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Biostratigraphy of the lower Burgersdorp Formation (Beaufort Group; Karoo Supergroup) of South Africa – implications for the stratigraphic ranges of early Triassic tetrapods

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The Beaufort Group (Karoo Supergroup) of South Africa comprises a thick sequence of fluvio-lacustrine sedimentary rocks that accumulated in a landlocked, intracratonic foreland basin in southwestern Gondwana during the Middle Permian to Middle Triassic. To the south this basin was bounded by the Cape Fold Belt, which acted as the major source of both sediment and discharge. Rocks of the Beaufort Group are renowned for their rich fossil record and eight tetrapod-based biozones are currently recognized. The uppermost two biozones of the Beaufort Group, the *Lystrosaurus* and *Cynognathus* assemblage zones, record terrestrial biotic recovery following the Permo-Triassic mass extinction event. Stratigraphic overlap between these biozones occurs in the proximal sector, but their separation by an unconformity in the distal sector reflects the incomplete preservation of the sequence in this part of the basin. Our results afford chronostratographic control that impacts on current theories on the development of the Karoo Basin, and on the relative age of the sequence.

Keywords: Early Triassic, Karoo Basin, *Lystrosaurus* and *Cynognathus* Assemblage Zones, stratigraphic range, overlap.

INTRODUCTION

Rocks of the Beaufort Group (Karoo Supergroup) outcrop over approximately 300 000 km^2 in South Africa (Smith 1990) and are renowned for their wealth of terrestrial tetrapod fossils, which have enabled the present eightfold biostratigraphic subdivision of this succession (Rubidge *et al.* 1995). This largely uninterrupted record represents a period extending from the Middle Permian to Middle Triassic (Hancox & Rubidge 2001; Rubidge 2005). It fulfils a prominent role in the correlation of terrestrial sequences and Lucas (1998), who advanced a global tetrapod biochronology scheme for the Triassic, based his Lootsbergian and Nonensian land vertebrate faunachrons on fossil assemblages from the Beaufort Group. Owing to the reciprocal flexural profile of the Karoo Basin (Catuneanu *et al.* 1998), the Beaufort Group accumulated in a strongly partitioned foreland basin. Base-level changes in the proximal and distal regions of the basin, corresponding to the southern and northern parts of the basin respectively (Fig. 1), were consequently out-of-phase, and display contrasting stratigraphies.

Triassic strata of the Beaufort Group, encompassing the uppermost Palingkloof Member of the Balfour Formation, as well as the overlying Katberg and Burgersdorp formations (Fig. 2), have been the focus of much research over the past decade (Smith 1995; Groenewald 1996; Hancox 1998, 2000; Smith & Ward 2001; De Kock & Kirschvink 2004; Neveling 2004). The basal part of the Burgersdorp Formation displays thin, weakly lenticular channel sandstones which are dominated by horizontally stratification, indicating strong genetic links with the arenaceous Katberg Formation. This proposed genetic relationship (Marais & Johnson 1965; Groenewald 1996; Hancox 1998), allied to the apparent gradational nature of the contact between these two formations (Johnson & Hiller 1990; Groenewald 1996), prompted several workers to postulate lateral equivalency for the upper Katberg, and lower Burgersdorp formations (Johnson 1976; Stavrakis 1980; Johnson & Hiller 1990; Groenewald 1996; Hancox 1998; Neveling *et al.* 1999).

