdat. Akad. Nauk SSSR [In Russian].

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

Schenk, A. 1888. Die geologische Entwicklung Sudafrikas. *Petermann's Geographische Mitteilungen,* 34**,** 225-232.

Schoch, R. R. & Milner, A. R. 2000. Stereospondyli: Stem-Stereospondyli, Rhinesuchidae, Rhytidostea, Trematosauroidea, Capitosauroide, 3B. *Handbuch der Palaoherpetology*. Munchen: Verlag Dr. Friedrich Pfeil.

Schwab, F. L. 1986. Sedimentary 'signatures' of foreland basin assemblages: Real or counterfeit? *In:* Allen, P. A. & Homewood, P. (eds.) *Foreland Basins*. Special Publications of the International Association of Sedimentologists, 8, 395–410.

Schwartz, E. H. L. 1897. Geological Survey of the Beaufort West district. *First Annual Report of the Geological Commission 1896, Cape of Good Hope*, 15–26.

Scott, E.D., (1997). *Tectonics and sedimentation: the evolution, tectonic influences and correlation of the Tanqua and Laingsburg subbasins, southwest Karoo basin, South Africa.* Unpublished PhD Thesis, Louisiana State University.

Seeley, H. 1888. Croonian Lecture: Researches on the Structure, Organization, and Classification of the Fossil Reptilia. II. On *Pareiasaurus bombidens* (Owen), and the Significance of Its Affinities to Amphibians, Reptiles, and Mammals. *Philosophical Transactions of the Royal Society of London. B,* 179**,** 59-109.

Seeley, H. G. 1889. Researches on the Structure, Organization, and Classification of the Fossil Reptilia. VI. On the Anomodont Reptilia and Their Allies. *Philosophical Transactions of the Royal Society of London. B,* 180**,** 215-296.

Seeley, H. G. 1892a. Researches on the structure, organization and classification of the fossil reptilia. *Philosophical Transactions of the Royal Society,* 182**,** 311-370.

Seeley, H. G. 1892b. On a New Reptile from Welte Vreden (Beaufort West), *Eunotosaurus africanus* (Seeley). *Quarterly Journal of the Geological Society,* 48**,** 583,NP,585.

Seeley, H. G. 1892c. On *Delphinognathus conocephalus* (Seeley) from the middle Karoo beds, Cape Colony, preserved in the South African Museum, Cape Town. *Quarterly Journal of the Geological Society,* 48**,** 469–475.

Seeley, H. G. 1894. Researches on the structure, organization, and classification of the fossil Reptilia: Part IX, Section 1, On the Therosuchia. *Philosophical Transactions of the Royal Society of London, Series B,* 185**,** 987–1078.

Seeley, H. G. 1895. Researches on the structure, organization and classification of the fossil Reptilia. Part IX, Associated remains of two small skeletons from Klipfontein, Fraserburg. *Philosophical Transactions of the Royal Society, Series B* 186**,** 149–162.

Shen, S.-Z., Henderson, C. M., Bowring, S. A., Cao, C.-Q., Wang, Y., Wang, W., Zhang, H., Zhang, Y.-C. & Mu, L. 2010. High-resolution Lopingian (Late Permian) timescale of South China. *Geological Journal,* 45**,** 122–134.

Shen, S.-Z. & Shi, G. 2009. Latest Guadalupian brachiopods from the Guadalupian/Lopingian boundary GSSP section at Penglaitan in Laibin, Guangxi, South China and implications for the timing of the pre-Lopingian crisis. *Palaeoworld,* 18**,** 152-161.

Shen, S. & Shi, G. 1996. Diversity and extinction patterns of Permian Brachiopoda of South China. *Historical Biology,* 12**,** 93-110.

Shishkin, M. A., Rubidge, B. S. & Hancox, P. J. 1995. Vertebrate biozonation of the Upper Beaufort Series of South Africa—a new look on correlation of the Triassic biotic events in Euramerica and southern Gondwana. *In:* Sixth Symposium on Mesozoic Terrestrial Ecosystems. China Press, Beijing, 39–41.

