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**Life After Extinction: Palaeoenvironments of the earliest Triassic  
lower Katberg Formation, Including the Origin of *Lystrosaurus*  
Bonebeds from the Karoo Basin, South Africa**

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## DECLARATION

I hereby declare that all of the work presented in this thesis is my own, except where otherwise stated in the text

P.A. Viglietti



"Nature is full of infinite causes that have never occurred in experience." – Leonardo da Vinci

## Abstract

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The most devastating mass extinction event Earth has experienced occurred at the end of the Permian period approximately 251 Million years ago (Ma). The southern Karoo Basin is one of the few places in the world that preserves an almost continuous stratigraphic record of terrestrial sedimentation through the Permian-Triassic Boundary (PTB). Emphasis on the rapid annihilation of marine and tetrapod faunas during the PTB extinction event has generally overshadowed the nearly as rapid radiation and regeneration of fauna in earliest Triassic Karoo environments. The expansion of mammal-like reptiles (therapsids) of the *Lystrosaurus* Assemblage Zone fauna into an increasingly arid, but not necessarily warmer Karoo Basin, is associated with changes in fossilization mode. Isolated skulls and postcranial material in the latest Permian are replaced by articulated, “curled up” skeletons and multi-individual accumulations (bonebeds) in the earliest Triassic. Lack of epiphyses and skull sizes suggest only sub-adult *Lystrosaurus* are present in bonebeds. Clustered articulated ribs among disarticulated material and minor weathering of bones are evidence of a period of desiccation where bones lay on or near the soil surface for up to five years before burial (Behrensmeyer, 1978; Smith and Botha, 2005; Botha and Smith, 2006). The lithology surrounding the bonebeds consists of floodplain mudrocks, carbonate nodules; and sand-filled mud cracks capped by coarse sediments, the latter indicative of rapid deposition during floods. The presence of ichnofossils such as vertebrate burrow-fills suggests the use of burrows possibly by *Lystrosaurus* and other fauna to escape extreme environmental conditions. Other rare associated vertebrate taxa suggest *Lystrosaurus* bonebeds were preferentially preserved due to climatic regime in place. Carbonate nodules have  $\delta^{13}\text{C}$  values ranging from -8.5 to -5‰ and  $\delta^{18}\text{O}$  values of 13.5 to 16 ‰ respectively. These values support the formation of the carbonate nodules under a highly seasonal, cool, semi-arid climate at higher latitude (~50° S) than the modern Karoo Basin. This study argues for the formation of bonebeds by aggregation of sub-adult *Lystrosaurus* during extended episodic periods of extreme climatic conditions, such as cold or drought, in the earliest Triassic Karoo Basin.

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## 1. Introduction

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The End-Permian mass extinction event at approximately 251 Ma (Bowring et al., 1998; Coney et al., 2007; Shen et al., 2011) is believed to be one of the most profound mass extinctions Earth has ever witnessed. This extinction event, which caused the loss of up to 90% of marine life, 60% of land vertebrates, 30% of insects, and nearly all land plants (Sepkoski, 1985; Labandeira and Sepkoski, 1993; Stanley and Yang, 1994; Retallack, 1995; 1999; Erwin et al., 2002) has been hard to define up until recently. It is generally agreed that a combination of triggers or kill mechanisms caused a run-away greenhouse effect from the failure of feedback processes. This resulted in the chemical and temperature regulators in the atmosphere and oceans undergoing catastrophic breakdown (Benton, 2003). The culprits for this end Palaeozoic biological crisis include 1) global marine anoxia associated with sea-level rise (Wignall and Hallam, 1992), 2) a combination of regression, volcanism, and anoxia (Erwin, 1993), 3) Siberian trap volcanism (Renne et al., 1995; Bowring et al., 1998), and 4) dissociation of gas hydrates (Heydari and Hassanzadeh, 2003).

Geological evidence from Spitsbergen and the palaeo-equatorial sections of Italy and Slovenia indicate that the world's oceans became anoxic at both low and high paleolatitudes in the Late Permian (Wignall and Twitchett, 1996) whereas terrestrial rocks from the Late Permian indicate sudden facies and fluvial style changes (Newell et al., 2010; Michaelsen, 2002; Smith and Botha, 2005). The Karoo Basin of South Africa harbours one of the few terrestrial Permo-Triassic Boundary (PTB)

successions, preserving the Permian-Triassic transition as a 7 m thick zone of purple laminated mudstones in the lower Palingkloof Member of the upper Balfour Formation (Smith 1995; Ward et al, 2000; Smith and Ward, 2001; Ward et al, 2005; Retallack et al, 2003; Smith and Botha, 2005; Botha and Smith, 2006; Tabor et al., 2007). The terrestrial Beaufort Group lithologies vary from the mudstone-dominated Late Permian formations (Teekloof, Middleton, Balfour), through the PTB (lower Palingkloof Member), into the sandstone-dominated Early Triassic Katberg Formation. This lithological succession has been interpreted by Smith (1995), and Smith and Botha (2005), as representing changes in the depositional environment across the PTB. These changes may have been due to global climate change brought about by Siberian trap volcanism (Renne et al., 1995; Bowring et al., 1998) and also local episodic tectonism in southwest Gondwana, associated with the Cape Orogeny (Smith and Botha, 2005). The change in fluvial style coincided with a faunal and floral turnover as the wet-floodplain adapted therapsid fauna of the *Dicynodon* Assemblage Zone were replaced by the dry-floodplain *Lystrosaurus* Assemblage Zone fauna. Due to the relatively sudden appearance of the new fauna, it has been proposed these *Lystrosaurus* Assemblage Zone fauna migrated from elsewhere into the drying Karoo Basin (King and Jenkins, 1997; Botha and Smith, 2007).

The therapsids (of the synapsid reptile lineage) were one of the most diverse tetrapod fauna from the Early Late Permian to Middle Triassic in both Laurasia and Gondwana. Before the dinosaurs, the therapsids had diversified into many types of land vertebrates, helping to establish the foundations for complex ecosystems (Sumida and Martin, 1997). Fossil evidence suggests therapsid origins lie in southern

Gondwana as fossils of some of the most basal therapsids (biarmosuchia, dinocephalia and anomodontia have been found in the Karoo Basin (Rubidge and Sidor, 2001). Because they make up a relatively large proportion of the Late Permian tetrapod fauna, therapsids can provide critical information on the nature of the Permo-Triassic extinction in the terrestrial realm. Beginnings of this extinction on land are seen with the arrival of the dicynodont *Lystrosaurus* into the basin, prior to the End-Permian mass extinction.

*Lystrosaurus* was one of few therapsid species (including the cynodonts), and the only dicynodont, if one does not consider the almost unknown *Myosaurus* (Cluver, 1971), to survive the End Permian mass-extinction event. Of the 48 tetrapod families living in the last 5 Myr of the Late Permian, only 12 survived the extinction event. It was the most dramatic mass extinction in Earth's history, dubbed "the mother of all mass extinctions" (Benton, 1997; Erwin, 2006; Ward, 2007). Along with many of the tetrapods, the *Glossopteris* flora also became extinct, and many have speculated that the key to the success of *Lystrosaurus* was its pre-adaptation to the arid climate *Dicroidium* flora that replaced *Glossopteris* in the Triassic (Botha and Smith, 2007). *L. maccaigi* was the first and largest *Lystrosaurus* species identified from the *Dicynodon* Assemblage zone. *L. maccaigi* was replaced by *L. curvatus* during the End-Permian mass extinction event, and by *L. murrayi*, and *L. declivis* in the earliest Triassic. *L. declivis* is the main taxa represented in the *Lystrosaurus* bonebeds (Figure: 1.1). Attempting to understand the success of *Lystrosaurus*, during and after the extinction event, may help us to understand the dynamics of this mass extinction and, possibly, the recovery of the faunal diversity in the Karoo Basin including the

origins of mammals (from the cynodonts). Studies of the *Lystrosaurus* bonebeds could play a pivotal role in helping answer some of these questions.



**Figure 1.1:** A reconstruction of *Lystrosaurus declivis* from the "Stone Bones" exhibit at Iziko South African Museum, Cape Town. *Lystrosaurus* had a significantly downturned snout when compared to the other dicynodonts, and this adaptation may have allowed it to process tough vegetation.

## 1.1 Previous Work on Karoo Fossils

To date, most studies of the therapsids and coeval vertebrate fauna of the main Karoo Basin of South Africa have concentrated on taxonomy (Broom, 1907; Kemp, 1972; Modesto et al., 1999; Rubidge and Sidor, 2001; Botha et al., 2007; Sidor and Smith, 2004; ), functional morphology (Owen, 1876; Cluver, 1971; King, 1990; Kinlaw, 1999; Ray and Chinsamy-Turan, 2003; Cisneros et al., 2011) and biostratigraphy (Haughton, 1919; 1969; Hotton, 1967; Boonstra, 1969; Keyser, 1973; Keyser and Smith, 1979; Smith 1990; 1993, 1995; Smith et al., 1993; Rubidge, 1990; Rubidge et al., 1995; Macleod et al., 2000; Smith and Ward, 2001; Smith and Botha, 2005; Botha and Smith, 2006; 2007; Van der Walt et al., 2010) and there have been very few taphonomic investigations of the fossil occurrences. Beginning with the discovery of vertebrate fossils in the Beaufort Group strata by Bain in 1838, early works by Owen (1876), Broom (1907) and Haughton (1919), were not very precise concerning the modes of occurrence and collecting procedures. Often, little to no attention was paid to the host rock lithology, bedding planes or sedimentary features nor even to accurately recording the locality of the fossil; sometimes only the skulls or individual bones were collected and the rest was left behind. This has led to problems relocating sites and accurately assigning them to a stratigraphic interval for relative dating of the fossils, and also identifying the palaeoecosystems.

In the last 50 years great strides have been made concerning the Beaufort Group fossils in the Karoo Basin. Scientists such as Colbert (1963), Hotton (1967) and Boonstra (1969) were some of the first to consider the mode of fossilisation and utilize it for palaeoclimatic and taphonomic interpretations. Refinements of the

biostratigraphy by Keyser and Smith (1979), and Rubidge et al (1995) have helped to further increase the resolution of faunal turnovers in the Karoo Basin from the Middle Permian to Early Jurassic including the End-Permian mass extinction and the smaller End Triassic extinction event.

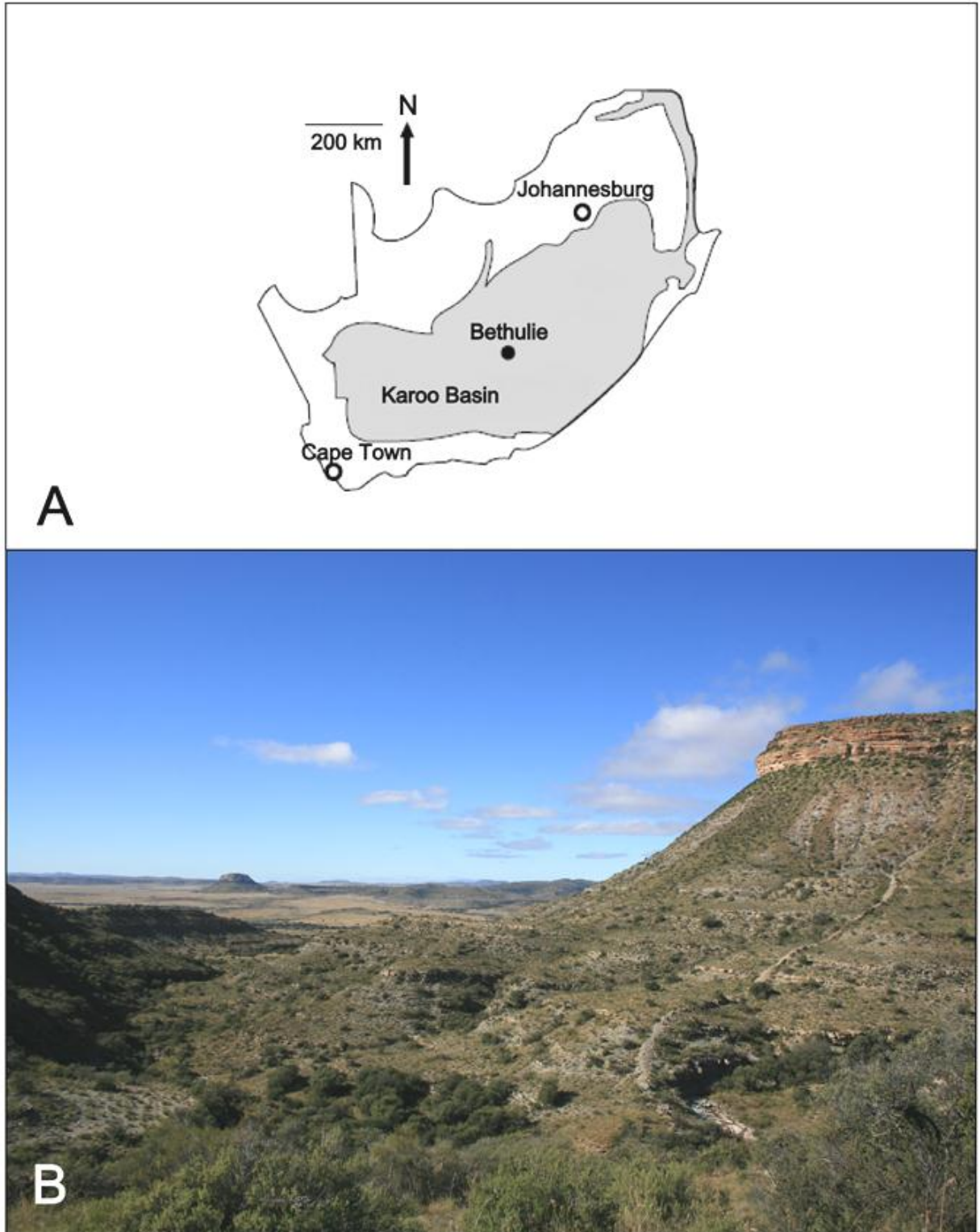
A fossil represents the end-product of a series of events that led to the death of the organism: burial, mineralization and exposure at the surface. The science of taphonomy or “the transition of an organism from the biosphere to the lithosphere” as Efremov (1940) first defined this field of study, has great palaeontological and geological significance. According to Weigelt (1989), the confluences of unusual biological and geological processes make the most substantial contributions to the fossil record. Fossils are thus potentially windows into the dynamics of catastrophic geological and climatic events, and bonebeds are effective indicators of particular environmental processes occurring at the time of deposition.

This thesis presents data relating to sedimentological, geochemical, and taphonomic observations of the lower Katberg Formation in the southern Karoo Basin with emphasis on the occurrence of *Lystrosaurus* bonebeds. The field observations are augmented with laboratory analyses and are presented in the context of the Karoo Basin’s general tectonic and geologic setting with emphasis on the origin of the bonebeds and what they reveal about the biotic recovery following the End Permian extinction. Understanding the occurrences of these fossils and bonebeds will contribute to further understanding the environment of the earliest Triassic. This is because these bonebeds provide a window into the extreme environmental changes

that followed after the End-Permian mass extinction event. If *Lystrosaurus* was struggling to cope with the conditions, so were other animals. There was a drying trend in the Karoo Basin up until desert conditions were reached by the end of the Stormberg Group (Smith et al., 1993). Why the cynodonts flourished and evolved into mammals in the process, while *Lystrosaurus* disappeared after surviving the largest mass extinction event on Earth, is not understood.

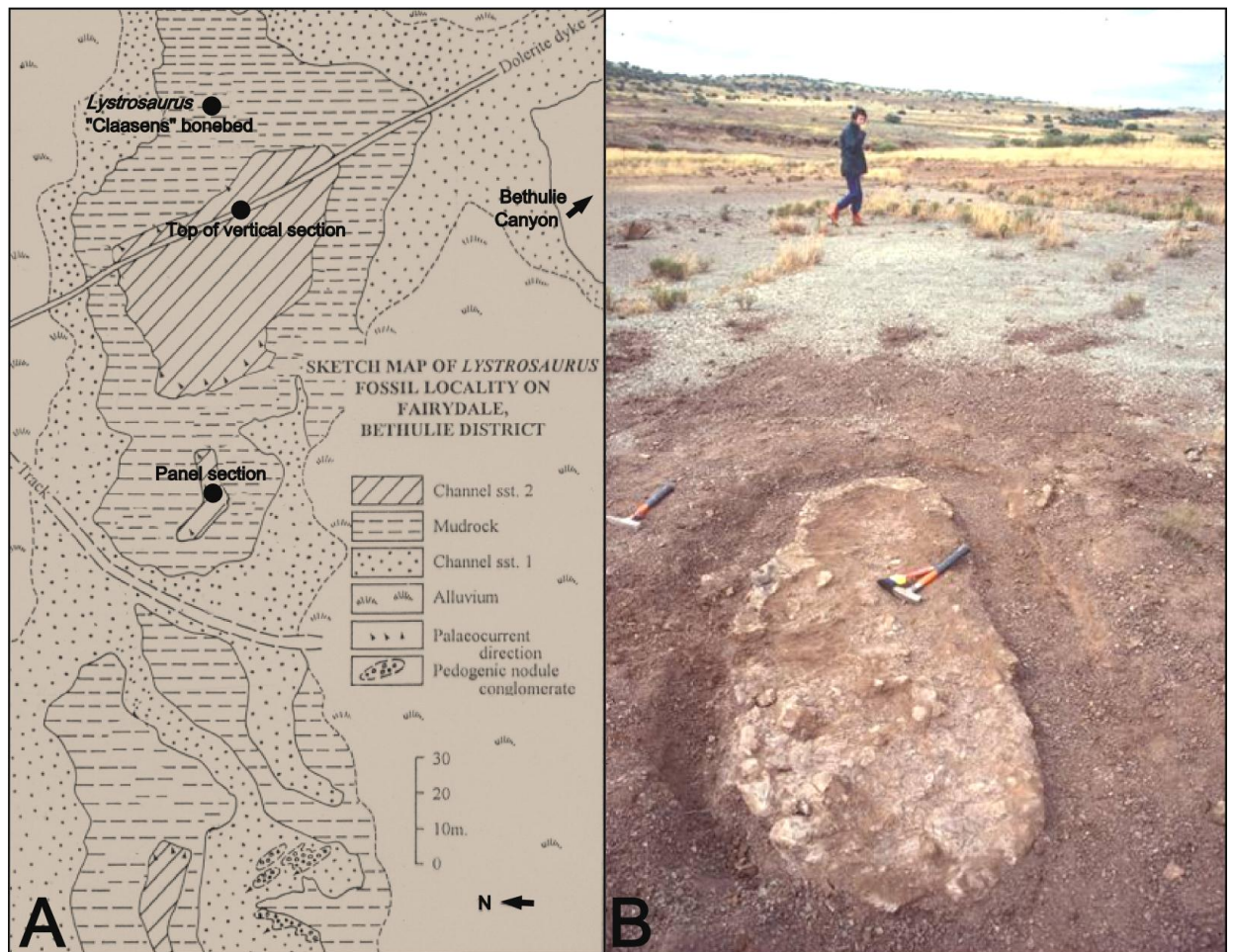
## 1.2 Locality of Study

The main locality for this study on the Early Triassic Katberg Formation is the Donald 207 Farm (was up until recently part of an adjoining Farm, Fairydale 193). The farm is a well-known and productive fossil locality first discovered by James Kitching in 1977 (Abdala et al., 2006). The farm and its adjoining property (Heldemoed 667) include a large canyon named Bethel Canyon, and this is where Smith (1995) first documented the End-Permian extinction and described a fully preserved PTB sequence in the Karoo Basin (Figure: 1.2). Prior to Smith's 1995 study, it was believed that the PTB in the Karoo was an erosional hiatus (Anderson and Cruikshank, 1978).



**Figure 1.2:** (A) The position of Bethulie, the closest town to the field area on Donald 207 in the context of South Africa and the Karoo Basin. Taken from Macleod et al. 2000. (B) South of the Donald 207 Farm is Bethel canyon (part of Heldemoed 667). This is where Smith (1995) first documented a fully preserved PTB in the Karoo Basin that coincided with the largest ever extinction event in the terrestrial vertebrate fossils.

Bethel Canyon preserves one of the best terrestrial exposures of the PTB in the World, and is one of few places in the Karoo Basin where one can walk from the upper Permian (*Dicynodon* AZ), through the PTB and into the Triassic (*Lystrosaurus* AZ) on continuous outcrop. Many fossils from Farms Fairydale 193, Donald 207, and Heldemoed 667 are housed in collections of the Bernard Price Institute (BPI) at the University of the Witwatersrand, the National Museum in Bloemfontein, and Iziko South African Museum in Cape Town. Dr. Roger Smith and his field team have been visiting the site regularly for 15 years, and over the past 5 years they have been working on a project funded by the National Research Foundation of South Africa entitled "Anatomy of Extinction". It is aimed at using the rocks and fossils of the Karoo Basin to find out what happened to the terrestrial ecosystems of southern Gondwana during the most devastating of mass extinctions, approximately 251 Ma, how the survivors succeeded, and how the ecosystems recovered from the extinction event giving rise to mammals and dinosaurs in the process. During the 2004 field season, the first large multiple accumulation of *Lystrosaurus* (nicknamed the "Claasens bonebed" in honour of the landowner) was uncovered by Annelise Crean (Figure: 1.3).



**Figure 1.3:** (A) Sketch geological map of Fairrydale Farm (now an adjoining property named Donald 207) showing the locality of the *Lystrosaurus* "Claasens" bonebed (SAM-PK-K8551) and also the position of the vertical and panel sections done in the study. Taken from Smith, 2005 (unpublished). (B) Photograph of the *in situ* *Lystrosaurus* "Claasens" bonebed found by Annelise Crean in 2004. Photograph taken by R. Smith, 2004.

The bonebed was excavated in a single block, stabilized with a Plaster of Paris jacket, and then taken to the Iziko South African Museum where it was given the accession number SAM-PK-K8551. Over the next 2 years, Hedi Stummer cleaned and prepared the bonebed with pneumatic air scribes to ensure all the individual bones were made visible, but left in position as they were buried. After all the preparation, the bonebed was described and figured (Smith and Botha, 2005). During this time, many *Lystrosaurus* fossils in this stratigraphic position of the lower Katberg

showed similar preservation style to the large bonebed discovered. About 227 in situ *Lystrosaurus* remains have been logged by Botha and Smith (2006) in this approximately 8m thick stratigraphic interval, dubbed the “*Lystrosaurus* abundant Zone” by Botha and Smith (2006).

### 1.3 Project Objectives

The Claasens bonebed formed the basis of my honours thesis (Viglietti, 2009); the major outcome of which was that it represents an accumulation of individuals of similar age that succumbed during an earliest Triassic drought event. Thus the main objectives of this MSc project are to understand the origin of the Claasens bonebed and a number of other *Lystrosaurus* bonebeds logged in the same stratigraphic interval on the Fairydale Farm. At the locality where the majority of these bonebeds occur a 2-D panel section was documented as well as a vertical section through the lower Katberg strata exposed on hillslopes and river gullies in the area. A geochemical study on carbonate nodules and fossil bone and tooth enamel collected from the lower Katberg Formation was undertaken in an attempt to gain information on the climatic influences on the floodplain environments and their resident animals and plants. A taphonomic study of the bonebeds and other vertebrate fossils encountered in the vertical section was done in order to gain more information on individual fossil occurrences and what this can tell us about the palaeoenvironmental conditions at the time of death and burial. In the following section, a geological setting of the Karoo Basin, with emphasis on the Beaufort Group, will present the Katberg Formation in its full context.

## 2. Geologic Setting

### 2.1 Tectonic Setting

The Katberg Formation outcrops over an estimated 150 000 km<sup>2</sup> within the central, south-eastern sections of the main Karoo Basin, a broad foreland basin in the centre of South Africa supported by the Kaapvaal Craton in the northeast and the Namaqua-Natal Metamorphic Belt (NNMB) in the southwest (Catuneanu et al., 1998; Tankard et al., 2009). This basin formed within the continental interior of south western Gondwana (Figure 2.1) and once formed part of a 6000 km long x 1000 km wide foreland system along the southern periphery (Catuneanu et al., 1998; Catuneanu and Elango, 2001).



**Figure 2.1:** A reconstruction of Late Permian-Early Triassic southwest Gondwana. The plate margin is based on accreted terranes and massifs. The position of the study area is indicated by an orange circle. Taken from Tankard et al. (2009).

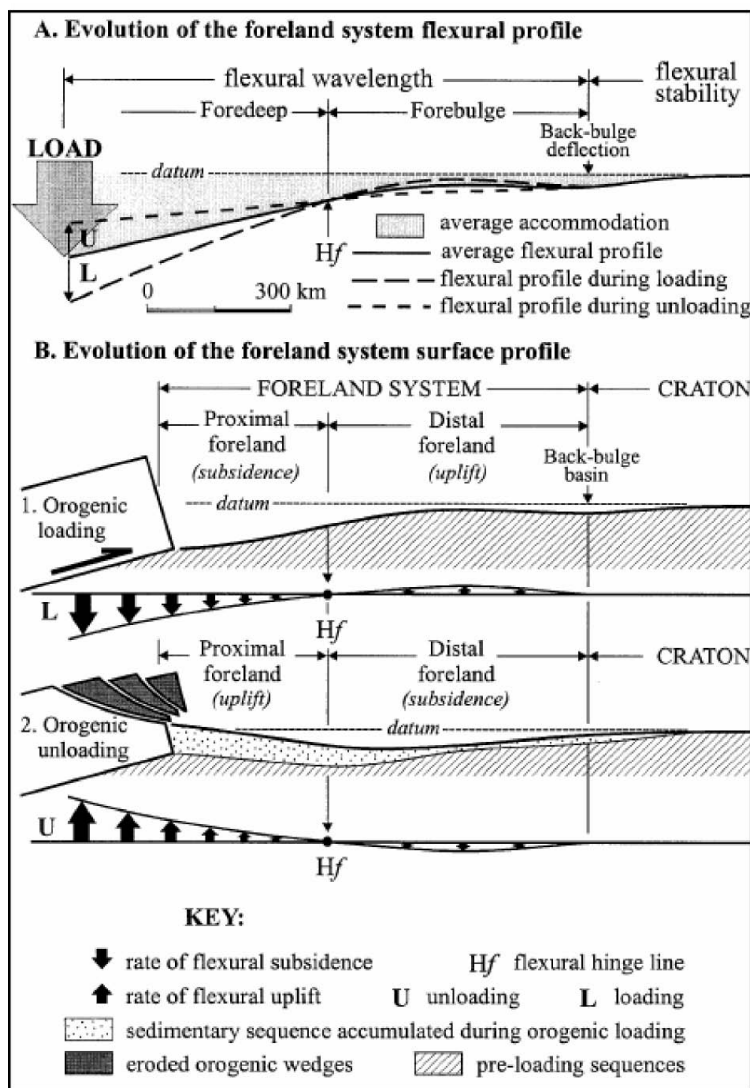
This system was produced by (in the Late Carboniferous – Early Permian (~300 Ma)) flat plate subduction of the Paleo-Pacific plate beneath the Gondwanan plate (Lock, 1980; De

Wit et al., 1988). The subduction zone consisted of volcanic arcs, a fold thrust belt called the Gondwanide Mobile Belt, and a retroarc foreland basin (Catuneanu et al., 1998). The Cape Fold Belt (CFB) is a relict portion of this mountain range. Crustal flexure in response to the over-thickening resulted in a series of foreland basins along the landward side of the Gondwanide Mobile Belt. The associated foreland basin fragmented at a later period due to Gondwana break-up, but the remnants are preserved today in South America (Paraña Basin), South Africa (Karoo Basin), Antarctica (Beacon Basin) and Australia (Bowen Basin) (Lock, 1978; Winter, 1984; De Wit et al., 1988; Johnson, 1991; De Wit and Ransome, 1992). The Karoo Basin and adjacent fold-thrust belt (the present CFB) were located some 1500 km from the collision margin, significantly further from the proposed margin than the other Karoo aged basins. According to Cole (1992), this interior position on the Gondwana plate was controlled by a zone of weak underlying continental crust – the Southern Cape Conductive Belt.

De Wit et al. (1998) hypothesized that the reactivation of this geophysical anomaly may have also controlled the CFB orogeny. Lock (1980) theorised that lithospheric deflection (flat slab subduction) of the subducting Paleo-Pacific plate beneath the Gondwana plate was the main cause of the Karoo Basin's position. North – verging thrusts seen in the Cape Supergroup rocks are believed by Lock (1980) to have been the result of lithospheric decoupling in a subduction zone, causing the translation of plate deformation and subsidence further into the plate interior. The flat slab model requires there to be thin and thick-skinned deformation present, and there is still a lot of contention concerning what kind of deformation is indeed present in the CFB (Tankard et al., 2009). Flat slab subduction is believed to cause landward migration and possibly total cessation of arc volcanism (Lock, 1981). It is known that volcanic

arcs were present, as much of the sedimentary material preserved in the Karoo Basin (the Karoo Supergroup) was sourced from typical arc setting volcanic compositions (Turner, 1978). This is known from the presence of ash beds in the lower successions, detrital zircons, and presence of other minerals and elements (i.e. uranium) (Turner, 1978; Haycock et al., 1997).

It is thus generally agreed that flexural tectonics (imposed by orogenic loading) and dynamic subsidence (imposed by flat slab subduction) are the two most important controls on accommodation in the main Karoo Basin, whose foreland nature is now widely accepted (Catuneanu et al., 2005). Depocentres of the Karoo sequence were greatly controlled by crustal loading during the Cape Fold Belt orogenic cycles (8 dated in all by Hälbig and Söhne, 1983 using mineralization along thrust planes). Orogenic loading was the initial subsidence mechanism acting on the Karoo Basin (Catuneanu et al., 1998; 2004; 2005). Flexural tectonics partitioned the Karoo Basin into the foredeep, forebulge, and back-bulge flexural provinces (Catuneanu et al., 1998). Orogenic loading and unloading caused changes in position of the forebulge and foredeep flexural provinces, and thus resulted in deposition in the proximal (with reference to the Gondwanide Mobile Belt) or distal regions of the Karoo Basin (Catuneanu et al., 1998) (Figure: 2.2).



**Figure 2.2:** Diagram (A) shows parameters that controlled sedimentation and erosion in the Karoo foreland system. The "load" represents orogenic loading from the formation of the Cape Fold Belt. Flexural wavelength depends on the rheology and elastic thickness of the lithosphere, basement tectonics, and mass distribution of the applied loads (Catuneanu et al., 2000). These factors affect horizontal distance of the foredeep and forebulge. It is generally accepted that a lithosphere with a high flexural rigidity produces a flexural wavelength of large horizontal scale, like the Karoo foreland system. Diagram (B) 1 and 2 show the effect orogenic loading and unloading have on the distribution of sedimentation respectively. They clearly show the depocenter of the foreland system alternating between the foredeep during loading and foresag during unloading. In the stratigraphic record this is preserved as proximal and distal facies changes in the Karoo Basin that are separated by the stratigraphic hinge line. Taken from Catuneanu et al. (1998).

Flat slab subduction (dynamic subsidence) was a larger influence in subsidence rates and distribution later in the evolution of the Karoo Basin. Because this dynamic subsidence was controlled by the drag force generated by viscous mantle corner flow coupled to the low angled subducting plate (the flat slab condition) (Mitrovica et al., 1989; Gurnis, 1992; Holt and Stern, 1994; Burgess et al., 1997), the onset of dynamic loading lags in time behind the initiation of subduction and tectonic loading, as it takes time for the subducting slab to reach far enough beneath the overriding plate to generate a viscous corner flow (Mitrovica et al., 1989; Catuneanu, 2005).



**Figure 2.3:** Photographs show two palaeosurfaces from different stratigraphic positions and locations in the Karoo Basin. **(A)** Palaeo-surface at the Ecca-Beaufort contact near Escourt, Kwazulu-Natal Province. Drag impression (right) is interpreted by Rubidge (PSSA conference, 2010) as being made by a large amphibian. **(B)** Footprints of a dinocephalian on Gansfontein palaeosurface (*Tapinocephalus* Assemblage Zone), near Fraserburg, Northern Cape Province. Although **(A)** is stratigraphically lower by 2000m, it has in fact been dated as younger than **(B)** by 6 million years (~254 Million years old). The diachronous ages of the Ecca-Beaufort contact were caused by migration of sedimentation from the foredeep northwards into the basin due to orogenic unloading during this time period (Catuneanu et al., 1998; 2005).

This caused loading and subsidence to happen out of phase throughout the Karoo Basin, thus many of the upper and lower boundaries of the lithostratigraphic groups are diachronous in age (i.e. Dwyka –Ecca, Ecca-Beaufort etc.) (Catuneanu et al., 1998, Rubidge et al., 1995) (Figure: 2.3). Extensional tectonics also influenced the deposition of the Stormberg Group (Bordy and Catuneanu, 2001; Bordy et al., 2004).

Many formations in the Karoo Basin as a result, are proximal and distal equivalents (i.e. Whitehill and Vryheid formations) (Turner, 1975). This fact has also caused controversy concerning correlating certain formations with orogenic paroxysms (i.e. the Katberg Formation). Tankard et al. (2009) proposed that the Katberg Formation depocenter, a northward-propagating alluvial wedge of sandstones and minor mudstones, was a direct response to the onset of the Cape Fold Orogeny. This initial tectonic pulse from the Cape Fold Belt orogeny was coupled with later foundering of the Natal Block, allowing deposition of the mudstone dominated Burgersdorp Formation (Tankard et al., 2009). This Katberg-Burgersdorp transition has been regarded a mega fining-upward cycle that has distal equivalents in the northern parts of the Basin (The Verkykerskop and Driekoppen formations respectively) (Catuneanu et al., 1998). These lateral movements of the Karoo Basin's depocenter, as well as varying provenance and transport directions led to the accumulation of a cumulative thickness of more than 12 km of terrestrial and non-marine sediments known as the Karoo Supergroup. Due to the focus of this study, only the Karoo Supergroup's Beaufort Group sediments will be discussed in more detail.

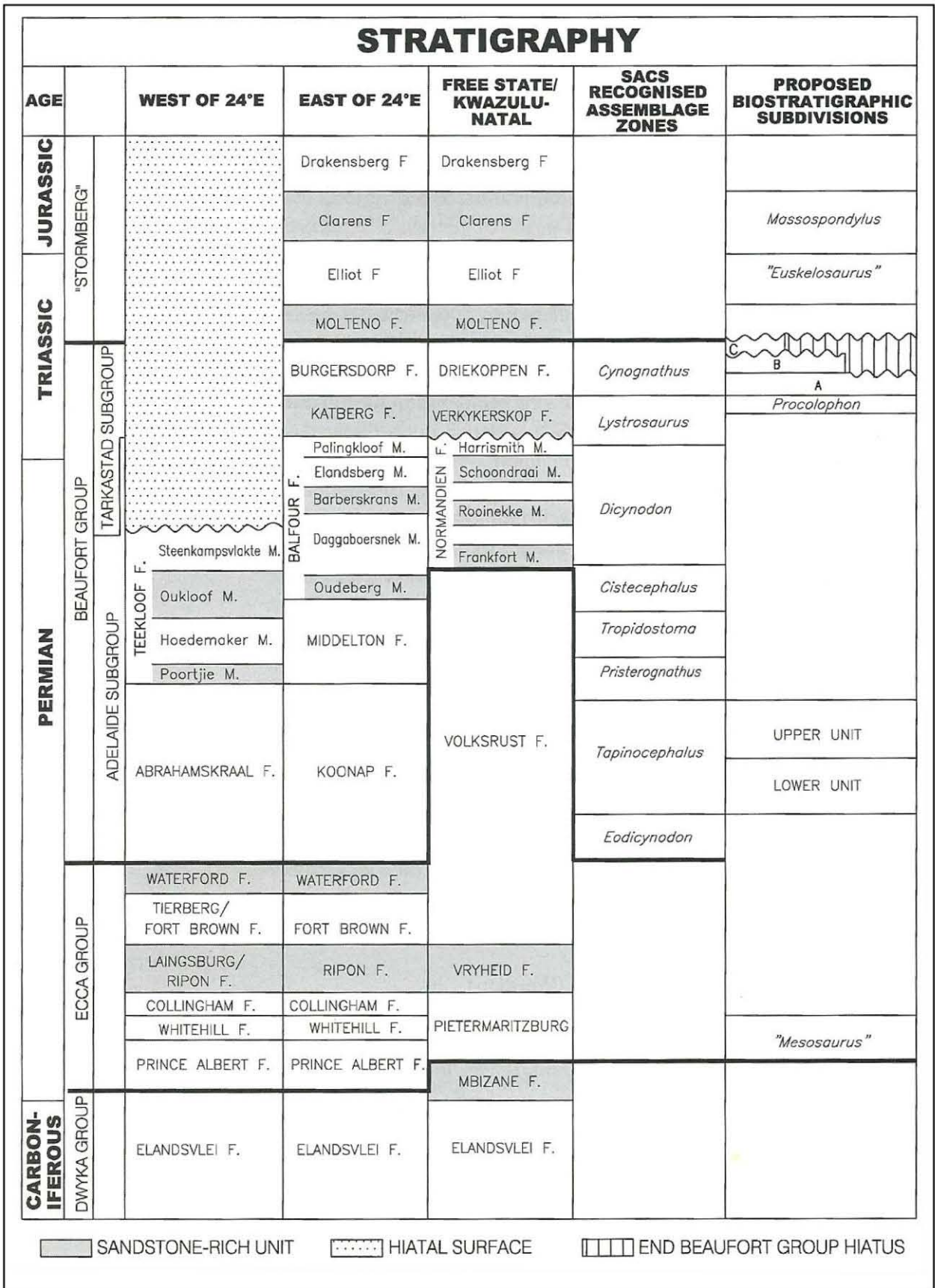
## 2.2 Stratigraphy of the Beaufort Group

### Lithostratigraphy

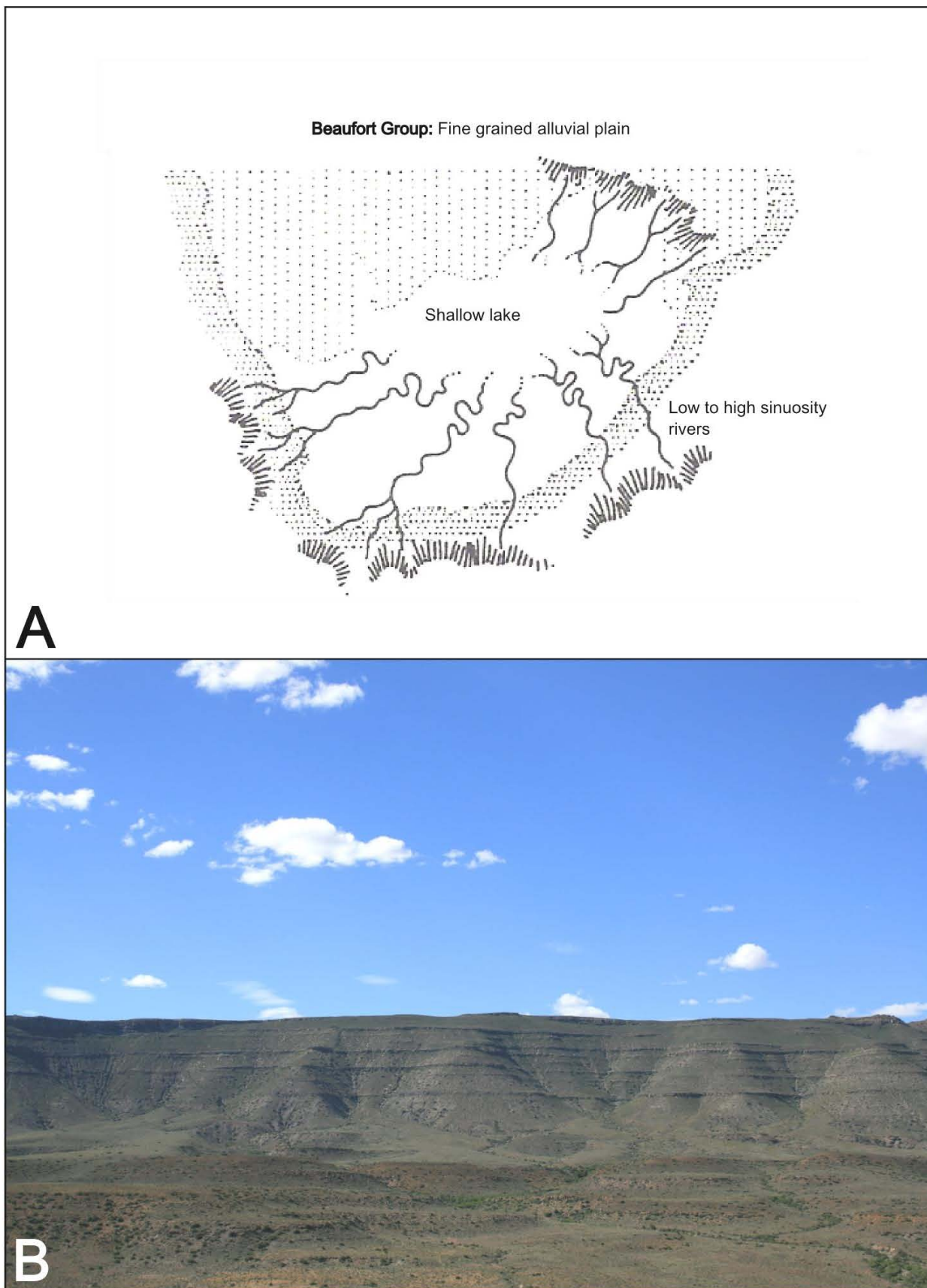
The Karoo Basin covers an area of ~ 600 000 km<sup>2</sup> (Smith et al., 1993; Johnson et al., 2006; Fildani et al., 2009) and contains an accumulative 12 km thick sedimentary succession of the Karoo Supergroup. The Karoo Supergroup, which consists of the Dwyka, Ecca, Beaufort, and Stormberg groups, unconformably overlies the dominantly marine Cape Supergroup (Table Mountain, Bokkeveld, and Witteberg Groups), a sedimentary sequence deposited in the earlier Cape extensional Basin (Rust, 1973; Cloetingh et al., 1992; Tankard et al., 2009) . There are also many other Karoo aged basins present in southern Africa that are less understood but contain a broadly similar sedimentation history which has allowed most of them to be reasonably correlated to the Karoo Basin (Smith et al., 1993; Catuneanu and Elango, 2001; Bordy and Catuneanu, 2001, 2002). Deposition of the Karoo Supergroup began when Gondwana was reaching the end of a long glacial period, with the Dwyka Group (320-280 Ma). The Dwyka Group was followed by dominantly marine (Ecca Group) and terrestrial sequences (Beaufort and Stormberg groups), finally terminating after 100 million years of sedimentation with the Early Jurassic aged Karoo volcanics (Duncan et al., 1997) (Figure: 2.4). Details concerning the sedimentation of the Beaufort Group will now be discussed with an emphasis on the Tarkastad Subgroup and the Katberg Formation as the focus of this study.