Biostratigraphically the Triassic rocks of the Beaufort Group incorporate the *Lystrosaurus* and *Cynognathus* assemblage zones (AZs). The fauna and distribution of these biozones have been the focus of much recent research (Hancox 1998; Hancox & Rubidge 2001; Hancox *et al.* 2002; Damiani & Jeannot 2002; Neveling 2002, 2004; Damiani & Hancox 2003; Abdala *et al.* 2005). Various workers have investigated the terrestrial expression of the end-Permian mass extinction at the base of the *Lystrosaurus* AZ (Smith 1995; MacLeod *et al.* 2000; Ward *et al.* 2000; Smith & Ward 2001; Hancox *et al.* 2002 Latimer *et al.* 2002; Retallack *et al.* 2003; Steiner *et al.* 2003; De Kock & Kirschvink 2004). Higher in the succession the recognition of faunal elements of the *Cynognathus* AZ in the northern part of the Karoo Basin (Welman *et al.* 1991) sparked new interest in the latter biozone which resulted in the description of a number of new tetrapod taxa (Damiani 1999, 2001; Neveling *et al.* 2001; Damiani & Jeannot 2002). Of greater significance was a proposal by Hancox and others (Hancox *et al.* 1995; Hancox & Rubidge 1997; Hancox 1998, 2000) for an informal threefold subdivision of the

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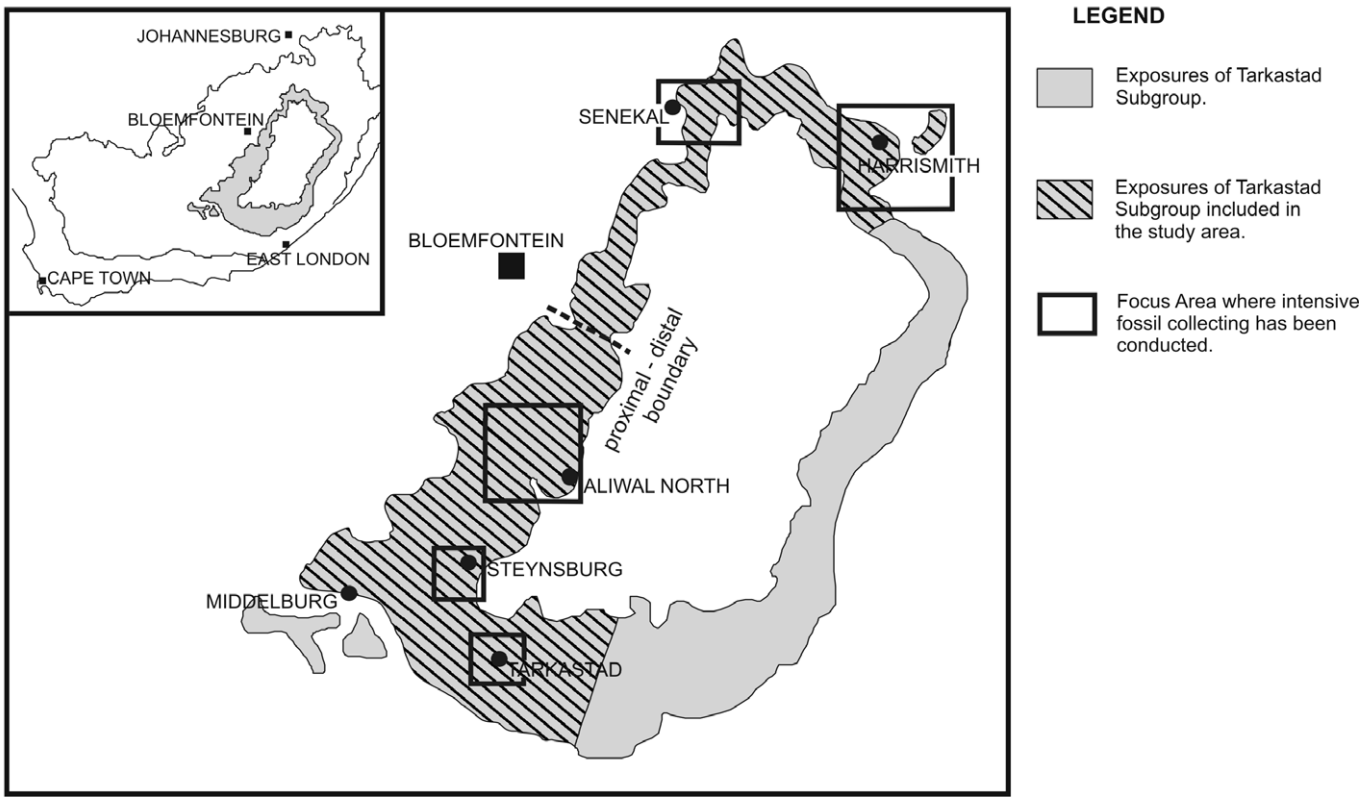


Figure 1. Map showing the distribution of the Tarkastad Subgroup and location of the study area.