Sidor, C. & Hopson, J. 1995. The taxonomic status of the Upper Permian eotheriodont therapsids of the San Angelo Formation (Guadalupian), Texas. *Journal of Vertebrate Paleontology,* 15**,** 53A.

Sidor, C. A. 2000. *Evolutionary trends and rela- tionships within the Synapsida.* Unpublished PhD Thesis, University of Chicago, Chicago.

Sidor, C. A., Angielczyk, K. D., Weide, D. M., Smith, R. M., Nesbitt, S. J. & Tsuji, L. A. 2010. Tetrapod fauna of the lowermost Usili Formation (Songea Group, Ruhuhu Basin) of southern Tanzania, with a new burnetiid record. *Journal of Vertebrate Paleontology,* 30**,** 696-703.

Sidor, C. A., Hopson, J. A. & Keyser, A. W. 2004. A new burnetiamorph therapsid from the Teekloof Formation, Permian, of South Africa. *Journal of Vertebrate Paleontology,* 24**,** 938-950.

Sidor, C. A. & Smith, R. M. 2007. A second burnetiamorph therapsid from the Permian Teekloof Formation of South Africa and its associated fauna. *Journal of Vertebrate Paleontology,* 27**,** 420-430.

Sigogneau, D. 1970. *Révision systématique des Gorgonopsiens sud-africains*. Paris, Centre National de la Recherche Scientifique.

Sigogneau-Russell, D. 1989. *Theriodontia I: Encyclopedia of Palaeoherpetology Part 17B, Wellnhofer, P.* (ed.). Gustav Fisher, Stuttgart.

Simon, R. V., Sidor, C. A., Angielczyk, K. D. & Smith, R. M. H. 2010. First record of a tapinocephalid (Therapsida: Dinocephalia) from the Ruhuhu Formation (Songea Group) of southern Tanzania. *Journal of Vertebrate Paleontology,* 30**,** 1289-1293.

Smith, R. H. M. 1981. *Sedimentology and Taphonomy of the Lower Beaufort strata near Beaufort West, Cape Province.* Unpublished Msc Thesis, Universty of the Witwatersrand, Johannesburg.

Smith, R. H. M. 1989. *Fluvial facies, vertebrate taphonomy and palaeosols of the Teekloof Formation (Permian) near Beaufort West, Cape Province, South Africa.* Unpublished PhD Thesis, University of Cape Town, Cape Town.

Smith, R. H. M. 1990. Alluvial Paleosols and Pedofacies Sequences in the Permian Lower Beaufort of the Southwestern Karoo Basin, South Africa. *Journal of Sedimentary Research,* 60.

Smith, R. & 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. H. M. & Keyser, A. W. 1995a. Biostratigraphy of the *Tapinocephalus* Assemblage Zone. *In:* Rubidge, B. S. (ed.) *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy Biostratigraphic Series, 1: Council for Geoscience, 8–12.

Smith, R. H. M. & Keyser, A. W. 1995b. Biostratigraphy of the *Pristerognathus* Assemblage Zone. *In:* Rubidge, B. S. (ed.) *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy Biostratigraphic Series, 1: Council for Geoscience, 13-17.

Smith, A. G. & Keyser, A. W. 1995c. Biostratigraphy of the *Tropidostoma* Assemblage Zone. *In:* Rubidge, B. S. (ed.) *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy Biostratigraphic Series, 1: Council for Geoscience, 18–22.

Smith, A. G. & Keyser, A. W. 1995d. Biostratigraphy of the *Cistecephalus* Assemblage Zone. *In:* Rubidge, B. S. (ed.) *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy Biostratigraphic Series, 1: Council for Geoscience, 23–28.

Smith, R. H. M., Rubidge, B. S. & Van Der Walt, M. V. M. 2012. Therapsid Biodiversity Patterns and Palaeoenvirnoments of the Karoo Basin, South Africa. *In:* Chinsamy-Turan, A. (ed.) *Forerunners of Mammals*, 31–64. Bloomington and Indianapolis: Indiana University Press.

Smith, R. M. 1987. Helical burrow casts of therapsid origin from the Beaufort Group (Permian) of South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 60**,** 155-169.