## **Depositional History of the Beaufort Group**

A shift from aqueous depocentres to non-marine depocentres is seen in the Beaufort Group and is one of the best uninterrupted Late Permian – Early Triassic non-marine sequences in the world. It consists of mudstones, siltstones, sandstones, intraformational conglomerates, palaeosols, carbonate nodules, and fossils of a once diverse vertebrate fauna and flora which thrived on the floodplain environments (Figure: 2.5). The Beaufort Group is subdivided into the Middle to Late Permian Adelaide and Early to Middle Triassic Tarkastad subgroups. The Katberg Formation occurs at the base of the Tarkastad Subgroup; however to place it into its palaeoenvironmental context the upper Adelaide Subgroup also needs to be included in this review.



**Figure 2.4:** Lithostratigraphic and biostratigraphic subdivisions within the Karoo Supergroup formations. The far right column shows proposed biostratigraphic subdivisions not yet approved by SACS. Taken from Smith et al. (2011).



**Figure 2.5:** (A) Simplified palaeogeographic model for the Beaufort Group taken from Smith et al. (1993). Meandering rivers provided much of the Adelaide Subgroup sediments. Meandering rivers were replaced by braided rivers in the deposition of the Tarkastad subgroup and this change is seen by changes in sandstone geometry and frequency. (B) A typical Beaufort Group (Adelaide Subgroup) sequence seen at the Karoo National Park, Beaufort West. Note the higher weathering resistance of the sandstone beds. View is to the northeast.

## Adelaide Subgroup

Sediments of the Adelaide Subgroup were deposited in the Karoo foreland basin, about 150 km north of the foredeep (Johnson, 1991). Palaeocurrent analyses indicate a source area to the south and south-east (Johnson, 1976). Sedimentary cyclicity is evident in the Adelaide Subgroup, with sandstone packages, and overlying mudrock defining upward-fining megacycles of up to 500 m thick (Visser and Dukas, 1979). Episodic uplift in the provenance may have produced these megacycles, with each event causing progradation of sandy sediment, followed by source-ward retrogradation of muddy sediment, as rivers gradients declined (Allen, 1978). It is also possible that sandstone packages accumulated due to differential subsidence rates between adjacent areas of the basin (Smith, 1989). Proximal formations of the Adelaide Subgroup includes the Abrahamskraal Formation and the Teekloof Formation (with its Poortjie, Hoedemaker, Oukloof, and Steenkampsberg members) being the lateral equivalent of the Koonap and Middleton formations in the Eastern Cape. The Adelaide Subgroup terminates with the Balfour Formation (consisting of the Oudeberg, Barberskrans, and Elandsberg members, and finally, the PTB within the Palingkloof Member). The distal portion of the Upper Balfour Formation is represented by the Normandien Formation in northern Free State and Kwa-Zulu Natal (Catuneanu et al., 1998).

The Adelaide Subgroup consists of mudrock and subordinate sandstone, with a mudstone-sandstone ratio ranging from 1:6 and 1:3 in places. Mudstones are predominantly greenish-grey, grey to dark grey, olive grey and less commonly reddish-purple. Individual mudstone units are up to 40 m thick, and colours are more than often variegated between red and greyish green (Cole et al., 2001). Slickensided surfaces (which signify multiple cycles of wetting and drying), invertebrate burrows and presence of rhizcretions are often associated

with the colour mottling. This indicates pedogenic modification of the original mud (Smith, 1990; 1995). Calcareous nodules are common and represent pedogenic calcretes, which formed under a semi-arid climate with seasonal rainfall (Smith, 1990; 1993; 1995). The rare occurrence of fossil desert rose clusters, composed of quartz pseudomorphs after gypsum (Keyser, 1973; Smith, 1990, 1993), is further evidence of a semi-arid palaeoclimate.

The sandstone units of the Adelaide Subgroup are both lenticular and tabular, reaching thicknesses of 20m (Johnson, 1976). These buff-weathered sandstone units range in colour from light grey to greenish-grey, ranging from a fine to medium sand grained texture. The sandstones can be massive, but can also display horizontal and planar bedding, trough cross-bedding, ripple cross-lamination and rarely, planar cross-lamination. The thicker sandstones are multistoried and commonly display fining-upward sequences. Basal contacts with mudrock are undulatory and erosional. Mudstone-pebble conglomerates are periodically present in the basal parts of sandstone bodies and on scour and/or erosion surfaces within bodies. Thinner sandstone beds have sharp planar bases with either gradational or sharp tops. These beds normally display parallel lamination, but grade upwards into ripple cross-lamination towards the top of upward-fining sequences (Johnson, 1976). Sometimes rippled surfaces are preserved on the top surfaces of individual beds, and at several localities (i.e. Fraserburg in the Northern Cape, Escourt in Kwa-zulu Natal) these rippled surfaces also preserve tetrapod and invertebrate footprints and trackways (See Figure: 2.3). Fossil plant fragments of mostly *Glossopteris* occur in the basal portions of the sandstones, and are often associated with the precipitation of uranium-bearing minerals (uraninite and coffinite being the most common) (Turner, 1978). The uranium mineralisation has an association with sandstones and is mostly confined to the Poortjie Sandstone Member of the lower Teekloof

Formation with potentially economic deposits (Turner, 1978). Large laterally persistent sandstone bodies locally form marker horizons (Le Roux and Keyser, 1988). The Poortjie Sandstone Member near Beaufort West is one of these marker horizons. Further up section, a large 40m thick sandstone package corresponds to the Oudeberg Member of the base of the Balfour Formation. Another sandstone package named the Barberskrans Member (Johnson et al., 2006) crops out between 100-150 m below the Katberg Formation in the Graaff-Reinet and Nieu-Bethesda area. The Barberskrans is overlain by the Elandsberg Member and the reddish mudrocks of the earliest Triassic Palingkloof Member. Thin sandstone beds are thought to be levee and crevasse-splay deposits, which resulted from overbank flooding onto the floodplains (Jordaan, 1990). Smith (1995), and Smith and Botha (2005) showed that the fluvial style of rivers began to change in the Palingkloof Member from perennial meandering to the ephemeral braided condition.

### **Tarkastad Subgroup**

This subgroup is Early to Middle Triassic in age (Rubidge et al., 1995) and directly overlies the Adelaide Subgroup. Sandstone predominates and inter-bedded between are mainly red mudrocks, but also minor siltstones. The Tarkastad Subgroup is divided into the sandstone-rich Katberg Formation and the mudstone-dominated Burgersdorp Formation. The boundary between the two is transitional over a 100 m thick stratigraphic interval (Johnson, 1976, 1984; Johnson and Hiller, 1990). The Katberg Formation consists of buff-weathered, greenish-grey and light grey tabular and minor ribbon-shaped sandstone bodies up to 30 m thick. These are inter-bedded with units of red, greyish-red and, less frequently, greenish-grey and dark greenish-grey mudstone. These mudstone units contain thin greenish-grey and light grey sandstone, and grey-blue or greenish-grey siltstone beds. The sandstone-

mudstone ratio is about 1:2, but changes to 1:0.8 in some areas such as Lootsberg Pass between Graaff-Reinet and Middleburg (Groenewald, 1996). Sandstone bodies are multistoried, with individual stories displaying repeated gradational sequences from medium to very fine grained sand. The basal sandstone contacts are undulatory and have an erosional relationship with the underlying mudstone. Basal units commonly consist of mudstone-pebble conglomerate up to 1 m thick. The lower section of the Katberg Formation typically consists of thick, cliff forming multistoried sheet sandstone bodies. This is seen at several localities such as Bethel Canyon near Bethulie, Lootsberg Pass, and on Ripplemead near Nieu Bethesda. Fossil vertebrates are relatively common, whereas plant remains are rare, and fossil bone fragments, peloids and calcareous nodules occur in the mudstone-pebble conglomerate. Sandstone packages become increasingly thicker up section where they reach maximum thickness in the upper portion of the Katberg Formation in the Swartberg Member (Smith and Botha, 2005).

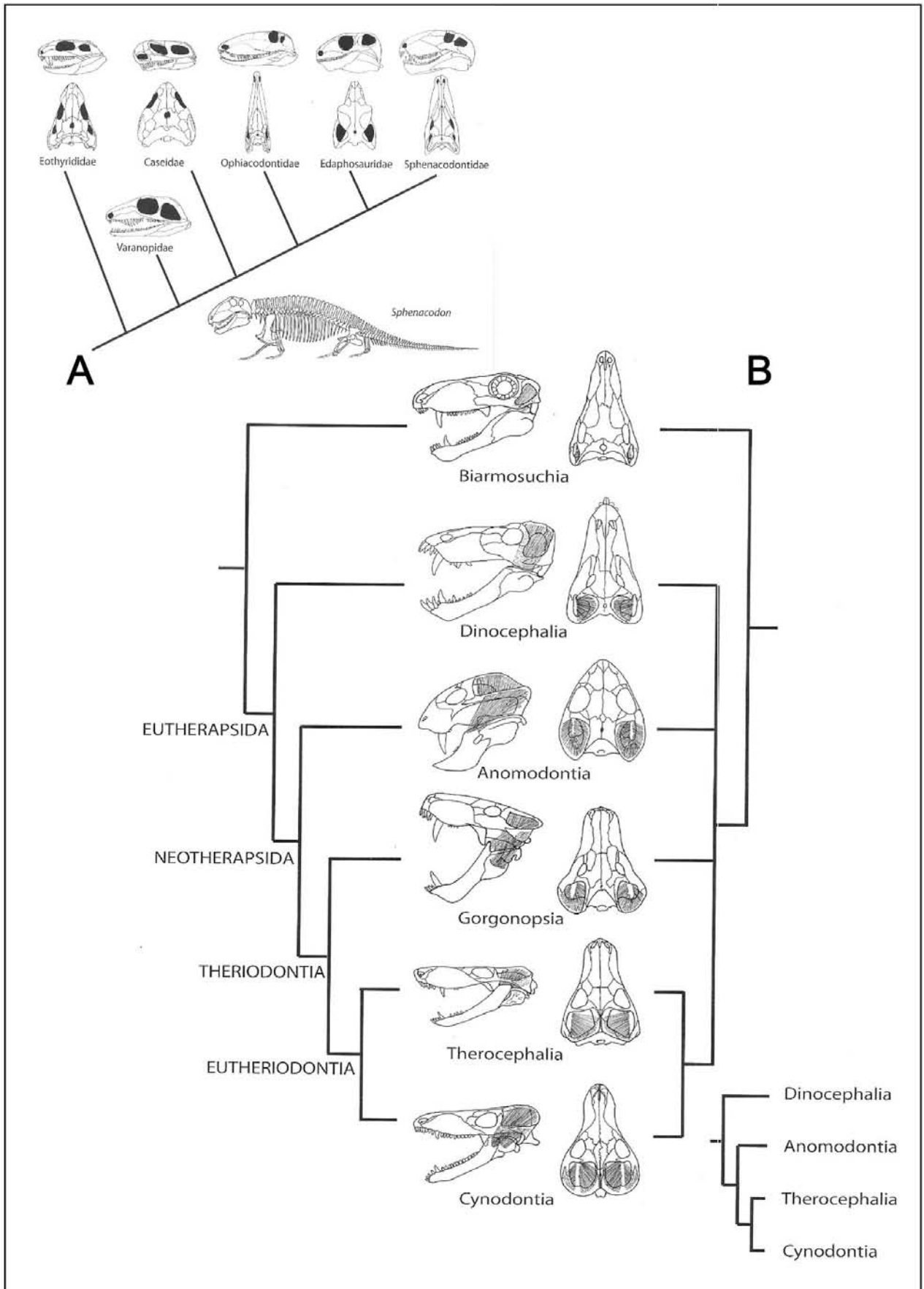
The mudstones are massive and contain calcareous nodules. Isolated trace fossils in the form of invertebrate burrows believed to have formed by an organism named *Katbergia sp.* (Gastaldo and Rolerson, 2007) often occur in the mudstones in association with colour mottling. The thin sandstone and siltstone beds within the mudstone normally have sharp planar bases with either sharp or gradational tops. Desiccation and mud cracks are locally present, often near sandstone bases and this may imply crevasse-splay type deposition (Groenewald, 1996). The predominantly red colour of the mudstones indicates well drained depositional conditions (Sheldon, 2005) and the calcareous nodules most likely represent pedogenic calcrete (Smith, 1990, 1995).

Depositional conditions begin to change as one move up section into the Burgersdorp Formation. Red, greyish-red and, greenish-grey and grey mudrocks become abundant. These mudstones contain minor 10 m thick sandstone bodies, with the mudstone-sandstone ratio at 1:3. But this ratio is subject to variability, periodically increasing. Mudstone units are 30 m thick and contain calcareous concretions, minor invertebrate burrows and desiccation cracks (Groenewald, 1996). Greenish-grey, grey, and light grey 0.5 m siltstone beds with sharp planar bases and gradational or sharp tops are also present. Sandstone bodies are buff-weathered, grey, greenish-grey, and light olive-grey, fine to medium grained. They form upward-fining units and are transitional to the overlying mudstone (Groenewald, 1996). They are generally lenticular in shape, but the thicker ones are multi-storied and extend laterally for a few kilometres (Johnson, 1984). Sedimentary structures in the sandstone include horizontal lamination, trough cross-bedding, and ripple cross-lamination. Massive sandstones are also relatively common. Palaeocurrent readings indicate a north-northeasterly palaeocurrent direction for the Burgersdorp Formation (Groenewald, 1996).

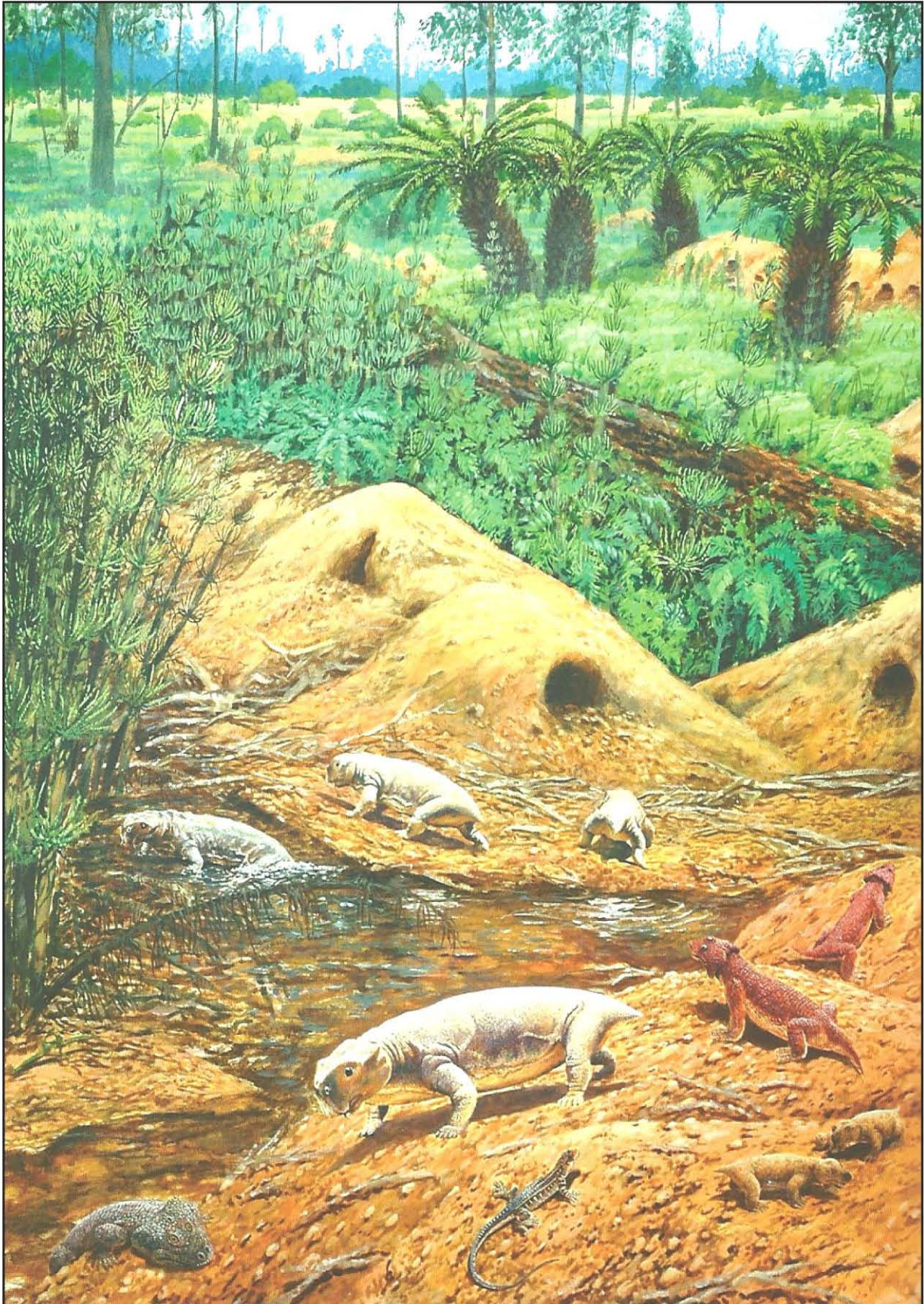
### **2.3 Biostratigraphy of the Beaufort Group**

The Karoo Basin is famed for its richness in Late Palaeozoic and Early Mesozoic fossils. The Karoo sequence records the drift of a supercontinent out of polar climates (the Dwyka Group), through temperate (Ecca-Beaufort groups), to near tropical latitudes (Stormberg Group) (Smith, 1993). The biosphere also reacted to these changes as Gondwana moved equator-ward, preserved as distinct floral and faunal turnovers. The Beaufort and Stormberg Groups preserve the bulk of this fossil diversity, however only the Beaufort Group will have its biozonation discussed in this study.

The Late Permian - Middle Triassic Beaufort Group supported a diverse tetrapod fauna and the Karoo Basin, the bulk of the fauna being the therapsids. Therapsids lived in Pangaeian times and have been found on almost every continent (Smith et al., 2011). However the Karoo Basin is by far the best place in the world to collect fossils of these unique animals. The therapsids were apart of ecosystems comprising amphibians (notably temnospondyls) and other reptile species that were beginning to diversify during this period. These reptile lineages (sauropsid, synapsid) are distinguished from one another by the number and position of temporal fenestrae in the skull (Osborn 1903; Sherwood- Romer, 1967; Steyer, 2012). The sauropsids comprise the parareptiles and diapsids. The parareptiles are a complex group comprising an array of different temporal fenestrae (although commonly do not have temporal fenestrae). Diapsid reptiles have two pairs of temporal fenestrae in the skull. Crocodylians, archosaurs, pterosaurs, dinosaurs, modern lizards and snakes have the diapsid skull arrangement. Synapsids have a single temporal fenestrae at the base of the skull (Rubidge and Sidor, 2001; Steyer, 2012). Therapsid ancestry lies in the Synapsid reptile lineage, evolving from the sphenacodontid line of the "pelycosaurs" (*Dimetrodon* being the most well-known). Therapsid diversification really took off in the Late Permian (Figure: 2.6). These non-mammalian synapsids were the dominant vertebrate fauna in southern Gondwana (Botha and Smith, 2007), showing adaptations that would one day define many modern mammals. The dicynodontia often outnumber other species by 60:1 as fossils in much of the upper Permian Karoo strata (Smith, 1993). In the earliest Triassic *Lystrosaurus* carried on the dicynodont legacy by comprising over 95% of fossil finds. This justifies the notion that the dicynodonts were not only the first, but likely one of the most successful herbivorous tetrapods to have evolved on Earth (Figure: 2.7).



**Figure 2.6:** (A) The relation of sphenacodontids in the paraphyletic group – the “pelycosaurs”. Therapsid origins are believed to lie within the sphenacodont group. (B) All six therapsid groups and their relation to one another. Taken from Kemp (2011).



**Figure 2.7:** *Lystrosaurus* (middle), part of the highly successful dicynodont clade is shown here in an artist's reconstruction. In the picture are also the amphibian *Lydekkerina* (bottom left), the archosauromorph *Prolacerta* (above), the cynodont *Thrinaxodon* (bottom right) and the parareptile *Procolophon* (right). Source: The Albany Museum, Grahamstown (Chinsamy-Turan, 2011).

## Biozonation of the Karoo Supergroup

The biostratigraphy of the Karoo Supergroup is based on 150 years of collecting an estimated 30,000 tetrapod fossils of which at least 12,277 are therapsids (Smith et al., 2011). The fossil remains of therapsid groups (dinocephalians, gorgonopsians, therocephalians, dicynodonts and cynodonts), parareptiles (parieasaurs, procolophonids, owennetids), amphibians (temnospondyls and stereospondyls), divide the Beaufort Group into eight biozones, based on the original six subdivisions compiled by Broom (1907).

Refinements to these divisions were made by Keyser and Smith (1979) who introduced the concept of assemblage zones and Rubidge (1990) who added the basal-most *Eodicynodon* zone. The biozones, or assemblage zones, are correlated with certain formations and members within the Beaufort Group and names are derived by the most common genus present in the unit. Recently work done by Van der Walt et al. (2010) has contributed further resolution concerning the distribution of these biozones in the Karoo Basin (Figure: 2.8). These eight biozones will now each be discussed briefly before the sedimentology of the study area is discussed.

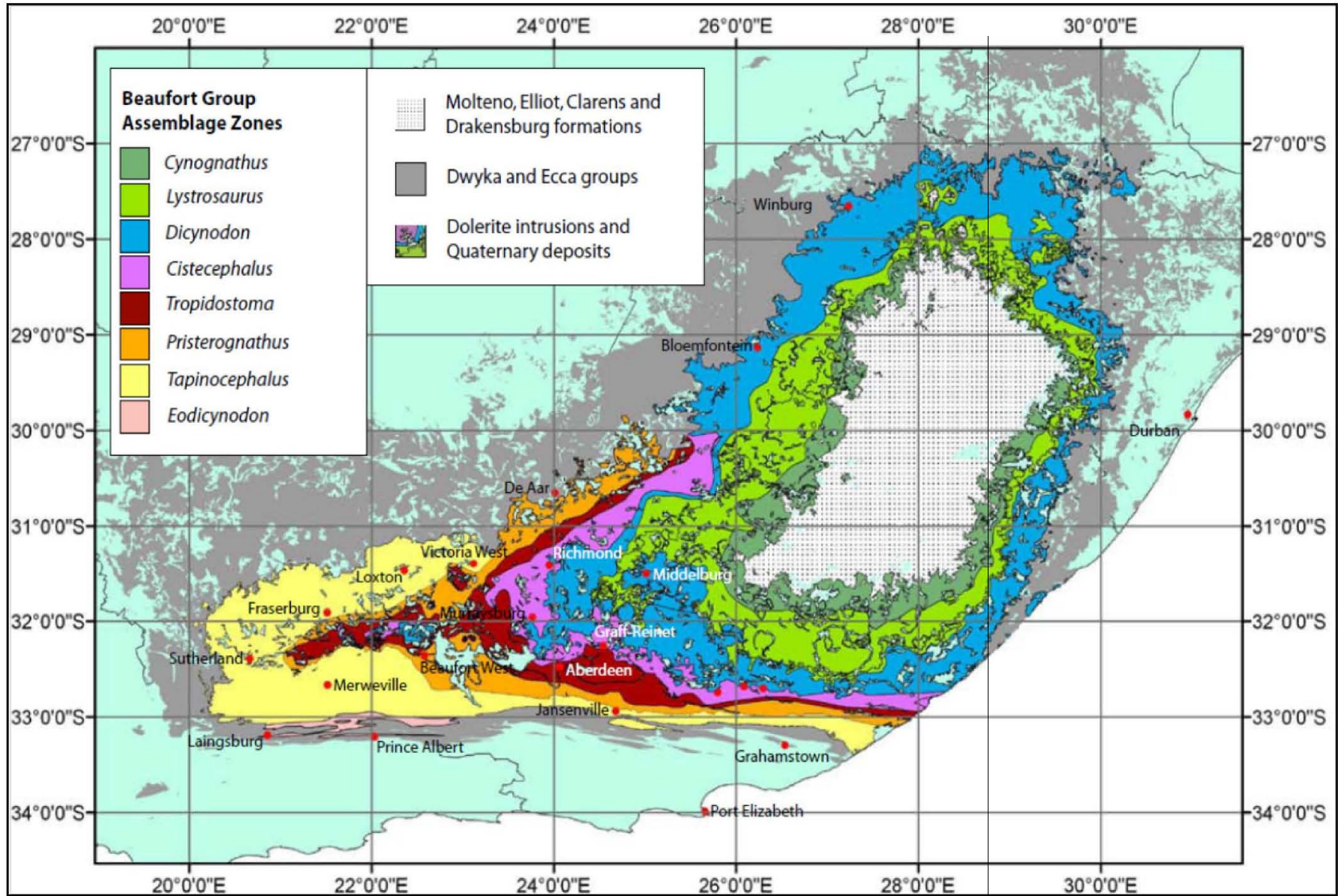


Figure 2.8: The biozones of the Beaufort Group (Van der Walt et al., 2010).

### ***Eodicynodon* Assemblage Zone**

The *Eodicynodon* assemblage zone (EAZ) is the lowermost biozone of the Beaufort Group sequence. The zone underlies the *Tapinocephalus* Assemblage zone and lithostratigraphically it falls within the Abrahamskraal Formation, directly overlying the Ecca Group's Waterford Formation. As the name suggests, this zone is characterised by the First Appearance Datum (FAD) of the dicynodont *Eodicynodon*. Generally the zone is fossil poor, but a wide variety of other fossil fauna have been found such as anomodonts (*Pantranomodon*), dinocephalians (*Tapinocanius*, *Australosyodon*), pristerognathid therocephalians (*Glanosuchus*, *Alopecodon*), gorgonopsians (only two fragmentary skulls found by Rubidge, 1988), and amphibians (fragmentary material found by Rubidge, 1988). They normally occur as individual fossil specimens within mudrock sequences, enveloped by brown weathering calcareous nodules (Rubidge, 1995).

### ***Tapinocephalus* Assemblage Zone**

The *Tapinocephalus* Assemblage Zone underlies the *Pristerognathus* Assemblage Zone, spanning the middle units of the Abrahamskraal Formation (Rubidge, 1995). This zone documents the replacement of *Eodicynodon* with large herbivorous pareiasaurs (*Bradysaurus* and *Embrithosaurus*) and a radiation of the dinocephalians (Haughton, 1969). The dicynodonts begin to radiate and the long ranging *Diictodon* makes its FAD in this biozone. Thus, in the field, the biozone is characterised by the co-occurrence of *Tapinocephalus*, *Bradysaurus*, and *Diictodon* (Rubidge, 1995). The dinocephalians consisted of *Tapinocephalus* and *Titanosuchus* (herbivores) and the carnivorous *Anteosaurus*. The dinocephalians are only found in the *Eodicynodon* and *Tapinocephalus* zones. Because they are commonly found as disarticulated, single bone specimens,

Boonstra (1969) argued that they lived in upland areas away from the rivers. The pareiasaurs however are commonly found as complete skeletons in mudstones with their heads dorsal up, appearing as if they had died after becoming mired (Boonstra, 1969). Fossil footprints, preserved on the Gansfontein palaeosurface near Fraserburg in the southern Karoo, are believed to have been made by these early therapsids (De Beer, 1986) on a proximal crevasse-splay surface (Smith, 1993) (See Figure: 2.3).

### ***Pristerognathus* Assemblage Zone**

This zone's lithostratigraphic position spans the uppermost strata of the Abrahamskraal Formation and lowermost strata of the overlying Teekloof Formation, including the Poortjie Sandstone Member (Smith and Keyser, 1995). The faunal assemblage has been described as an impoverished *Tapinocephalus* Assemblage Zone due to the extinction of the dinocephalians. The therapsid fauna diversity is low, dominated by the dicynodont *Diictodon*, in association with the therocephalian *Pristerognathus*. Other scarce elements of the fauna are the pareiasaur *Bradysaurus* and parareptile *Eunotosaurus*, gorgonopsian *Eoarctops*, biarmosuchid *Hipposaurus* (also found in the underlying *Tapinocephalus* Zone), the therocephalian *Ictidosuchoides*, and the crocodile-like amphibian *Rhinesuchus*. The dicynodonts *Pristerodon* and *Endothiodon* make their FAD in the upper strata and become much more common in the succeeding biozone (Smith and Keyser, 1995).

### ***Tropidostoma* Assemblage Zone**

The *Tropidostoma* Assemblage Zone overlies the *Pristerognathus* Assemblage zone and is located in the lower part of the Teekloof Formation. The name of this zone is derived from a dicynodont confined to this biozone that is often characterised by its association with the

larger dicynodont *Endothiodon*. Other fossil fauna include amphibian *Rhinesuchus*, pareiasaur *Pareiasaurus*, other dicynodont species such as *Emydops*, *Rhachiocephalus*, and *Pristerodon* which appear for the first time in this biozone. Gorgonopsids *Lycaenops*, *Gorgonops*, and *Cynosaurus*, and the eosuchid *Youngina* also make their FAD (Keyser and Smith, 1979; Rubidge, 1995).

### ***Cistecephalus* Assemblage Zone**

The *Cistecephalus* Assemblage Zone occupies the central units of the Teekloof Formation, the uppermost part of the Middleton Formation and lowermost units of the Balfour Formation (Oudeberg Member) east of 24° E (Smith and Keyser, 1995). This biozone is well-known for its fossil richness and fossil fauna diversity, in particular of the dicynodonts. For the first time many large dicynodonts make an appearance such as *Oudenodon* and *Aulacephalodon*. *Endothiodon* and *Rhachiocephalus* are still present but as rare fossils (2% of fossils found). *Diictodon* is still the most common fossil accounts for 60% of the fauna. However a new distinctive small dicynodont makes an appearance, *Cistecephalus* after which the biozone takes its name. *Cistecephalus* has a flattened box shaped skull and eyes positioned on the front of the face which suggests binocular vision. Although forming a lesser component of the fossil fauna (~3%) gorgonopsids reach a diversity peak and are present as many large predatory species such as *Gorgonops*, *Cynosaurus*, *Lycaenops*, and *Prorubidgea*. Whaitsiid therocephalians (Kemp, 1972) also form part of the predators of this biozone. The small procolophonid *Owenetta* makes its first appearance as does the biarmosuchid *Lemurosaurus* (Smith and Keyser, 1995).

### ***Dicynodon* Assemblage Zone**

The *Dicynodon* Assemblage Zone strata fall within the upper units of the Teekloof Formation. Between 24° E and 25° E the zone occupies the Balfour formation extending above the Oudeberg Member. Fossil diversity is higher in the lower units of the biozone, where dicynodonts from the lower Assemblage Zone (*Diictodon*, *Pristerodon*, *Oudenodon*, and *Dicynodon* which the zone takes its name after) are joined by cow sized *Dinanomodon*, *Pelanomodon*, and *Emydops* (Kitching, 1995). Large carnivores are diverse and represented by several groups such as lion-sized gorgonopsids *Dinogorgon*, *Lycaenops*, *Prorubidgea*, *Rubidgea*, *Leontocephalus*, and bear and wolf-sized therocephalians *Moschorhinus* and *Theriongnathus*, respectively. These carnivores most likely hunted the large dicynodonts that lived on the floodplains. The cynodonts (the line of therapsids that mammals later evolved from) make their FAD and are represented by three species at this time (*Cynosaurus*, *Nanictosaurus* and *Procynosuchus* (*Procynosuchus* has also been confirmed in the top of the *Cistecephalus* Zone by Botha et al. (2007)). Crocodile-sized *Rhinesuchus* is still common and was most likely an ambush predator in the Late Permian meandering waterways (Damiani and Rubidge, 2003). However, nearing the top of the biozone, diversity begins to noticeably decrease particularly within the predatory gorgonopsians with a final termination of nearly all the species represented in the biozone at its top contact with the *Lystrosaurus* Assemblage Zone.

### ***Lystrosaurus* Assemblage Zone**

The Triassic *Lystrosaurus* Assemblage Zone overlies the Permian *Dicynodon* Assemblage Zone. This biozone includes the Palingkloof Member of the Balfour Formation, the Katberg Formation and the lower third of the Burgersdorp Formation (Groenewald and Kitching,

1995). Smith and Ward (2001) described the so named “event beds” for the End-Permian mass extinction event within the Palingkloof Member. The lowermost contact of the biozone was originally placed at the FAD of the genus *Lystrosaurus*; however it is now clear that one *Lystrosaurus* species (*L. maccaigi*) lived in the latest Permian alongside the Permian fauna (Botha and Smith, 2007). The *Lystrosaurus* zone is defined by low reptilian species diversity and an abundance of *Lystrosaurus* (present as *L. curvatus* in the PTB beds and *L. declivis* and *L. murrayi* in the lower Katberg Formation). These species are in association with the anapsid *Procolophon* and newly described procolophonid *Phonodus dutoitorum* (Modesto et al., 2010). Absence of *Dicynodon lacerticeps* and other Permian groups is apparent. Although diversity is low, fossils are abundant with *Lystrosaurus* comprising the bulk of finds (95%).

Other common genera in the lower units of the zone are the therocephalians *Moschorhinus* and *Promoschorhinus*, and archosauromorphs *Proterosuchus* and *Prolacerta* (Modesto and Botha-Brink, 2008). Well into the biozone salamander-sized amphibians *Lydekkerina* and *Micropholis* (Damiani and Rubidge, 2003) are commonly found within brown weathering nodules. Weasel-sized cynodonts such as *Galesaurus* and *Thrinaxodon*, therocephalians *Regisaurus* and *Scaloposaurus*, and archosauromorph *Prolacerta* are the only main carnivores. Studies have revealed an increase in procolophonid abundance towards the top of the biozone, and above the Last Appearance Datum (LAD) of *Lystrosaurus* (Neveling et al., 1999, 2000; Hancox and Rubidge, 2001). Thus it has been proposed that the *Procolophon* Zone of Watson (1914) between the LAD of *Lystrosaurus* and the FAD of the amphibian *Kestrosaurus* (Neveling et al., 2000) be reinstated.

### ***Cynognathus* Assemblage Zone**

The uppermost biozone of the Beaufort Group overlies the *Lystrosaurus* Assemblage Zone and is restricted to the Burgersdorp Formation. The occurrence of fossils as complete skeletons is rare, but well preserved specimens do occur in mudrock units as dispersed and isolated skeletons, associated with calcareous concretions. Recent collecting efforts, and taxonomic and biostratigraphic studies on the Burgersdorp Formation have resulted in a proposed subdivision of the *Cynognathus* Assemblage Zone into three subzones informally known as A, B, and C (Hancox et al., 1995; Hancox and Rubidge, 1996; Damiani, 1999; Neveling et al., 1999, 2000; Abdala et al., 2005). The presence of *Cynognathus* in all three subzones confirms that this genus is the correct choice of index taxon for the Assemblage Zone (Abdala et al., 2005). The subdivisions are mainly based on the stratigraphic and geographic distribution of capitosaurid amphibians (*Kestrosaurus* sp., *Paratosuchus* sp., and *Paracyclotosaurus* sp.) as these species do not overlap (Hancox and Rubidge, 2001).

### **Causes of Faunal Change in the Karoo Basin**

The faunal changes that occur within the Karoo Basin biozone divisions highlight some noteworthy faunal turnovers (Smith et al., 2011). The nature of these turnovers are not entirely understood, particularly the end –Guadalupian extinction of the dinocephalians (Boonstra, 1969; Keyser and Smith, 1998; Rubidge et al., 1995) and the dicynodont changeover between the *Tropidostoma*, *Cistecephalus*, and *Dicynodon* Assemblage Zones (Smith et al., 2011). These faunal turnovers are believed to have been caused by environmental changes which resulted in changes in fluvial behaviour and water table fluctuations that may have killed off different vegetation types (Smith et al., 2011). These smaller changes are however are cast in the shadow of the End-Permian mass extinction

event occurring at the boundary between the *Dicynodon* and *Lystrosaurus* Assemblage Zones (Smith, 1995, 2005; Smith et al., 2011).

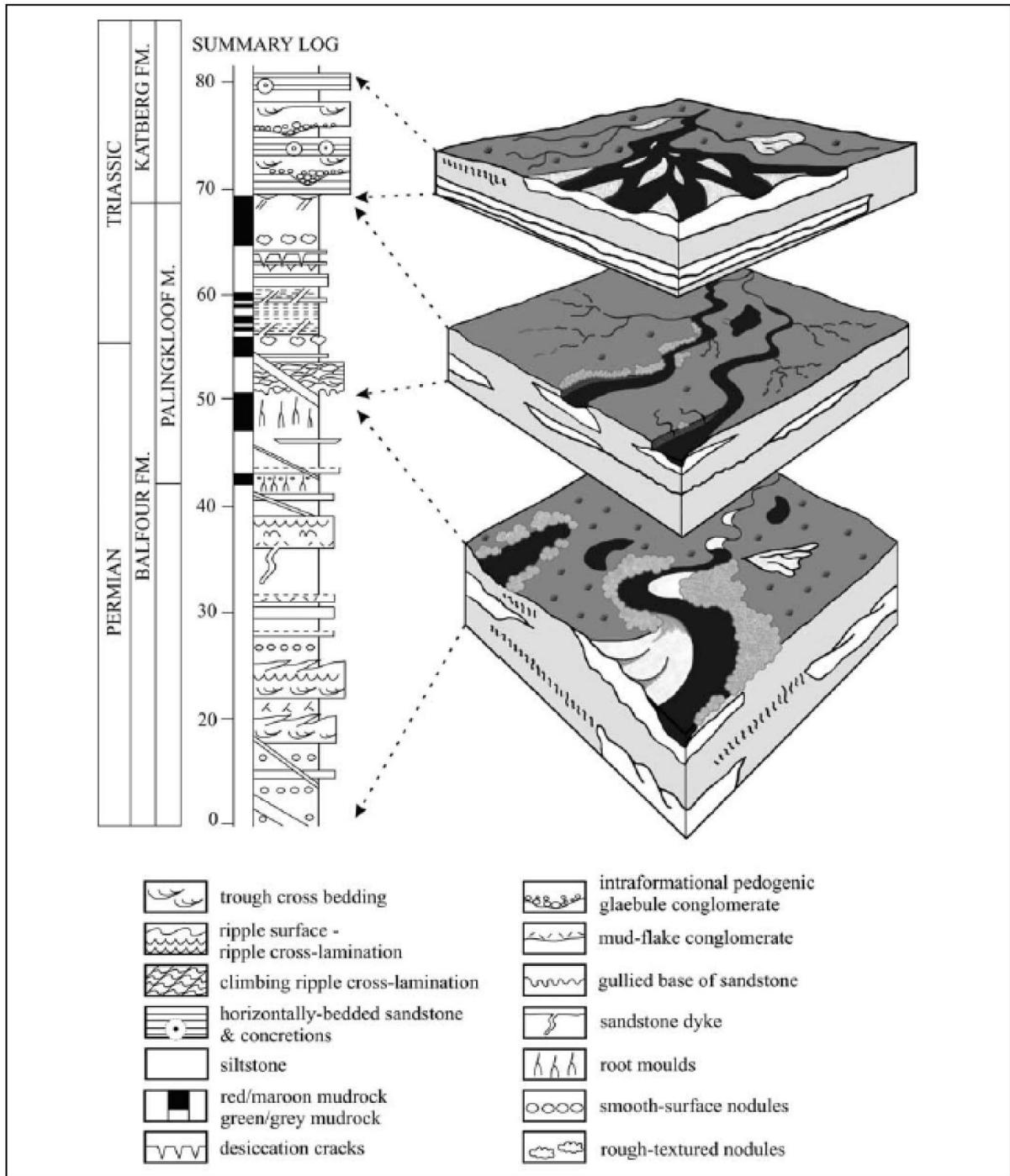
### **The End Permian Mass Extinction**

The End-Permian mass extinction event that occurred at approximately 251-252 Ma (Bowring et al., 1998; Coney et al., 2007; Schien et al., 2011) is regarded as the most catastrophic of the five major Phanerozoic extinctions. Despite excellent exposure of the “event beds” (Smith and Ward, 2001), application of the non-marine Permian International Timescale to the Karoo Basin is a challenge due to the timescale being primarily based on Northern Hemisphere marine taxa (Fildani et al., 2009). It has been unclear as to whether global (Siberian Trap volcanism (Renne et al., 1995) or local influences such as the CFB orogeny (Catuneanu and Elango, 2001) altered the Karoo Basin environments in the latest Permian. The PTB within the central Karoo Basin is defined by magnetic stratigraphy, highly negative  $\delta^{13}\text{C}$  excursion, and faunal turnover (Coney et al., 2007). The timing of the PTB has as of yet not been determined in the Karoo Basin, but the 252.5 Ma (Coney et al., 2007) age for a single zircon crystal from Commando Drift Dam section, Eastern Cape gives a maximum constraint for the age of the event bed, and is in agreement with the accepted age of the boundary globally (Bowring, 1998; Coney et al., 2007; Schien et al., 2011). However, the isochronous nature of the PTB in the Karoo Basin is currently being challenged by Gastaldo et al. (2009) and Fildani et al. (2009).

Gastaldo et al. (2009) believe that the PTB exposed in the Bethulie district is not regionally correlative, whereas Fildani et al. (2009) have dated zircons sampled from the upper Skoorsteenberg and Laingsburg formations which show Early Triassic ages. Nevertheless,

the PTB in the Karoo Basin is well represented by sudden faunal turnover and by sudden facies changes (Smith 1995; Smith and Botha, 2005) (Figure: 2.9). Comparable changes in fluvial depositional systems at the PTB are apparent in other parts of the Karoo Basin (Smith et al., 1993; Smith, 1995; Smith and Botha, 2005), and in other major Gondwana basins such as the Fremouw Formation in the central Transantarctic Mountains (Veevers et al., 1994; Catuneanu, 2004), the Bowen Basin in Australia (Michaelsen, 2002), and at the Vyazniki and Gorokhovets locality on the Russian platform (Newell et al., 2010). Zircon dates compiled by Fildani et al. (2009) contradict much of the sedimentological and fossil evidence within the rocks of the Karoo Supergroup (Broom, 1907; Hotton, 1967; Haughton, 1919, 1969; Keyser and Smith, 1979; Rubidge et al., 1995; Rubidge and Hancox, 2001).

Abrupt changes in sandstone geometries and internal architecture are interpreted as a switch from meandering to braided fluvial style in the Karoo Basin during the End-Permian mass extinction event (Smith, 1995; Smith and Botha, 2005; Smith et al., 2011). This is believed to have been caused by global warming and drying of the Karoo Basin. A stepped extinction of small herbivorous dicynodonts and their gorgonopsian predators before the onset of the main extinction pulse of the larger herbivores and carnivores coincided. This pattern suggests smaller foragers feeding on undergrowth plants died off before larger browsing fauna, which is in keeping with increasingly drier conditions as plant died off (Smith et al., 2011).