Cynognathus AZ, based on the stratigraphic and temporal distribution of key mastodonsaurid (amphibian) genera. Subsequent research further revealed the presence of a more cosmopolitan tetrapod fauna in the uppermost Burgersdorp Formation than previously recognized (Hancox & Rubidge 1994, 1996; Hancox 1998; Hancox *et al.* 2002; Damiani & Hancox 2003; Abdala *et al.* 2005).

The contact between the *Lystrosaurus* and *Cynognathus* AZs, from both a palaeontological and geological point of view, has been a particular focus of Karoo Triassic research in recent years. Kitching (1977) was the first to observe that these are the only two biozones of the Beaufort Group with no common fossil taxa. Later researchers attributed the abrupt nature of this faunal turnover to: the presence of a fossil-barren interval separating the two biozones (Keyser & Smith 1977–78); a stratigraphic gap (Anderson & Cruickshank 1978; Cosgriff 1984; King 1990; Battail 1993); or an extinction event (Lucas 1998). Geological data do not support the existence of a major unconformity within the exposures of the proximal sector, and hypotheses proposing the presence of a stratigraphic gap or fossil-barren zone, have been discredited (Neveling 2002, 2004). In the Rouxville and Burgersdorp districts, stratigraphic overlap has been documented between fossil tetrapod taxa of the *Lystrosaurus* AZ and the lowermost subzone of the *Cynognathus* AZ (Neveling 1998; Neveling *et al.* 1999). Based on the data then available, these authors suggested that an 'Impoverished Zone', encompassing the *Procolophon* Zone of Broom (1906) and part of the lowermost *Cynognathus* AZ as defined by Hancox *et al.* (1995), existed between the *Lystrosaurus* AZ of Groenewald and Kitching (1995) and the *Cynognathus* AZ of Kitching (1995).

NEW BIOSTRATIGRAPHY

An extensive study, incorporating exposures of the Tarkastad Subgroup in both the proximal and distal sectors, and an intensive fossil collecting programme in five selected focus areas (Fig. 1), has enabled us to determine the stratigraphic ranges of various tetrapod taxa and to test earlier hypotheses. Stratigraphic ranges of the fossil tetrapod taxa are summarized in Fig. 3, and it is evident that the patterns differ in the northern (distal) and southern (proximal) parts of the basin.

Our new data do not support the existence of an 'Impoverished Zone' between the *Lystrosaurus* and *Cynognathus* of the proximal sector, but shows the taxa previously reported from this interval to have long stratigraphic ranges extending into the adjacent biozones. The *Procolophon* Zone of Broom (1906) constitutes a very thin horizon that occurs only in isolated geographical localities [for example on the farm Elandskop (S31°57.93' E26°07.78') in the Tarkastad district; Neveling 2002] right at the top of the *Lystrosaurus* AZ (*sensu* Groenewald & Kitching 1995). The only two tetrapod genera we recorded from the '*Procolophon* Zone', *Procolophon* and the amphibian *Micropholis,* also occur in traditional exposures of the *Lystrosaurus* AZ lower down in the stratigraphic sequence, with *Procolophon* considered an index taxon of the latter biozone (Groenewald & Kitching 1995). Due to a dearth of distinguishing characters, we are of the opinion that there are no grounds to recognize a distinct and separate '*Procolophon* Zone'. However, the dramatic increase in the number of *Procolophon* fossils towards the top of the *Lystrosaurus* AZ, may in future lead to the recognition of a '*Procolophon* Abundance Zone'.