Smith, R. M., Rubidge, B. S. & Sidor, C. A. 2006. A new burnetiid (Therapsida: Biarmosuchia) from the Upper Permian of South Africa and its biogeographic implications. *Journal of Vertebrate Paleontology,* 26**,** 331-343.

Smith, R. M. H., Eriksson, P. G. & Botha, W. J. 1993. A review of the stratigraphy and sedimentary environments of the Karoo-aged basins of Southern Africa. *Journal of African Earth Sciences (and the Middle East),* 16**,** 143-169.

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.

Stanley, S. M. & Yang, X. 1994. A double mass extinction at the end of the paleozoic era. *Science,* 266**,** 1340-1344.

Stavrakis, N. 1980. Sedimentation of the Katberg Sandstone and adjacent formations in the south-eastern Karoo basin. *Transactions of the Geological Society of South Africa,* 83**,** 361–374.

Stear, W. M. 1980. *The sedimentary environment of the Beaufort Group uranium province in the vicinity of Beaufort West.* Unpublished PhD thesis, University of Port Elizabeth, Port Elizabeth.

Steiner, M. B. 2006. The magnetic polarity time scale across the Permian-Triassic boundary. *Geological Society, London, Special Publications,* 265**,** 15-38.

Stevens, L. G., Hilton, J., Bond, D. P., Glasspool, I. J. & Jardine, P. E. 2011. Radiation and extinction patterns in Permian floras from North China as indicators for environmental and climate change. *Journal of the Geological Society,* 168**,** 607-619.

Sullivan, C., Reisz, R. R. & Smith, R. M. 2003. The Permian mammal-like herbivore *Diictodon*, the oldest known example of sexually dimorphic armament. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 270**,** 173-178.

Sun, Y., Lai, X., Wignall, P. B., Widdowson, M., Ali, J. R., Jiang, H., Wang, W., Yan, C., Bond, D. P. & Védrine, S. 2010. Dating the onset and nature of the Middle Permian Emeishan large igneous province eruptions in SW China using conodont biostratigraphy and its bearing on mantle plume uplift models. *Lithos,* 119**,** 20-33.

Tankard, A., Welsink, H., Aukes, P., Newton, R. & Stettler, E. 2009. Tectonic evolution of the Cape and Karoo basins of South Africa. *Marine and Petroleum Geology,* 26**,** 1379-1412.

Tankard, A. J., Jackson, M. P. A., Eriksson, K. A., Hobday, D. K., Hunter, D. R. & Minter, W. E. L. 1982. *Crustal Evolution of Southern Africa: 3.8 Billion Years of Earth History,* 523. Berlin, Springer.

Tatarinov, L. P. 1987. A new primitive cynodont from the Upper Permian of the southern Urals. *Paleotological Journal,* 21**,** 103–107.

Tate, R. 1867. On some Secondary Fossils from South Africa. *Quarterly Journal of the Geological Society,* 23**,** 142–144.

Theron, J. C. 1975. Sedimentological evidence for the extension of the African continent southwards during Late Permian-Early Triassic times. *In:* Campbell, K. S. W., ed. *Gondwana Geology*. Australian National University Press, Canberra, 61-71.

Theron, J. N. 1983. Explanation of geological map sheet 3220 (Sutherland). 18. Council for Geoscience, Pretoria.

Thissen, J. M., Marpmann, J. S. & Ronge, T. A. 2010. Litho- and biostratigraphic analysis of the Abrahamskraal to the Teekloof Formation near Prince Albert, South Africa. Unpublished report: Universitat Bonn & University of the Witwatersrand.

Thommasen, H. & Carroll, R. L. 1981. *Broomia*, the oldest known millerettid reptile. *Palaeontology,* 24**,** 379-390.

Toerien, M. J. 1953. Evolution of the palate in some anomodonts and its classificatory significance. *Palaeontologia Africana,* 1**,** 49–117.

Tsuji, L. A. & Müller, J. 2009. Assembling the history of the Parareptilia: phylogeny, diversification, and a new definition of the clade. *Fossil Record,* 12**,** 71-81.