**Figure 2.9:** Summary taken from Smith and Botha (2005) of the PTB sequence sedimentological log compiled from study sections in the Bethulie District. Interpreted palaeolandscapes reconstructions show a change in fluvial style across the PTB from meandering rivers in the Late Permian, to braided rivers in the EarlyTriassic. Vertical scale is in metres.

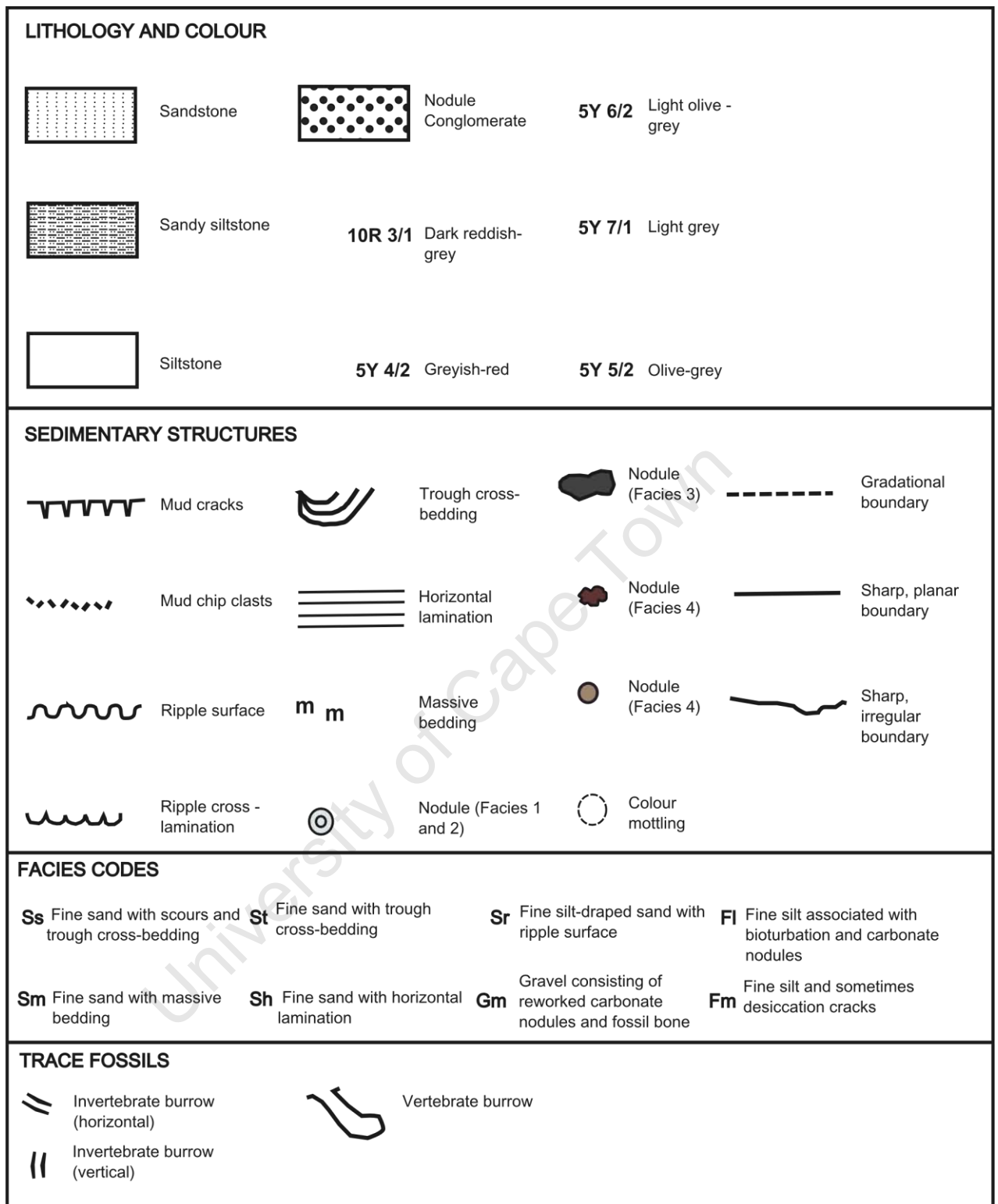
## Earliest-Triassic Recovery

In amidst the catastrophic disappearance of the *Dicynodon* fauna was the seemingly sudden appearance and colonization of the drying floodplains by the *Lystrosaurus* fauna. Although the therapsids never regained the ecosystem domination they once enjoyed in the Late Permian (Smith et al., 2011) *Lystrosaurus* appeared to flourish, becoming the most successful herbivorous tetrapod (arguably of all time) on the earliest Triassic Karoo Basin floodplains. *Lystrosaurus*, like many of the other *Lystrosaurus* assemblage zone fauna, was clearly well adapted to the highly seasonal, monsoonal conditions (Smith and Botha, 2005). Their adaptations were not always sufficient to cope with the extreme conditions brought about by the unreliable climatic regimes, and it is argued that many of the fossils from the earliest Triassic represent preservation of animals that succumbed in drought, in particular multiple accumulations of *L. declivis* (Smith and Botha, 2005; Smith et al., 2011). Thus the aim of the chapters to come is to argue for or against the hypothesis that *Lystrosaurus* bonebed accumulations are that of drought afflicted animals using sedimentological, isotopic and taphonomic evidence in the hope a serious conclusion can be made.

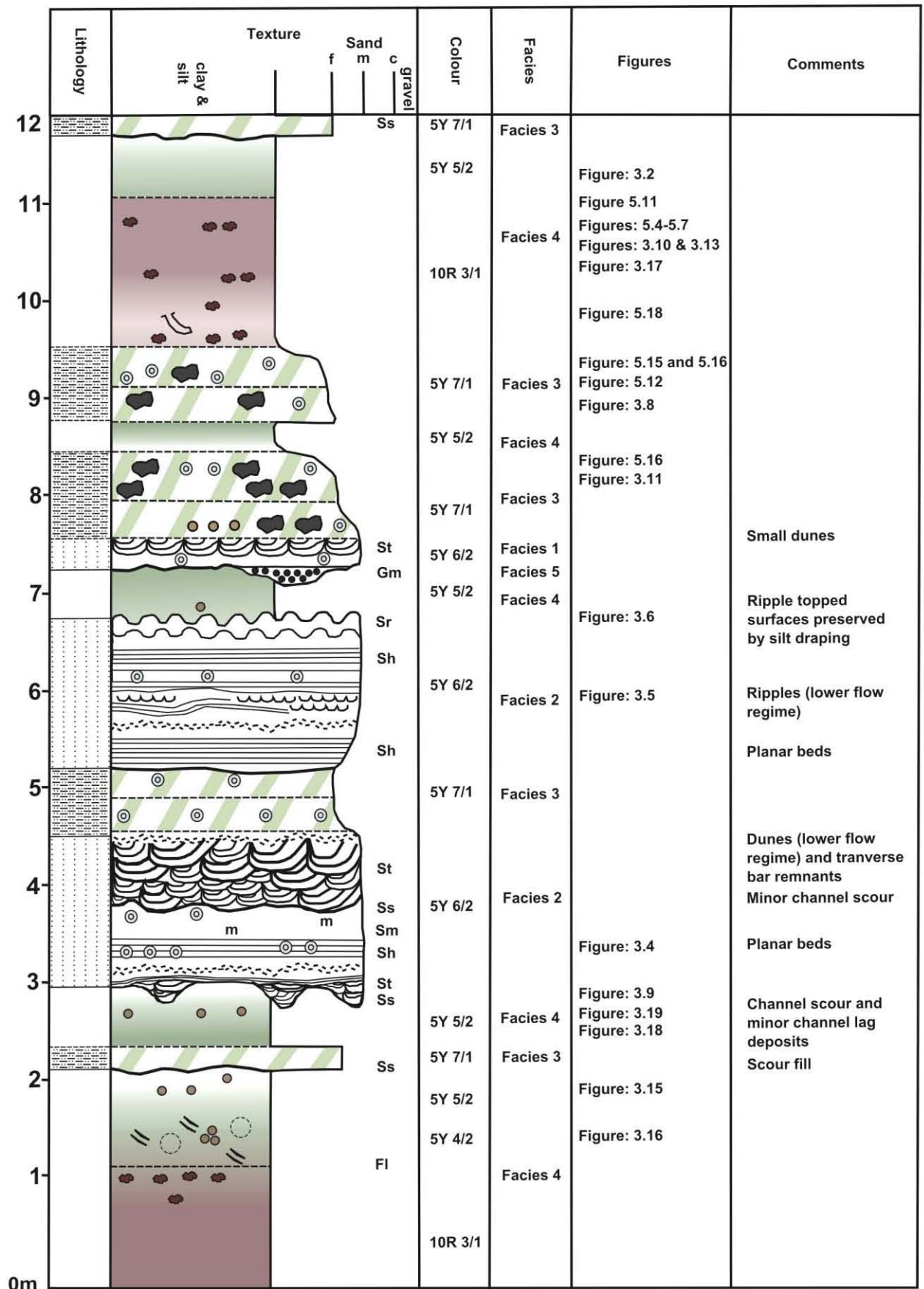
### 3. Sedimentology of Study Area

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The sedimentology of the study area was mostly derived from a portion of the Donald 207 Farm in the Smithsfield District of the southern Free State Province, where there is an easily accessible, extensive exposure of fossil-rich lower Triassic Katberg Formation. A detailed sedimentological log of approximately 29 m of vertical section of the Katberg Formation was recorded using a Jacob's staff with levelling eyepiece recorded to an accuracy of 5 cm and major bounding surfaces were traced 50 m laterally to establish their rank (Figure: 3.1). The log starts in the lowermost strata exposed in a riverbed, and terminates at the top of a small hill (koppie) capped by a resistant flat-lying sandstone body cut by a vertical dolerite dyke. In addition to the vertical section, a 2-D panel section which consisted a 10 m thick by 50 m wide transect on an exposed cliff within the study area (Figure: 3.2). This exposed cliff contains numerous bonebeds and these were measured and logged in detail. All features of palaeoenvironmental interest were incorporated into the vertical and panel section. These included rock lithologies, textures, colours, sedimentary structures, bounding surfaces, scours, nodules, fossils, burrows, etc. Samples collected for petrographic thin section and geochemical and stable isotopic analysis included *Lystrosaurus* canine enamel, fossil bone, and various types of carbonate nodules. The vertical sections (Figure: 3.1) and the detailed panel section (Figure: 3.2) will be referred to throughout this chapter.

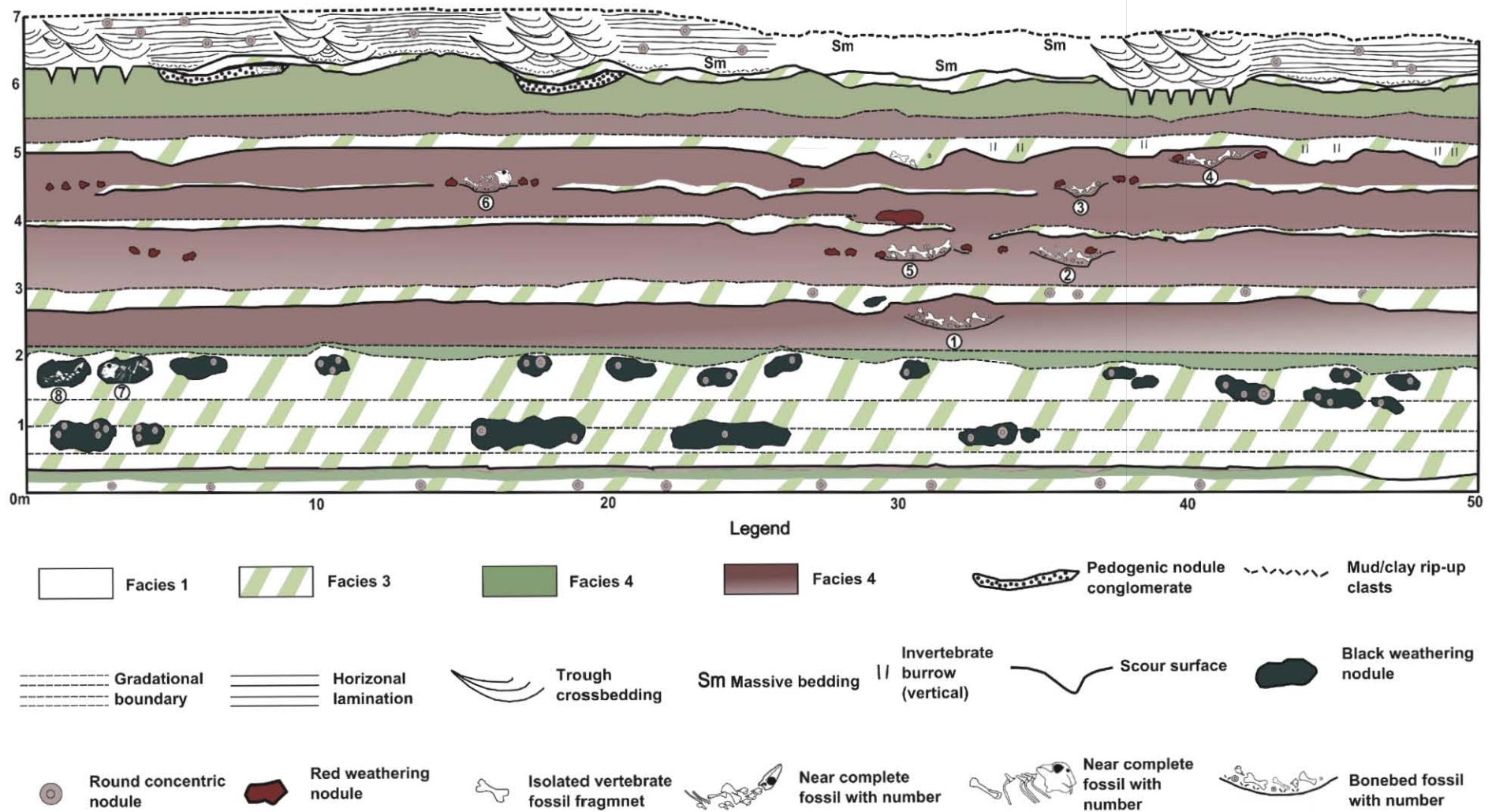


**Figure 3.1:** Above are lithological symbols used in the vertical section construction from the study area on Donald 207 Farm near Bethulie. The 29 m section was constructed over three pages that follow this legend, starting a 0 m (base) and ending at 29 m (top) on the last page. The position of the panel section, nodule and rock samples, and fossils are shown by the position of their figure numbers. The positions of figures from other chapters are also shown on the graphic log, alongside field comments.



Lithology	Texture				Colour	Facies	Figures	Comments
	clay & silt	f	m	c gravel				
24					5Y 6/2	Facies 1		Minor channel scour
23					5Y 5/2	Facies 4		
					5Y 7/1	Facies 1		
22					5Y 6/2	Facies 1		Minor channel scour
					5Y 7/1	Facies 3		
21					5Y 5/2	Facies 4		
					5Y 6/2	Facies 1		
20					5Y 7/1	Facies 3		Sharp contact
					5Y 5/2	Facies 4		
19					10R 3/1	Facies 4		
					5Y 5/2	Facies 4		
18					5Y 5/2	Facies 4		
					5Y 7/1	Facies 3		
17					5Y 7/1	Facies 3		Sharp contact
					5Y 5/2	Facies 4		
16					5Y 7/1	Facies 3		Sharp contact
					5Y 5/2	Facies 4		
15					5Y 7/1	Facies 3		
					10R 3/1	Facies 4	Figure: 5.3	Minor scour hollow
14					5Y 7/1	Facies 3	Figure: 5.14	Large desiccation cracks
					5Y 5/2	Facies 4	Figures: 5.12 and 5.13	
13					5Y 7/1	Facies 3	Figure: 3.14	Ripples (lower flow regime)
					5Y 6/2	Facies 1	Figure: 3.5	Channel dunes and planar beds
12m					5Y 7/1	Facies 3	Figure: 3.7	Mud cracks
					5Y 5/2	Facies 4	Figure: 3.12 Figures: 3.20 & 3.21 Figure: 5.18 Figure: 5.17	Channel lag deposit (consists of winnowed material)





**Figure 3.2:** The Donald 207 panel section, 2x vertically exaggerated, constructed between 9 and 13 m on the vertical section. It shows sedimentological detail and the positions of the *Lystrosaurus* bonebed occurrences in this interval, in association with other fossils found on the panel section.

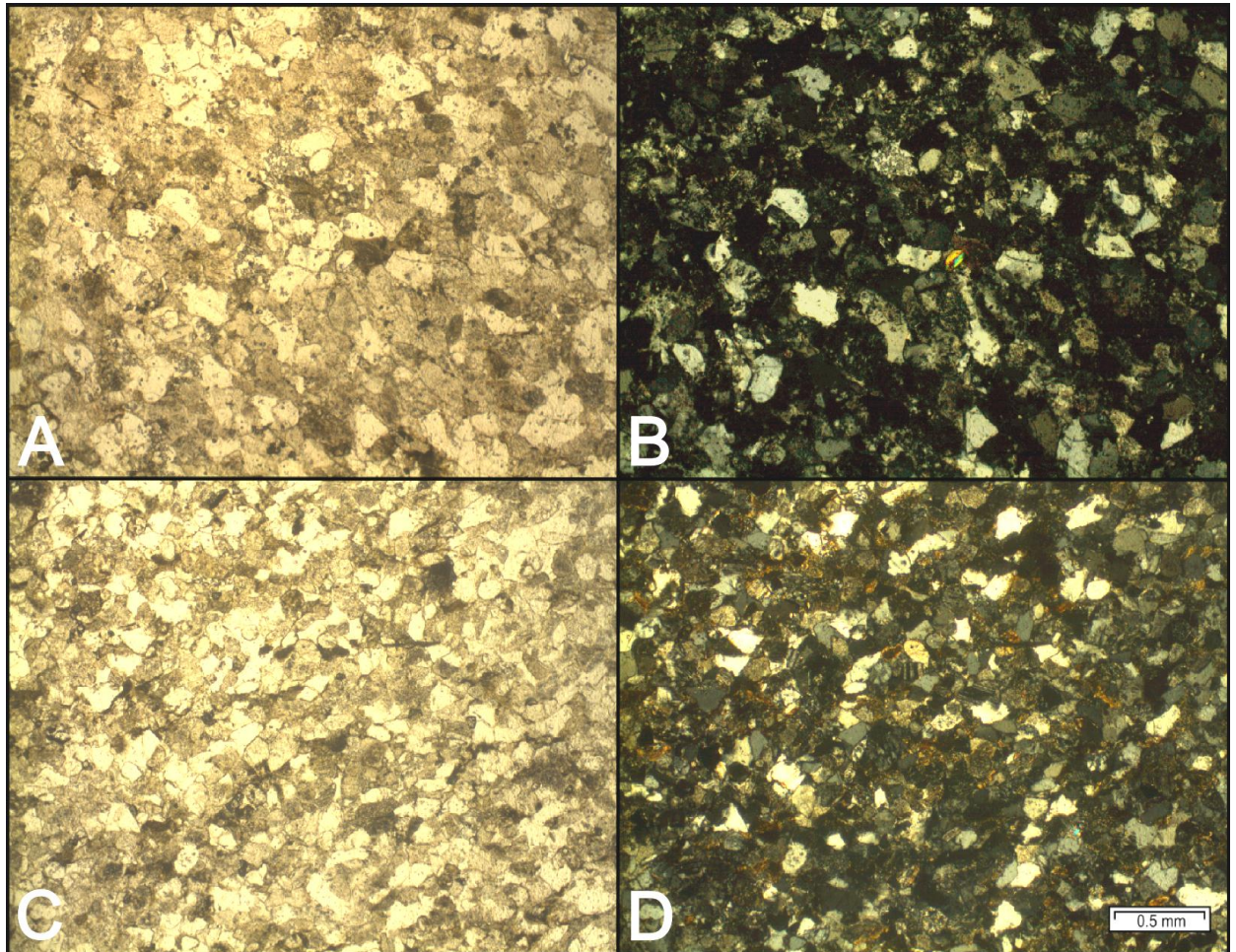
### 3.1 Sedimentological Facies of the lower Katberg Formation

Five different sedimentological facies were recognised in the study area. They are: single storey sandstones (Facies 1), multi-storied sandstones (Facies 2), massive sandy siltstone (Facies 3), massive siltstone (Facies 4), and intraformational nodule conglomerate (Facies 5). The sandstones on Donald 207, although identical in colour and thin section description, are divided into two facies as they occur either as a single unit (single storey) or as multiple vertically stacked units separated by laterally continuous erosional surfaces (multistoried). Facies 1 and 2 together make up 31% of the total logged section, Facies 3 24%, Facies 4 40%, and Facies 5 2% of the total logged section respectively. In the following section these facies and their stratigraphic occurrence are described and these data are then used to interpret the depositional environment. The stratigraphic position of figures referred to in the facies descriptions are also plotted on the vertical logs and panel section.

#### **Facies 1: Single Storey Tabular Sandstone Bodies**

The single storey sandstone beds vary in colour from olive-grey to light olive-grey (5Y 5/2, 5Y 6/2 on the Munsell colour charts). They vary in thickness from 0.5-1 m and commonly fine upward from medium-grained at the base of the bed (1/4-1/2 mm on the Wentworth scale) to fine-grained towards the top of the bed (~1/8-1/4 mm on the Wentworth scale). The sandstones are well-sorted, with sub-angular to angular grains. Bulk mineral composition is dominantly quartz (~45 wt%). Feldspar is present (30 – 35 wt%) although hard to identify whether plagioclase and orthoclase feldspar due to most of the grains being in an advanced state of alteration. Altered clay minerals (10 wt%) are present, along with indiscernible lithic fragments (5%) and

trace minerals such as zircon and rutile (Figure: 3.3). Tiny mudrock clasts were also observed concentrated on trough cross-bedded foresets.



**Figure 3.3:** (A and B) Thin section images (ppl and xpl) of the +3 m Facies 1 sandstone on the Donald 207 section. Note the zircon grain present in (B) (grain showing high birefringence colours in xpl). (C and D) Thin section images (ppl and xpl) of the +6.5 m Facies 3 sandy siltstone. Note the presence of less weathered feldspar (Twinned grains in xpl). Scale bar is indicated bottom right.

Single storey, tabular sandstone bodies logged on Donald 207 are almost always bounded above and below by Facies 3 and 4 siltstones and mudrocks, and have undulatory and erosive basal contacts with the underlying lithologies present. Upper contacts are gradational. Rarely coarse-grained pebbly intraformational nodule conglomerate (Facies 5) occurs as scour-fill deposits near or at the sandstone bases.

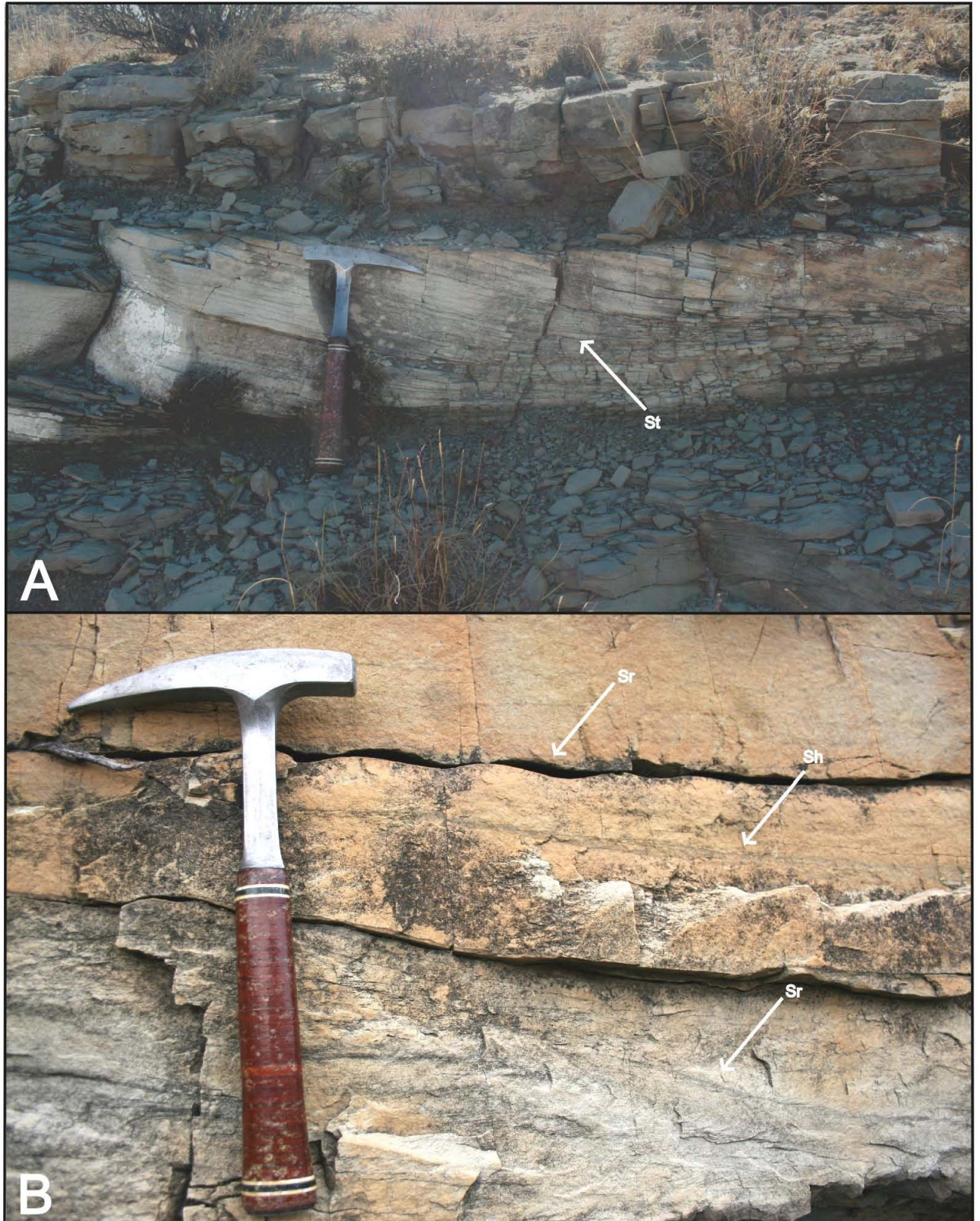
Overlying the basal contact massively and trough cross-bedded occur followed by horizontally laminated sandstone that sometimes contain mud and rip up clast layers. The trough cross-bedding indicate north-northwest palaeoflow directions deduced from parting lineation orientation. This importantly supports palaeocurrent data from previous studies (Johnson, 1976; 1989; Stavrakis, 1980; Hiller and Stavrakis, 1984; Smith, 1995; 2005; Groenewald, 1996; Haycock et al., 1997; Pace et al., 2009). The mud and clay rip up clast layers also line bedding planes of sandstone bases and trough cross-bed foresets. These rip up clasts are commonly plastically deformed which indicates that the rounded mud pebbles (rip up clasts up to 4 cm in diameter) were pliable and soft when they were deposited. Rare plant stem impressions have been found in these mud layers (Figure: 3.4).

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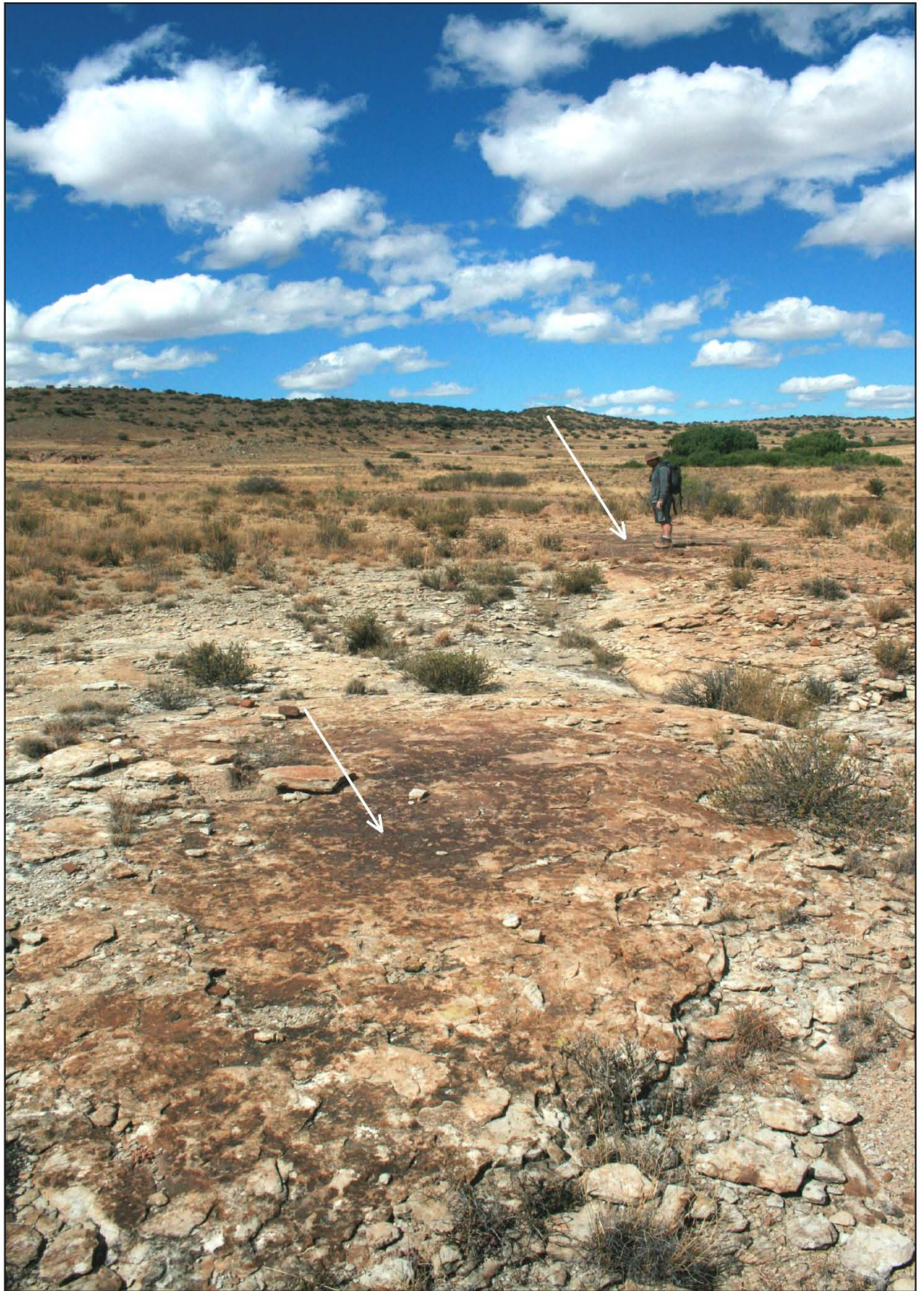


**Figure 3.4:** Rare stem fragment impression from the base of the +3 m Facies 1 sandstone on the Donald 207 log. The longitudinal grooves are indicative of *Equisetalian*, one of few plant species alongside *Dicroidium* seed ferns that survived into the Early Triassic.

Upwards from the base of the tabular sandstone bodies sedimentary structures change to climbing ripple cross-laminations and ripple-cross lamination at the top (Figure: 3.5). The upper surfaces of some of the tabular sandstone units are undulatory, resembling erosively-bound bar forms (Figure: 3.6). The flanks and depressions between these bar forms commonly display ripple forms and terminate in ripple-topped surfaces preserved beneath thin siltstone drapes (Figure: 3.7). Some of the ripples crests are planed-off. Possible *Lystrosaurus* footprints and other small tracks of cynodonts have been found in Bethel Canyon (Heldemoed 667 Farm) on the top surface of single storied sandstone (R. Smith pers. comm, 2011).



**Figure 3.5:** (A) and (B) show evidence of change in sandstone sedimentary structures as fluid velocity changes. (A) Facies 1 sandstone bases often have trough cross-bedding (St), as in the + 13 m Facies 1 sandstone on Donald 207 and horizontal lamination (Sh). (B) As velocity and water depth decrease, ripple cross-lamination (Sr) dominate, terminating in a mudstone-draped ripple-topped surface (Sr) such as sandstone from Bethel Canyon. This bed is approximately correlative with +3 m Facies 2 sandstone on Donald 207. Both beds indicate a north-westerly palaeocurrent direction. Hammer is 32 cm long.



**Figure 3.6:** Arrows point to the tops of two bar forms preserved on Donald 207 Farm. Their undulatory appearance in the field is apparent, and they are present on the same horizon as the +6.5 m ripple surface on the vertical section (~ 200 m northwest from the bar forms).



**Figure 3.7:** (A) Ripple topped Facies 1 sandstone surface + 6.5 m on Donald 207 section. Photograph from R. Smith (2010). (B) On closer inspection ripple crests are asymmetrical and sinuous, typical of wind rearranging sand surface in shallow water (R. Smith pers. comm, 2010). In some places the ripples bivate, and plane off, commonly with secondary ladder-backs. All of these features are interpreted as indicating shallow water depths. Paint brush is 18 cm long.

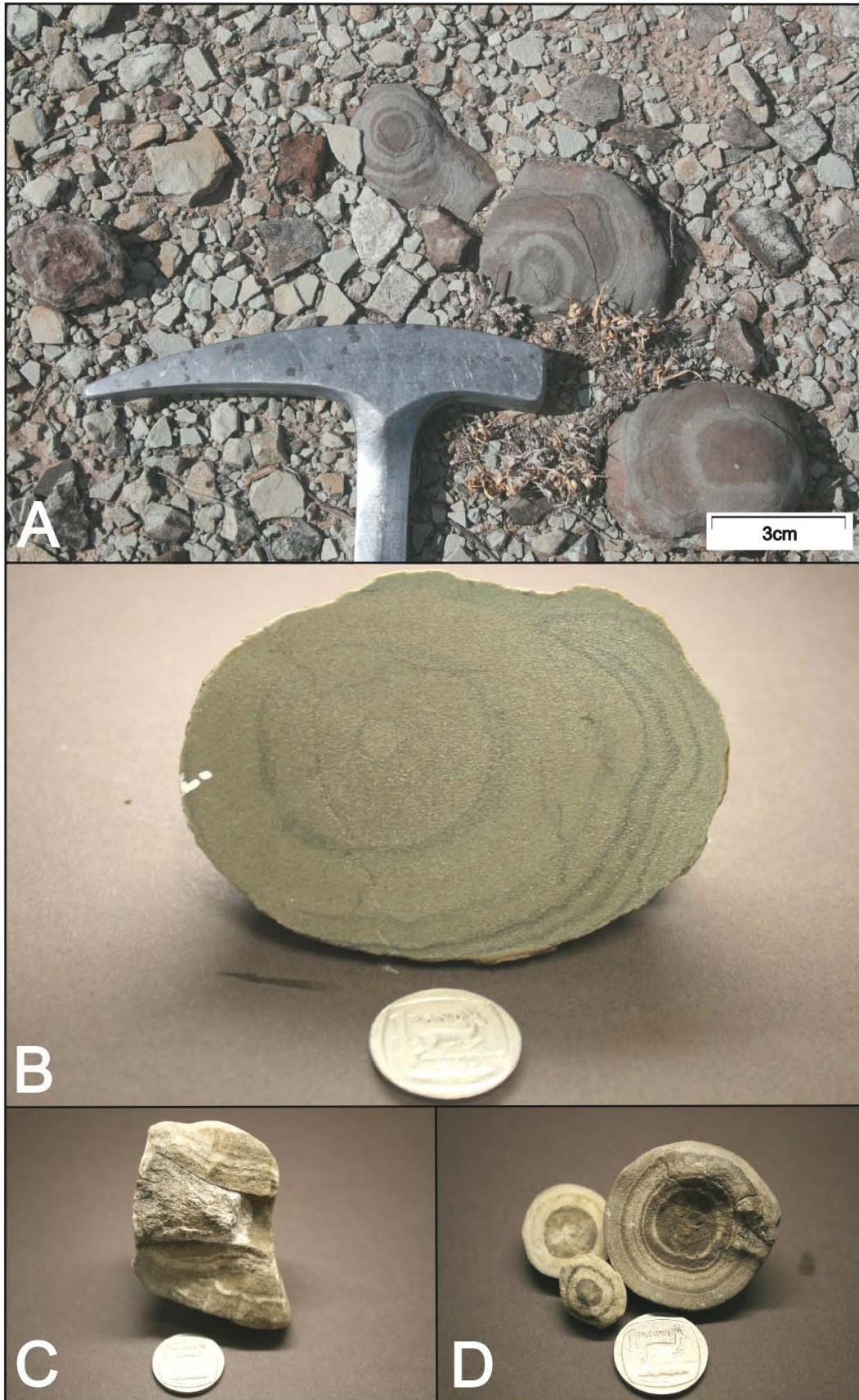


**Figure 3.8:** Bioturbation and filled mud cracks beneath a dislodged block of the +13 m Facies 1 sandstone on Donald 207. Differences in mud crack width are interpreted as reflecting variation in thickness of the mud layer (R.Smith pers. comm, 2010). Some of the knobs were initially interpreted as sole markings, but upon closer inspection are sandstone filled depressions in the mud surface and may in fact be invertebrate burrows. Lens cap is 6 cm in diameter.

Sole marking and sand-filled mud cracks are often found at or beneath the basal contact of sandstone beds (Figure: 3.8). The sandstone capping the panel section study (Figure: 3.2) is a typical single storey sandstone in the study area and shows sand-filled mud cracks beneath the erosional base with conglomeritic material filling some of the scours. The trough cross-bedded strata were mostly confined to the most scoured based sections of the sandstones.

Carbonate nodules with concentric colour banding are present within the horizontally laminated and massive sandstone beds of Facies 1 and 2 (Figure: 3.9). This concentric pattern suggests that the carbonate was precipitated incrementally round a core, possibly organic. A few have been found with bone fragments in their cores. In some areas these nodules show apparent favourable directions of growth, and in these cases they become elongate as the ring thickness varies. The concentric nodules are found either as solitary concretions in Facies 1 and 2 sandstone and Facies 3 sandy siltstone or as groups merged together into irregular masses. Individual nodules range in size from 2-20 cm in diameter.

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**Figure 3.9:** Concentrically patterned nodules associated with Facies 1, 2, and 3 lithologies. (A) nodule samples collected from +8.5 m sandstone top. (B) Nodule sample cut in cross section showing presence of concentric rings within nodule and varying thickness of rings. Hammer's head 15 cm across. (C) Nodule sample from +8.5 m horizon containing bone fragment within nodule core, concentric rings mimic bone's shape. (D) Nodules have great size ranges and this may be product of their maturity. R1 coin is 1.5 cm in diameter.

## **Facies 2: Multi- storied Tabular Sandstone Bodies**

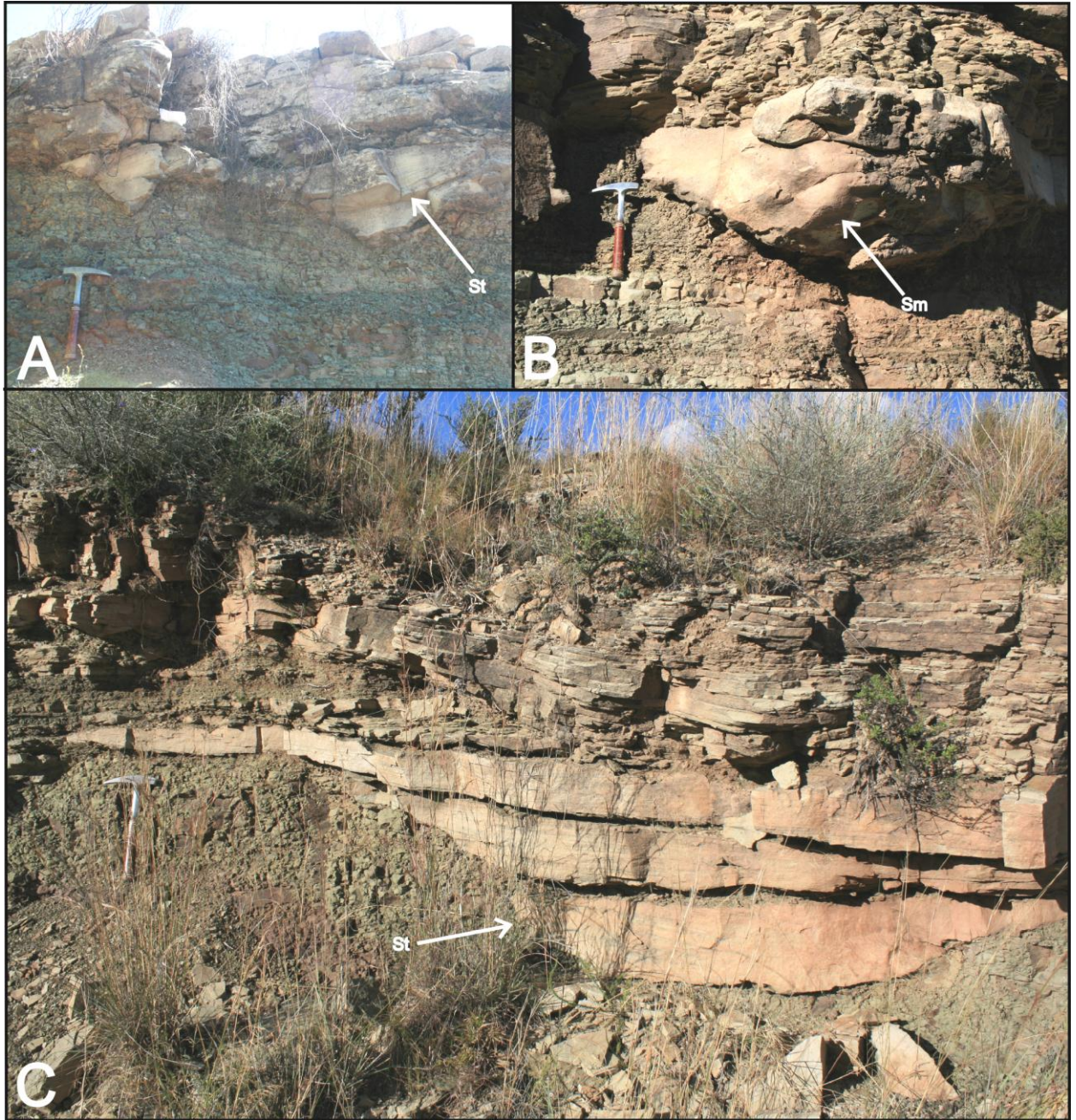
Facies 2 sandstones are light olive-grey (Munsell 5Y 6/2), and consist of two or more vertically nested single storey tabular sandstones. Petrographic analysis shows that the well-sorted mineral grains are sub-angular and medium-to fine-grained in size (1/4-1/2 mm on the Wentworth scale). Bulk mineral composition is dominantly quartz (50%). Altered feldspar grains are also present (35%), along with altered clay minerals that are likely a combination of weathered biotite and muscovite (10%). Unidentifiable lithic fragments (5%) and trace minerals such as zircon and rutile are also present. There there are no notable differences when compared to Facies 1 petrography (Figure: 3.3).