Our research demonstrates that the range of *Thrinaxodon*

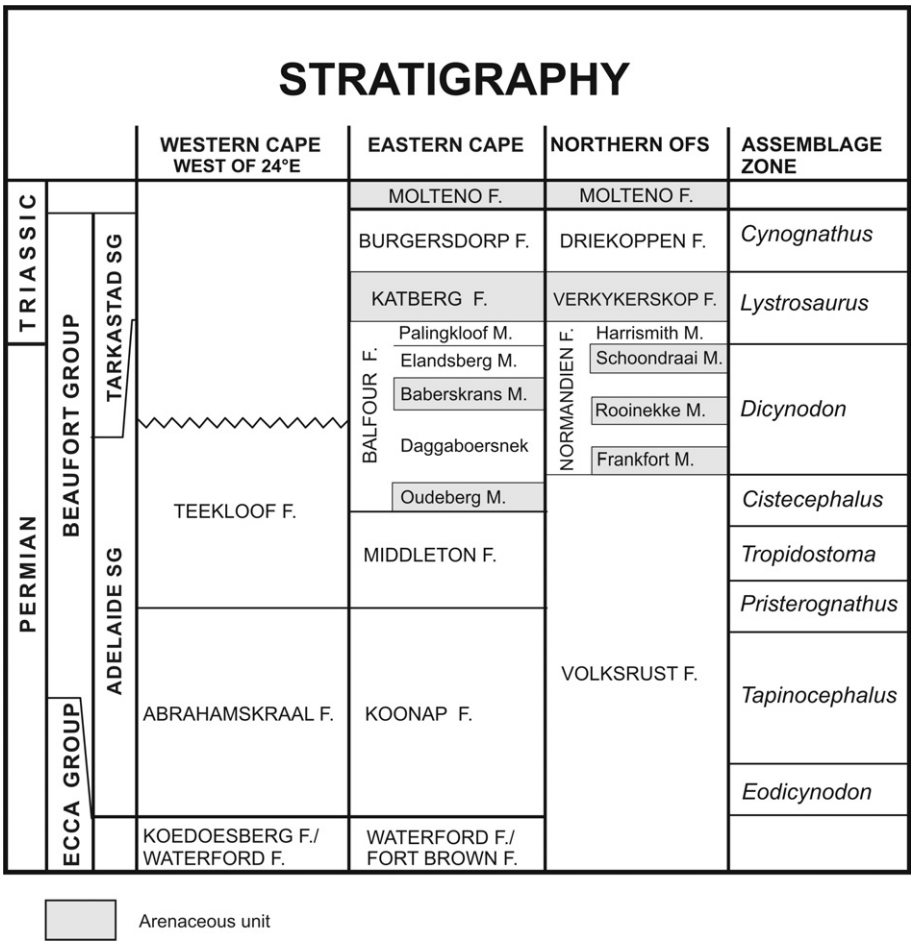


Figure 2. Stratigraphic units of the Beaufort Group. After Rubidge *et al.* (1995).

extends throughout the *Lystrosaurus* AZ; and that *Lystrosaurus* is absent from the very top of this biozone (its last appearance datum [LAD] being more than 50 m below that of *Procolophon* in the proximal exposures of this AZ). *Lystrosaurus* thus disappears before the other elements of the *Lystrosaurus* AZ faunal assemblage (Groenewald & Kitching 1995). The presence of *Thrinaxodon* at the top of the succession in the proximal sector contradicts Groenewald & Kitching's (1995) contention that this genus, together with *Galesaurus,* is restricted to the middle part of the *Lystrosaurus* AZ.