Turner, B. R. 1979. *Excursions Guidebook, Geocongress '79*. Geological Society of South Africa, Port Elizabeth.

Turner, B. R. 1981. Revised Stratigraphy of the Beaufort Group in the southern Karoo Basin. *Palaeontologia Africana,* 24**,** 87–98.

Turner, B. R. 1985. Uranium mineralization in the Karoo Basin, South Africa. *Economic Geology,* 80**,** 256-269.

Tverdokhlebov, V. P., Tverdokhlebova, G. I., Minikh, A. V., Surkov, M. V. & Benton, M. J. 2005. Upper Permian vertebrates and their sedimentological context in the South Urals, Russia. *Earth-Science Reviews,* 69**,** 27-77.

Van Den Heever, J. 1987. *The comparative and functional cranial morphology of the early Therocephalia (Amniota: Therapsida).* Unpublished PhD thesis, University of Stellenbosch, Stellenbosch.

Van Den Heever, J. 1994. The cranial anatomy of the early Therocephalia (Amniota: Therapsida). *Annals of the University of Stellenbosch,* 1**,** 1–59.

Van Der Walt, M., Day, M., Rubidge, B., Cooper, A. & Netterberg, I. 2010. A new GIS-based biozone map of the Beaufort Group (Karoo Supergroup), South Africa. *Palaeontologia Africana,* 45**,** 1-5.

Van Hoepen, E. C. N. 1916. A new Karroo Reptile. *Annals of the Transvaal Museum,* 5 (3, supplement 3).

Van Hoepen, E. C. N. 1934. Oor die indeling van die Dicynodontidae na aanleiding van nuwe vorme. *Paleontologiese Navorsinge van die Nasionale Museum, Bloemfontein,* 2**,** 67–101.

Visser, J. N. 1987. The palaeogeography of part of southwestern Gondwana during the Permo-Carboniferous glaciation. *Palaeogeography Palaeolimatology Palaeoecology,* 61**,** 205-219.

Visser, J. N. J. 1992. Deposition of the Early to Late Permian Whitehill formation during a sea-level highstand in a juvenile foreland basin. *South African Journal of Geology,* 95**,** 181–193.

Visser, J. N. J. & Dukas, B. A. 1979. Upward fining fluviatile megacycles in the Beaufort Group north of Graaff Reinet, Cape Province. *Transactions of the Geological Society of South Africa,* 82**,** 149–154.

Vitali, F. 2001. Stratigraphic column and descriptions of the stratigraphic section of the lowermost Beaufort in the area near Prince Albert Road (Dwyka River). *Unpublished report.*

Von Eichwald, E. I. 1846. *Geognosy of Russia,* 572. St. Petersburg.

Von Huene, F. 1925. *Die südafrikanische Karroo-Formation als geologisches und faunisches Lebensbild,* 124. Verlag yon Gebrfider Borntraeger, Berlin.

Von Huene, F. 1931. Beitrag zur Kenntnis der fauna der südafrikanischen Karrooformation. *Neues Jahrbuch für Geologie und Paläontologie Abh,* 18**,** 159–227.

Von Huene, F. 1940. Die Saurier der Karroo-, Gondwana- und verwandten Ablagerungen in faunistischer, biologischer und phylogenetischer Hinsicht. *Neues Jahrbuch fur Geologie und Palaontologie Beil. Bd.,* 83, Abtsteilung B**,** 246-347.

Von Huene, F. 1942. Die Anomodontier des Ruhuhu-Gebiets in der Tübingen Sammlung. *Palaeontographica Abt. A,* 94**,** 154–184.

Wadley, R. G. & Hoffmann, J. 1986. A case history of the DR-3 uranium anomaly, Laingsburg District. *In:* Anhaeusser, C. R. & Maske, S. (eds.) *Mineral Deposits of Southern Africa. Volume II*, 2141–2147. Johannesburg: Geological Society of South Africa.

Wang, W., Cao, C. & Wang, Y. 2004. The carbon isotope excursion on GSSP candidate section of Lopingian–Guadalupian boundary. *Earth and Planetary Science Letters,* 220**,** 57-67.