In the vertical section two sandstone bodies (the +3 m and +25 m) are multi-storied tabular sandstone bodies 2-5 m thick, much thinner than the amalgamated (>50 m) sandstone bodies that occur higher in the Katberg Formation forming the Swartberg Member (Botha and Smith, 2006). They are commonly bounded above and below by Facies 3 and/or Facies 4 strata. The bases of Facies 2 sandstones are erosive, but show more extensive and deeply scoured bases when compared to Facies 1. These scoured bases display distinctive scour troughs, gutters, or gullies that range in shape and size (30 cm – 1 m wide and 20-50 cm in depth), even along the same sandstone base (Figure: 3.10). The scour troughs are elongate and are mostly a symmetrical in cross-sections. The gullies are filled with massive, trough or planar cross-bedded sandstone. The sandstone bodies commonly comprise two or three vertically stacked fining-upward sequences with the upper surface of each sequence having been eroded by the overlying storey. Sedimentary structures reflect a trend in

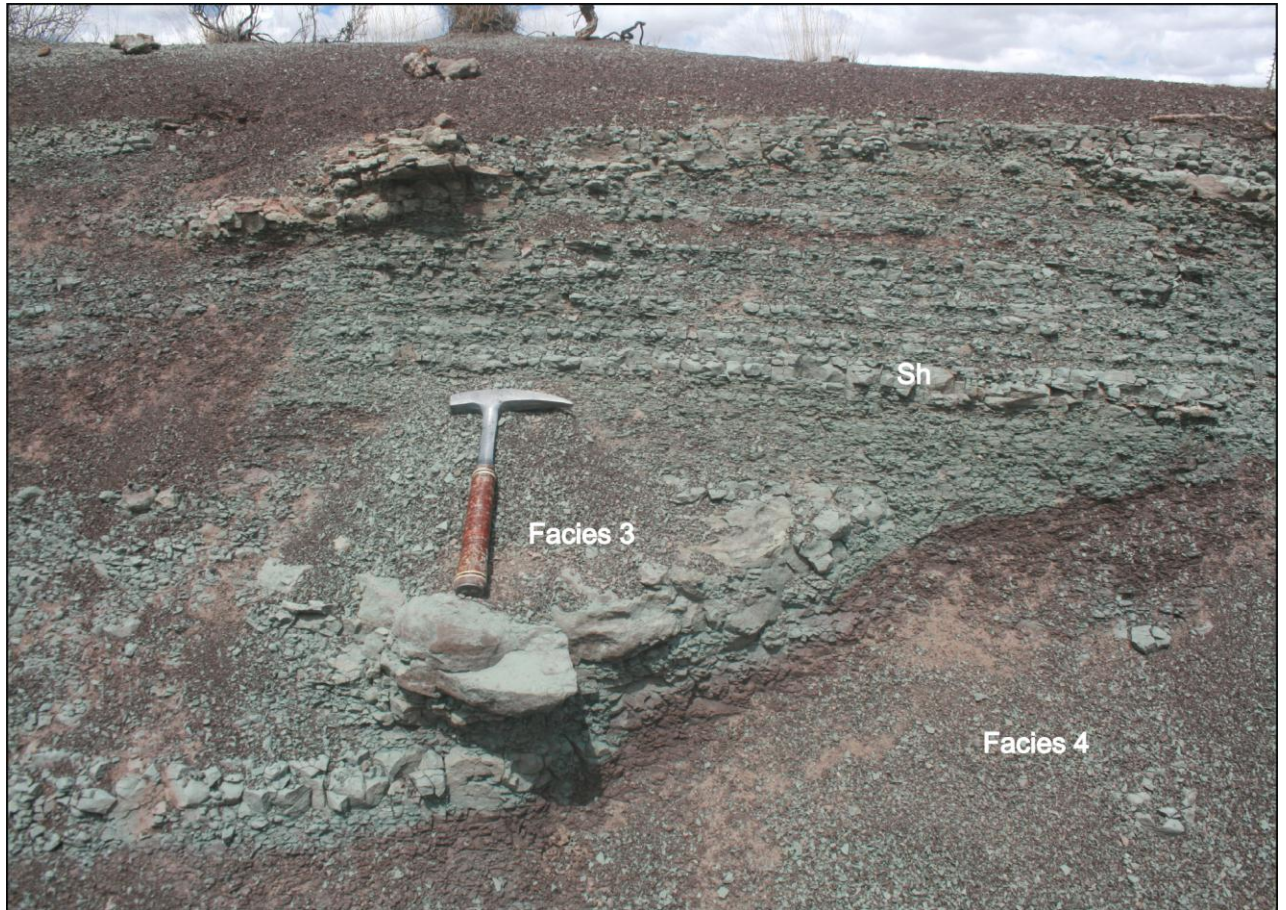
each storey passing from horizontal to trough cross-bedding and ripple cross-lamination. Rarely a finer grained Facies 3 sandy siltstone bed can be preserved between the nested sandstone bodies. Concentrically grown carbonate nodules are found within the horizontally laminated and massive sandstones and occur identically as in Facies 1. These nodules bare similarity to nodules that occur in association with fossils and have been locally eroded and reworked into internal scour depressions and basal conglomerates of the channel sandstones (See Facies 5 descriptions).

### **Facies 3: Massive Sandy Siltstone**

Thin (~ 0.3-1 m thick) light bluish-grey (Munsell 5Y 7/1) sandy siltstone beds occur throughout the Donald 207 section. They make up 24% of the succession logged and occur most commonly immediately above single and multistoried sandstone beds. They also occur within the massive mudstone facies (Facies 4) as laterally restricted scour-fill deposits (Figure: 3.11). Grain size is similar to the fine grained sandstones (~1/8-1/4 mm on the Wentworth scale). In addition, the grains show a similar degree of angularity to the sandstones however, their mineral modal abundances differ slightly.



**Figure 3.10:** Basal scours of a Facies 2 sandstone base equivalent to the +3 m on the Donald 207 vertical section showing similar fill of fine-grained sandstone but variation in basal scour shape and size. **(A)** Two basal scours that are V-shaped and filled with trough cross-bedded (St) sandstone. **(B)** A scour filled with massive sandstone (Sm) and has a shallow, rounded shape. **(C)** The base of a laterally equivalent sandstone bed to the +13 m sandstone bed on the vertical section. This basal scour has a shallow rounded shape (asymmetrical) and filled with trough cross-bedded sandstone. The size however, is significantly larger than the basal scours shown in the previous photographs. Hammer is 32 cm long.

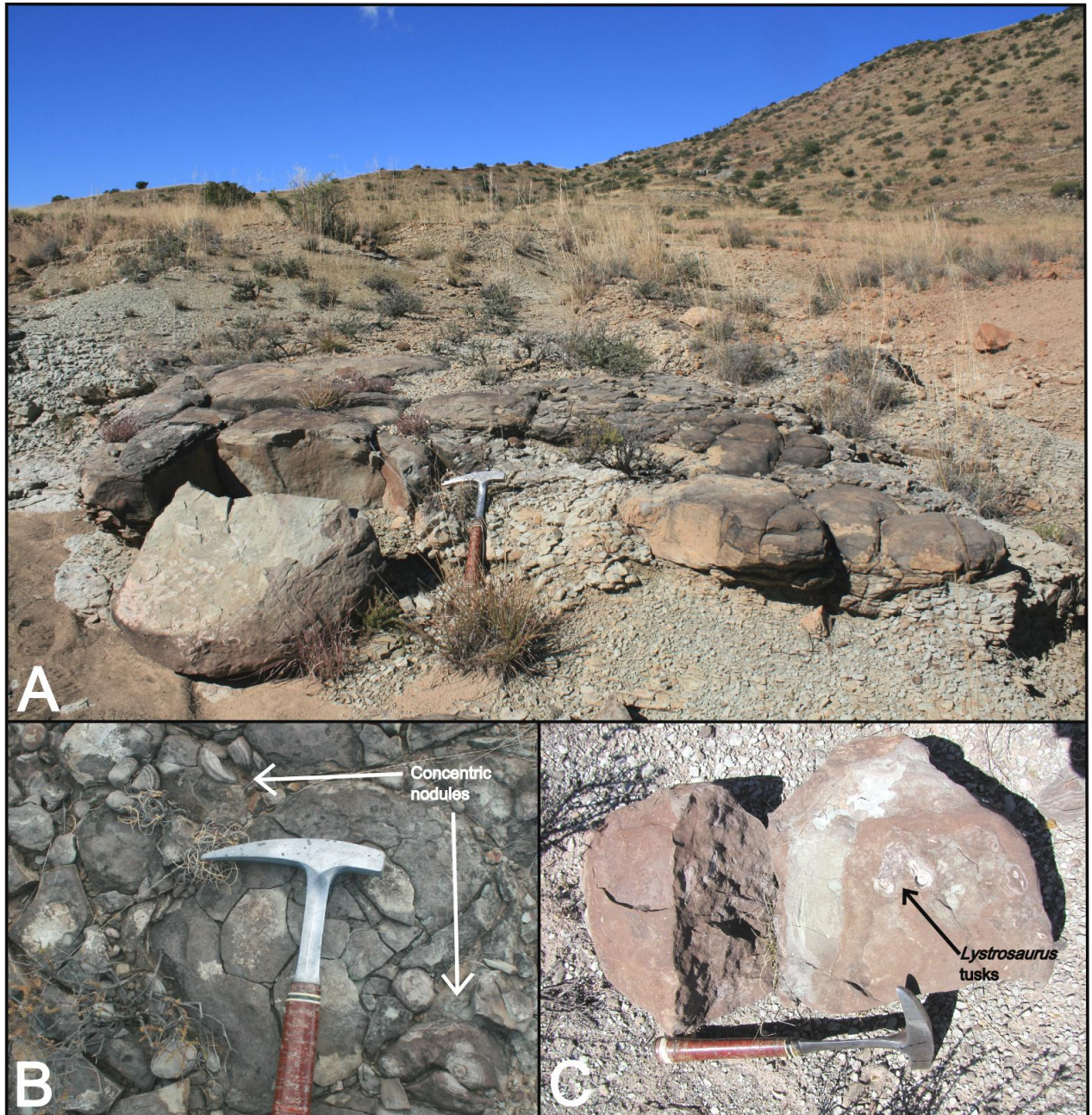


**Figure 3.11:** Photograph shows a Facies 3 scour within Facies 4 red siltstone (labelled). The coarsest material is below geological hammer, whereas laminations (Sh) are visible in the finer units above the geological hammer. Hammer is 32 cm long.

Feldspar grains are more abundant (35%), fresher, more visible (mostly consisting of thin twinned alkali feldspars) (Figure: 3.3). There is also a higher percentage of biotite (up to ~25% modal abundance) which has been altered to clay (~90 wt% of the biotite is altered). Quartz and trace minerals such as zircon have similar modal abundances to the Facies 1 and 2 sandstones (~40 wt% and trace respectively). Sedimentary structures present are mainly in the form of horizontal lamination, although blocky weathering makes it nearly impossible to discern finer detail structures in outcrop. However, these details are revealed in the baked contact zones of dolerite intrusions.

The concentrically patterned nodules present in Facies 1 and 2 are also found in Facies 3, but here they occur as inter-grown clusters of about 5-7 nodules in the coarsest beds of this facies in association with another nodule type unique to Facies 3. The latter being large, black/dark brown weathering, irregular shaped nodules (~ 1-5 m long) occurring in nearly all the Facies 3 beds logged and in the panel section area. These large nodules are rarely solitary and occur in close association with other similarly sized black/brown-weathering nodules. Facies 3 clustered concentric nodules, mud-filled invertebrate burrows, and articulated vertebrate remains are frequently found inside these large black/brown weathering nodules (Figure: 3.12 and 3.13). Petrography of these nodules revealed fine laminations lined with siltstone which indicates bedding continues through them.

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**Figure 3.12:** Photographs show the mode of occurrence of the large Facies 3 black-weathering nodules on Donald 207. (A) One of the larger black-weathering nodules weathering out the +9 m Facies 3 beds as a round, domed feature. These nodules are unique to Facies 3. (B) A black-weathering nodule containing round concentric patterned nodules within (arrowed). (C) Another black-weathering that contains the fossilised remains of a *Lystrosaurus*. Hammer is 32 cm long.



**Figure 3.13:** Facies 3 black-weathering nodule with mud-lined, vertically orientated invertebrate burrows. The colour of the interior of the Facies 3 back-weathering nodules is identical to the Facies 3 sandy siltstone.

#### **Facies 4: Massive Siltstone facies**

Facies 4 makes up 40% of the section and consists of 0.5-2m thick beds of massive siltstone which occur as predominately thin beds that are inter-bedded with Facies 3 sandy siltstones near the bases of the thicker sandstone beds of Facies 1 and 2.

Sedimentary structures within Facies 4 siltstone beds are masked by a blocky weathering texture however, next to dolerite intrusions, the sedimentary structures are discernable as centimetre-scale flat-lying discontinuous sheets with horizontal lamination. The beds alternate between fine silt and clay (1/125-1/64 mm on the Wentworth scale) and coarse silt (1/32-1/16 mm) with occasional sandy siltstone lenses.

The colour of the siltstones is predominantly maroon or dull reddish grey (Munsell 10R 3/1) but olive-grey (Munsell 5Y 5/2) colours do occur and the colour boundaries are commonly gradational and irregular, suggesting post-depositional pedogenic overprint. The individual cm-scale thin beds within this facies are not laterally continuous; however, a single maroon siltstone unit is traceable throughout the study area (1 km<sup>2</sup>). Within this siltstone there is evidence of scouring and pinching out of beds (Figure: 3.14).

Troughs filled with coarser sandy siltstone are common and even pods and lenses of massive fine-grained silty sandstone are present (see Figure: 3.10). The colour of the siltstones invariably grades upwards from dull reddish-grey to olive-grey. Large (~60 cm long) mud-filled structures named stellate structures by Smith and Botha (2005) were observed in the siltstones in some parts of the study area (Figure: 3.14). These structures are star-shaped in cross section. Desiccation cracks not associated with sandstone bases were found in the study area, but not at the locality where the section was logged (Figure: 3.16). Near horizontal *Katbergia* burrows (Gastaldo and Rolerson, 2007) of possible crustaceans are common throughout the lower Katberg siltstones and are particularly abundant where colour mottling is present (Figure: 3.17).



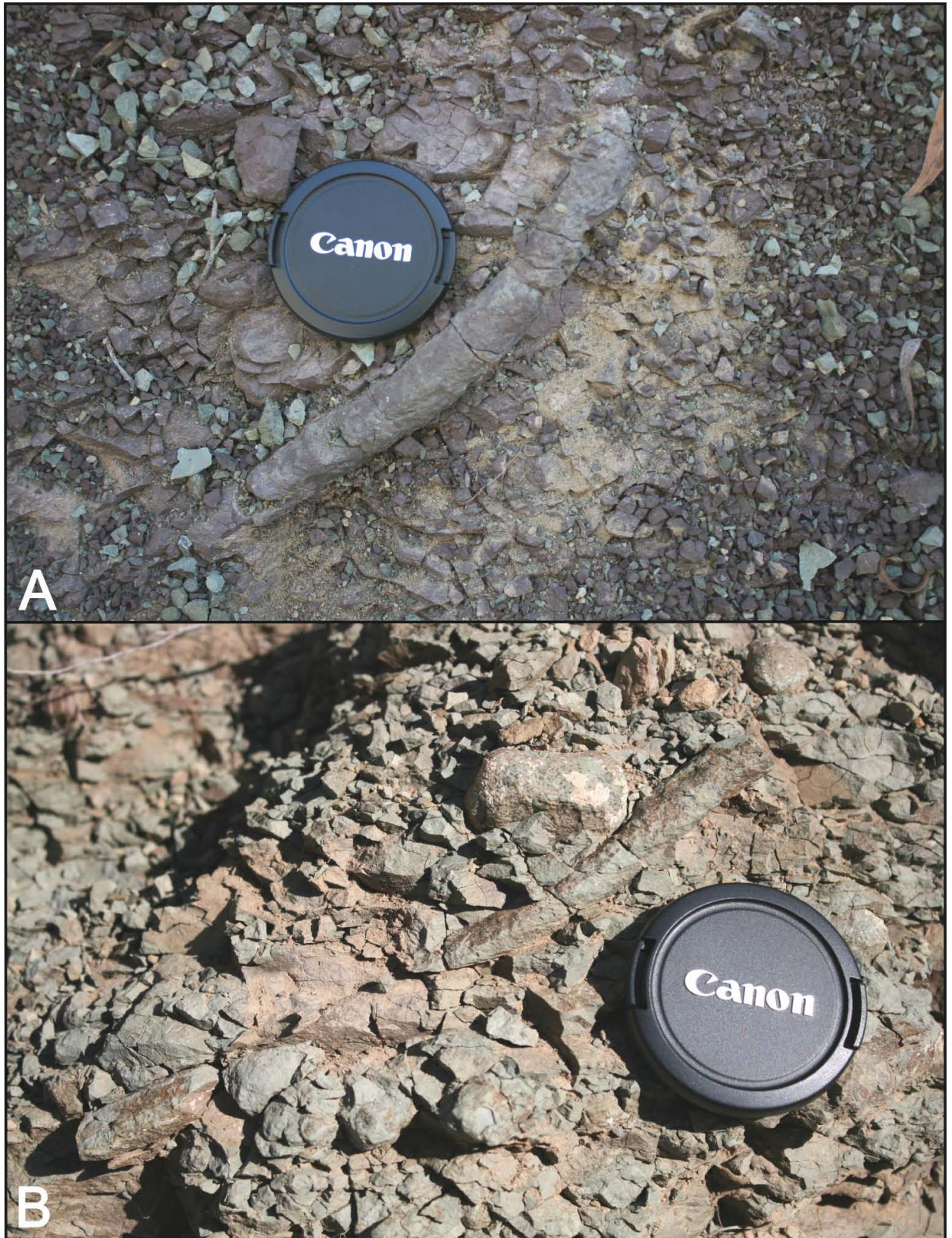
**Figure 3.14:** Outcrop of Facies 4 siltstones on Donald 207 Farm. The beds are mostly discontinuous, and alternation from red to green siltstone happens frequently through the section, so the post-depositional subsurface environment chemistry switched frequently from reducing to oxidising and back again. Scour fill of the coarser Facies 3 sandy siltstone has been highlighted. Hammer is 32 cm long.



**Figure 3.15:** A stellate structure filled with micrite from Facies 4 siltstone in Bethel canyon (laterally equivalent to +2.5 m on the Donald 207 logged section). They are believed by Smith and Botha (2005) to either represent fossil tree roots, or cracking and shrinking within soil during dry periods. Hammer is 32 cm long.



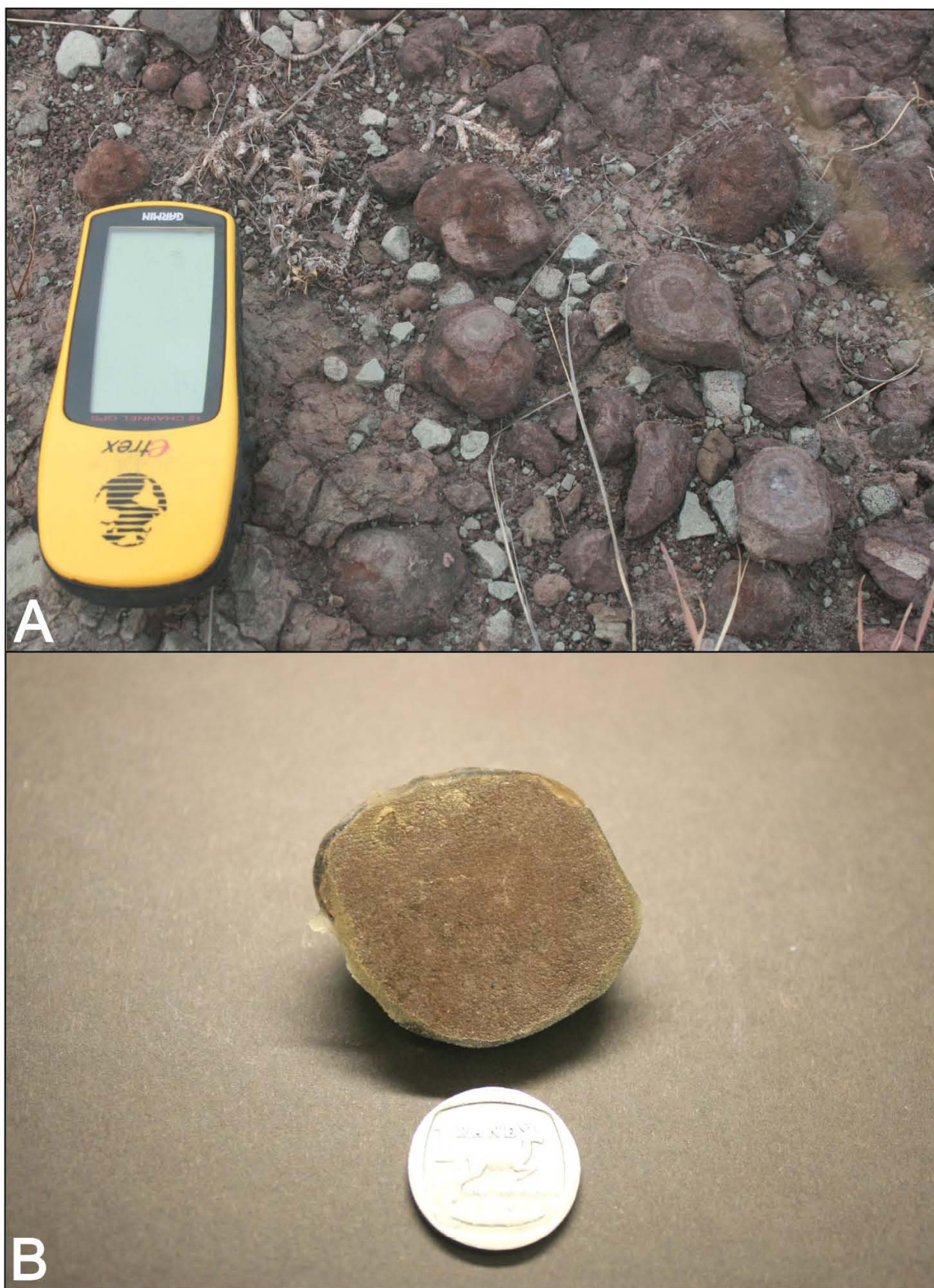
**Figure 3.16:** Partially excavated desiccation cracks in Facies 4 siltstone from +14.5 m on the vertical section. The large size of the desiccation cracks and width of sand-filled cracks are significant as they indicate intense drying out of the soil profile (Khadiqkar et al., 1998). These large desiccation features are commonly observed under hyper-arid conditions in modern semi-arid environments (Smith and Botha, 2005) and also indicate good drainage (Fielding et al., 2012). Hammer is 32 cm long.



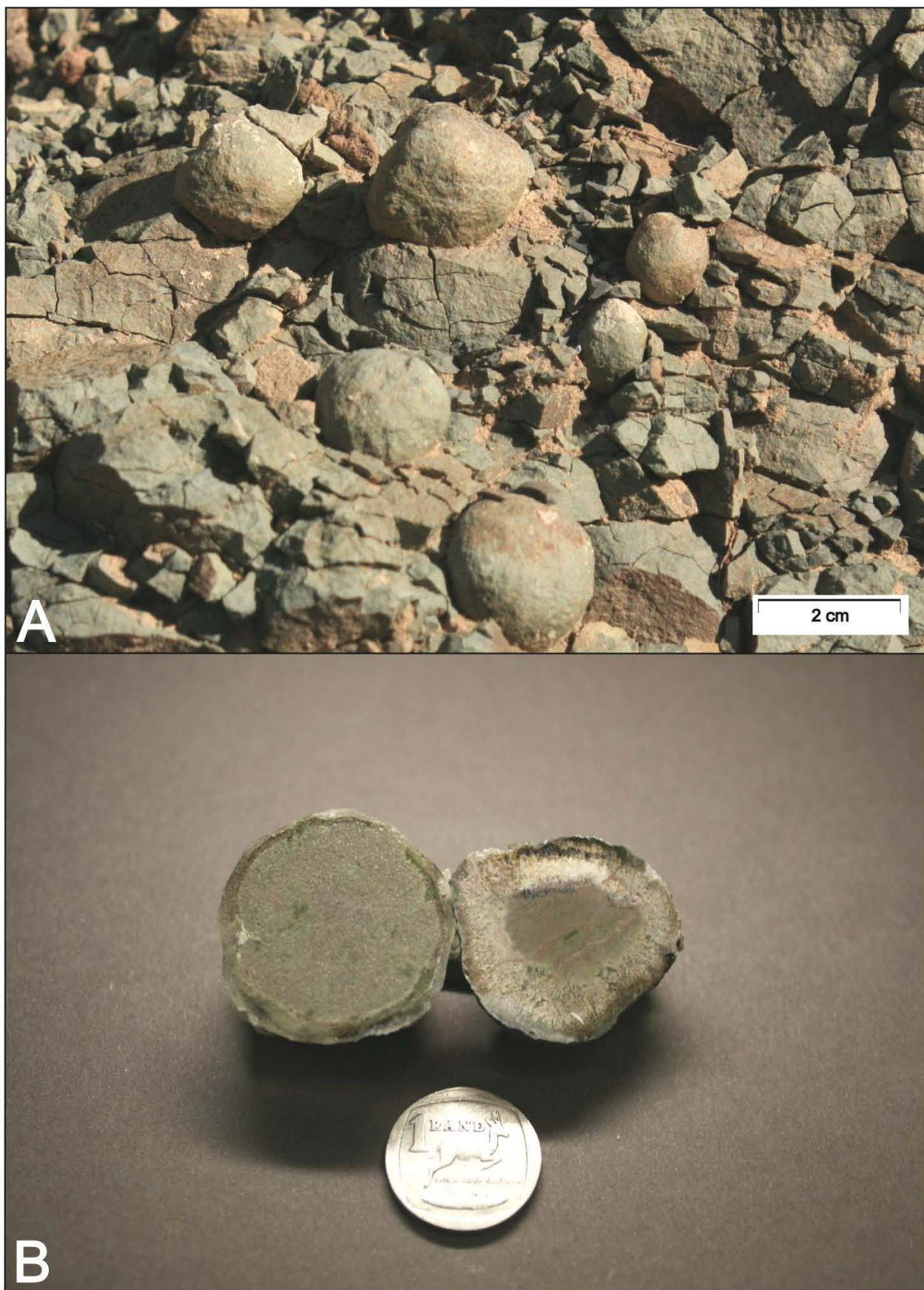
**Figure 3.17:** Facies 4 invertebrate burrows of *Katbergia sp.* (Gastaldo and Rolerson, 2007). The burrows occur in both the red (A) and green (B) Facies 4 siltstone, often in association with nodule horizons and colour mottling. The burrows incline at an angle of  $\sim 35\text{-}45^\circ$  and show chevron-shaped ridges on their outer surface. The two burrows were logged at  $\sim +1$  m (A) and  $+1.5$  m (B) on the Donald 207 vertical section respectively. Lens cap is 6 cm in diameter.

Medium sized sandstone-filled burrow casts attributed to cynodonts, and larger ones possibly constructed by *Lystrosaurus* (Smith and Botha, 2005) are quite common, particularly in the red siltstone. The burrows are preserved by infilling of fine grained sandstone or coarse silt. Petrography of burrow-fill sandstone reveals a similar composition to the massive sandy siltstone (Facies 3).

Two distinct types of carbonate nodules occur in Facies 4. In the maroon siltstone small (2-5 cm across), discrete round-to oblong-shaped reddish-brown weathering nodules occur (Figure 3.18). These nodules normally have a spherical or oblate shape and a smooth or pustular surface and are never larger than 4-8 cm in diameter. They often occur in clusters along specific horizons in association with bioturbation and invertebrate burrow fills. The olive-grey siltstone contains small rounded peloid- type nodules (Figure 3.19). These nodules superficially do not resemble the red siltstone pedogenic nodules in hand specimen. They are generally small (1-5 cm in diameter) smooth, round peloids or glaebules (Smith, 1990). They do however occur in clusters along bioturbated horizons, sometimes in direct association with *Katbergia sp.* burrows, some present within the infilling of the burrow itself. They normally occur as inter-grown clusters of 2-5 nodules, sometimes stacked vertically upon one another. These peloids are commonly encountered as intraformational pedogenic nodule conglomerate having been reworked and deposited on the scoured bases of Facies 1 and 2 sandstones.



**Figure 3.18:** Carbonate nodules from the Facies 4 red-brown coloured siltstone. **(A)** The red-brown nodules collected on the outcrop and sampled for isotope data. **(B)** One of the nodules cut in cross-section showing not much of the inside detail is visible with the naked eye. GPS and R1 coin are 10.5 cm and 1.5 cm respectively.



**Figure 3.19:** (A) Carbonate nodules collected from the Facies 4 green-grey siltstone beds. (B) Two of the nodules cut in cross section. Note the presence of a rim of calcite regrowth present in the right hand nodule. R1 coin is 1.5 cm in diameter.

The massive red siltstone beds of Facies 4 host many of the vertebrate remains found in the Katberg Formation (Botha and Smith, 2006). Vertebrate remains are present as isolated fragments, complete skeletons or chaotic melanges of multiple and/or single individuals. The fossils consist predominantly of *Lystrosaurus* (*L. declivis* and *L. murrayi*), but also other therapsids (cynodonts *Thrinaxodon* and *Galesaurus*, therocephalians *Regisaurus* and *Scaloposaurus*). Other vertebrate taxa are also found include amphibians (*Lydekkerina* and *Micropholis*), the archosauromorphs *Prolacerta*, and rarely *Proterosuchus* (which has yet to be found in the study area, but has been found in Bethel Canyon). Some of the fossil fauna were noted to have facies associations.

Most of the complete *Lystrosaurus* skeletons are hosted by the olive-grey sandy siltstone and siltstone of Facies 3 and 4. Cynodonts and therocephalians are mostly confined to the siltstones of Facies 4 whereas *Proterosuchus*, *Prolacerta* and *Lydekkerina*, are found in both Facies 3 and Facies 4. Vertebrate bone fragments are common in Facies 5 and rarely found in Facies 1 and 2, but due to their condition it is hard to identify to species level.



**Figure 3.20:** A pod of Facies 5 nodule conglomerate filling a scour beneath the base of the +3 m sandstone bed on the Donald 207 vertical section. Most of the peloids and nodule clasts have eroded out of the rock in this in situ example. Hammer is 32 cm long.

### **Facies 5: Intraformational Nodule Conglomerate**

The clast-supported intraformational nodule conglomerate of Facies 5 is rarely found in situ in the study area and constitutes only 2% of the succession. The conglomerate is never laterally extensive and occurs as scour fills at the bases of the larger sandstone beds (Figure: 3.20). The in situ examples are almost always strongly weathered, forming negative exposure and the less resistant mudrock clasts erode out leaving voids. In places large blocks of the Facies 5 conglomerate lie eroded out of the outcrop. They are more cemented and show minimal weathering, and although not useful in log construction, they are useful to study the composition (Figure: 3.21).

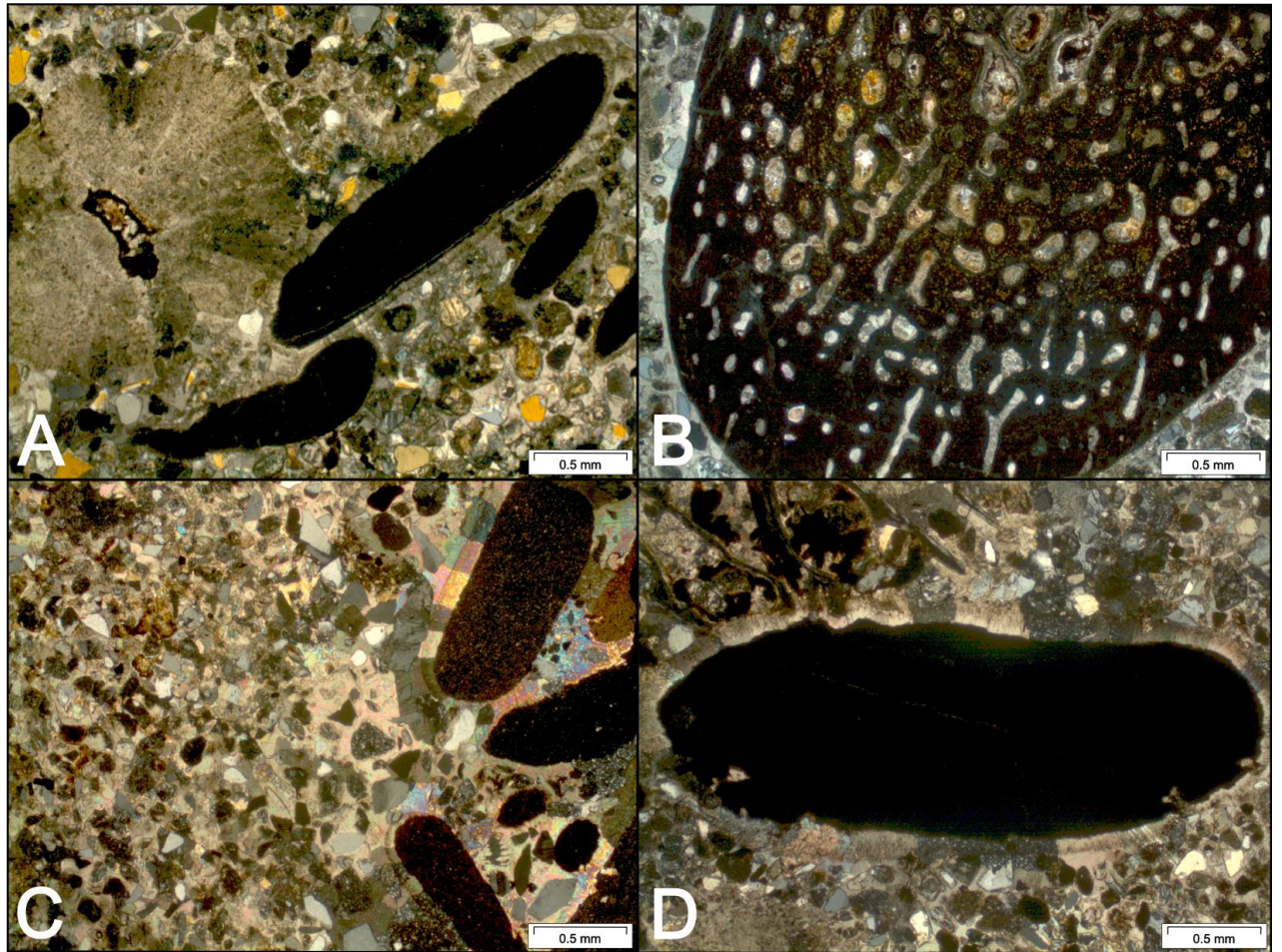


**Figure 3.21:** Close inspection of a fresh, but loose fragment of Facies 5 nodule conglomerate from the base of the +13 m panel section sandstone. Note the presence of septarian cracks in many peloids and nodules. They also show evidence of being abraded and rounded along with isolated fossil bone fragments.

The Facies 5 conglomerate consists of nodules of varying clast size, mostly from medium to pebble-sized grains (1/4 mm -4 cm). Most of the nodule intraclasts are spherical to oblate and have septarian shrinkage cracks which suggest they are pedogenic nodules (peloids), which agrees with observations by Smith (1995) and Smith and Botha (2005). Some nodules have bone fragments within them. The nodules are similar to nodules found in Facies 4. Amongst the nodule clasts, isolated fossil, unidentifiable lithic, and mudrock fragments are also present. Fish teeth and bone fragments have been found in this conglomerate by R. Smith (pers. comm,

2010). Often in the field these conglomeritic pods show elephant skin weathering texture which indicates cementation by carbonate.

Petrography reveals rounded oblate mudrock fragments and calcareous cement of microspar calcite (Figure: 3.22). Some of the mudrock fragments and unidentifiable lithic fragments appear to be preferentially orientated and show a small degree of imbrication. The fragments are commonly rimmed by radial calcite growth, and minor grading of grains and fragments is rarely observed. Small bone fragments are present, usually as fragmentary pieces, but some have been rounded. From histological observations, the bone fragments are considered to be from either small or infant animals (A. Chinsamy-Turan pers. comm, 2010). The histology reveals spongy bone (seen on the ends of long bone shafts) where bone growth originates which, in young animals, has more blood vessels. Many of the very tiny fragments are possibly of fish.



**Figure 3.22:** Cross polarised thin section images of Facies 5 nodule conglomerate. The photographs show the following features: (A) Imbricated mudstone fragments and a pedogenic nodule, (B) small bone fragment, (C) calcareous-lithic matrix and (D) a mudstone fragment with rim of crystalline radiaxial calcite.

### 3.2 Interpretation

Fluvial models for the Early Triassic Katberg Formation have been suggested by Johnson (1976), Stavrakis (1980), Hiller and Stavrakis, (1984), Smith (1995, 2001), Smith and Botha (2005), Groenewald (1996), Haycock et al. (1997), and Pace et al. (2009). Although most of this work has been influenced by facies models of braided, meandering, and straight river systems compiled by Leopold and Wolman (1957), Allen (1965), Miall (1977, 1996), and Walker (1979); the precise fluvial system of the lower Katberg Formation is still contentious, but authors have accepted the braided model as a best fit. It is now acknowledged that there are another two channel pattern morphologies that exist besides Leopold and Wolman's (1957) braided, meandering and straight (Ashworth and Lewin, 2012). They are 1) wandering rivers that are transitional between meandering and braided with typically large permanent islands (Burge and Lapointe, 2005), and 2) anastomosing rivers with multiple channels that are laterally inactive and can be meandering, braided, straight, wandering or anastomosing (Miall, 1977; Nanson and Knighton, 1996; Ashworth and Lewin, 2012) (Table: 1).

Type	Morphology	Sinuosity	Load Type	Erosive Behaviour	Depositional Behaviour
<b>Meandering</b>	Single channels	>1.3	Suspension or mixed load	Channel incision, meander widening (or loop cut-off)	Point bar formation
<b>Braided</b>	Two or more channels with bars and small islands	<1.3	Bedload	Channel widening	Channel aggradation, mid-channel bar formation
<b>Straight</b>	Single channel with pools and riffles, meandering thalweg	<1.5	Suspension, mixed or bedload	Minor channel widening or incision	Side-channel bar formation
<b>Wandering</b>	Alternating single and multiple channels, with large permanent islands	Varies from >1.3 to <1.3.	Suspension or mixed load, or bedload	Minor meander and/or channel widening	Formation of islands, minor point bar and channel aggradation
<b>Anastomosing</b>	Multiple channels, often wetlands and lakes between levee-flanked channel branches	>2.0	Suspension load	Slow meander widening, often channels are laterally inactive	Slow bank accretion

**Table 1:** Classification of river types taken from Miall (1977), Nanson and Knighton (1996) and Ashworth and Lewin (2012).

Authors agree that the Katberg channel sandstones do not represent a meandering system like the underlying Adelaide Subgroup formations (Hiller and Stavrakis, 1984; Haycock et al., 1997; Smith, 1995; Smith and Botha, 2005). Hiller and Stavrakis

(1984) were the first to compare the Katberg's clastic alluvial sequence to fluvial models of Miall (1977; 1996), in particular the Platte River (Colorado-Nebraska) model. This model consists of alternating facies in the following order: linguoid bars (trough cross bedding (St)) and sand waves (planar cross bedding facies (Sp)), horizontally laminated facies (Sh), climbing ripples facies (Sr), minor floodplain interbed facies (FI) (Miall, 1977). The Platte River model has been used for a number of decades to describe typical braided river system deposits however, a recent review of the Platte River model by Horn et al. (2012) concluded the Platte River model does not incorporate sufficient data relevant to the rock record as Miall's (1977) sequence model does not fully describe the vertical succession within the Platte River itself. The discussion will now move towards comparing the earliest Katberg Formation to more recent literature on braided river deposition and morphology (ancient and modern) in an effort to conclude if indeed the lower Katberg Formation deposits are typical of braided rivers.

### **Braided Rivers in Literature**

According to Leopold and Wolman (1957) and Miall (1977; 1996) typical modes for identification of braided rivers in the ancient rock record constitutes normal grading sequences with channel deposits resting on scoured surfaces, and these commonly contain basal lag deposits. Sandy braided river systems typically preserve vertically stacked sequences of bedforms which decrease in size with sediment grading.

Stacked bedform size is related to the depth of the channel as seen by Sambrook et al. (2006) in their study on the sandy braided Saskatchewan River, and in a case study by Fielding et al. (2012) on the braided fluvial, Lower Jurassic Precipice

sandstone, Queensland Australia. The position and migration of bars within braided river system channel result in high lateral continuity of sandstone beds in the rock record (Miall, 1977; 1996; Smith and Botha, 2006; Long, 2006). Levee, channel bank, and floodplain deposits are generally less important in braided systems. More anastomosing branches in braided rivers may preserve levee channel bank, and floodplain deposits due to their nature of being less laterally active (Nanson and Knighton, 1996; Ashworth and Lewin, 2012). Bars form in the middle of channels and migrate downstream with flow in braided rivers (Miall, 1977, 1996; Smith, 1995; 2005; Ashworth and Lewin, 2012). Migrating bars in the braided condition erode the channel causing widening and vertical aggradation. Aggradation in braided rivers also causes the channel to become raised relative to the floodplain. Since many braided rivers are the result of variable discharge rates (Allen, 1962; Miall, 1977; 1996; Smith, 1995; 2005; Tooth, 2000; Sambrook Smith et al., 2010), inevitably a trigger (such as a flood event) will cause sudden avulsion and subsequent abandonment of the channel.