Overlap in the stratigraphic ranges of taxa of the *Lystrosaurus* AZ and the lowermost subzone of the *Cynognathus* AZ is restricted to a very thin stratigraphic interval. In the rocks of the proximal sector the abrupt faunal change-over between the *Lystrosaurus* and *Cynognathus* AZs occurs in the uppermost sandstones of the Katberg Formation and lowermost mudstones of the Burgersdorp Formation (Neveling 2002, 2004; Fig. 3). Our research has also demonstrated that the *Cynognathus* AZ correlates with the entire Burgersdorp Formation, contradicting earlier workers (Keyser & Smith 1977–78; Groenewald & Kitching 1995) who considered the lowest third of the Burgersdorp Formation as part of the *Lystrosaurus* AZ. This means that the latter AZ is restricted to the Palingkloof Member of the Balfour Formation, and the Katberg Formation.

We have traced the lowermost subzone of the *Cynognathus* AZ (Hancox *et al.* 1995) from the northern part of the Karoo Basin (Hancox *et al.* 1995; Shishkin *et al.* 1995) as far south as the Tarkastad and Queenstown districts (Neveling 2002, 2004), and support formal recognition of this biostratigraphic interval. Mastodonsaurid amphibians (Damiani 2001) assignable to the genus *Kestrosaurus* (Shishkin *et al.* 2004) dominate this interval, while the fragmentary medium to large cynodonts from this interval, previously assigned to *Cynognathus* and *Diademodon* (Welman *et al.* 1991; Hancox *et al.* 1995; Hancox 1998) have recently been identified as *Cynognathus* (Hopson, pers. comm., 2002), confirming this faunal assemblage as representing a lower interval of the *Cynognathus* AZ. In the southernmost part of the basin the fauna of this subzone is represented by very scarce amphibian, trirachodontid and archosauriform material from the mudstones and sandstones of the lowermost Burgersdorp Formation. As one proceeds northwards in the basin there is a gradual increase in fossil abundance within this horizon, such that most of the fossils from this interval have been collected from the Senekal and Bethlehem districts in the Free State Province.

Differences between the ranges of taxa in the northern and southern parts of the basin are significant. Overlap between faunas traditionally described from the *Cynognathus* AZ (*sensu* Kitching 1995) and those of the underlying *Lystrosaurus* AZ (*sensu* Groenewald & Kitching 1995) is limited to the southern part of the basin (proximal sector), while no overlap has been recorded in the northern part of the basin (distal sector; see Fig. 3).