Wang, X. D. & Sugiyama, T. 2000. Diversity and extinction patterns of Permian coral faunas of China. *Lethaia,* 33**,** 285-294.

Wardlaw, B. R., Davydov, V. & Gradstein, F. M. 2004. The Permian period. *In:* Gradstein, F. M., Ogg, J. G. & Smith, A. G. (eds.) *A Geologic Time Scale 2004*, 249–270. Cambridge: Cambridge University Press.

Watson, D. M. S. 1914a. The zones of the Beaufort Beds of the Karoo System in South Africa. *Geological Magazine, New Series,* Decade 6**,** 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. 1914c. *Broomia perplexa*, gen. et sp. nov. a fossil reptile from South Africa. *Proceedings of the Zoological Society of London*, 1914, 995-1010.

Watson, D. M. S. 1914d. *Eunotosaurus africanus* Seeley, and the ancestry of the Chelonia. *Proceedings of the Zoological Society of London***,** 1011–1020.

Watson, D. M. S. 1914e. The Deinocephalia, an order of mammal-like reptiles. *Proceedings of the Zoological Society of London,* 1914**,** 749–786.

Watson, D. M. S. 1921. The bases of classification of the Theriodontia. *Proceedings of the Zoological Society of London,* 1921**,** 35–98.

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

Watson, D. M. S. 1952. Robert Broom 1866-1951. *Obituary Notices of the Royal Society of London,* 8**,** 37-70.

Watson, D. M. S. & Romer, A. S. 1956. A Classification of Therapsid Reptiles: A Rectification. *Bulletin of the Museum of Comparative Zoology,* 114**,** 37–89.

Welman, J., Loock, J. C. & Rubidge, B. S. 2001. New evidence for diachroneity of the Ecca-Beaufort contact (Karoo Supergroup, South Africa). *South African Journal of Science,* 97**,** 320–322.

Wignall, P. B., Sun, Y., Bond, D. P. G., Izon, G., Newton, R. J., Védrine, S., Widdowson, M., Ali, J. R., Lai, X., Jiang, H., Cope, H. & Bottrell, S. H. 2009a. Volcanism, Mass Extinction, and Carbon Isotope Fluctuations in the Middle Permian of China. *Science,* 324**,** 1179-1182.

Wignall, P. B., Védrine, S., Bond, D. P. G., Wang, W., Lai, X.-L., Ali, J. R. & Jiang, H.-S. 2009b. Facies analysis and sea-level change at the Guadalupian–Lopingian Global Stratotype (Laibin, South China), and its bearing on the end-Guadalupian mass extinction. *Journal of the Geological Society,* 166**,** 655-666.

Williams-Jones, G. & Rymer, H. 2000. Hazards of volcanic gases. *Encyclopedia of volcanoes***,** 997-1004.

Williston, S. W. 1925. *The osteology of the reptiles, Gregory, W. K.* (ed.). Cambridge, USA, Harvard University Press.

Winter, H. D. L. R. & Venter, J. J. 1970. Lithostratigraphic correlation of recent deep boreholes in the Karroo-Cape Sequence. Soekor.

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*, 1–62. Cape of Good Hope Parliament, Cape Town.

Yang, X., Jiarun, L. I. U. & Guijun, S. H. I. 2004. Extinction process and patterns of Middle Permian Fusulinaceans in southwest China. *Lethaia,* 37**,** 139-147.

Yang, X. N., Shi, G. J., Liu, J. R., Zhou, J. P. & Sun, L. 1999. A study on the Maukou Formation(Middle Permian) ofPanxiang, Guizhou Province and its fusilinacean fossils. *Journal of Stratigraphy,* 23**,** 170–181 [In Chinese].

Zhou, M.-F., Malpas, J., Song, X.-Y., Robinson, P. T., Sun, M., Kennedy, A. K., Lesher, C. M. & Keays, R. R. 2002. A temporal link between the Emeishan large igneous province (SW China) and the end-Guadalupian mass extinction. *Earth and Planetary Science Letters,* 196**,** 113-122.