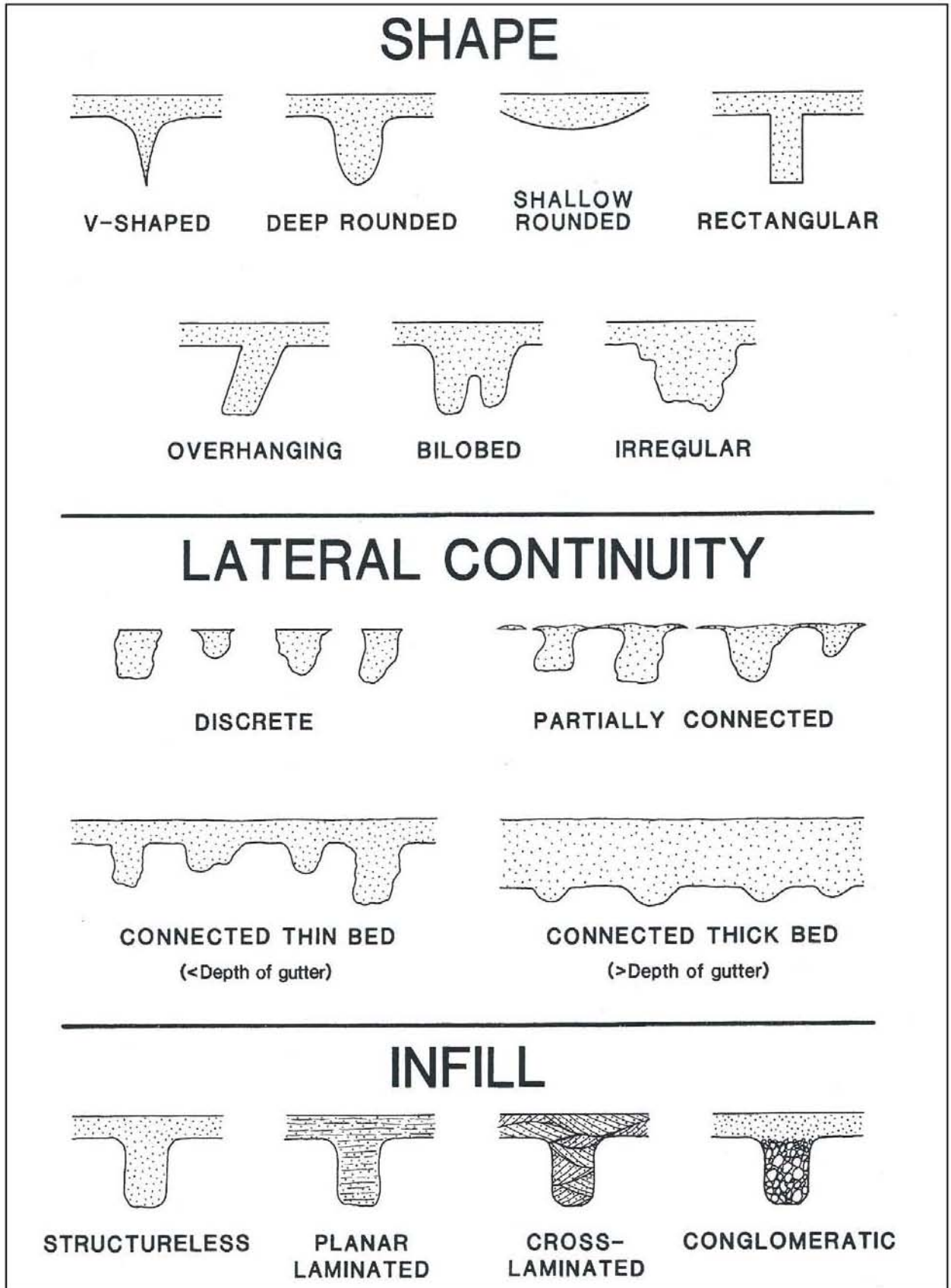
There are many factors that determine the nature of a stream channel, and the manners in which they combine to influence a system are very complicated and involve at least nine variables (Leopold and Wolman, 1957). These include discharge (amount and variability which generally fluctuates in braided systems), sediment load (amount and grain size, typically large amounts of coarse material), width, depth, velocity, slope and bed roughness. Amount and type of vegetation growth affects stream type (Schumm, 1968; Tooth, 2000; Long, 2006; Ashworth and Lewin, 2012), and therefore climatic and geologic factors must also be considered. Since braided

streams are common in many different modern and ancient climatic regions (Leopold and Wolman 1957; Allen, 1962; Moody-Stuart, 1966; Schumm, 1968; Walker, 1976; Miall, 1977, 1996; Myrow, 1992; Tooth, 2000; Long, 2006; Ashworth et al., 2007; Shambrook Smith et al., 2009; 2010; Ashworth and Lewin, 2012); vegetation growth and climate can be misleading. There are two main reasons for this: 1) Sediment load and discharge of a river partially reflects the climate and relief of the source, which may be hundreds of kilometres away, and 2) The causes of fluctuating discharge are diverse and include relief, dominance of mechanical weathering, flooding following glacial melting, arid monsoonal climate, lack of vegetation and consequent flash flood response to storms.

#### **Fluvial Style of the lower Katberg on Donald 207**

Deposition of the lower Katberg Formation supports data on sandy braided rivers (Ashworth et al., (2007); Shambrook Smith et al., (2006; 2009); Fielding et al., (2012); Horn et al., (2012)) along with meandering to braided fluvial style changes observed by Smith (1995), Smith and Botha (2005) and Botha and Smith (2006) for the upper Balfour and lower Katberg formations. Facies 1 and 2 sandstones on Donald 207 show architectural and morphological features of fine sand deposited in braided river channels. Bedform sizes are relatively small, the largest being in the range of 30-50 cm in thickness. This shows that in peak flood the channel was no more than 0.5 m deep. Bar tops are sometimes preserved and their undulatory tops can be seen on Donald 207 (Figure: 3.7). On the downstream sections of these bars, ripples form in the shallow water once the flood event has passed (Smith, 1995; Sambrook Smith et al., 2006; Horn et al., 2012) and many ripple surfaces have also

been preserved on Donald 207. The 3-D preservation of these ripples implies the ripples were not completely sub-aerially exposed before being buried by suspension settling silt (R. Smith pers. comm, 2010 ). Facies 1 and 2 sandstone bases show evidence of erosion, gulleying, and channel scouring, which most likely are the result of initial formation of a new channel following a local avulsion (Smith and Botha, 2005). They can also be formed by local erosion within the active channel (Horn et al., 2012). These scours may have not been filled by the same event that created them and Smith (1995) has interpreted the scours as rapidly dumped sandy sediment during waning flood events. Most deposits in scours show a massive texture, however some are trough cross-bedded and some may have been filled by in-channel migration of bars due to the presence of trough cross-bedding in many of the scours. Nevertheless, their shape, size, and differing internal sedimentary structures suggest a polygenetic nature to their origin. A study of “pot, gutter, and scour” casts on the bases of channel sandstones of the Chapel Island Formation Newfoundland, by Myrow (1992) suggests that depending on shape, lateral continuity and infill, scour fills can have an array of origins. Shape refers to the margin gradients and on Donald 207, V-shapes, overhanging, irregular, and deep rounded margined scour shapes as described by Myrow (1992) are the most common (Figure: 3.23). Steep sided scours are interpreted as early fill during rapid flow (Goldring and Aigner, 1982; Myrow, 1992). However, many can be explained by in-channel erosion by bars migrating downstream within an active braid channel or a newly avulsed channel as observed by Sambrook Smith et al. (2006; 2009) in the South Saskatchewan River, Canada, and large braid bar deposits in the Rio Parana, Argentina; as well as by Horn et al. (2012) in the Platter River, USA.



**Figure 3.23:** Characteristics of gutter casts in cross-section. These features were observed to occur on small (cm) and large (m) scale much like on Donald 207. Taken from Myrow (1992).

The sedimentary structures overlying the scoured surface indicate vertical accretion in the waning flow following a flood event (Smith, (1995); Smith and Botha, (2005); Ashworth et al., (2007); Shambrook Smith et al., (2006; 2009); Fielding et al., (2012); Horn et al., (2012)). Because little preservation occurs during the high velocity flow in the immediate flooding conditions of braided rivers, erosional boundaries between sandstone packages of the multi-storey sandstone facies most likely indicate successive erosion and waning flood cycle deposits in an active channel. Alternatively, the single storey sandstones could represent failed avulsion events that were immediately abandoned after the deposition of the channel deposit.

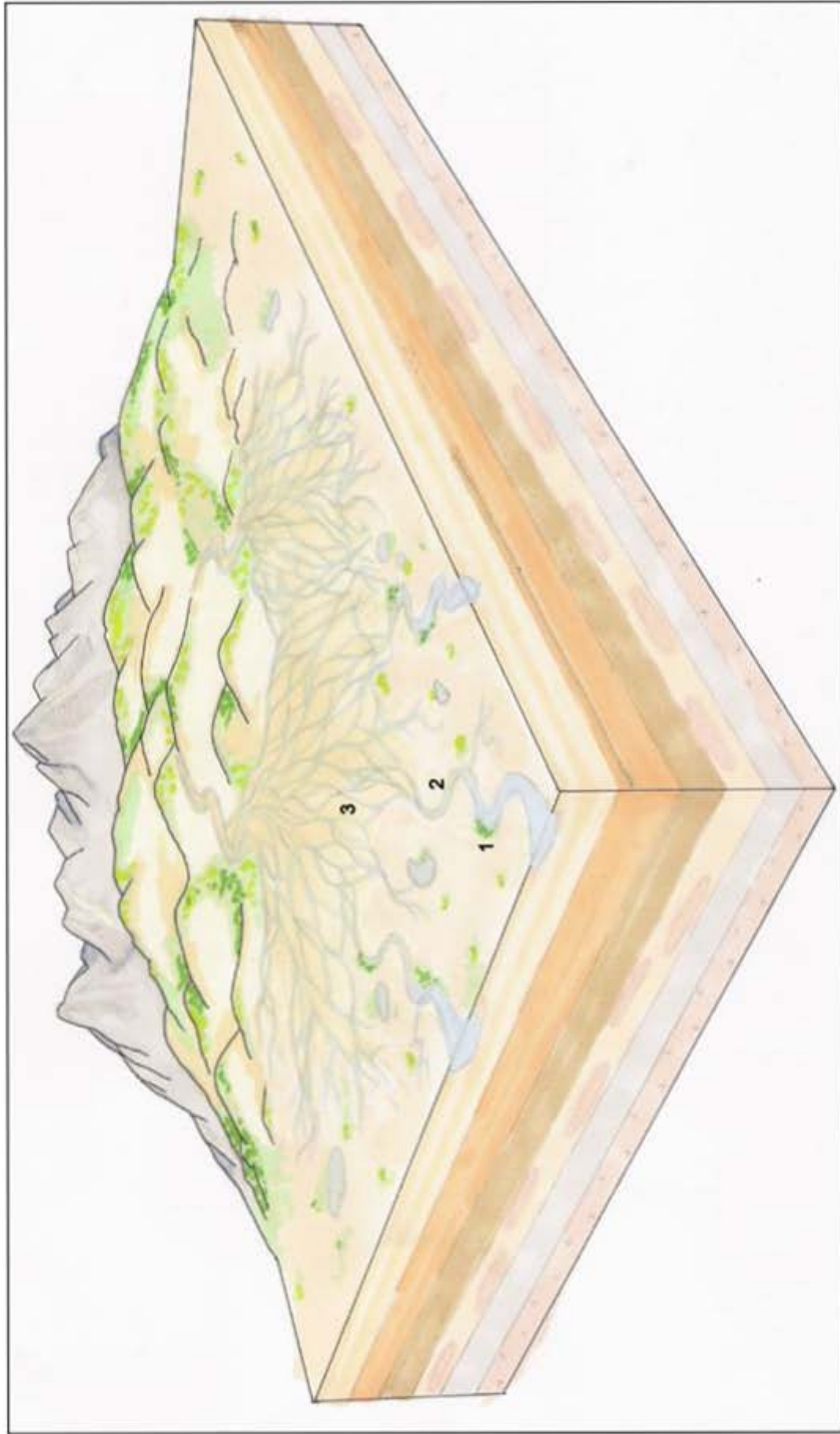
Aggradation in sandy braided rivers is normally a result of linguoid or transverse bars migrating downstream (Miall, 1977; Horn, et al., 2012). The preponderance of trough cross-bedding and horizontal lamination in the fine to medium-grained Katberg sandstones was interpreted by Smith (1995) as flood dominated sedimentation in wide, shallow, ephemeral stream channels. The lack of planar cross-bedding in the lower Katberg Formation on Donald 207 appears to show the internal structure of bars was dominated by deposits of downstream-migrating dunes, however Horn et al. (2012) observed a similar paucity of planar cross-bedding in some reaches of the Platte River and they propose that this is because linguoid and transverse bar deposits have not been preserved. Erosional scours within stacked sandstone beds in the lower Katberg may explain why these deposits have not been preserved, and also supports Smith's (1995) interpretation of flood-dominated deposition.

Smith (1995), Smith and Botha (2005) and Botha and Smith (2006) propose that much of the sandy Katberg sedimentation is controlled by strongly seasonal flooding. Flood intensities required for causing reworking and sedimentation in braided river systems is hard to quantify in the rock record according to a study by Shambrook Smith et al. (2012) on flood events in the Saskatchewan River, Canada. After observing surface (digital elevation models) and subsurface (ground penetrating radar) changes following a large (1 in 40 yr) flood event, it was discovered that although this flood reworked the entire braidplain, the scale of scour and style of deposition were similar to those associated with lower magnitude floods where the river was laterally unconstrained with extensive low relief floodplain.

Climatic regimes may be able to help with this conundrum as Smith and Botha (2005) believe much of the flooding was controlled by a monsoonal climate in a semi-arid dryland setting. According to Tooth (2000) floods in dryland environments are defined as the occurrence of water within a normally dry floodplain irrespective of amount. Dryland flooding can also be channel confined, partly channelized or unchannelized (Tooth, 2000). This may explain scour features seen in the Katberg sandstones; as well as the floodplain facies sediments and could be analogous to sheetfloods described by Graf (1988) in Piedmont settings and sheet-like deposits in unconfined Precambrian braided rivers by Long (2006), due to lack of rooted land plants. Although flood intensities in the lower Katberg Formation cannot be confidently quantified there is a lot of evidence for flood controlled sedimentation.

Inevitably as the flow is re-directed by more advantageous gradients, avulsion occurs and channels are abandoned. This leads to a gradual loss of flow energy such that fines suspended in the flow are able to settle (Smith, 1995). This explains the gradational tops of sandstone beds and silt-draped ripples. On the logged sections, as many as eight in-channel sand dominated successions can be observed dispersed between the finer-grained overbank and inter-channel deposits. Depending on how often the channel belt was reoccupied, either the Facies 1 or Facies 2 sandstone bodies are present. Mohrig et al. (2000) during their analysis of ancient alluvial sequences in Spain interprets numerous stacked channel fills as indicating repeated reoccupation of the same site by avulsing channels. They also indicate inherited floodplain topography was an important control on newly avulsed channels, which are strongly attracted toward pre-existing channels as they represent low points in the landscape (Mohrig et al., 2000). Although studies by Ashworth et al. (2006) indicate a positive relationship between avulsion and sedimentation rates, this relationship does not imply an increase in sedimentation with avulsion rate. This means the stacked channel sandstones on Donald 207 may represent margins of braid channels rather than the active channel itself as according to Ashworth et al. (2006), where flow occupancy is higher, and sedimentation rates are lower. If the channel does not flow for a long period of time, other finer sediments can be deposited above the old channel, but the type of sediment deposited depends on the proximity of the new channel.

Rocks of Facies 3 and Facies 4 were deposited as sediment in the inter-channel parts of the section of Donald 207. Facies 3 deposits may represent crevasse-splay deposits as they bear similarities with decimetre thick sheet sandstones from the Oligocene Guadalop-Matarranya System (northern Spain) described by Mohrig et al. (2000) and also sheetfloods described by Graf (1988) and Long (2006). They may also represent levee deposits due the presence of large black/brown weathering nodules and clustered nodule horizons, as Moody-Stuart (1966) describes large concretionary mergers in Devonian overbank deposits from Spitsbergen believed to represent levees on either side of the coarser low sinuosity channel deposits. Since levee deposits are common in anastomosing rivers (Nanson and Knighton, 1996; Ashworth and Lewin, 2012), it is likely some parts of the Katberg braided system were anastomosing as this is seen today in many modern braidplains such as the Platter River (Horn et al., 2012) and in many dryland fluvial sequences (Tooth, 2000). The Facies 4 siltstones are accepted to represent floodplain deposits (Smith, 1995; 2005; 2006). These finer over bank deposits are not normally a dominant feature in braided streams and this is due to the frequency with which anabranching streams can comb across the floodplain and erode these sediments (Allen, 1965). The relative abundance of overbank relative to channel deposits is supports deposition by both braided and anastomosing in the earliest Triassic Katberg Formation floodplains and supports observations by Smith and Botha (2005) and Botha and Smith (2006) that a transition from meandering to braided rivers occurred over the PTB, with only true braidplains appearing in the Early Triassic with the onset of deposition of the Swartberg Member, some 112 m above the logged section on Donald 207 (Figure: 3.24).



**Figure 3.24:** 3D block diagram based on fluvial style change interpretation by Smith and Botha (2005) and Botha and Smith (2006) across the PTB in the Karoo Basin. Numbers indicate the depositional environment of the (1) Palingkloof Member, (2) lower Katberg Formation and the (3) Swartberg Member.

It is tempting to compare Moody-Stuart's (1966) concretionary horizons to the Facies 3 meter wide concretions found in the Donald 207 study area. The presence of levee deposits has also been observed in modern rivers on the banks of highly braided streams (such as the Yellow River in China by Chien (1961), but do not normally last long enough to get preserved in the geological record (Moody-Stuart, 1966).

The floodplain deposits of Facies 4 that occupy long abandoned channel areas gradually raise the landscape in these areas by slow vertical accretion and suspension settling of fines, such as silt and clay during submersion by floodwaters. Slow accretion of fines on the floodplains is the norm in modern river systems and according to Walker (1979) rates of accretion on the floodplains of the Brahmaputra are estimated to be of 2 cm/yr or less. This is most likely a similar rate for the earliest Triassic floodplains, as individual beds and laminations are very thin and most often not continuous. Coarser beds of bluish-grey Facies 3 material is often inter-bedded, and could be interpreted as scour fills or distal portions of small avulsions onto on the floodplain following especially heavy floods. These deposits often contain bioturbation evidence such as vertical burrows.

These Triassic Beaufort floodplains must have been vegetated to some degree, but no rhizcretions were found on the logged section. However plant stem impressions were found in some mud rip up clast layers within the sandstones and in other parts of the field area. Moreover, stellate nodules in Facies 4 deposits are interpreted here to be fossil tree roots (Smith and Botha, 2005). Khadkikar et al. (1998) describe vertical fissures from Quaternary deposits in the Gujarat region of western India while formed in response to extreme drying events when the soil started cracking. These cracks were infilled by detrital sediment or calcium carbonate precipitating from incoming solutions. Fielding et al. (2009) also observed desiccation cracks in the PTB Amery Group, Antarctica, that are used as evidence for free drainage in the alluvial landscape.

These fissures are undoubtedly similar to the structures seen in the Donald 207 study area. However, the lack of rhizcretions in the logged area may suggest lack of vegetation, but their presence may have been obscured by the weathering profile of the rocks since we know that plants were present from rare plant stem impressions (Figure 3.4). If floodplain accretion occurs over long periods of time, plants can take hold and soil forming processes begin. Evidence of this in the study area include the formation of palaeosol horizons, which are often noticed as horizons of carbonate nodules, slickensides (evidence of soil movement according to Khadkikar et al. (1998), and colour mottling of deposits in the field area (Smith, 1995; 2005).

Eventually these floodplain deposits normally become eroded by the introduction of an avulsed channel into the immediate area following a flood, as is evidenced by intraformational conglomeratic material of Facies 5. Miall (1977) describes a similar facies in his review on braided river models. The cobble-gravels are described as

being clast-supported, which indicates the sand and silt matrix filtered into the interstices following deposition. In Miall's (1977, 1996) facies, clasts are commonly imbricated and lateral changes in grain size may be apparent, which has been interpreted as representing channel-lag deposits (Miall, 1977, 1996).

This is similar to Facies 5 described in this study, only the clasts are more pebble to gravel-sized, and consist of reworked carbonate nodules and bone material. Petrographic studies revealed radial calcite surrounding many of the grains (Figure 3.21). This has been interpreted by Tabor et al. (2007) as representing precipitation within a supersaturated near surface environment, such as a phreatic backwater swamp. Bone and nodule samples in Facies 5 do not show significant rounding, thus they may have been sourced locally. It is likely then that Facies 5 may have had relatively high energy beginnings in its deposition, reworking nodule material from earlier channel and over bank deposits during flash floods. However, once the floods had ceased, low oxygen conditions caused precipitation of radial calcite around Facies 5 grains (Tabor et al., 2007). The nodules in Facies 5 have an unknown origin. However their association with bone fragments, some of which showing evidence of being fossilized prior to incorporation into conglomerate (R. Smith pers. comm, 2011), and the occurrence of fossil bone on Donald 207 in Facies 4 siltstones, suggests their source must be from the floodplain deposits. It is speculated that they have been locally eroded, transported, abraded and re-deposited in the channel setting by reworking old channel deposits, or re-deposited

into the channel by floodplain tributaries (Smith and Botha, 2005; Botha and Smith, 2006). Nodules often occur as pods in lag deposits or scour fills beneath multi and single storied sandstone beds and they possibly show the position of the thalweg in the braided channel, as only the coarsest material would be able to be deposited in this position (Smith and Botha, 2005; Botha and Smith, 2006). The presence of Facies 5 vindicates the occurrence of floodplain winnowing in this environment, probably during the onset of wetter conditions and incision into the older landscape by a river channel avulsion onto the floodplain (Pace et al., 2009). No thick horizons of peloids have been found in the Facies 4 deposit which also supports the notion that floodplain peloids and fossil bone fragments have been concentrated by these winnowing processes.

Field observations suggest that the different types of nodules of Facies 1, 2, 3, and 4 can be divided into those formed during pedogenesis (soil formation), and those formed during early diagenesis (formation immediately after burial). These nodules are termed: a) pedogenic; micritic calcite formed during active soil formation, while in direct communication with the atmosphere (also known as peloids) (Packham et al., 1960), and b) early diagenetic; microspar calcite precipitation around organic cores via groundwater activity, respectively (Smith, 1990). Smith (1995) considers the Facies 4 nodules to be pedogenic as they are associated with fossil palaeosol horizons whereas the Facies 1, 2, and 3 nodules are early diagenetic due to their apparent alignment with palaeoflow directions in the sandstone beds (Johnson, 1989).

Many of the carbonate nodules contain fossil material within them indicating that the bones may act as nucleation sites which promote early calcite precipitation either during soil forming (pedogenesis), or lithification processes such as diagenesis. The bone preserved in these nodules is black and has not been affected by compaction.

Fossils not encased within nodules often show evidence of compaction during the lithification process. Identical observations have been recorded from Permian fossils lower in the stratigraphy (Smith, 1993; Rubidge, 1995). The presence of undeformed fossils inside nodules suggests that the nodules formed around the fossils before the onset of compaction, and that the nodules on Donald 207 are pedogenic (Facies 4) and early diagenetic (Facies 1, 2 and 3). Fossil bone fragments have been found in the Facies 5 conglomerate which may indicate that partially fossilized material is also being incorporated into this intraformationally derived conglomerate. The rivers must have altered course relatively frequently and when they did, they did so rapidly, destroying much of the floodplain facies deposits in their immediate area, and leaving a select fraction in their wake following inevitable abandonment of the cut channel.

### **Aridity Hypothesis**

It was first proposed by King (1961), and later Stavrakis (1980) that depositional features in the lower Triassic sections of the Katberg Formation indicate seasonal aridity. Hiller and Stavrakis (1984) later outlined parameters in the Katberg Formation that indicated an arid fluvial setting. These included a dominant red colour to floodplain sediments, sedimentary structures that indicate erratic or periodic rainfall (i.e flash flood events), pedogenic carbonate, and palaeontological evidence. Smith

and Botha (2005), and Smith and Botha (2006) believe sedimentological evidence in the Karoo Basin from this time represent a change to a strongly seasonal monsoonal climatic regime in the Karoo Basin.

The dominant red colour of floodplain sediments, which is seen in many other formations worldwide, is believed to represent fines deposited in an arid setting (i.e. the Permian Clent Formation, British Isles, Late Triassic Chinle Formation, Arizona, and Jurassic Elliot Formation, South Africa). This theory comes from the generally accepted idea that green sediments are deposited under predominantly reducing conditions, and red sediments in dominantly oxidizing conditions. In arid climates the oxidizing environmental conditions are favoured (Van Houten, 1973; Walker, 1976). More recently Dubiel and Smoot (1994) put forth a model suggesting continental red bed formation is favoured by monsoonal desert to savannah vegetation. Parrish (1998) later constructed a similar terrestrial red bed formation model indicating their association with warm and dry or seasonal climates, with respect to rainfall.

However, it has been debated as to how reliable rock colours are. Reineck and Singh (1980) proposed that diagenetic processes alter colour, and these can develop under a much wider range of environmental conditions. Retallack (1991; 1997; 2001) has also contested these older models and refers to many examples of diagenetic reddening of non-desert paleosols by dehydration of iron oxides. In the desert and monsoonal environments of modern Pakistan and India, Retallack (1991) shows both grey and red paleosols are found. Wyn (2000) and Wyn and Retallack (2001) also describe lack of significant reddening in Cenozoic paleosols in Africa. Due to the lack of savannah grassland environments prior to the Cenozoic, Dubiel and Smoot's

(1994) model does not provide an exact explanation for the origin of redbeds in the past. A case study by Sheldon (2005) on the origin of Late Permian red beds from northwestern Sardinia suggests their red colour merely represents well-drained conditions and provides no information on palaeoclimatic conditions at the time of their formation. Studies on carbonate content, ichnofossils, and pedotypes suggest a high mean annual rainfall (~ >1300 mm/year) that is not consistent with desert conditions. Lack of carbonate nodules also suggests neither a wet or dry monsoonal climatic regime was present (Retallack, 1991; Sheldon, 2005).

From these results it shows that red colour origins should be seen as able to form in a variety of settings and must not be generalised into one genetic model. Red colour alone is therefore not diagnostic. On Donald 207 red floodplain deposits are not apparently more common than green floodplains deposits. On the vertical log green and red siltstone occur in equal abundance. In fact it was apparent that the green siltstone was found in greater abundance, and almost always occurred in close proximity to the Facies 1 and 2 sandstone beds, either directly in contact above or below their bases. This pattern relates to Sheldon's (1995) observations that redness cannot be used as a proxy for aridity and merely denotes better drainage. It is intuitive that floodplain deposits more proximal to the river channels would be exposed to low drainage (reducing) conditions whereas away from the river channel more free drainage occurs thus a red colour to sediments would be adopted.

Sedimentary features such as tabular single and multi-storied sandstone beds (Facies 1 and 2) with basal lag deposits (Facies 5) and basal scours are regarded by

Smith and Botha (2005) to suggest braided to anastomosing rivers subjected to seasonal flash flood events. This alone does not support an arid climate, but it does suggest seasonal extremes. Tooth (2000) emphasises the importance of large floods and variable flow regimes in dryland river morphology, particularly in Australian and southern African arid zones. Haycock et al (1997) mention the possibility of seasonal snowfall of the Gondwanides, and due to the latitudinal position of the Karoo Basin in the earliest Triassic (50° S) (Smith et al., 1981; Faure et al., 1995), seasonal snow melt may have also played a role in fluvial pulses.

Retallack et al. (2003) interpret LAZ paleosols with greater depth to calcic horizon as presence of a seasonally lower water table than in the Permian DAZ. Desiccation features such as mud-cracks (sand-filled ones the only easily visible ones on Donald 207) and nodules with septarian shrinkage cracks also suggest seasonal wetting and drying of the soil and soil profile (Retallack, 2003; Smith and Botha, 2005; Botha and Smith, 2006). Root and stem traces on Donald 207, believed to belong to *Equisetium* flora, are also suggestive of at least a seasonally dry climate. This is because these plants, along with the *Dicroidium* flora, survived the End-Permian mass extinction event (Smith and Botha, 2005; Botha and Smith, 2006). It is believed that many of the floodplains during earliest Triassic times were sparsely vegetated, if vegetated at all during particularly dry spells (Smith and Botha, 2005; Botha and Smith, 2006). This caused fluvial river systems to become increasingly braided as the lack of vegetation allowed wide channels to form and lowered constraint of fluid flow to the channels.

Long (2006) describes similar features in Precambrian braided river deposits in the Late Paleoproterozoic Athabasca Basin of northern Saskatchewan and Alberta, Canada. Although these features would have formed under an array of climatic conditions in the Precambrian due to lack of rooted land plants, Long (2006) suggests they appear to be fairly similar to those of modern braided and ephemeral systems in dryland climates described by Tooth (2000). Tooth (2000) emphasises the erosive effects of floods in dryland systems due to lack or loss of vegetation cover in dry seasons. This may also explain how floodplain winnowing can easily occur (and produce Facies 5 nodule conglomerates found on Donald 207) as lack of vegetation combined with flash flood events could easily erode floodplain silt. This means that in an attempt to understand and identify dryland fluvial deposits (modern and ancient) Precambrian fluvial deposits may provide good facies models for these systems.

Ubiquitous apparent early-formed carbonate nodules on Donald 207 could support the idea of seasonal climatic differences during their formation. Carbonate nodules are present in calcic palaeosols in the floodplain Facies 4 deposits, encasing solitary bone and complete fossils sandstones and sandy siltstones of Facies 1, 2 and 3, respectively. The nodules preserve evidence of fluid flow in cut hand specimen (Facies 3 black weathering nodules) which indicates that they formed as groundwaters flowed through these more porous beds (Johnson, 1989). Previous studies on the ancient stratigraphic record mark the presence of nodules as indicating periods of seasonal monsoonal climates (McPherson, 1979; Retallack, 1991; Smith, 1995; Smith and Botha, 2005).

Calcretes and other carbonate precipitates are important components of modern semi-arid depositional systems and characteristic of regions experiencing a mean annual rainfall of around 500mm (Khadkikar et al., 1998; Retallack, 1991; Rowe and Maher, 2000; Srivastava, 2001; Neymark et al., 2005; Schmid et al., 2006; Ringrose et al., 2009) forming during seasonal wetting and drying cycles at the sediment water interface in the soil profile. Carbonate nodules on Donald 207 support their formation in an environment subject to possibly a highly seasonal or monsoonal climatic system (Retallack, 1991; Smith, 1995; Retallack et al, 2003; Smith and Botha, 2005). However, this says nothing about the aridity or temperature of the Earliest Triassic Karoo Basin environment during the deposition of the lower Katberg Formation.

Much of the sedimentological evidence for aridity in the lower Katberg Formation braided system is purely circumstantial and there is much scope to rectify this. If red colouring cannot be used to study possible aridity in the earliest Triassic Karoo basin, then other aspects of the Katberg Formation sediments need to be considered, such as sedimentary features, pedogenic carbonate, root traces, trace fossils, and taphonomic information from abundant vertebrate fossils (which will be considered in later chapters). In the next chapter evidence for aridity will be explored further by use of stable isotope data collected from the carbonate nodules, but also fossil bone and tusk material from fossils found on the logged section.

## 4. Stable Isotope Analysis

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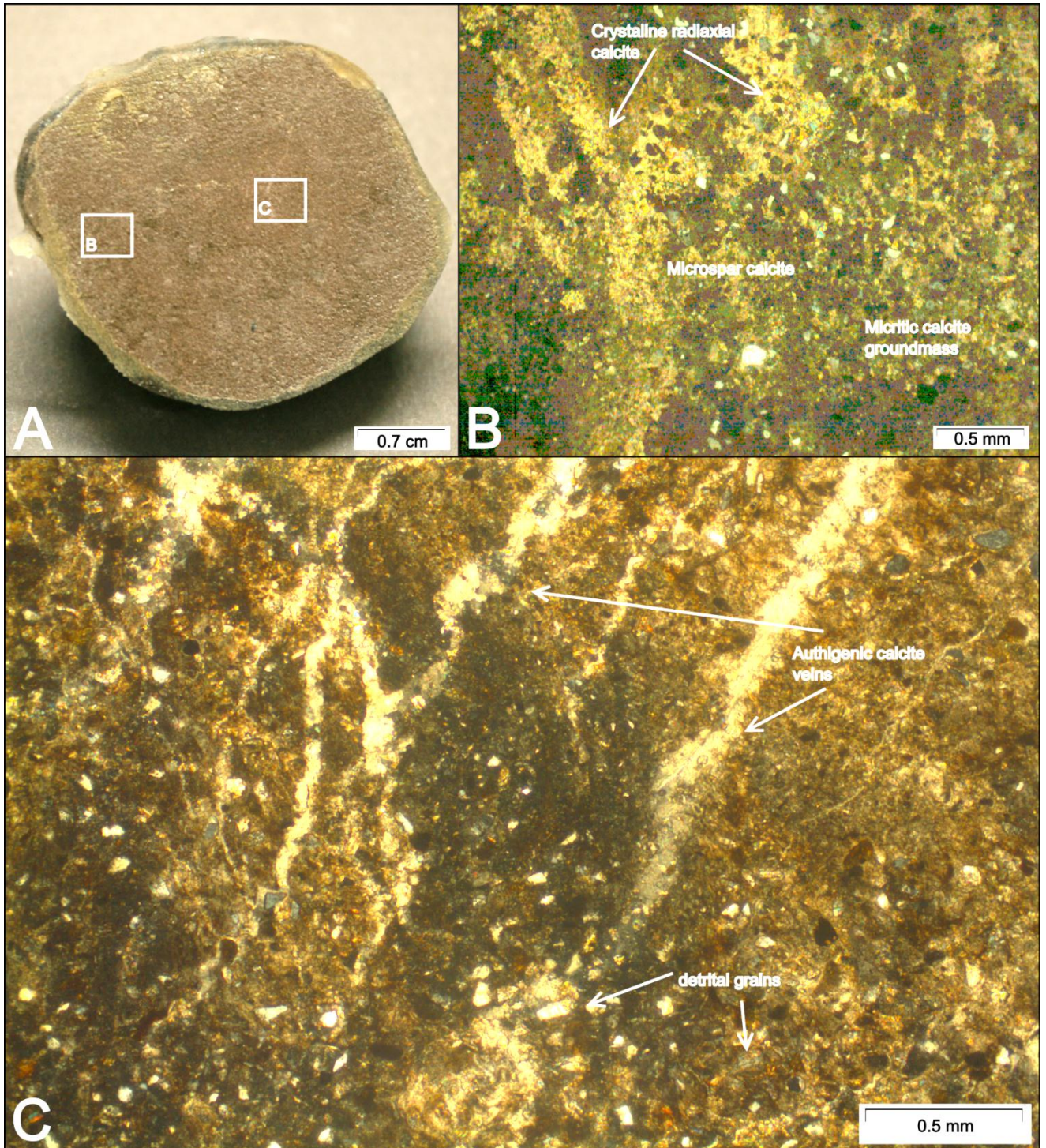
### 4.1 Introduction

This chapter focuses on the stable isotope composition of carbonate nodules, fossil bone, and fossil tusk. Samples were collected in the field area in the interval between 8-10 m above the base of the 29 m thick logged section where the largest number of *Lystrosaurus* vertebrate accumulations occurs. The positions of collected nodule, fossil tusk, and fossil bone samples are shown on the panel section (Figure: 3.2). Some additional nodules were collected from a horizon 7 m below the 29 m thick panel section for comparison. Initially the intention was to measure isotope changes within single nodules (i.e. from rim to centre of nodules) to document any trends as the nodule formed. However, no significant rim to centre isotope patterns emerged from the analyses and the centre to rim analyses are thus reported as single mean values for each nodule type. The tusk and bone analyses represent the mean of two *Lystrosaurus* specimens from bonebeds numbered 2 and 3 on the Figure 3.2 panel section. Nodule, bone and tusk samples were analysed for stable oxygen and carbon isotopes to provide data, independent of sedimentology, on the degree of aridity during deposition of the Katberg Formation. If the data show evidence for aridity, it will support the hypothesis that the fossiliferous floodplain bonebed horizon may represent a period of seasonal aridity or drought (Smith and Botha, 2005).

This study involved bone samples collected from the *Lystrosaurus* bonebeds and tusk material from *Lystrosaurus* on the same or similar horizons to the vertebrate bonebed accumulations. Because fossil bone and tusk material can be problematic in isotope studies, as will be explained later in the chapter, the three types of co-occurring calcareous nodules were sampled and analysed for comparison with associated bone and tusk material.

#### **Nodule Types: Facies 4 Red Siltstone Nodules**

The majority of Facies 4 red siltstone nodules show a concentric ring pattern in cross-sectioned hand specimen. The rings are defined by darker and lighter red banding on the surface of and within the nodules. In thin section no ring structures are observed but rather a homogenous red micritic matrix cemented by microspar calcite. This microspar calcite is particularly apparent in the core of the nodules (Tabor et al., 2007). Along the outer 0.2-0.5mm rims of the nodules growth of fibrous textured elongate calcite crystals (radial calcite) prevails and decreases away from the rims toward the centre (Figure: 4.1). The nodule rims are harder than their centres and this may be due to the crystalline radial calcite growth. Some detrital grains are present as isolated grains within the micrite matrix. Although hard to identify, many of the grains appear to be quartz and minor feldspar grains that are weathered or chemically altered. Veins of calcite radiate outwards from the nodule centres but do not extend as far as the radial calcite nodule rims. These calcite veins are believed to represent septarian shrinkage cracks refilled with secondary calcite growth (Smith, 1990). This nodule type is referred to as Facies 4 i.



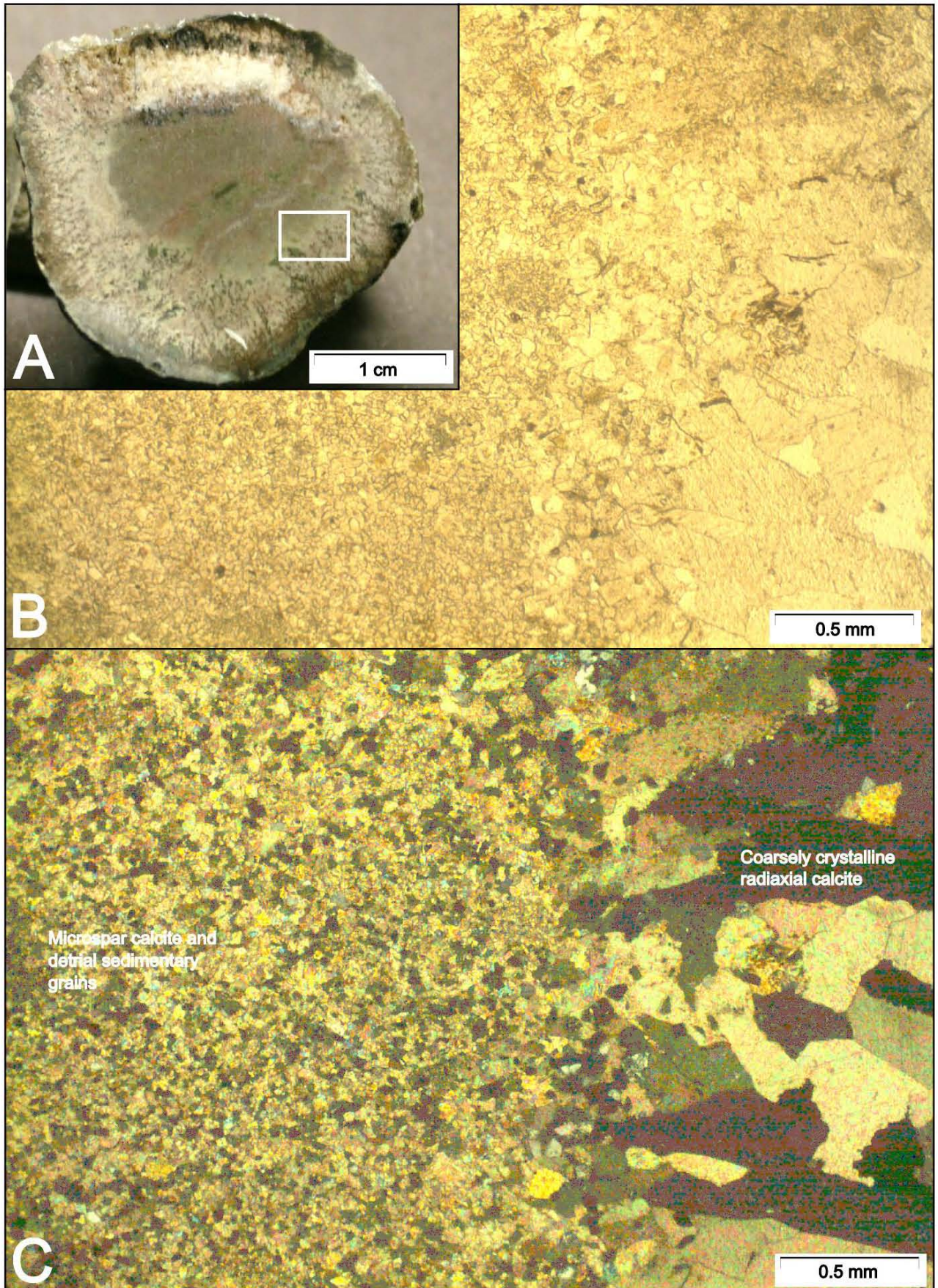
**Figure 4.1:** Thin section photographs of Facies 4 red siltstone nodules that were used for the stable isotope analysis. **(A)** cut calcareous nodule, and the positions micrographs **(B)** and **(C)**. **(B)** The position of radiaxial calcite and microspar calcite close to the rims (arrowed). **(C)** The central area of the nodule. Cracks are infilled with secondary calcite and micrite (microspar calcite and mudstone gains), and detrital quartz and feldspar grains are also shown.