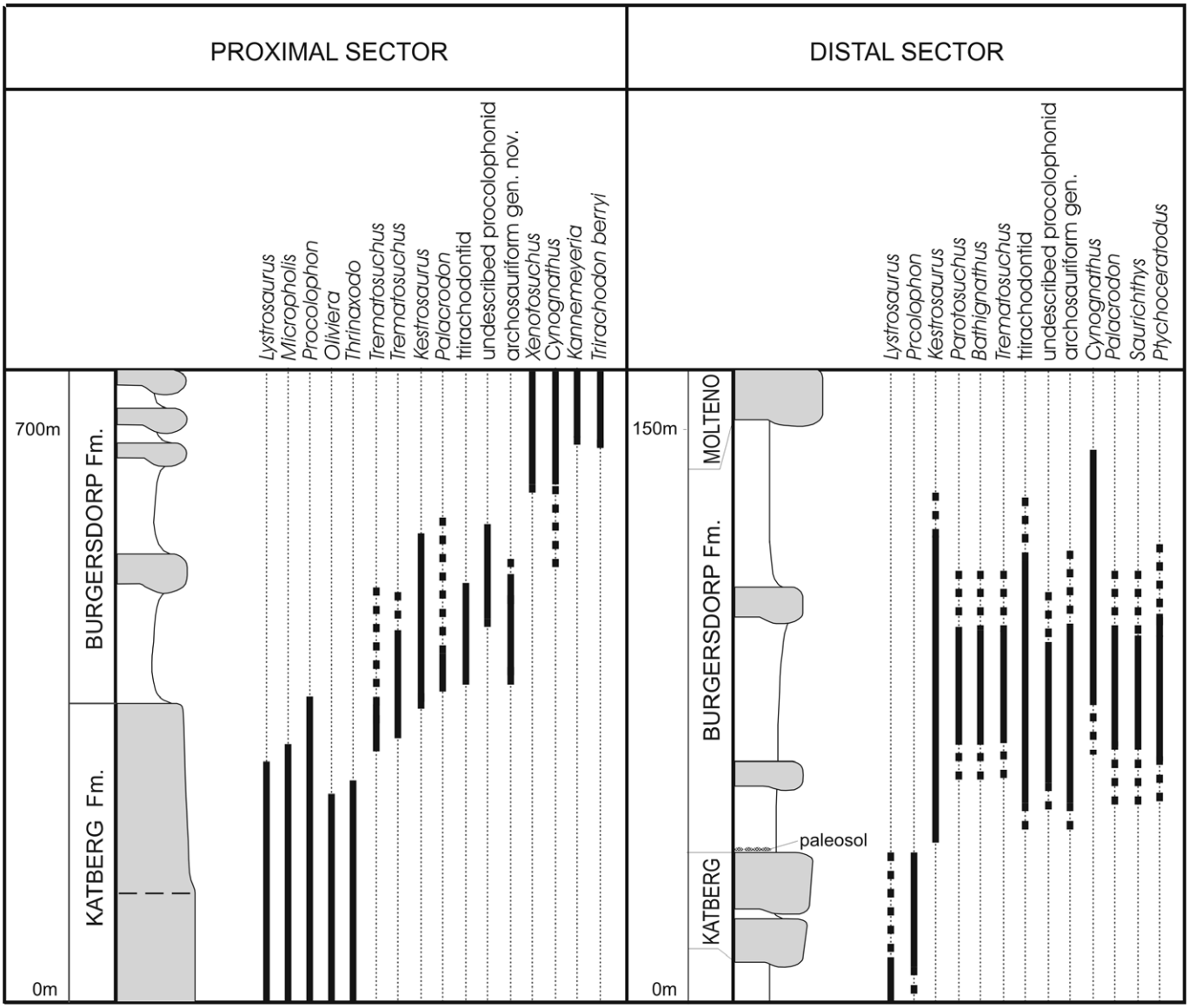


Figure 3. The ranges of important fossil taxa as documented in the studied interval for the proximal and distal sectors of the Karoo Basin. Dashed lines represent inferred stratigraphic ranges based on fragmentary fossil material or literature data. The actinopterygian material is described in Bender & Hancox (2004). (Note sections are not to scale.)

NATURE OF OVERLAP

In the southern half of the study area, west of Aliwal North, the LAD of *Lystrosaurus* is situated in the sandstones of the uppermost Katberg Formation, below the first appearance datum (FAD) of the amphibians *Trematosuchus* and *Kestrosaurus*. *Procolophon* occurs above the LAD of *Lystrosaurus* and overlaps the ranges of *Trematosuchus, Kestrosaurus* and *Palacrodon,* traditionally considered to be from the *Cynognathus* AZ, by more than 20 metres. Above the LAD of *Procolophon* the fauna of the lowermost *Cynognathus* AZ increases dramatically in abundance with the appearance of trirachodontid cynodonts, procolophonid material that resembles *Thelerpeton* and *Teratophon* in appearance (Cisneros, pers. comm., 2006) and a new erythrosuchid archosauriform. *Cynognathus, Bathignathus, Saurichthys* and *Ptchychoceratodus* have been recorded in the richer northern deposits and do not appear to overlap with *Lystrosaurus* AZ representatives (Neveling 2002). Significantly no dicynodonts, or indeed any medium to large herbivores, have been documented from this subzone, the only interval in the Beaufort Group in which dicynodonts are absent.