### **Nodule Types: Facies 4 Green Siltstone Nodules**

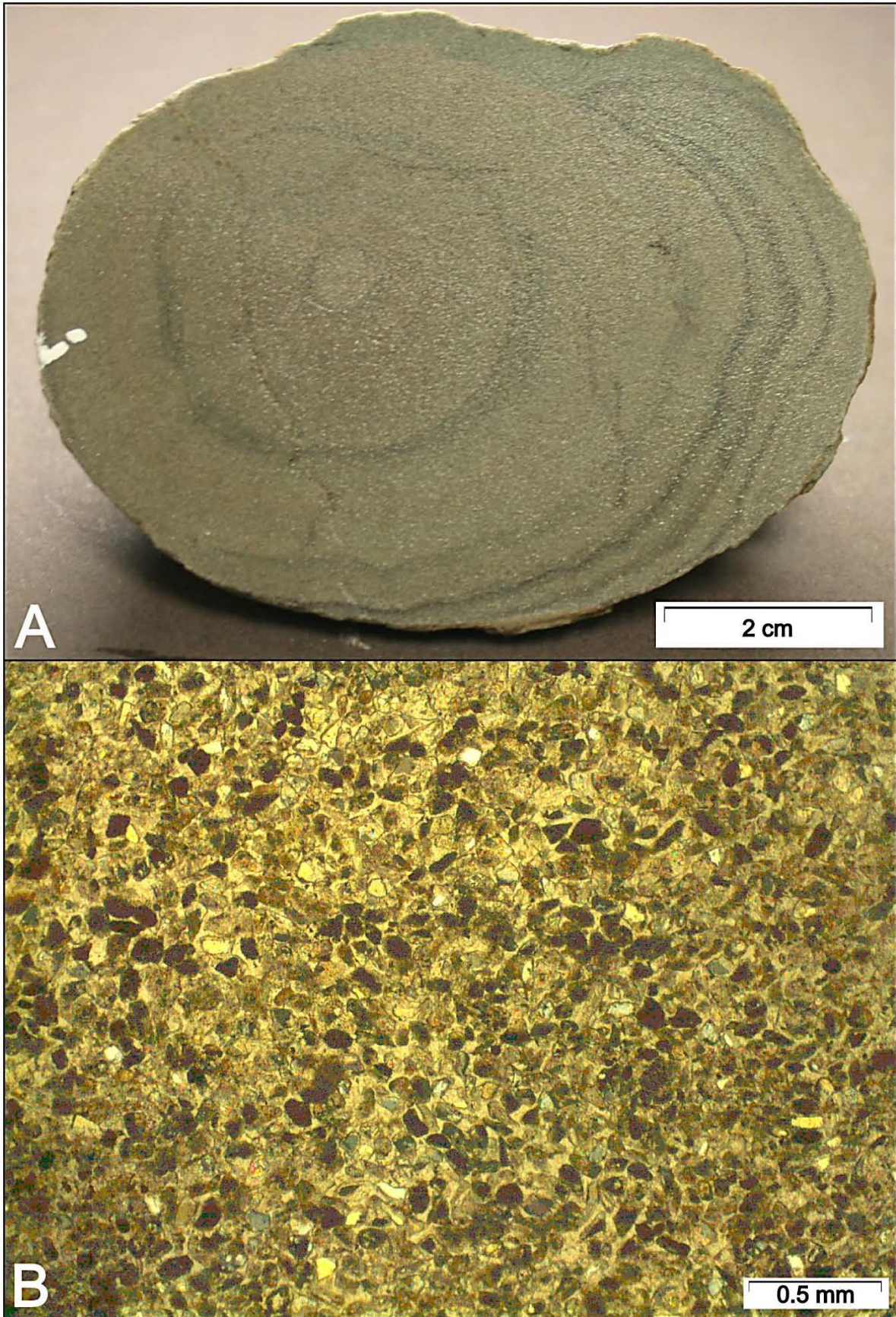
Facies 4 green siltstone nodules are similar to the nodules found in the red siltstone, only they do not show any form of concentric growth and their outer rim of crystalline radial calcite is up to twice as thick and consists of larger inter-grown calcite crystals (Figure: 4.2). Within their centres there are detrital grains of quartz and feldspar within a matrix of micrite and cemented by microspar calcite crystals. Cracks within nodules are common and are filled with sparry calcite crystals. This nodule type is referred to as Facies 4 ii.

### **Nodule Types: Concentric Nodules**

Concentric nodules were found only in the sandstones and sandy siltstones of Facies 1, 2, and 3; often occurring in inter-grown clusters or small groups. Although the concentric pattern is obvious in hand specimen as circular light and dark rings following the contours and shape of the nodule; in thin section the concentric pattern is not obvious. It is not clear why the pattern cannot be seen when the nodules are cut, but it may be possible that weathering in the field reveals the concentric growth pattern on the surface of the nodules. Fine grained quartz, feldspar, and lithic fragments seen in the concentric nodules are in modal abundances identical to what are observed Facies 3 sandy siltstone thin sections. The only differences are microspar calcite crystals cementing the groundmass (Figure: 4.3). No observable radial calcite is present.



**Figure 4.2:** Thin section micrographs showing internal detail within a Facies 4 green siltstone nodule sampled for stable isotope analysis. **(A)** The nodule sampled and the position of micrographs **(B)** and **(C)**, which are of the same image in plane polarised light **(B)** and crossed polarised light **(C)**. **(B)** and **(C)** show clearly radiaxial calcite growth in the rims and microspar calcite growth in the central parts of the nodule (labelled).



**Figure 4.3:** (A) Concentrically banded carbonate nodule sampled in the stable isotope analysis. (B) The similarity to the Facies 1 and 2 sandstone under thin section is apparent, the only difference is the presence of calcite (nodule fizzes under HCl).

Concentric nodules are believed to have a diagenetic origin and were used to compare to the other types of nodules regarded as pedogenic by Smith (1995). Generally nodules consisting of micritic calcite are more reliable than nonmicritic nodules as a proxy for palaeoatmospheric CO<sub>2</sub> δ<sup>13</sup>C and δ<sup>18</sup>O (Tabor et al., 2007). This is because micritic calcite is typical of soil carbonate that forms in well drained soils open to gaseous diffusion between soil and atmosphere. Coarsely crystalline radiaxial calcite is a form of crystal growth more typical of phreatic, closed system environments (Tabor et al., 2007). For these reasons, the most likely pedogenic or soil-formed nodules taken from Facies 4 successions were given more attention in this study as they consist of more micritic than radiaxial calcite.

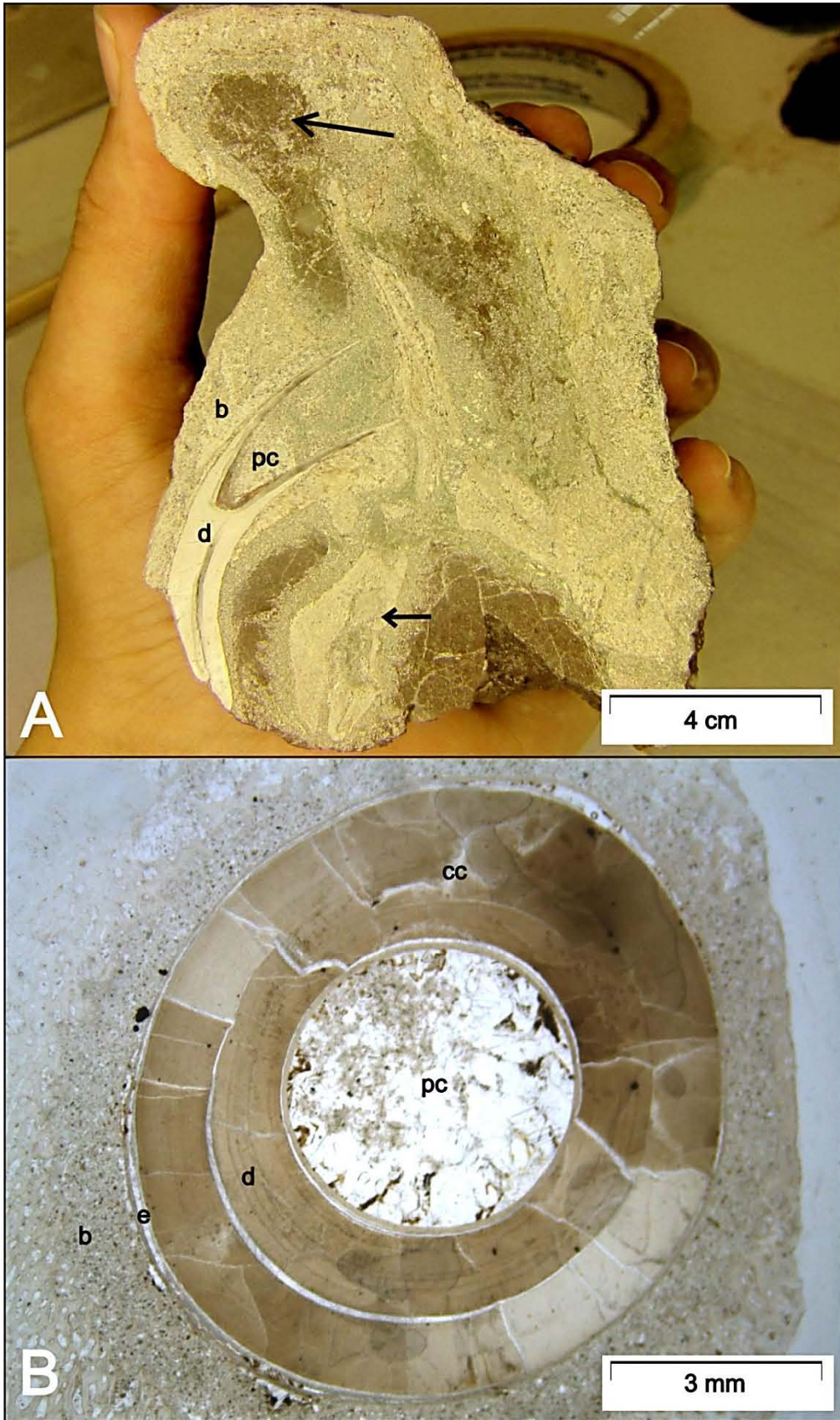
Samples of the smaller concentric nodules were also taken but were utilised only as a comparison to decide whether any kind of late stage overprinting (such as from the intrusion of the Jurassic Karoo dolerites) may have affected their isotope ratios. The larger nodules, unique to Facies 3, were not sampled in this study. As previously mentioned, the isotopic study was mainly aimed at sampling Facies 4 micritic nodules which, based on the field evidence, are thought to have been formed more or less contemporaneously on similar stratigraphic horizons to the *Lystrosaurus* bonebeds.

### **Fossil Bone and Tusks**

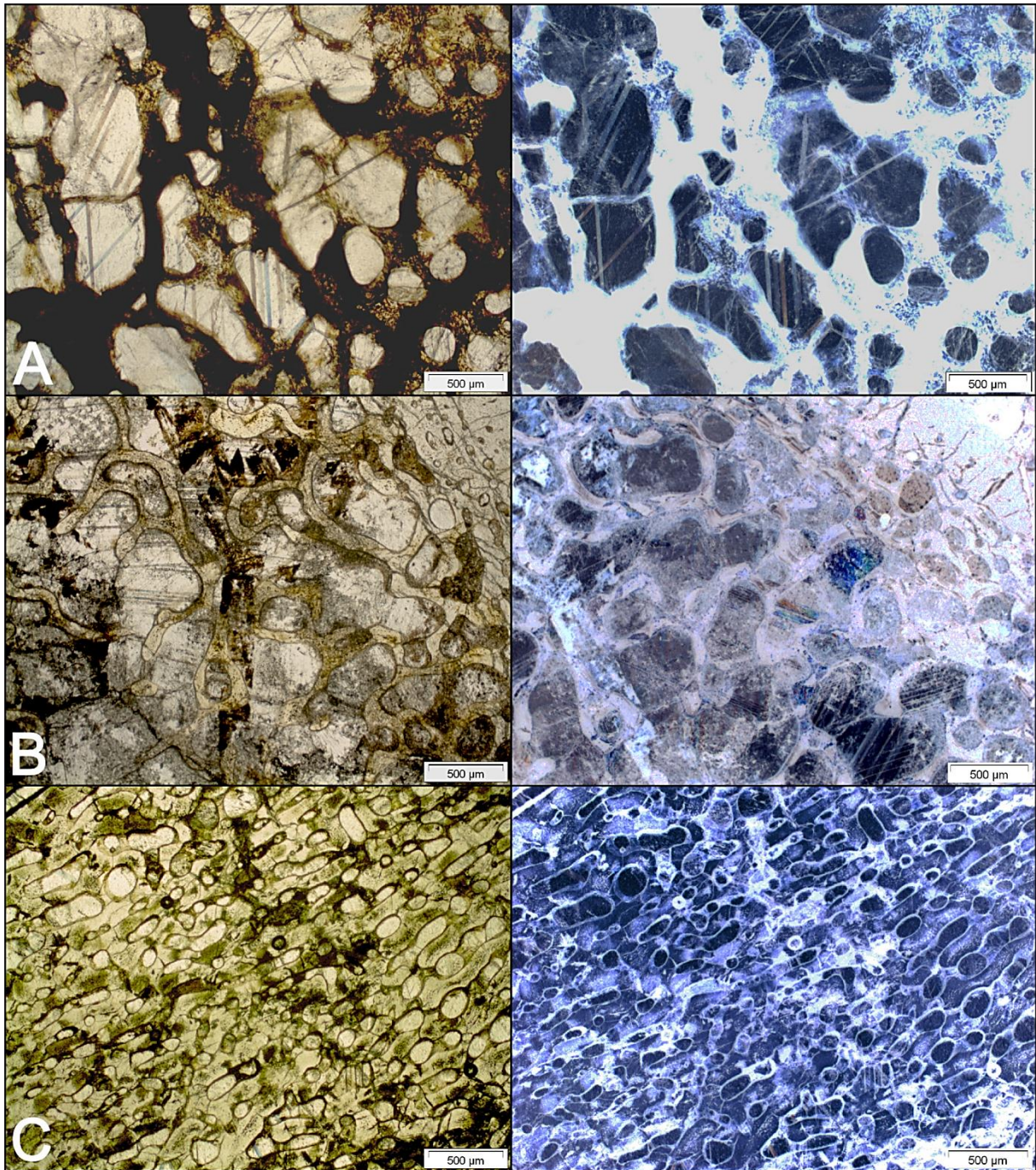
Fossil bone was collected from the five bonebeds of *Lystrosaurus* present in the panel section (only bone from three bonebeds were analysed isotopically however) along with tusk material from *Lystrosaurus* (two specimens) found on or near the same stratigraphic

horizons (Figures 4.4 and 4.5). Key to any isotope study is the need to understand the internal structures that comprise bone, how they formed, and how fossilization may preserve or alter these internal structures. Bone has a complex structure which is still not entirely understood, but according to work done by Weiner and Wagner (1998) the basic building block of living bone is the mineralized collagen fibril (Figure: 4.6).

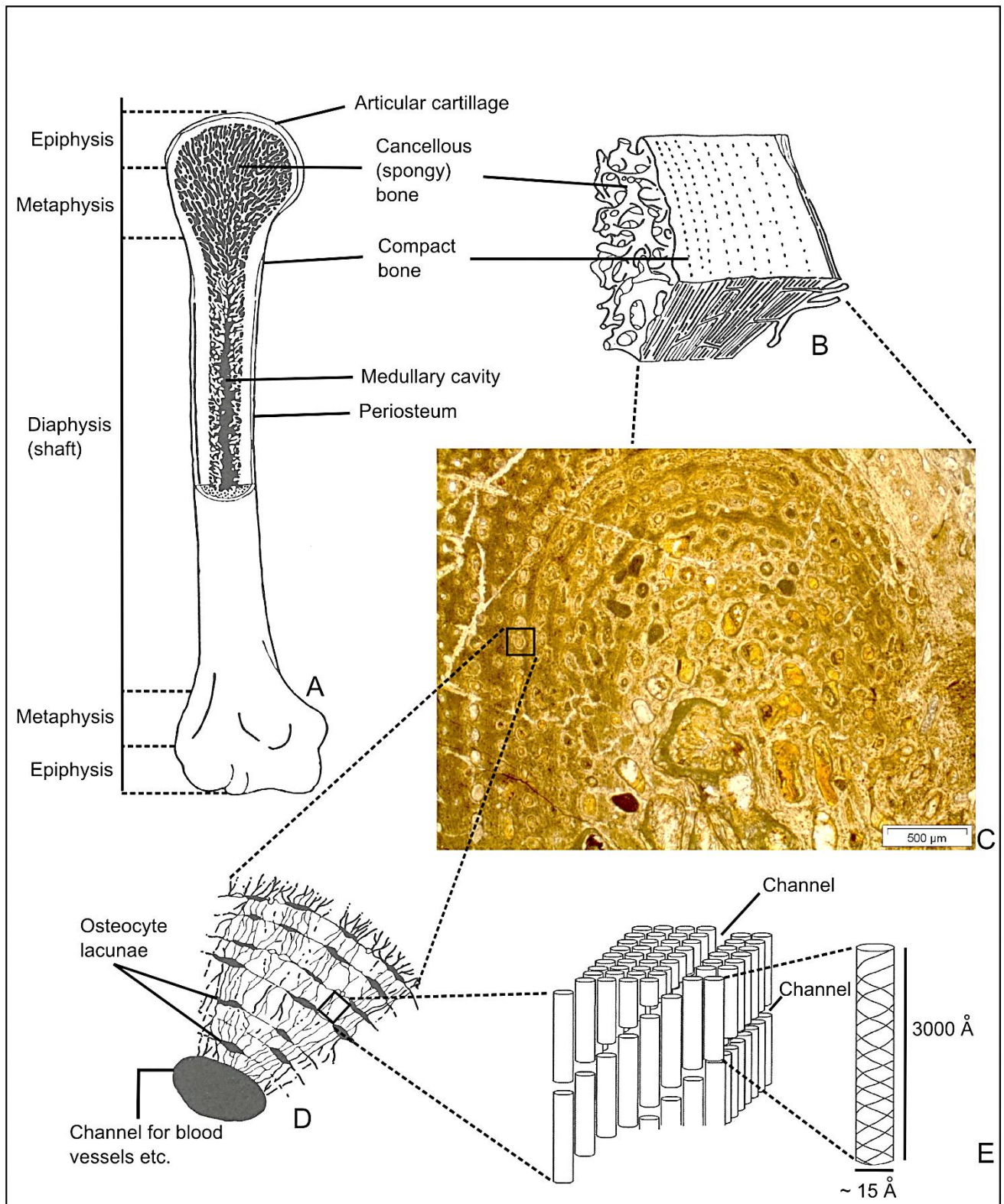
These fibrils consist of fibrous protein collagen which constitutes the main component of a three-dimensional matrix into which, parallel layers of plate-shaped crystals grow 20-30 Å thick and 100 Å long having hexagonal symmetry not exhibited macroscopically. The mineral is known as dahllite, or carbonate hydroxy apatite ( $\text{Ca}_5(\text{PO}_4, \text{CO}_3)_3(\text{OH})$ ). Dahllite most likely occurs as the smallest crystals known to be formed biologically and align themselves with the collagen fibril framework in the living animal (Weiner and Traub, 1992). Depending on the type of bone these mineral-organic composite materials are organized into layers or lamellae to form an array of different hierarchical structures that provide the bone with flex from the collagen and rigidity from the mineral component (Chinsamy-Turan, 2005). Upon death the original bone structure becomes compromised from soft tissue decay including decay of collagen. The decay rate of bone is largely controlled by the decay rate of the carcass, not only by microorganisms within the animal, but also by colonization by bacteria and fungi from the surrounding environment (Trueman and Martill, 2002).



**Figure 4.4:** (A) *Lystrosaurus* skull from Donald 207 sampled for this study. The skull was cut tangentially exposing a deep tusk root, pulp cavity (pc) and dentine (d). Bone (b) surrounding the tusk is indicated as is the eye socket (large arrow) and lower jaw (small arrow). (B) A thin section of a tusk from another *Lystrosaurus* specimen found in the study area but was not used in the stable isotope study. The detail shown is important as authigenic calcite (cc) can potentially contaminate stable isotope studies if one does not factor in their presence. Calcite has also completely replaces the pulp cavity (pc). The incremental growth in the dentine (d), the enamel (e) and surrounding bone (b) are also shown.



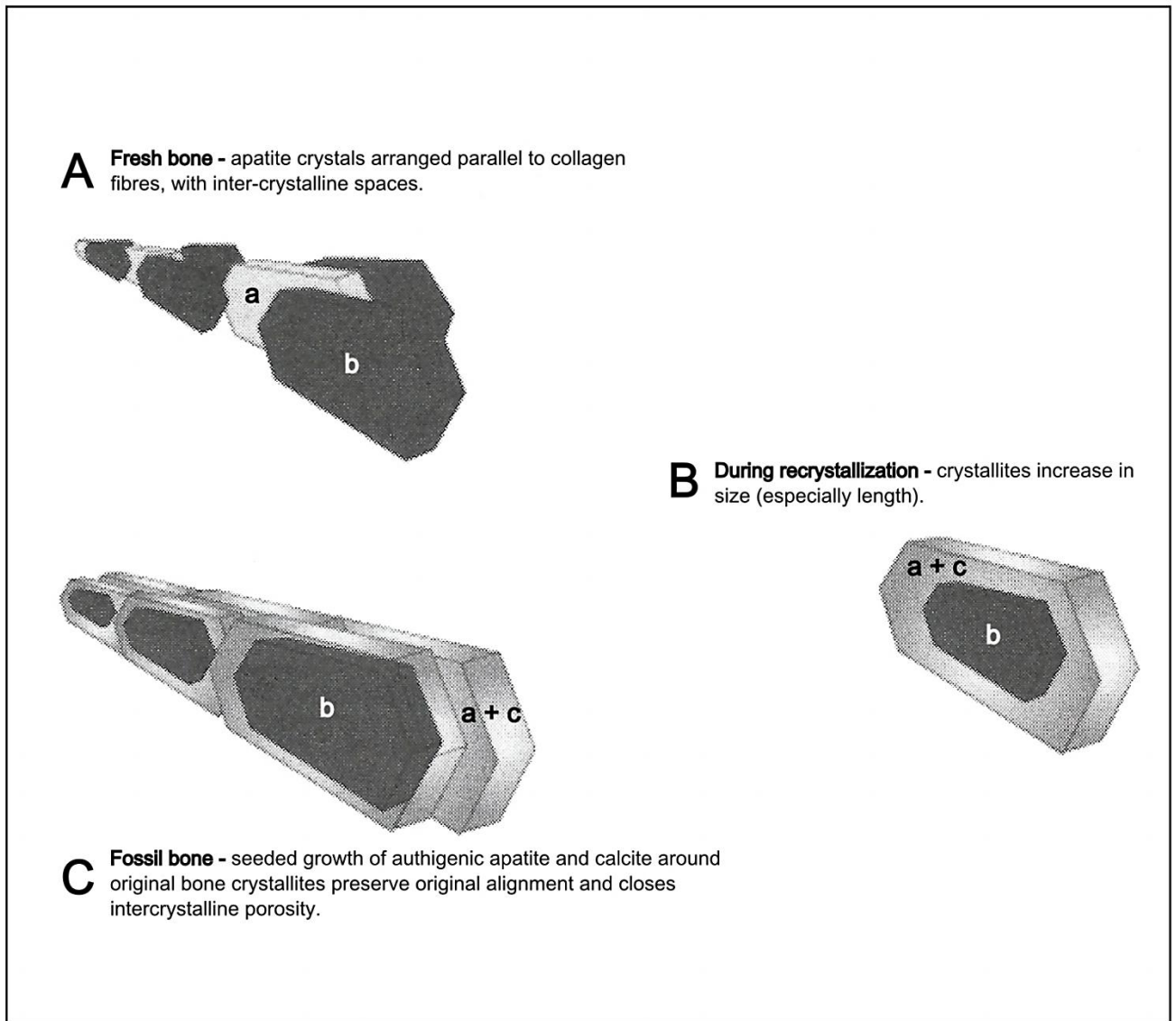
**Figure 4.5:** Thin section micrographs of fossil *Lystrosaurus* limb bones sampled from *Lystrosaurus* accumulations 1 (A), 2 (B) and 3(C). The bonebeds are numbered in this manner on the panel section and in the taphonomic study. The photographs are shown under plane polarised light (left images) and as an inverted colour image (right images) in order to help show bone microstructure and authigenic calcite crystal growth. The thickness of the osteonal cavities varies in the images due to the orientation the bone was sectioned. (A) and (B) were cut parallel to the shaft of the limb bone whereas (C) was sectioned across the limb bone shaft.



**Figure 4.6:** Diagrams shows internal and micro-structure of a typical mammal bone (not drawn to scale). Reptilian bone may differ by the presence of growth lines and evidence of arrested growth during harsh conditions (Chinsamy-Turan, 2005). (A) The position of outer protective layer (periosteum), inner compact and spongy bone. (B) A cross-section sketch through the compact and spongy bone. (C) A transverse thin section image of the miniature long bone from an unidentified fossil reptile from the Donald 207 section. Note the presence of compact and spongy bone and also circular osteon structures that house a central blood vessel. (D) A section of the osteon and blood vessel detail. Smaller capillary-like features surround the vessel (canaliculi) which house the bone forming cells (osteocytes). (E) The final microscopic bone forming material that is created (collagen mineral composite fibrils). Taken from Weiner and Traub (1992) and Chinsamy-Turan (2005).

The decay rate of bone is normally a function of the environment of death and burial, with rapid burial and dry climate being the most conducive to bone preservation into the fossil record (Trueman and Martill, 2002). Many have argued that the variation in bone decay relative to environment may result in a preservation bias in the fossil record. Once all the organic components of the bone have decayed, the crystalline phases of the bone then undergo authigenic regrowth of calcite and carbonate fluorapatite under diagenetic processes (Trueman and Martill, 2002) (Figure: 4.7).

Incorporation of isotopically heavy and light carbon and oxygen isotopes into the bone and tooth enamel structure is primarily controlled by diet, which is a function of processes such as digestion, excretion, tissue synthesis and turnover or the replacement of bone by growth of animal over its lifetime. A comprehensive palaeoenvironment reconstruction requires input from studies of pollen and plant material as well as vertebrate remains, but in the study area the former are not available. Bone geochemistry has the potential to provide a rich array of isotopic evidence concerning the animal's diet as a proxy for climatic data. To make accurate assertions about the animal's biology the geochemical evidence should be combined with histological and taphonomic data (Hedges et al., 2005) particularly for animals such as *Lystrosaurus* that have no modern, living counterparts to use as biological and physiological analogues. Carbon and oxygen isotopes occur in both organic (as part of the collagen) and inorganic (as part of crystalline bioapatite) phases.



**Figure 4.7:** Simplified diagram showing the alteration of bone microstructure during diagenetic and fossilization processes. Labels represent original bone collagen fibers (b), apatite (a) and regrowth of apatite and calcite (a+c). See text for further detail. Taken from Chinsamy-Turan (2005).

Carbon and oxygen remaining after decomposition, burial and fossilization commonly have altered isotope ratios (Hedges et al., 2005), and the older the fossil material, the more potential for chemical and isotopic alteration by diagenetic, metamorphic, and hydrothermal processes. Tusk and tooth material is generally more robust than fossil bone as it consists partly of enamel which is a less porous and more stable form of bioapatite and, for these reasons, is most commonly used in stable isotope studies (Hedges et al., 2005).

## 4.2 Sampling Strategy and Analytical Methods

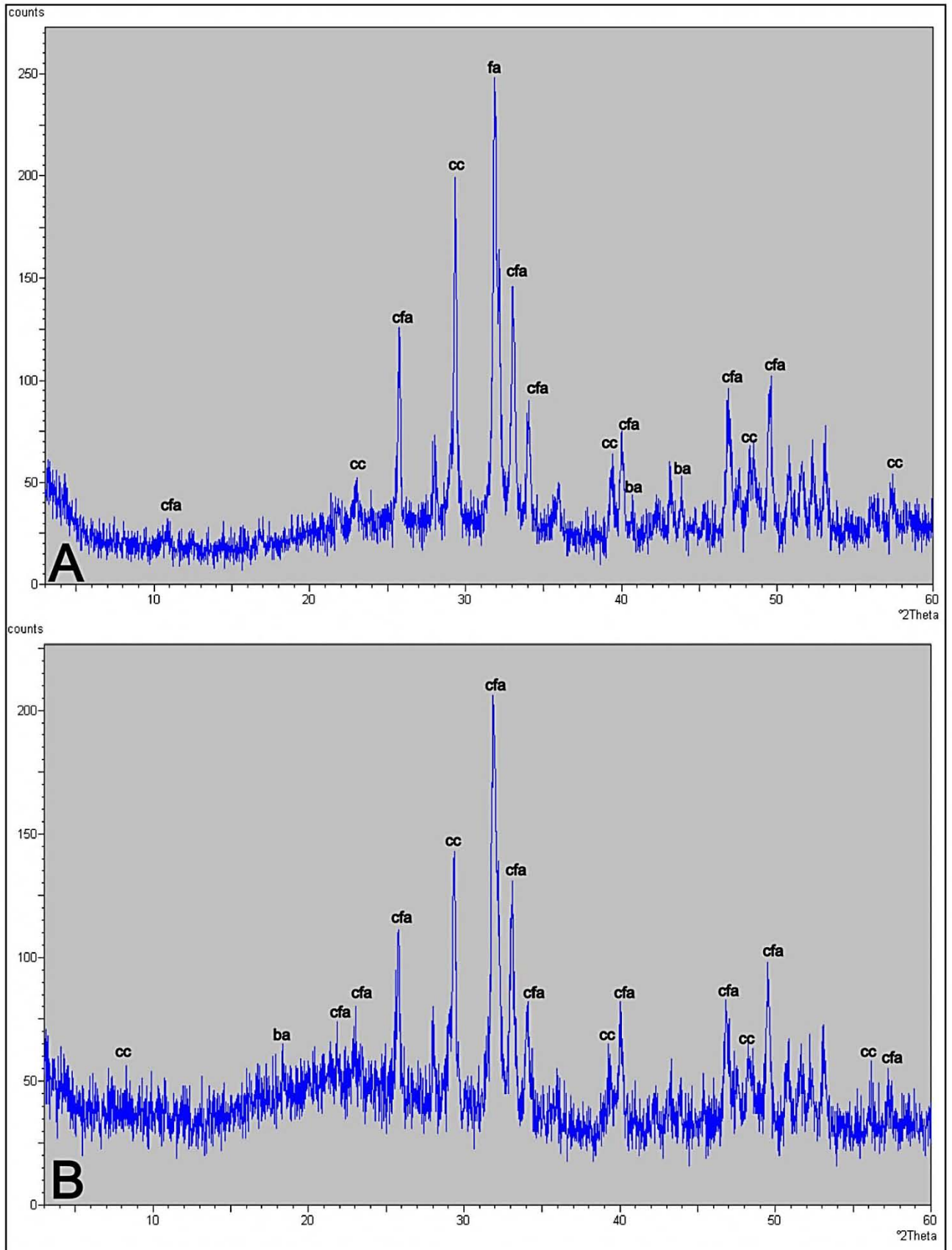
The stable isotopes of carbon and oxygen were of interest in this study for what they might reveal about the palaeoenvironments at the time of deposition or during burial diagenesis. Isotopic analyses were performed at the stable isotope laboratory in the Department of Geology, University of Cape Town. Drilled, powdered bulk samples from the centre to the rim of cut calcite concretions, bone, and tusk were reacted offline with 100% phosphoric acid, following the method of McCrea (1950). For a minimum of 24 hours the reaction vessels were transferred to a water bath set at 25°C. CO<sub>2</sub> released during the reaction was captured online and sealed in glass vials for further analysis. Samples were run on a MAT252 mass spectrometer and corrected using the CO<sub>2</sub> calcite fractionation factor of 1.01025. The standard normally used to report isotope values of calcite are the Pee Dee Belemnite (PDB; Craig, 1957) and Standard Meteoric Ocean Water (SMOW; Gonfiantini, 1984) the “in-house” standard Namaqualand Carbonate (pure calcite) was used as a standard in this study. The stable isotope data were also compared to the results of Macleod et al., (2000) who analysed the isotope composition of nodules and fossil tusks of *Dicynodon* and *Lystrosaurus* in the Bethulie area.

In conjunction with the isotopic study, bone, tusk and nodule mineralogy was analysed using the X-ray powder diffractometry (XRD) laboratory in the Dept. of Geology, University of Cape Town. Qualitative powder XRD analysis was performed on samples ground to less than 50 µm in a pestle and mortar. The mineralogy of the fossil material was obtained using a Philips (PW1130/90) X-ray diffractometer with an accelerating voltage of 15 kV, a beam current of 20 nA and a beam diameter of 20 µm. Minerals were identified from *d* values and relative

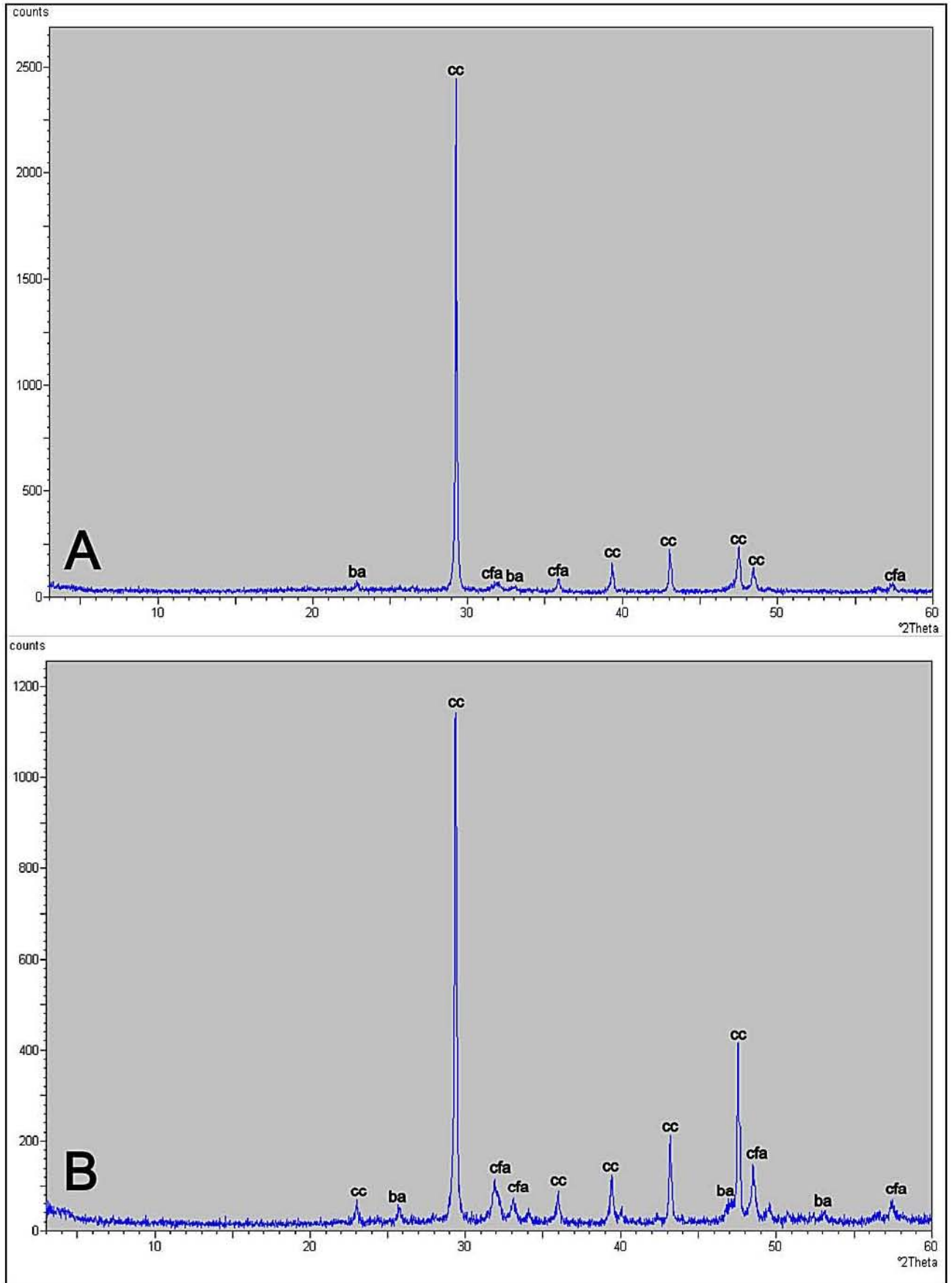
peak intensities using the JCPDS PDF-2 database retrieval/display system (Faure et al., 1995) (Figures: 4.8 and 4.9). Weight % calcite values were determined from wika readings taken during the capture of the samples' CO<sub>2</sub> on the carbonate line in the stable isotope lab.

### 4.3 Results

The calcite content varied significantly among the fossil bone, fossil tusks and nodule samples. The fossil bone had between 66 and 90 wt % calcite. The Facies 1, 2 and 3 carbonate nodules had 46.8-50.4 wt % calcite and the Facies 4 carbonate nodules had 46.4-67.5 wt % calcite. The fossil tusk material had between 8.7 and 13.5 wt % calcite. The XRD data are in agreement with the weight % calcite content determined by the stable isotope analysis procedure. The carbonate nodules and fossil bone samples are almost entirely calcite, with minor carbonate fluorapatite and possibly trace barite in the fossil bone; whereas the fossil tusk samples contained mainly carbonate fluorapatite and minor calcite and also possibly trace barite (Figures: 4.8 and 4.9).



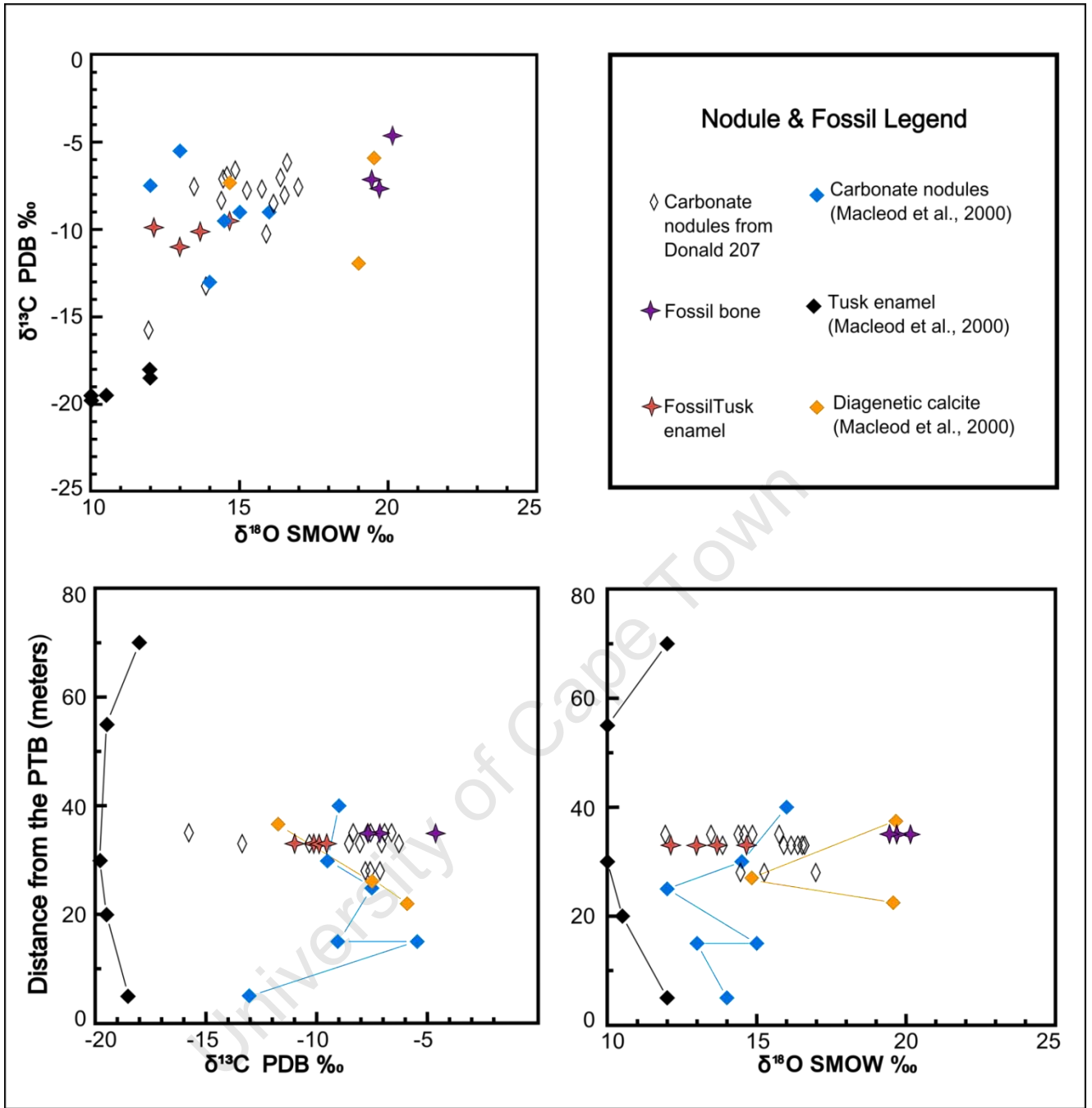
**Figure 4.8:** XRD data of fossil *Lystrosaurus* tusks sampled from two specimens associated with the *Lystrosaurus* accumulations in this study. Tusk sample numbers are: (A) T2a; (B) T3. These samples were also used for the stable isotopic analysis. Peaks that most fitted calcite (cc), carbonate fluoroapatite (cfa), and barite (ba) are shown.



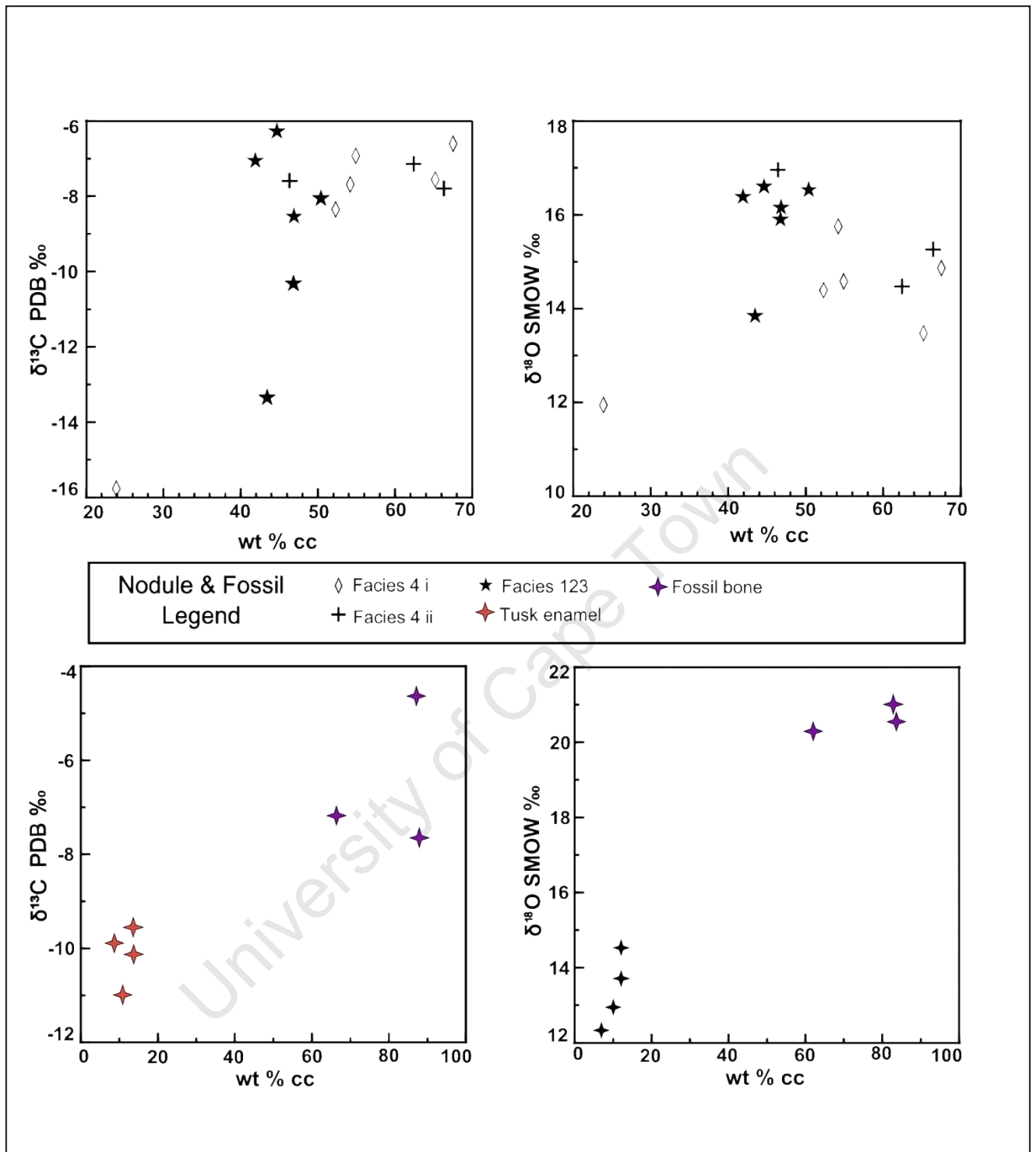
**Figure 4.9:** XRD data of bone samples taken from *Lystrosaurus* accumulations (A) 1 and (B) 3. These samples were also used in the stable isotope analysis. Peaks that most fitted calcite (cc), carbonate fluoroapatite (cfa), and barite (ba) are shown.

The  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values from Donald 207 are plotted against each other and also are plotted with isotope values obtained by Macleod et al., (2000) from nodules in the Bethulie area (Figure: 4.10). Donald 207 data are also shown plotted with their weight percent calcite (Figure: 4.11) and are shown with ellipses highlighting data clusters (Figure: 4.12). Data collected are also compared to global stable isotope data of calcrete and carbonated duricrusts from modern day arid zones (Figure: 4.13). Absolute values for all Donald 207 data are shown in Appendix 1.

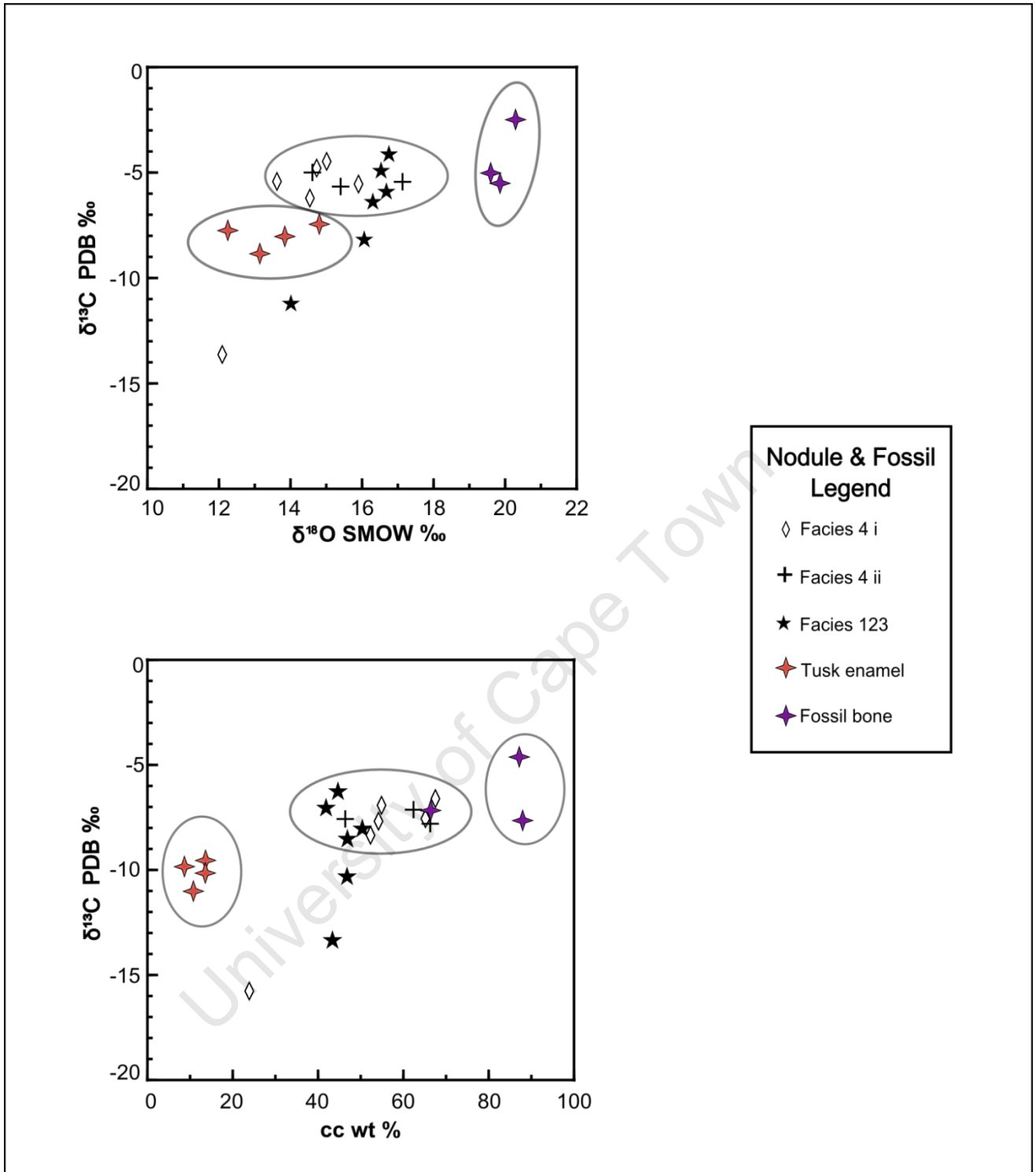
All nodule types show similar  $\delta^{13}\text{C}$  values, within a range of -8.5 to -5 ‰ if one excludes two outliers (Figures: 4.10, 4.11, 4.12).  $\delta^{18}\text{O}$  is slightly more variable between nodule families as Facies 1 and 2 nodules have a narrow range of 15.9 - 16.6 ‰, whereas Facies 4 nodules show a less narrow range (13.5-16 ‰ for Facies 4i and 14.5-17 ‰ for Facies 4ii). However Facies 4ii represents samples from three different nodules and the others only two nodules. There was no pattern or trend in isotope values for samples from rim to centre of the same nodule. The  $\delta^{13}\text{C}$  values collected by Macleod et al. (2000) from carbonate nodules in the Bethulie area show similar values to this study from Donald 207 Farm, however  $\delta^{18}\text{O}$  values are generally lower (Figure: 4.10). Nevertheless when observing the stratigraphic position of the samples across the PTB, the heaviest  $\delta^{18}\text{O}$  value (17 ‰) is located at 40 m which is the same stratigraphic position as the Claasens bonebed (Figure: 4.10). Different types of nodules generally had a similar range in percent calcite (40-60 wt %) (Figure: 4.11).



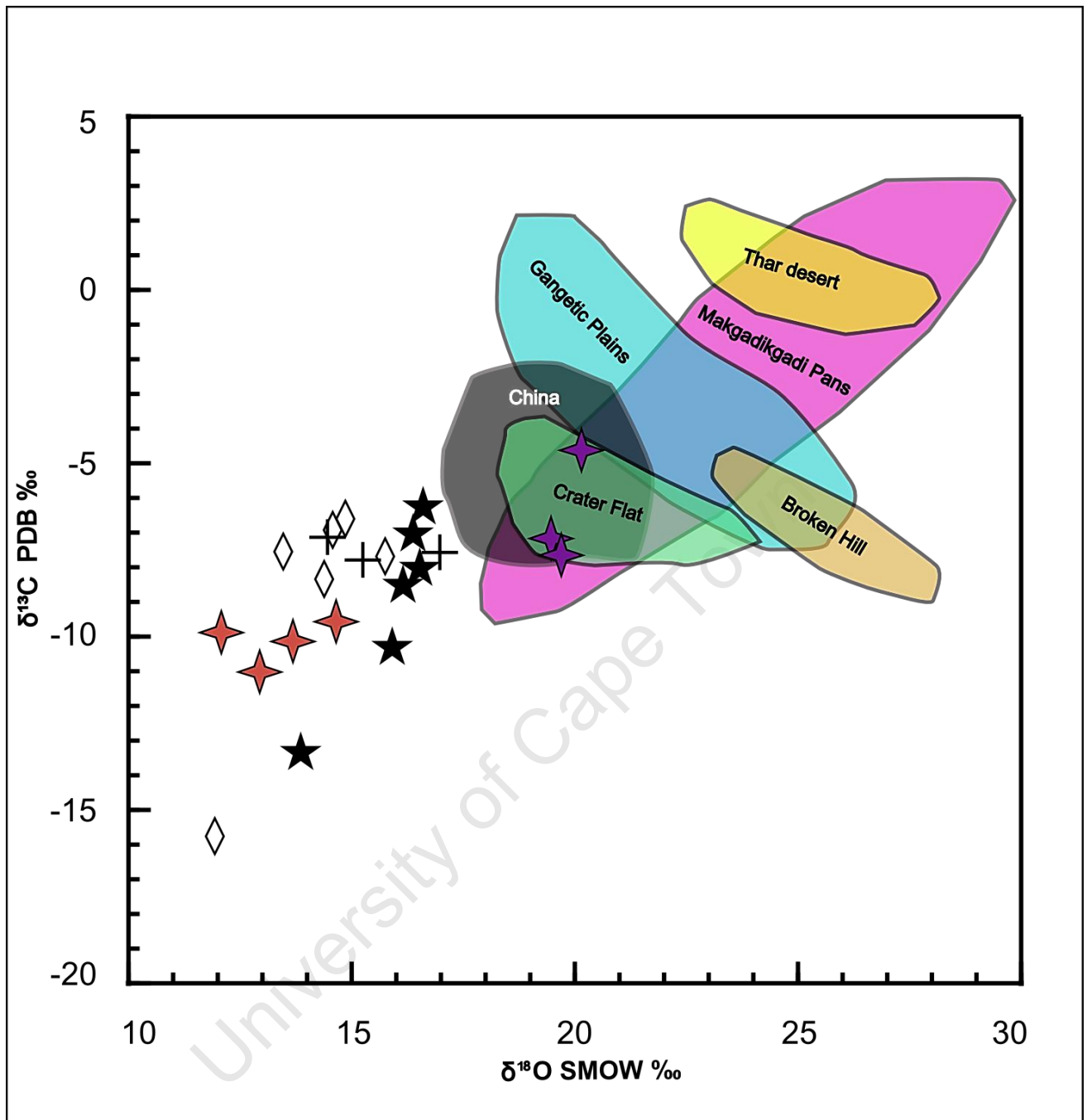
**Figure 4.10:** Stable isotope data collected from Donald 207 Farm. Samples have been plotted alongside nodule, diagenetic calcite and tusk data collected by Macleod et al. (2000) in the Bethulie area (top). The  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  data were also plotted in relation to their distance from the PTB (bottom).



**Figure 4.11:** The graphs above show  $\delta^{13}\text{C } \text{‰}$  and  $\delta^{18}\text{O } \text{‰}$  values plotted against wt % calcite collected from carbonate nodules, fossil tusk and fossil bone of *Lystrosaurus declivis* from the study area. Carbonate nodule and fossil material values are plotted separately.



**Figure 4.12:** Graphs show  $\delta^{18}\text{O}$  (top) and wt% percent calcite (cc) (bottom) data plotted against  $\delta^{13}\text{C}$ . Ellipses indicate where majority of the nodule, tusk and fossil bone data plot respectively.



**Figure 4.13:** Stable isotope data from samples collected on Donald 27 Farm in comparison to global stable isotope results. Fields shown are from the Makgadikgadi Pans duricrusts and calcretes (Botswana) (Ringrose et al., 2009); the Gangetic Plains arid calcretes (Srivastava, 2001); Thar Desert (NW India) (Andrews et al., 1998); Pleistocene calcrete nodules from the Chinese Loess Plateau (Rowe and Maher, 2000); Crater Flat calcretes Nevada, U.S.A (Neymark et al., 2005) and Broken Hill, Australia (Schmid et al., 2006). See text for discussion.

Fossil tusk isotope values have a similar range to the carbonate nodules; however the tusks have lighter  $\delta^{18}\text{O}$  values (Figure: 4.11). The  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values range between -9 and -11.5 ‰ and 12 and 14.5 ‰, respectively (Figures: 4.11, 4.12). Fossil bone has the most contrasting values with reference to the other data with  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values ranging between -7 and -4.5 ‰ and 19.5 and 20 ‰ respectively (Figures 4.11, 4.12).

#### 4.4 Interpretation

##### Petrography

Thin section observations support evidence for the pedogenic origin of Facies 4 nodules and early diagenetic origin of Facies 1, 2 and 3 nodules. The presence of micrite or microcrystalline calcite inter-grown with small lithic fragments and detrital grains, chemically weathered feldspar grains, and fracture systems are all consistent with a pedogenic origin of Facies 4 nodules. These petrographic textures are comparable to microstructural descriptions of Quaternary pedogenic calcretes, and carbonate bearing soils (Netterberg 1967; 1971; Goudie, 1983). Crystalligraphic textures of the Facies 1, 2, and 3 nodules support previous descriptions from Chapter 3 for early diagenetic nodules, such as the presence of microspar calcite inter-grown between detrital grains. There are also no observable cracks refilled with calcite in the Facies 1, 2, and 3 nodules, which are believed to indicate wetting and drying events in the soil profile (Smith, 1990).

## Isotope Data

The isotope data collected from Donald 207 carbonate nodule and fossil *Lystrosaurus* bone and tusk show a trend with global terrestrial calcrete and nodule values from the literature, but are not in complete agreement (See Figure: 4.13). The values from Donald 207 are not in agreement with arid calcretes from the Thar Desert (Andrews et al., 1998) or Gangetic Plains (Srivastava, 2001). However,  $\delta^{13}\text{C}$  values for the Donald 207 samples are in agreement with the terrestrial calcrete and nodule values of the Chinese Loess Plateau (Rowe and Maher, 2000), Crater Flat, Nevada (Neymark et al., 2005), Broken Hill, Australia (Schmid et al., 2006), and the more negative  $\delta^{13}\text{C}$  values collected from duricrusts and calcretes from Makgadikgadi Pans (Ringrose et al., 2009). These samples were all collected from Pleistocene and Holocene; seasonally cool semi-arid environments (Figure 4.13).  $\delta^{18}\text{O}$  values for the Donald 207 data are enriched, but still lighter than most of the global isotopic data (Figure: 4.13) and are the reason the isotope data from Donald 207 fall outside the coloured areas in Figure 4.13. Possible explanations for the  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values from Donald 207 samples will now be outlined.

### Carbonate Nodule $\delta^{13}\text{C}$ Values

Stable Carbon isotope percentages ( $\delta^{13}\text{C}$ ) of soil  $\text{CO}_2$  is predominantly controlled by biogenic sources such as the respiration of plants and decay of organic matter (Craig, 1953). Nevertheless,  $\text{CO}_2$  can also be sourced from rainwater (atmosphere), and from chemical weathering of rocks (carbonic acid reacting with limestone or with feldspar to produce bicarbonates) which will introduce different  $\delta^{13}\text{C}$  signatures to the soil. Organic matter  $\text{CO}_2$  in most soils will dominate but atmospheric and bedrock  $\text{CO}_2$  can be significant depending on

the setting and bedrock geology with carbonate rich lithologies weathering to provide a large source of carbonate. Factors that can influence  $\delta^{13}\text{C}$  values include the species composition of plant communities (Schmid et al., 2006). C3 land plants have average  $\delta^{13}\text{C}$  values of -25 ‰ and C4 plants -13 ‰. Under equilibrium conditions soils can become enriched by up to 14-16 ‰ according to Cerling (1999) which means carbonate concretions and calcretes forming under C3/C4 dominated plant community can have  $\delta^{13}\text{C}$  values of -12 ‰ and +2 ‰, respectively (Khadkikar et al., 1998).

C4 plants had not yet appeared in the Triassic, thus soil  $\text{CO}_2$  in the Triassic was most likely more enriched in  $^{12}\text{C}$  than modern soils and this is supported by the values seen for the carbonate nodules from the study area. Since  $\delta^{13}\text{C}$  values in the soil are generally not a reflection of atmospheric  $\text{CO}_2$ , but rather presence of organic matter  $\text{CO}_2$ , these data could reflect the amount of vegetation present on the surface (only C3 plants in the Triassic period). Schmid et al (2006) believe that shifting  $\delta^{13}\text{C}$  values in Holocene calcretes from Broken Hill, Australia are due to variation in moisture availability due to changes in precipitation and evaporation. Reduced moisture availability and reduced plant cover would increase the importance of atmospheric  $\text{CO}_2$  in the subsurface (Schmid et al., 2006). Thus if one compares these results to the Donald 207 carbonate nodules, nodule  $\delta^{13}\text{C}$  values that fall closer to -15‰ may represent wetter periods where there was plenty of C3 plant cover and thus less atmospheric  $\text{CO}_2$  influence on the subsurface.

The bulk of the data on the other hand may represent drier climate periods when there was less above-ground vegetation (and less soil organic in the soil) and also a higher influence of

atmospheric CO<sub>2</sub> in the soil profile, which supports the hypothesis of at least a seasonally dry climate since calcretes and carbonate nodules tend to form in well-aerated soils typical of semi-arid to arid environments (Schmid et al., 2006).

### Carbonate Nodule $\delta^{18}\text{O}$ Values

The  $\delta^{18}\text{O}$  values in carbonate nodules and other carbonate precipitates depend on the isotope composition of the water from which the carbonate formed as well as the average atmospheric temperature. Isotope fractionation is therefore a function of groundwater composition (Degens, 1967). Evaporation enriches the carbonate content of groundwater and the carbonate precipitated from that water is in the heavier  $^{18}\text{O}$  isotope and thus causing the loss of lighter  $^{16}\text{O}$  isotopes from the system. This is expected for terrestrial carbonates as they precipitate in semi-arid systems that experience seasonal wetting and drying and fluctuation of the water table (Smith, 1995).  $\delta^{18}\text{O}$  values from nodules from the lower Katberg Formation suggest a reasonable amount of evaporation was occurring in the soil however  $\delta^{18}\text{O}$  values for the Donald 207 are lighter than most of the global isotopic data (Figure: 4.13). The lighter  $\delta^{18}\text{O}$  values cooler temperatures in the earliest Triassic. This does not eliminate the presence of a dry climate. In order to determine the mean annual temperature from the  $\delta^{18}\text{O}$  data one would need to know the isotope composition of the groundwater.

Groundwater  $\delta^{18}\text{O}$  values are a function of latitude and elevation (Smith et al., 1981; Sheppard, 1986; Faure et al., 1995). South Africa was at a latitude of  $\sim 55^\circ$  S in the Late Permian (Smith et al., 1981). In a study by Faure et al. (1995)  $\delta\text{D}$  values were taken from

calcite lenses in coal bearing beds of the upper Grootegeluk Formation (Early Late Permian), Waterberg Basin. Samples of Permian coal from a similar latitude in Australia and were found to be in equilibrium with water with  $\delta D$  value of  $-90 \text{ ‰}$ . (Faure et al., 1995). This suggested to Faure et al. (1995) that the Late Permian Karoo Basin ambient meteoric water had a  $\delta^{18}O$  value of the order of  $-13 \text{ ‰}$  on the basis of the Meteoric Water Line (MWL) by Sheppard (1986). Using a  $\delta^{18}O$  value for meteoric water of  $-13 \text{ ‰}$ , the crystallization temperature was calculated for the analysed carbonate nodules using the O'Neil et al. (1969) calcite-H<sub>2</sub>O fractionation factor to be between  $15^\circ \text{ C}$  and  $20^\circ \text{ C}$  (Faure et al., 1995). This is a reasonable temperature for precipitation of freshwater carbonates. If South Africa's latitude did not change significantly during the Permian – Triassic transition, this Permian  $\delta^{18}O$  value for meteoric water can be used for the precipitation of the carbonate nodules in the earliest Triassic collected on Donald 207, supporting a cool temperate climate for the Karoo Basin in the earliest Triassic. The claim by Haycock et al. (1997) that snow cover may have existed on the highest peaks of the Gondwanide Mountains is thus a plausible estimate. A similar temperature range of formation ( $\sim 17.9\text{-}18.8^\circ \text{ C}$ ) was calculated for calcretes formed from 80 000-90 000 year old pan margins from the Makgadikgadi Pans, Botswana (Ringrose et al., 2009). Ringrose et al., (2009) propose that their low  $\delta^{18}O$  values indicate a cooler and drier climate prevailed during the formation of these calcretes. Rowe and Maher (2000) also discuss the formation of Quaternary calcrete nodules in loess deposits from the Chinese Loess Plateau during a cold period. Rowe and Maher (2000) propose calcrete concretion formation on the Loess Plateau under less humid, cold stage conditions. Since both these localities show the most similar  $\delta^{18}O$  values to the Donald 207 data, it is most probable that a colder, more seasonally dry climate than the present day Karoo Basin also formed the Donald 207 carbonate nodules.

## Fossil Tusk $\delta^{13}\text{C}$ Values

The fossil tusk stable carbon isotope results in this study do not show any similarity to those of Macleod et al. (2000). Tusk samples were treated by Macleod et al. (2000) with dilute NaOHCl and buffered 1M acetic acid prior to following procedures similar to sampling methods of the samples of this study. The pre-treatment is designed to dissolve away calcite to leave only carbonate fluorapatite (CFA) behind. Without this treatment Macleod et al. (2000) yielded  $\delta^{13}\text{C}$  values of -8.7 ‰ which are similar to values yielded in this study. Since the tusks were bulk sampled and not pre-treated to remove authigenic calcite within the enamel, it is most likely that their values represent a mixture of authigenic and biogenic  $\text{CO}_2$  as recrystallized calcite would also react with the phosphoric acid more readily and by weight contains more  $\text{CO}_2$  than the biogenic component of the tusk enamel.

Fractionation differences of the heavy isotope  $^{13}\text{C}$  between C3 and C4 plants also support contamination of bulk sample with recrystallized calcite. Since it is assumed *Lystrosaurus* fed on C3 plants, the Donald 207 data reflect  $\delta^{13}\text{C}$  values which are less than that are expected for animals that fed on C3 plants. If the Macleod et al. (2000) data are considered, these data fit the probable C3 diet quite well, which most likely means that the tusk data collected from Donald 207 represents a mixture of enamel and later calcite crystallization.

## Fossil Tusk $\delta^{18}\text{O}$ Values

Some of the lowest  $\delta^{18}\text{O}$  values belong to the fossil *Lystrosaurus* tusk collected in the study area.  $\delta^{18}\text{O}$  values are mostly somewhat heavier than those measured by Macleod et al. (2000). The similar values suggest that the  $\delta^{18}\text{O}$  values are less affected by later alteration of

the fossil tusk enamel to a mixture of calcite and CFA. It is not clear why the  $\delta^{13}\text{C}$  values are so much more dissimilar to Macleod et al. (2000) than  $\delta^{18}\text{O}$  values when it is clear from the  $\delta^{13}\text{C}$  values that alteration occurred via authigenic calcite veins entering tusks. It may reflect that there is a lot more oxygen than carbon in both  $\text{CaCO}_3$  and apatite, or that the later diagenetic waters that formed the calcite had a significantly different carbon but not so different oxygen isotope composition to the original waters.

Oxygen is less variable than carbon so this may be one of the reasons the oxygen values are most similar to Macleod et al. (2000). The phosphoric acid used on the fossil tusk bulk sample for the isotope analysis may be the another reason as phosphoric acid is used to estimate the  $^{18}\text{O}$  isotope composition of the original apatite mineral in fossil tooth enamel (Kolodny and Kaplan, 1970; McAuthur et al., 1980). Oxygen isotope values from the phosphate component of the bioapatite are the most robust in terms of recording original biological information. To confirm collection of only phosphate oxygen the samples must undergo a procedure that was not undertaken on the Donald 207 samples.

This procedure is explained involves treatment with phosphoric acid, and samples are dissolved in HF to remove more recent contaminants, and then added to an ion-exchange column to isolate phosphate. Following elution of phosphate from the column, silver phosphate, a non-hydrating mineral, is precipitated. To release the oxygen from the precipitate, samples are reacted under a vacuum with excess  $\text{BrF}_5$ . The oxygen generated by this procedure is converted to  $\text{CO}_2$  by hot graphite, collected, and analysed on a mass spectrometer (Clayton and Mayeda, 1963). This is a controversial procedure as the isotopic difference between carbonate and phosphate oxygen isotope values within a sample has

been used as evidence for endothermy/ectothermy and ecology of extinct animals, since isotopic values of precipitating apatite are believed to be dependent upon the body water temperature of animals as well as drinking water (Koch et al., 1994; Billon-Bruyat et al., 2005; Amiot et al., 2010).

### **Fossil Bone $\delta^{13}\text{C}$ Values**

The lightest  $\delta^{13}\text{C}$  obtained from this study belong to the fossil bone samples collected from three of the *Lystrosaurus* bonebeds. The calcite in the fossil bone likely represents altered material due to the presence of much calcite inter-grown within the cancellous bone which was then bulk sampled for analysis (Figure: 4.5). Nevertheless, it is not understood why the bone data are so different to the tusk and the rest of the data. The fossil bone data plots closest to diagenetic calcite samples from the Bethulie area done by Macleod et al. (2000) (Figure: 4.10). If the fossil tusks were also altered by this authigenic calcite one would expect the bone and tusk values to be more similar, but they are not. Interestingly the fossil bone is also similar to global isotopic data from arid calcretes (Figure: 4.13). Fossil bone data is most similar to diagenetic calcite data of Macleod et al. (2000). This may explain the isotopically lighter carbon isotope values for the fossil bone than for the fossil tusk in the Donald 207 data. What this difference also shows is that no obvious resetting of isotope data has happened in the Bethulie area by Jurassic-aged dolerite intrusions (Macleod et al., 2000). The data from all the carbonate nodules and fossils would be more similar than they are, since they are all from the same stratigraphic horizons.

## Fossil Bone $\delta^{18}\text{O}$ Values

The heaviest  $\delta^{18}\text{O}$  values obtained from the study belong to the fossil bone. Macleod et al. (2000) did not undertake isotope analyses on fossil bone so there is no comparison to stable isotope work done on bone in the Bethulie area. Under the right conditions, modern bone can become mineralised with calcite and other evaporitic minerals (barite and trona) quickly, and it happens on the exposed surface with no burial required as observed in Amboseli National Park in Kenya (Trueman and Behrensmeyer, 2004). In some cases this subaerial diagenesis of the bone significantly filled osteonal cavities and cracks in the bones within two years post-mortem (Trueman and Behrensmeyer, 2004) in association with evaporated swamp margins and mineralisation by calcite. Such rapid chemical change has been interpreted as being the result of a dynamic interaction of the bones, soil moisture, and evaporation at ground surface (Trueman and Behrensmeyer, 2004). A bone resting on the soil surface draws up pore water which evaporates on the exposed upper surface of the bone (Trueman and Behrensmeyer, 2004) a process comparable to the “wicking” mechanism of an oil lamp or candle. The high surface area and pore spaces in a bone make it an effective wick; allowing major changes in the bone mineral and organic matrix in a very short time period (Trueman and Behrensmeyer, 2004). Fresh bone does not have this same “wicking” capacity (Trueman and Behrensmeyer, 2004).

It is tempting to use the heavy  $\delta^{18}\text{O}$  values from the Donald 207 fossil bone samples to support work by Trueman and Behrensmeyer (2004) in Amboseli, Kenya. If the calcite taken for analysis from Donald 207 fossil bone samples was mainly calcite and possibly barite that precipitated in the 1-10 years that the bones of the *Lystrosaurus* lay on the soil surface

before final burial; they may reflect some environmental data in this regard. However a larger sample set would be required to verify this since only three bone samples were run in the isotope lab. In addition, chemical diagenesis of bone continues and the fossil bones are isotopically similar to diagenetic calcite samples from Bethulie. Thus the bulk of the calcite present in the fossil bone is likely diagenetic calcite. The possible presence of barite in the Donald 207 fossil bone is interesting however, as Trueman and Behrensmeyer (2004) observed its presence within their bone samples. Since Trueman and Behrensmeyer (2004) noted barite as an evaporitic mineral crystalizing within the bone before its burial, this mineral's presence within the Donald 207 fossil bone could show the possibility of some original pre-diagenetic  $\delta^{18}\text{O}$  values remaining. There is scope to study what information lies hidden in fossil bone, but any isotopic study (especially on bone) must have proof of preservation carefully demonstrated before it can be utilised for palaeoenvironmental interpretation. Thus for now, fossil bone data from Donald 207 cannot be assumed to reflect any meaningful isotopic values referring to palaeoenvironment.

### **Isotope Data and Drought Hypothesis**

The nodule oxygen and carbon isotopic data support the presence of a relatively cool climate in the earliest Triassic Karoo Basin. The  $\delta^{18}\text{O}$  values for the carbonate nodules are significantly lower than that seen in global isotope data, although a trend can be seen with data collected from carbonates believed to have formed under cool conditions (Rowe and Maher, 2000; Ringrose, 2009). This does dispute previous literature concerning a hot Triassic Karoo Basin (Hiller and Stavrakis, 1984; Smith, 1995; Smith and Botha, 2005), but does not rule out the presence of a semi-arid climate. There are many cold deserts in the

modern World (the Atacama, the Gobi, and the Antarctic Dry Valleys), so the Karoo Basin in the Early Triassic could still have been controlled by strongly seasonal cooler/drier periods and warmer/wetter periods (Smith, 1995; Smith and Ward, 2001; Smith and Botha, 2005; Botha and Smith, 2006; 2007). This means a time of seasonal aridity could have been present during the deposition of the stratigraphic horizon hosting the *Lystrosaurus* bonebeds, but this alone cannot prove that this stratigraphic horizon represents a strongly seasonal semi-arid episode that resulted in a drought. The  $\delta^{13}\text{C}$  values could support the drought hypothesis as much of the carbonate nodule data have more positive values which indicate low vegetation cover (Schmid et al., 2006). Since vegetation tends to die off in droughts (Shipman, 1975) this could indicate the presence of an extended dry period at this stratigraphic horizon.

It is difficult to assume any evidence of drought from the fossil tusk isotopic data as they most likely represent altered material. They are similar to the carbonate nodule's isotope data however, thus may reflect similar palaeoenvironmental signals to the nodules. Since only C3 plants were present in the Triassic, one can only assume that C3 plants were their only source of food. Certain C3 plants are more sensitive to aridification than C4 plants as the C4 photosynthetic pathway is more economical under these conditions (Cerling, 1994; Schmid et al., 2006; Ringrose et al., 2009). If the Macleod et al. (2000) data for fossil tusks are considered, the tusk data enriched in the  $^{12}\text{C}$  isotope could indicate the plants that the animals were consuming had to endure dry conditions at a time near to the death of these animals.

Although the fossil bones are a limited and unreliable dataset from which to make interpretations, it may be interesting to explore the possible data they may preserve. The high  $\delta^{18}\text{O}$  values and low  $\delta^{13}\text{C}$  of the Donald 207 bone support high amounts of evaporation and lack of organic matter in the soil which in turn could support the hypothesis of a drought event at this horizon whereby animal carcasses lay on surface unburied near a dried up water source or pan and bones became mineralised by the evaporative precipitates forming in the drying soil due to soil pore water interaction (Trueman and Behrensmeyer, 2004). Koch (2007) mentions in some instances fossil bone can retain biogenic  $\delta^{18}\text{O}$  values, thus if some of the  $\delta^{18}\text{O}$  values are partially indicative of biogenic  $\delta^{18}\text{O}$ , it could be speculated that the water drunk prior to death of the *Lystrosaurus* had experienced high evaporation. If the *Lystrosaurus* bones were recrystallized reasonably rapidly under conditions stipulated by Trueman and Behrensmeyer (2004) and quickly buried, diagenetic processes would allow preservation of some biogenic  $\delta^{18}\text{O}$  values (Koch, 2007). There would be the possibility of the isotope data reflecting some evidence of a cool semi-arid period immediately prior to, or immediately after the death of these animals.

What was causing the *Lystrosaurus* to aggregate prior to death may indeed have something to do with seasonal extremes acting on their environment. These speculative claims can only be tested once further analyses are done on more bone collected from *Lystrosaurus* bonebeds. The next chapter concerns the vertebrate taphonomy of the *Lystrosaurus* bonebeds which may provide more physical clues for quantifying the residence time of the *Lystrosaurus* bones on surface before burial and testing the drought hypothesis.

## 5. Vertebrate Taphonomy

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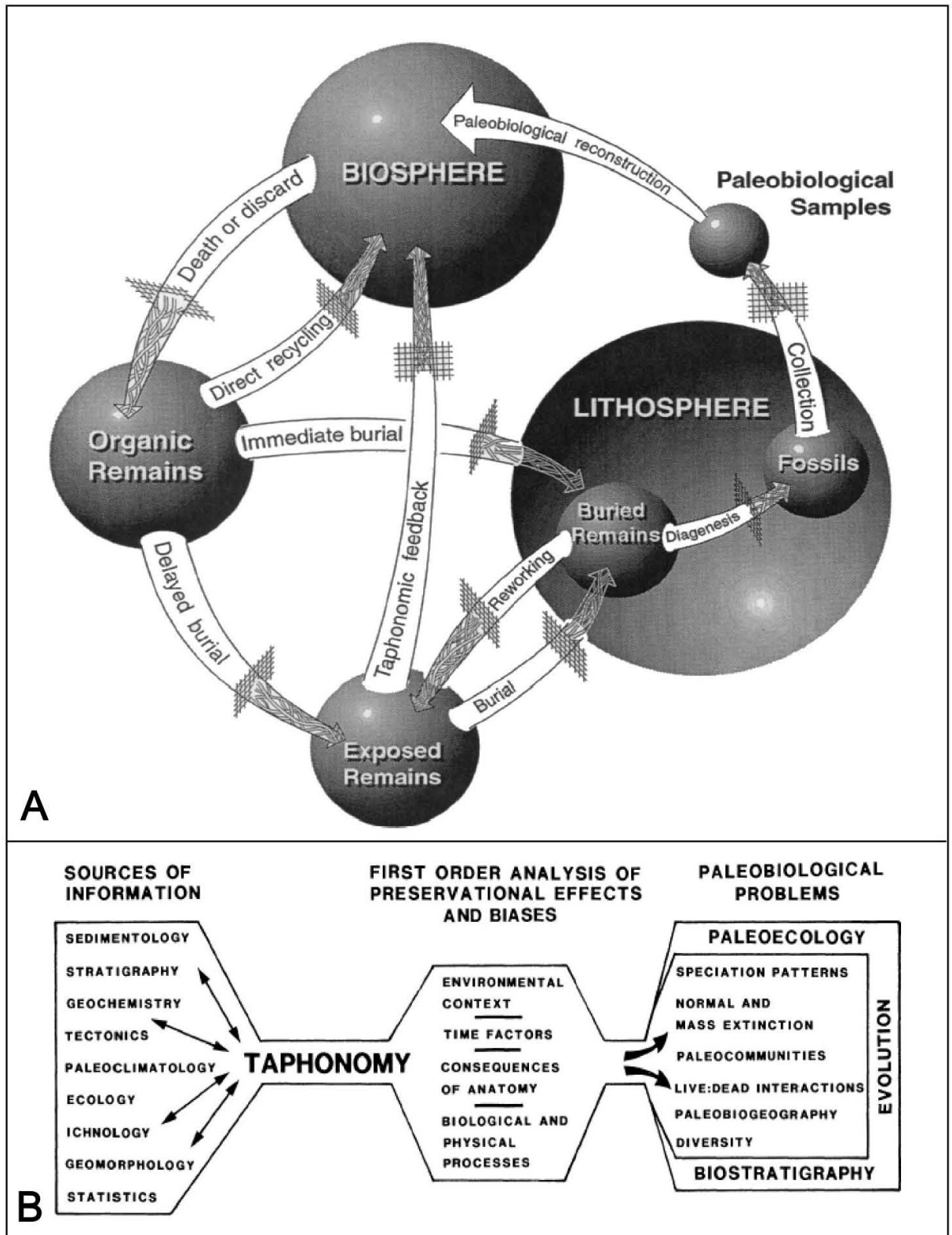
In this section taphonomic information collected from the Donald 207 Farm relating to the vertebrate fossils will be presented after some background information on the science of taphonomy is mentioned.

### 5.1. Foundations of Taphonomy

Leonardo Da Vinci (1452-1519) was possibly the first person to document the fact that fossils are the petrified remains of ancient life. Subsequent studies conducted by Steno (1669) and Hooke supported the assertion that fossils were of organic origin and were not the result of “plastic virtue” of the surrounding rocks. The term taphonomy was first coined by Efremov (1940) and was defined as the study of the transition of organic remains from the biosphere into the lithosphere. This was later modified as the study of the conversion of living communities (the biocoenosis) into a fossil or death assemblage (the thanatocoenosis), or simply the study of the passage “from death to diagenesis” (Martin, 1999). In the infancy of the modern discipline of taphonomy, German scientists such as Walter (1904; 1910), Abel (1912; 1927; 1935) and Weigelt (1989) mainly focused on its uses in palaeoenvironmental interpretation. Efremov (1940) used taphonomic principles to emphasize the incompleteness of the fossil record and thus taphonomy has become the documentation of information loss and bias in the fossil record. This is to a degree what taphonomy documents as it sits at the interface of many different scientific disciplines, between the death of an organism and its potential for long-term preservation in the fossil record, and the many ways in which alteration can lead to the loss of interpretive features in

between. Figure: 5.1(A) shows the processes or “pathways” that operate in the taphonomic realm which control how a dead organism becomes fossilised. These pathways indicate information that can be gained from a fossil assemblage, if one knows where and how to look. Taphonomic studies can in fact reveal many different types of information useful to a number of other scientific disciplines i.e. (stratigraphy, sedimentology, geochemistry, palaeoclimatology etc.) (Behrensmeyer and Kidwell, 1985) (Figure 5.1 (B)).

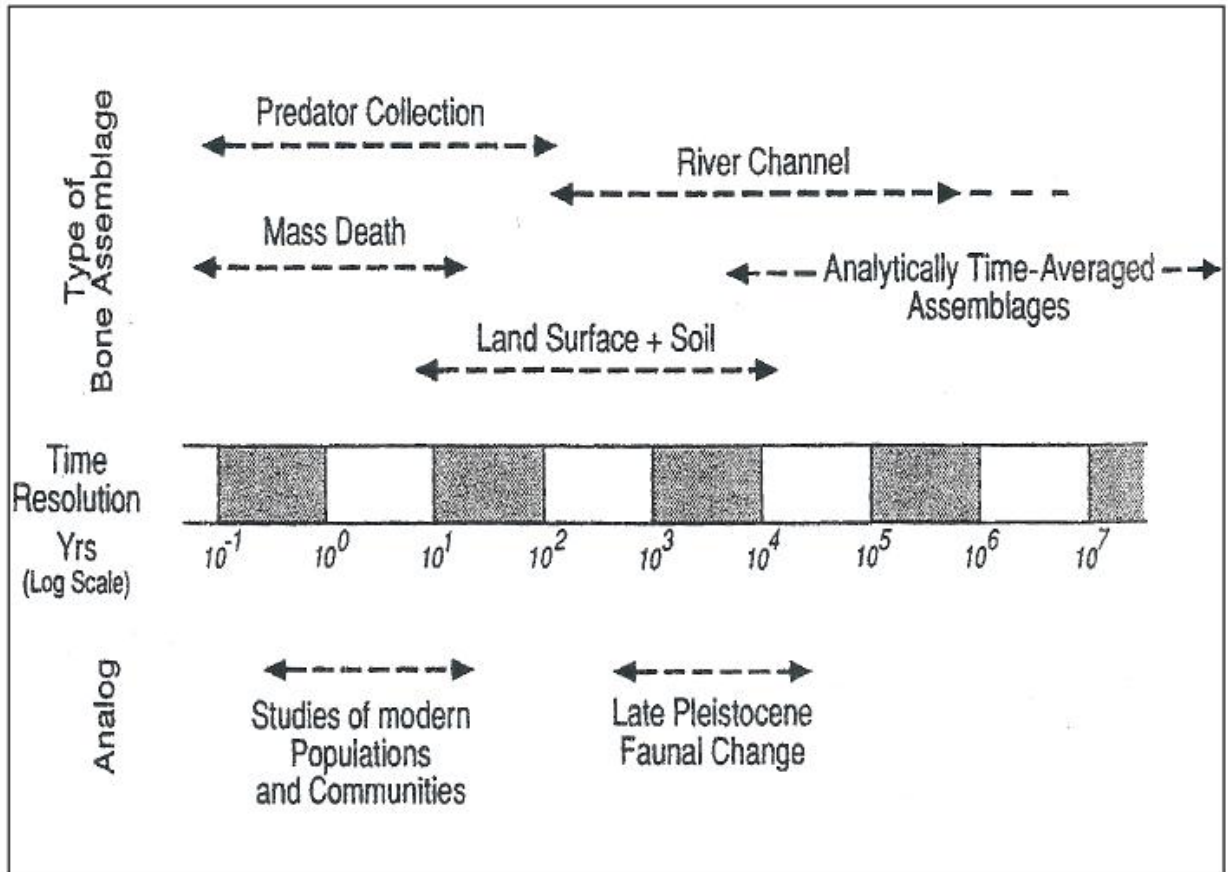
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**Figure 5.1:** The diagrams explain how information is gained (and lost) during taphonomic processes as well as how information can be gained from multiple sources of information and scientific disciplines. **(A)** The main pathways for organic remains from death to paleobiological inference. Each path is affected by taphonomic processes and circumstances that filter the information as it passes to the next stage. **(B)** The interdisciplinary connections, primary first-order research objectives, and some of the geological, and paleobiological problems to which taphonomic information contributes. Taken from Behrensmeyer and Kidwell (1985).

## 5.2. Time-Averaging

Time-averaging goes hand in hand with any taphonomic study and the rate of accumulation for fossil taxa varies with the depositional environment and type of accumulation (i.e. predator accumulation, mass death, natural “rain” of carcasses from non-catastrophic or normal mortality) (Figure: 5.2). Behrensmeyer (1982) studied the duration of accumulation of Quaternary mammalian bone assemblages. She calculated that channel lag assemblages tend to represent the longest time-averaging durations as bones and bone fragments in these assemblages are sourced from non-catastrophic mortality over extended time spans relative to the generation periods of animals being preserved (Behrensmeyer, 1982). For instance, Behrensmeyer (1982) noted the presence of *Bison* in a study on un-fossilized bone assemblages in fluvial channel deposits of the East Fork River in Wyoming, U.S.A. These animals have been extinct in the area for over a century. This river also flows through Pleistocene deposits, so in some instances even greater durations of time-averaging are possible ( $10^5$ - $10^6$ ) as these deposits are approximately 20 000 years old (Behrensmeyer and Chapman, 1993). Fossil remains found in floodplain deposits tend to represent a geologically short period of time ( $10^0$ - $10^4$  years) because low sedimentation rates allow carcasses to accumulate on the surface rather than being reworked under rapid sedimentation regimes (Behrensmeyer and Chapman, 1993).