LATERAL EQUIVALENCE

Short-snouted (trematosaurine) trematosaurid amphibians are the first elements of a post-*Lystrosaurus* fauna to appear in the stratigraphic record. In the proximal sector an isolated mandible, most likely assignable to *Trematosuchus* (Damiani *et al.* 2000), recovered from the uppermost Katberg Formation in the Burgersdorp district, represents the FAD of trematosaurids. *Trematosuchus* is well documented from the mudstones of the overlying Burgersdorp Formation (Shishkin & Welman 1994; Shishkin *et al.* 1995). As this represented the first record from the Katberg Formation of a taxon previously assigned to the *Cynognathus* AZ (Kitching 1995), it was interpreted as supporting evidence of lateral equivalence of the Katberg and Burgersdorp formations (Neveling *et al.* 1999).

Fossils collected during the course of this study do not

support a simple model of lateral equivalence. With the exception of the trematosaurid mandible discussed above and an *ex situ*, tabular fragment assigned to a *Kestrosaurus*-grade mastodonsaurid amphibian, only fossils of the *Lystrosaurus* AZ (*sensu* Groenewald & Kitching 1995) were found in the proximal outcrops of the upper Katberg Formation. *Procolophon* is the dominant tetrapod fossil in the uppermost exposures of the *Lystrosaurus* AZ. Besides two fragmentary *Procolophon* mandibles, only fossils assignable to Subzone A of the *Cynognathus* AZ are found in the lower Burgersdorp Formation of both the proximal and distal sectors of the basin (Fig. 3). The basin-wide correspondence of the *Lystrosaurus* AZ with the Katberg Formation, and the lower *Cynognathus* AZ with the Burgersdorp Formation, seems to suggest that the stratigraphic distribution of these biozones are facies-specific. However, the contact between the two formations is gradational and a detailed sedimentological analysis revealed the presence of similar local depositional environments within both the upper Katberg and lower Burgersdorp formations (Neveling 2002, 2004). Instead, we interpret this association to be indicative of an incomplete stratigraphic record, especially in the distal sector, which resulted from the complex interaction of dynamic subsidence and reciprocal flexure (Catuneanu *et al.* 1998; Pysklywec & Mitrovica 1999; Catuneanu & Elango 2001; Hancox *et al.* 2002; Neveling 2002) in the development of the Karoo Basin.

Our comprehensive biostratigraphic dataset does not support lateral equivalence of the Katberg and Burgersdorp formations, but rather suggests contemporaneous deposition of the lower Burgersdorp Formation in both the southern and northern parts of the basin. From our faunal analysis it is clear that the trematosaurid and mastodonsaurid amphibians, otherwise typical of the *Cynognathus* AZ, are earliest records from the uppermost exposures of the Katberg Formation in the proximal sector and that they predate the appearance of the rest of the *Cynognathus* AZ fauna.

AGE

The stratigraphic overlap between the faunas of the *Lystrosaurus* (*sensu* Groenewald & Kitching 1995) and *Cynognathus* (*sensu* Kitching 1995) AZs has significant consequences for the age determination and duration of the *Lystrosaurus* AZ. Although the earliest record of the genus *Lystrosaurus* is latest Permian (Cheng 1993; Smith 1993, 1995; Smith & Ward 2001), the typical *Lystrosaurus* AZ fauna appears only in the earliest Triassic (MacLeod *et al.* 2000; Smith & Ward 2001; De Kock & Kirschvink 2004; Ward *et al.* 2005). Correlation with *Lystrosaurus*-bearing strata in Russia (Kalandadze 1975; Shishkin *et al.* 2000) and Asia (Romer 1969; Lucas 1993) and more direct correlation with the amphibian fauna in the Andavakoera Formation (Sakamena Group, Madagascar) and Wordy Creek Formation (East Greenland) support an Induan age (Anderson & Cruickshank 1978; Cooper 1982; Ochev & Shishkin 1989; Hankel 1994). Close taxonomic affinities between the rhytidosteid amphibians of the South African *Lystrosaurus* AZ (Kitching 1978; Cosgriff 1984), various Australian assemblages (Cosgriff 1965, 1974, 1984; Cosgriff & Zawiskie 1979; Warren 1991) and the Sticky Keep Formation of Spitzbergen (Cosgriff 1965) also suggest an early Olenekian age (Tozer 1967; Tozer & Parker 1968; Cox & Smith 1973; Foster 1982; Helby *et al.* 1987; Retallack 1997).

The fauna of Subzone A of the *Cynognathus* AZ includes the mastodonsaurid amphibians *Parotosuchus* and *Kestrosaurus*, as well as batrachosuchid and trematosaurid amphibians and archosauriforms which have close taxonomic affinities with taxa from the *Parotosuchus* fauna in the Cis-Urals, and the Middle Buntsandstein in the Germanic basin (Ochev & Shiskin 1989; Shishkin & Ochev 1993; Shishkin & Welman 1994; Shishkin *et al.* 2000; Damiani 1999, 2002; Damiani & Jeannot 2002). This suggests an Upper Olenekian age for the lowermost *Cynognathus* AZ, as previously proposed by Hancox *et al.* (1995). Overlap between faunas of the *Lystrosaurus* and *Cynognathus* AZ's and the presence of a trematosaurid mandible high in the Katberg Formation, suggests that the fauna of the *Lystrosaurus* AZ in southern Gondwana survived up to (or very close to) the end of the Lower Olenekian, while its equivalent fauna in the northern hemisphere disappeared much earlier (Shiskin & Ochev 1993).

CONCLUSION

Detailed bio- and lithostratigraphic research on the contact between the *Lystrosaurus* and *Cynognathus* AZ's has shown that the stratigraphic ranges of faunal elements of both biozones overlap, but this is restricted to the Tarkastad Subgroup in the southern (proximal) part of the basin. In the north (distal sector) these biozones show no faunal overlap. The new biostratigraphic data disprove the previously proposed lateral equivalence of the Katberg and lower Burgersdorp formations and indicates a much longer duration for the *Lystrosaurus* AZ than formerly accepted (Anderson & Cruickshank 1978; Cosgriff 1984; Battail 1993; Lucas 1998). Our research supports the proposed basal subdivision of the *Cynognathus* AZ (Hancox *et al.* 1995) and extends the range of the lowermost subzone A southwards to the Tarkastad district. The entire fauna of the *Lystrosaurus* AZ is replaced by that of the lower *Cynognathus* AZ over a very narrow stratigraphic interval, which indicated the rapid nature of this transition. However, more research is needed to determine the causal factors responsible for the faunal turnover at the interface between these two biozones.

Our study area extended over twelve districts, ranging from Tarkastad in the south to Bergville in the northeast. J.N. extends his gratitude to Col. Van Schalkwyk of the Goedemoed Prison and P. Badenhorst (Oliviershoek), F. Bester (Driefontein), L. Borman (Fraaiuitzicht), C.F. Conradie (Jutland), J.F. du Plessis (Moerbeidal), W. du Plessis (Elandskop), S.E. Durand (Heuningkrans), A.M. Grobbelaar (Waschbank), J.C. Harding-Male (Odendaalstroom), S.G. Jacobs (Cypherfontein), W.J. Ludik (Klipkuil), F. Marais (Elandskop), B.G. Meyer (Driefontein), N. Miya (Kwa Miya), Mundy (Little Switzerland), F. Myburg (Saamwerk), W. Nel (Eldorado), P. Odendaal (Kaaimansgat), B. Oliphant (Jisreël), A. Porter (Hill and Dale), P.S. Potgieter (Drenthe), H. Prinsloo (Gwarriekop), A. Sehlu (Boshoek), C. Steyn (Teebus), F. Steyn (Driekoppen), J. Steyn (Erfdeel), A. van der Walt (Perdelaagte), A. van der Merwe (Rhebokkop), J. van Niekerk (Spreeuhoek) and J. Wilken (Klipplaatsdrif) for permission to work on the property in their care. F. Tshabalala, J. Sejake, D. Nkwinika and C.M. Hlatswayo provided invaluable assistance in the field, while A. Motgale, D. Nkwinika, J. Sejake, F. Tshabalala,

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