**Figure 5.2:** Approximate durations of time-averaging of mammalian assemblages. Taken from Behrensmeyer and Chapman (1993).

### 5.3 Donald 207 Taphonomic Study

A taphonomic study of the fossils logged on the Donald 207 section has the potential to contribute significant information to our understanding of the way an organism is fossilised, the processes that transported and buried its remains, and how the rate of burial processes impacted fossilisation. Fossils of the Karoo Basin tell an interesting taphonomic story in part because the taphonomy of fossils changes markedly across the PTB. Vertebrate fossils within inter-channel siltstones change from isolated skulls and lower jaws in upper Permian strata to nearly fully articulated skeletons and multi-individual accumulations (bonebeds) in the earliest Triassic beds (Smith, 1995).

It is generally agreed that there was a drying of the interior of the Karoo Basin in the Palaeozoic-Mesozoic transition following the effect of supercontinent formation (Pangaea), coupled with the possibility of local climate change in the rain shadow of the rising Gondwanide Mountains (Smith, 1995). These factors may have increased the Karoo Basin's susceptibility to periods of deficient rainfall, and drought.

Droughts are geologically short-lived events and therefore difficult to recognize in the geologic record (Rogers, 1991). Although one can recognize an arid environment in the rock record quite easily, a drought event is more elusive. Drought does not visibly affect the environment as much as it affects, or is injurious to local flora and fauna (Rogers, 1991). This is why a taphonomic study on bonebeds, such as the *Lystrosaurus* bonebeds, is important as bonebeds have the potential to provide insight into recognizing the occurrence of short-term climatic extremes (such as drought) in the geologic record (Shipman, 1975; Rogers et al., 1990; Smith and Botha, 2005). The stratigraphic position of the bonebeds in the lower Katberg Formation has a greater significance: they potentially provide information concerning the recovery of Gondwana ecosystems and environments following the End-Permian mass extinction event (Smith and Botha, 2005; Botha and Smith, 2006).

The current hypothesis is that the *Lystrosaurus* bonebeds resulted from drought events in the Karoo Basin (Smith and Botha, 2005). Thus the main aim of the taphonomic study on the *Lystrosaurus* bonebeds is to find out whether field observations and laboratory analyses can prove or disprove this hypothesis. If so, are these observations supported in the literature on similar bonebeds? If not, what

do the observations say about the origin of the *Lystrosaurus* bonebeds? These multi-individual fossil accumulations or bonebeds are discussed here in conjunction with fossils and ichnofossils on the logged section. All fossils found during this study are assigned a field number and a “taphonomic class” as defined by Smith (1993) (Table: 2). The Claasens bonebed was previously assigned an accession number (SAM-PK-K8551) by Roger Smith and his field team in 2004, but for the sake of clarity it will be referred to by its nickname (Figure 5.3).

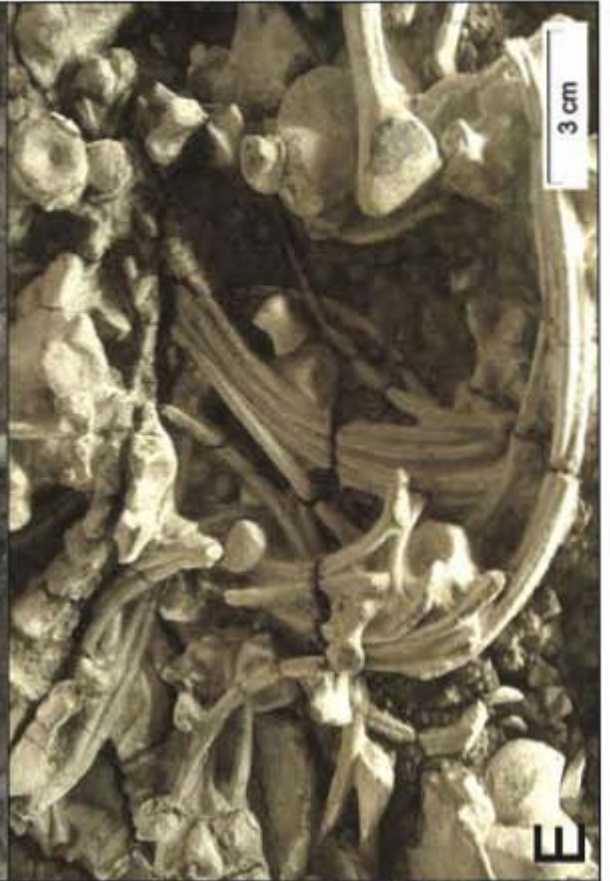
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Taphonomic class	Explanation	Transportation	Duration of post mortem/pre-burial period
A	Complete articulated curled up skeleton.	No transportation.	V. short.
B	Complete or near complete skeleton with straight or reflexed spinal curvature.	Slightly rolled, minimal transportation.	V. Short.
C	Skull with articulation cervical vertebrae and lower jaw.	Lag/ short distance transport.	V. Short.
D	Skull with displaced lower jaw.	Lag/ short distance transport.	V. Short.
E	Skull without lower jaw.	Lag/ short distance transport.	Short.
F	Lower jaw.	Lag/ short distance transport.	Short or Long.
G	Gradual accumulation of variety of postcranial elements.	Transport or winnowing.	Long.
H	Isolated and/or fragmented ribs, limb bones and vertebrae.	Long distance.	Long - V. long.
I	Associated disarticulated and semi-articulated skeletal elements into a "bonebed".	No transport.	V. Short - Short.

**Table 2:** Taphonomic classes (A-I) defined by Smith (1993) based on the degree of disarticulation of the skeleton alongside new taphonomic class (J) defined by Viglietti (2012) to describe the *Lystrosaurus* bonebeds. Duration of short versus long post mortem pre-burial is estimated to have been between  $10^0$ - $10^4$  (V. short – short) and  $10^5$ - $10^6$  (long – V. long) (Behrensmeier, 1982).



**Figure 5.3:** (A) The Claasens bonebed (SAM-PK-K8551) on display at the Iziko South African Museum in the Karoo Palaeontology exhibit (Viglietti, 2009; 2010). Different bone types were plotted as overlays on the image in order to observe attitudes and orientations of bones (i-vi). Aspects of interest in the bonebed (B,C,D,E) have their positions indicated and have been individually photographed. (B) Limb bones with missing articular ends (epiphyses). (C) Limb bones disarticulated but associated. (D,E) Articulated rib sections. The Claasens bonebed is 180 x 72 cm. Source: C. Payne (2007).



### ***Lystrosaurus* Bonebed Occurrences (Taphonomic Class I)**

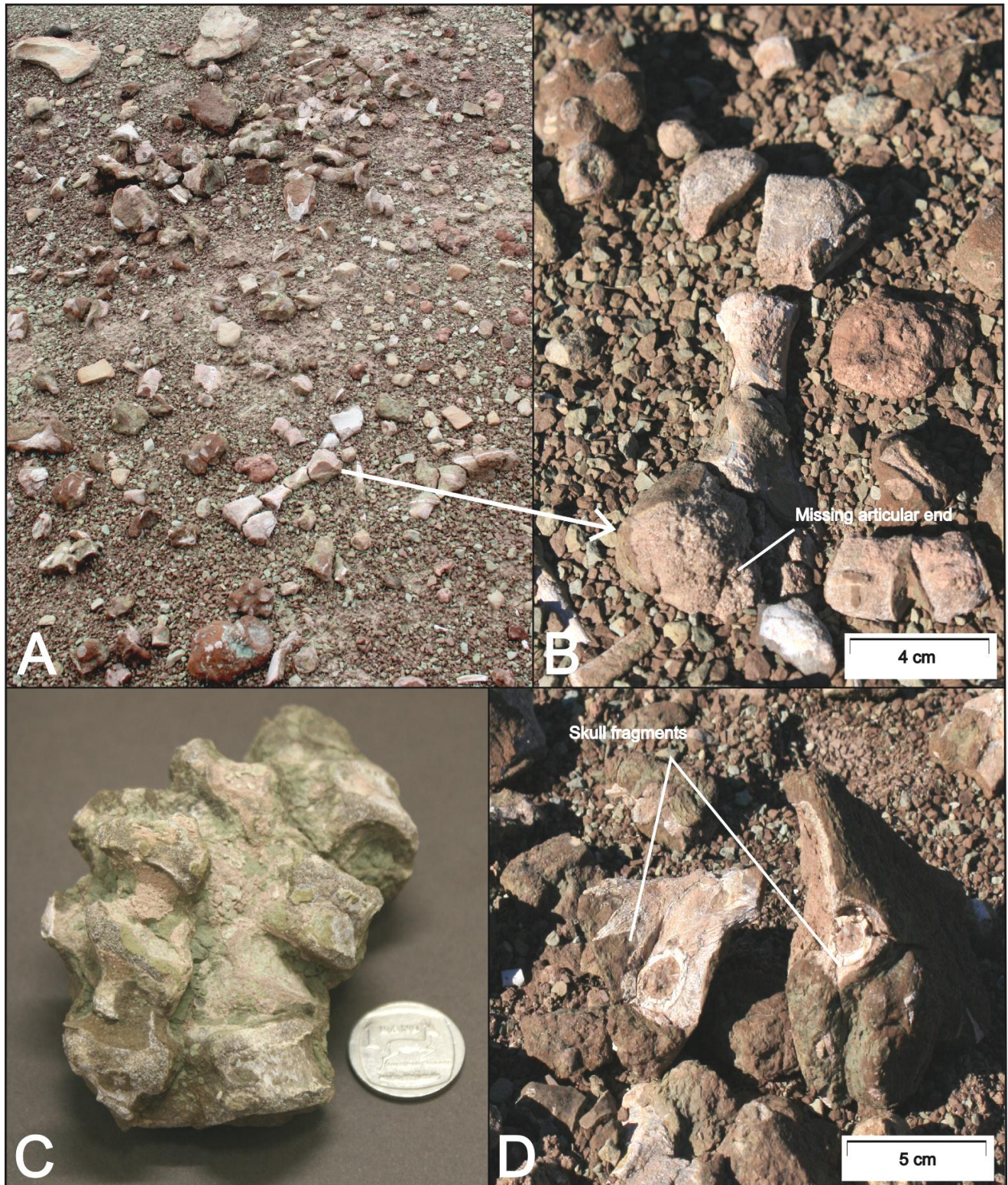
Fossils 1-5, 10 (Assigned the RS-379 field number but were never collected) and the Claasens bonebed (SAM-PK-K8551) have been assigned a new taphonomic class I as they consist of dominantly post cranial material preserved as bone-on-bone accumulations that do not appear to show evidence of reworking for reasons that will be explained in full later in the chapter (Figures: 5.3, 5.4-5.8, and 5.14). All of these enigmatic, multi-individual bonebed assemblages occur within two dark red siltstone horizons separated by a Facies 1 single story sandstone on Donald 207. The Claasens bonebed and its analyses will be used as a comparison to the other bone beds that were analysed in this study (Figure 5.3).

### **Quantitative Analyses**

Quantitative analysis is one of the first analyses done on fossils assigned taphonomic class G, or bonebeds because the following data need to be collected before further analyses is done: (1) Minimum Number of skeletal Elements (MNE) and (2) Minimum Number of Individuals present (MNI). These data are important as they will form the basis for almost every subsequent analysis or interpretation of the bonebeds. MNE consists of counting bones of the same type (humeri, femurs etc.). The Claasens bonebed underwent a bone mapping exercise by use of a bonebed grid made by preparator Hedi Stummer. The grid image was used as a template to map different bone types (humeri, femurs, skulls etc.) individually in order to make quantitative analyses and general observations on the bonebed easier, as well as to map out the original positions of the removed bone fragments (Figure: 5.3).

*Lystrosaurus* Accumulation: 1

Taphonomic Class: I



**Figure 5.4:** (A) Occurrence of *Lystrosaurus* accumulation 1 (RS-379) on the panel section outcrop. (B) Close up of fragmented but in situ femur is shown. (C) A close up of slightly disarticulated but associated vertebrae encrusted in micritic peri-mineralization. (D) Two broken but associated skull fragments so it is assumed the fragments belonged to the same skull. R1 coin is 1.5 cm in diameter.

*Lystrosaurus* Accumulation: 2

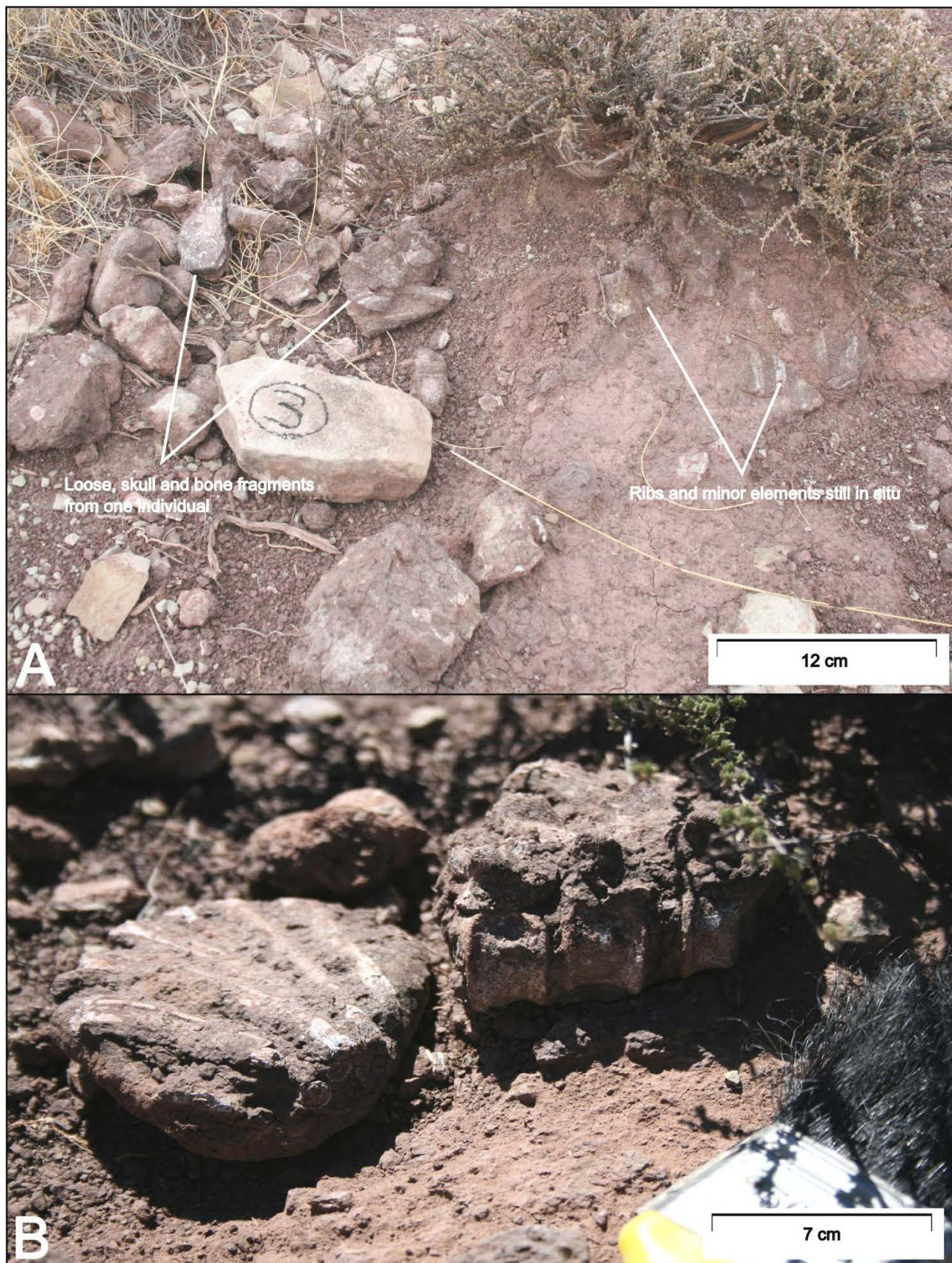
Taphonomic Class: I



**Figure 5.5:** (A) *Lystrosaurus* accumulation 2 (RS-379) on outcrop surface. (B) Close up of skull fragment exposing a cross section of the tusks. (C) Disarticulated rib and associated vertebrae resting above same skull fragment.

*Lystrosaurus* Accumulation: 3

Taphonomic Class: I



**Figure 5.6:** (A) *Lystrosaurus* accumulation 3 (RS-379) as present on outcrop. The majority of material is not *in situ*, and many of the loose fragments comprise fragmented bone and skull encrusted with micritic peri-mineralization. (B) On closer inspection the loose fragments contain articulated elements such as ribs, minor vertebrae, and broken skull fragments.

*Lystrosaurus* Accumulation: 4

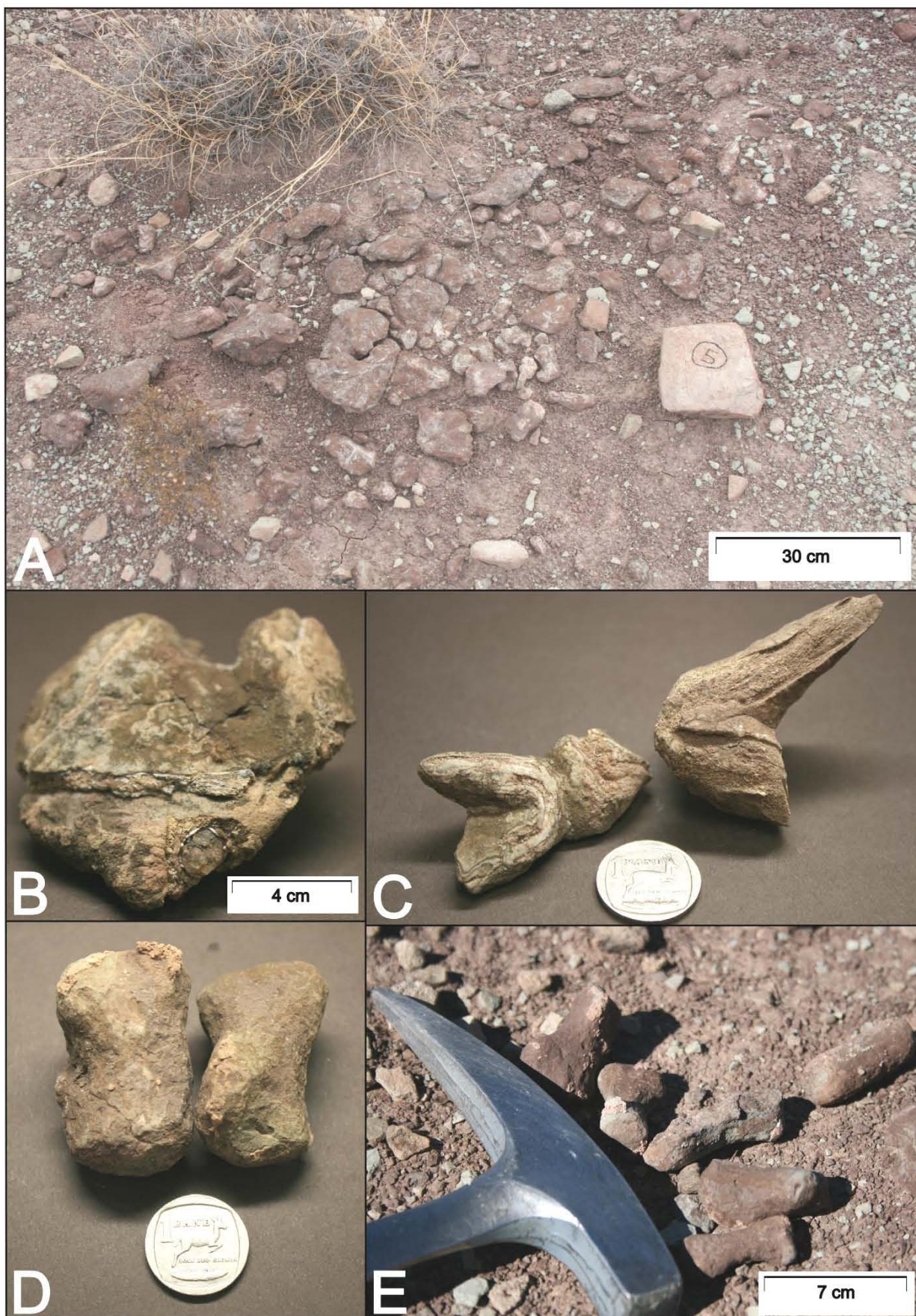
Taphonomic Class: I



**Figure 5.7:** (A) *Lystrosaurus* bonebed occurrence 4 (RS-379) as present on outcrop. (B) Close up of two elements of accumulation showing a well preserved humerus alongside skull fragment with loose vertebrae resting above. All encrusted in same micritic peri-mineralization which shows this occurred prior to fossilisation. (C) Small thin bones that cannot belong to *Lystrosaurus* indicate another fossil species is present in this bonebed. R1 coin is 1.5 cm in diameter.

*Lystrosaurus* Accumulation: 1

Taphonomic Class: I



**Figure 5.8:** (A) *Lystrosaurus* bonebed 5 (RS-379) as present on outcrop. (B) This bonebed comprises very young animals due to presence of small tusk and skull fragment and (C) Two small lower jaws. (D) Two tiny humeri were also found. (E) A number of small limb bones found encrusted in micritic peri-mineralization.

Bone fragments were counted if they belong to the same skeletal element in question. This was particularly important concerning the other bonebeds from the field area as many of the bones were broken or fragmentary, some were impossible to assign to a bone type. The other bonebeds are still in situ in the study area, unlike the Claasens bonebed they have not been prepared so most of the bones were encased in siltstone and/or micritic peri-mineralization and could not be identified. These are named “other” in the quantitative analysis. Since the bonebeds consisted almost solely of one species, *Lystrosaurus declivis*, the quantitative analysis was performed on this species only. The results of this analysis are shown in Table 3 and are shown alongside the Claasens bonebed data. Table 4 shows a calculated minimum number of individuals for each bonebed.

<i>Lystrosaurus</i> bonebed count	Claasens bonebed	Bonebed 1	Bonebed 2	Bonebed 3	Bonebed 4	Bonebed 5
Skulls	9	1	1	1	2	1
Lower Jaws	6	0	0	0	1	2
Humeri	12	1	1	1	2	3
Femurs	14	2	0	0	1	0
Ribs	117	4	20	7	8	6
Vertebrae	129	14	5	10	9	13
Other	16+	38	13	15	13	45

**Table 3:** Table shows minimum number of skeletal elements (MNE) counted in the six bonebeds studied on Donald 207. "Other" refers mainly to broken bone pieces that were unidentifiable as well as other bone types that were not used in the quantitative analyses (i.e. phalanges, ulnas, radii, tibiae, and fibulae).

<i>Lystrosaurus</i> <i>bonebed</i>	Claasens bonebed	Bonebed 1	Bonebed 2	Bonebed 3	Bonebed 4	Bonebed 5
MNI	9	1	1	1	2	2

**Table 4:** Calculated minimum number of individuals (MNI) for the Donald 207 bonebeds.

## Bone Loss

What can first be observed from the quantitative analysis is that the bonebeds from the panel section consist of much fewer animals than the Claasens bonebed. This does make sense as the bonebeds from the panel section are also significantly smaller in area as they tend to vary from ~50-100 x 20-40 cm in plan view with comparison to the Claasens bonebed which is 180 x 72 cm. From the quantitative analysis, it was realised that the first three accumulations are not a true bonebed as their MNI came to only one individual present. They show identical taphonomic class to the other bonebeds, so it is possible they formed in a similar process to the other true bonebeds and will be referred to as bonebed accumulations here. This conclusion reveals uncertainty with the MNI analysis, as there is always the possibility that more individuals are present, but not enough bones collected to prove this. Also the high degree of bone fragmentation, weathering, and micritic siltstone peri-mineralization (a thin carbonate nodule-like encrustation on fossil) (Smith, 1993) made it hard to identify the bulk of the bone fragments present, so adding to the uncertainty of the MNI for the smaller bonebeds from the panel section. If there is the opportunity to do preparation of the bone material curated at Iziko Museum in the future, it will be almost certain that more evidence of other individuals would be found, however at this point assumptions concerning further individuals present cannot be made.

Each *Lystrosaurus* has 2 humeri, 2 femurs, 54 ribs, and 41 vertebrae (Watson, 1913), so if the calculated MNI are taken into account, not nearly enough bone is present for one full animal in any of the bonebeds, besides the Claasens bonebed.

Bone loss depends on a variety of factors, such as the length of time a carcass lies on the surface after death, the presence of carnivores or scavengers dispersing remains, trampling by other animals and the distance the skeletal material is transported before final burial. Erosion or other processes after burial can further remove or add material to an accumulation (Rogers et al., 2007).

From all the bonebeds and accumulations, there has been exceptional loss of ribs and vertebrae. An intuitive reason for this is that ribs and vertebrae are generally less dense bones (lightweight) and are thus more easily destroyed or lost. Rogers (1991) discusses the importance of trampling by other animals in the loss of vertebrae, phalanges, and ribs in a *Hadrosaur* bonebed in north-western Montana and the resistance of limb extremities to disarticulation in dry conditions. There is not much evidence for trampling in the Claasens bonebed, or in fossils on Donald 207. Many of these bone fragments are encased in nodular material which may show bones were broken by diagenetic processes during fossilization (Figures 5.4, 5.5, 5.7 and 5.8). Expanding of cracks by crystallization of secondary calcite during diagenesis could be mistaken for trampling. If trampling were a significant factor, crunched or broken bones would be expected to be seen along with the bone fragments however, this is not evident. Carnivory may have caused preferential destruction of ribs and vertebral elements, but as explained later, little evidence of carnivory is present on the bonebed accumulations.

It is also very likely, in the scenario of the panel section bonebeds and accumulations, that bone loss occurred following exhumation of the fossils during

modern weathering processes as they are all highly eroded and only some of the elements are still embedded in fresh rock. Regardless, the amount of loss seen in the smaller bonebeds and accumulations are still significant, as it is possible that the accumulations represent carcasses that spent a longer amount of time on the surface than the Claasens bonebed, most likely being buried and exhumed a number of times before being finally buried.

### **Bone Articulation**

Upon first inspection, the Claasens bonebed appears to be a jumbled melange of post cranial and cranial material. However, there is an uneven distribution to the bones as most of the bones and skulls lie on one side of the bonebed. *Lystrosaurus* skulls are large and dense so one would assume that shallow sheet floods would not be capable of entraining and transporting them, thus their position should represent the closest point to the site of death. Most of the ribs lie in clusters throughout the bonebed in varying degrees of articulation. The rib clusters may signify the original resting place of some of the individuals. The orientation of the humeri and femurs are intriguing however, water action cannot be assumed the cause (Figure: 5.3). These observations could imply that the original position of the carcasses was inside the floodplain depression with bone loss occurring because of either local processes (burrowing) or the current removing bones from the depression before burial.

The other *Lystrosaurus* accumulations are more difficult to measure bone attitude and orientation as the fossils that are no longer completely in situ. However, in places the carbonate encrustation on bones do preserve clumps of disarticulated bone, and

also individual bones completely encased in the same micritic peri-mineralization material, which proves that that the bones were moved from their life position (i.e. disarticulated) prior to fossilisation. This is seen clearly in all the bonebeds and accumulations, but particularly in the Claasens bonebed, accumulations 1 and 2 and bonebed 4 (See Figures: 5.3(B), 5.4, 5.5 and 5.7). Here skull material is associated with disarticulated elements, such as loose vertebrae and ribs (Figure: 5.5 and Figure 5.7). These nodular clumps also preserve some articulated elements as well, mostly ribs and vertebrae sections. In accumulation 1, a small rack of vertebrae shows slight disarticulation and this is preserved in the nodular casing (Figure: 5.4). A rack of articulated ribs and vertebrae are also preserved in accumulation 3 (Figure: 5.6). This is an interesting observation as the articulated elements in the Claasens bonebed also consist of rib and minor vertebrae sections (See Figure: 5.3 (C and D)). Ribs and vertebrae are easily lost from a system due to their morphology and easy disarticulation from the rest of the carcass. This can be seen in the bonebeds by the significant loss of ribs and vertebrae, yet the ones that do remain appear to have retained some form of articulation. R. Smith (pers. comm, 2009) suggested that their articulation was the result of dried skin keeping the ribs together, almost as though some parts of the carcasses mummified as they lay on the surface, possibly resulting in the skin drying in the hot sun. There was some articulated material amongst the fragments removed from the bonebed, such as a front foot and some vertebrae. In a semi-arid climate, this often occurs in animals after death, as the hot sun dries cartilage, tendons, joints and skin, resulting in preservation of articulation (Hill and Behrensmeyer, 1984; Weigelt, 1989).

## Bone Weathering and Carnivory

Bones in these bonebeds have not been fragmented or broken by weathering processes and carnivory, and are generally well preserved, showing few cracks and fissures which are surprising observations considering all the evidence supporting long periods of exposure to the elements. This is particularly true for the Claasens bonebed as fine features have been preserved on the bones such as muscle scars (See Figure 5.3). These sorts of features are hard to see on the other bonebeds' elements due to micrite encasement. The generally fine preservation of bone does not completely exclude the possibility of carnivory, as carnivores may have removed bones within flesh from the carcasses. However, it cannot be assumed carnivores were a major influence as there is no evidence of carnivory in the bones preserved in the bonebeds.

Some evidence for desiccation is evident on certain bones in the form of minor longitudinal cracks and fissures on some of the longer bone shafts. Behrensmeyer (1978) defined five stages of bone weathering after an intensive study on bone weathering of recent mammals in the Amboseli Basin, southern Kenya. These stages can be used as a proxy for the time the bone spent lying on the surface. These stages are defined by easily observable criteria (cracking, flaking, skin and ligament presence, etc.). Using Behrensmeyer's (1978) weathering stage criteria, it was decided that the *Lystrosaurus* bonebeds show characteristics from weathering stages 1 and 2. Stage 1 criteria involve longitudinal cracks, the presence of fat, skin and/or other tissue (but fleshy material would not survive fossilisation). Stage 2 is similar, only cracks become deeper, flaking may be evident (but this is not seen in the

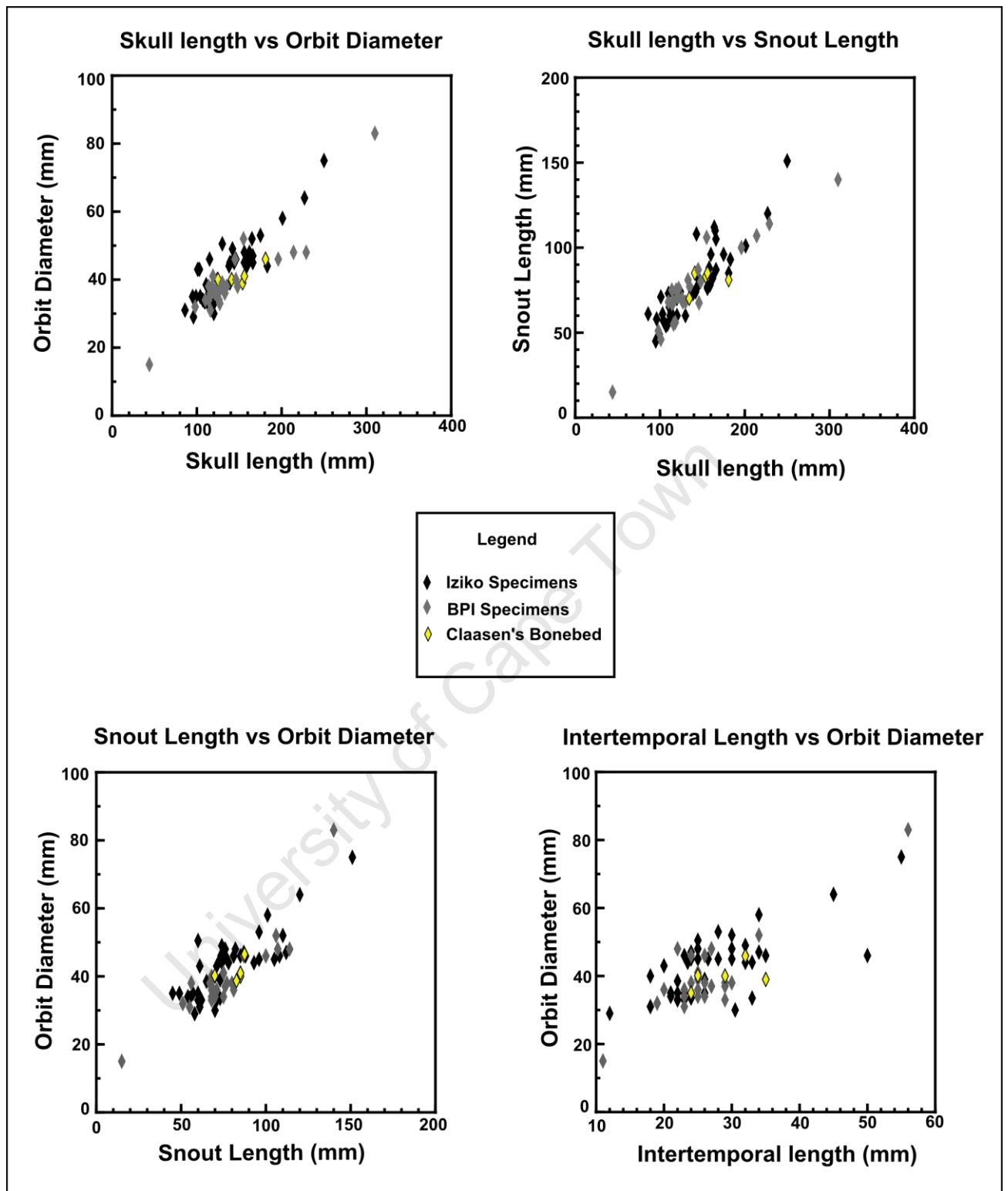
bonebeds) and ligaments, cartilage and skin can be present (Behrensmeyer, 1978). Stages 1 and 2 are interpreted as less than five years exposure to semi-arid climatic conditions on an exposed floodplain (Smith and Botha, 2005).

### **Juveniles vs. Adults**

The average skull length for an adult *Lystrosaurus* is within the range of 109-258 mm depending on the species (Botha and Smith, 2007). Thus to understand the growth stage of the *Lystrosaurus* that consisted the Claasens bonebed and the other smaller bonebeds, skull dimensions were compared to *L. declivis* specimens in the collections of Iziko South African Museum, and the Bernard Price Institute at the University of Witwatersrand, Johannesburg (Appendix 2). For each specimen the skull dimensions measured included total skull length, snout length, orbital diameter, interorbital region (skull length between two orbits), and finally the intertemporal region (width of the back of the skull). These measurements were then plotted on a graph to help show the position of the Claasens bonebed skull dimensions with respect to other specimens of *L. declivis* in the collections (Figure: 5.9). All measurements are shown on a spreadsheet in conjunction with photographs of each specimen measured (Appendix 2). Graphs were constructed comparing measurements of particular skull dimensions which are believed to reflect ontogenetic growth. Most of the graphs express as a positive correlation line which would be an intuitive result for growing animals. Due to degree of preservation of each specimen, some measurements were impossible to determine as a section of the skull is missing or is too deformed. Skulls were too fragmented to be quantitatively measured for their respective dimensions, thus the same constraints

apply to some of the specimens of the Claasens bonebed, with the result that not all nine individuals are represented on the graphs. The size range of animals in the other logged bonebeds has been predicted to be similar by comparing skull fragments and long bone sizes to the Claasens bonebed.

*L. declivis* was not as large as the Permian species *L. maccaigi*, but it was a relatively large species (larger than *L. curvatus* and *L. murrayi*) with the largest specimen measured having a skull length of 250 mm (SAM-PK-K10377) (Appendix 2). *L. declivis* is identified as different from *L. curvatus* and *L. murrayi* by its longer and ridged snout (Botha and Smith, 2007). Although all nine of the *L. declivis* individuals making up the Claasens bonebed fall within the adult range of skull lengths compiled by Botha and Smith (2007) they had not reached the maximum size of their species as their skull lengths range from 125-181 mm. This means we can comfortably say these animals were sub-adult at their time of death based on the size of the skulls and bone morphology. As mentioned previously, the skeletal and cranial accumulations of *Lystrosaurus* preserved within the panel section were not preserved as complete skulls. The sub-adult status of the individuals is apparent because features such as limb bones with missing epiphyses. In juvenile and sub-adult animals the epiphysis is still soft or cartilaginous, and is the point where new bone growth occurs. In adult animals, the bone epiphysis is fused to the main bone shaft as the animal has stopped growing. Many of the bones had missing epiphyses, which meant that the long bones belonged to sub-adult animals (See Figure: 5.3(A)).



**Figure 5.9:** Skull measurements of *Lystrosaurus declivis* specimens in collections housed at Iziko South African Museum in Cape Town, and at the Bernard Price Institute at the University of Witwatersrand, Johannesburg (See Appendix 2). Skull measurements collected from the Claasens bonebed individuals are also shown. Skull dimensions were unable to be measured from the other bonebeds on Donald 207 as skulls were too weathered or broken to make accurate measurements. Skull lengths within the 109-258mm range are considered sub-adult to adult for *Lystrosaurus* sp. (Botha and Smith, 2007).

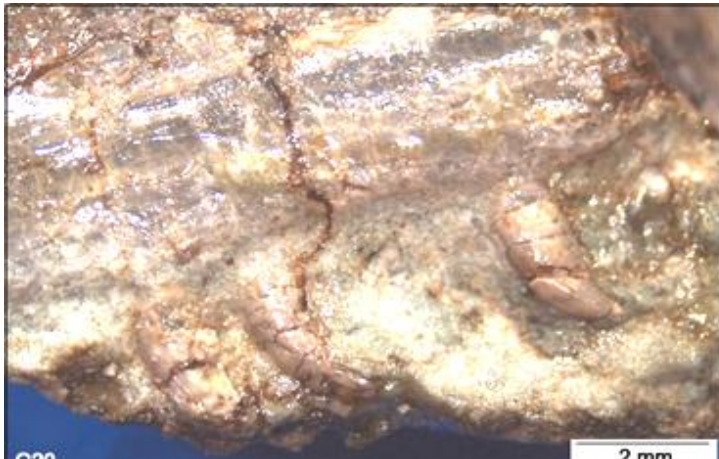
Although it appears that all the individuals are sub-adults, the fact that the skull elements are of different size indicates that they are not all the same age. This was particularly true when observing fossil accumulation 5. Here two lower jaws and limb fragments were found believed to have belonged to juvenile or even infant animals (See Figure 5.8). The other accumulations appear to have *Lystrosaurus* of similar size to the Claasens bonebed accumulation, so the age of the animals likely ranges from juvenile to sub-adult, but were not all the same size. Because of the range in size of animals from the bonebeds we can assume that they were not all from a single brood but rather indicates a gregarious behaviour and a situation where juvenile to sub-adult animals grouped together to form herds. For some reason, this age group were prone congregating together alive and then perishing together to form these accumulations and maybe their apparent grouping behaviour may be a clue as to why.

#### **Evidence of other Taxon than *L. declivis***

All these bonebed accumulations comprise the bones of almost exclusively *L. declivis*. *L. declivis* lived alongside one other species of *Lystrosaurus* during the earliest Triassic, namely *L. murrayi*. *L. declivis* is easy to tell apart from the coeval *murrayi* species due to its longer snout, two frontal grooves on its snout, and larger size (Botha and Smith, 2007). It is very likely the two species displayed different behavioural tactics and occupied different niches. *L. declivis* was a sheep sized member of the dicynodont clade and was one of the most common tetrapods on the earliest Triassic landscape. It was originally interpreted as having led a semi-aquatic, hippo-like lifestyle (Broom, 1907). However, this view has been mostly denounced

and it is presently the consensus that it was a fully terrestrial tetrapod that lived along braided ephemeral rivers, feeding on riparian vegetation, especially sphenopsids (horsetails) and *Dicroidium* (seed ferns) (Botha and Smith, 2007).

Within the Claasens bonebed are also small jaw fragments of an archosauromorph, possibly *Prolacerta*, and possible jaw fragments of small parareptiles (Figure: 5.10). Each jaw was allocated a letter and a number, which corresponds to a position on the grid (See Figure: 5.3), plotting its original position on the fossil. Because of their size, it has been deduced that these jaws belong to juvenile or infant animals of their species. The other five *Lystrosaurus* accumulations in this study do not contain other species. In accumulation 4 however, ribs were found associated with the *Lystrosaurus* remains but are too small to belong to the individual present which means it may belong to an infant animal of the same species, or some other small animal, such as *Prolacerta* (See Figure 5.7).

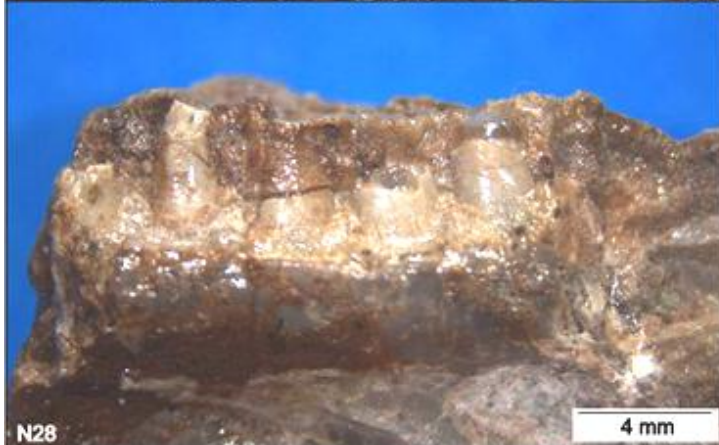


**Figure 5.10:** Jaw fragments collected from the *Lystrosaurus* "Claasens" bonebed (SAM-PK-K8551) during preparation. The jaws were given a grid number so they can be positioned as found back into the bonebed. Details about each jaw fragment are below.

Diapsid jaw fragment G20. Note the recurved unserrated teeth.



Diapsid jaw fragment J33. Similar to G20 but smaller in size.



Jaw fragment N28. The teeth are significantly damaged so difficult to identify. The pin-like teeth suggest a small parareptile.



Jaw fragment L27. Quite damaged teeth. The teeth are not recurved so been tentatively identified as small parareptile as cynodonts have multi-cusped teeth.

### **Other *Lystrosaurus* Remains**

*Lystrosaurus* is the most abundant fossil species found in the study area. R. Smith and J. Botha are meticulously documenting all these fossils as part of a NRF African Origins funded project on the Early Triassic Recovery. This is beyond the scope of this study, however a selection of taphonomically interesting fossils is described.

### **Fossil 6 (Taphonomic class C)**

Fossil 6 (Field number: RS-378) is the remains of a single *L. declivis* individual comprising an articulated skull and lower jaw associated with remnant vertebrae minor ribs and limb bones. It was found and position logged on the panel section on the same horizon as accumulation 3 in the Facies 4 red siltstone (Figure: 5.11). As the bone was badly weathered, this specimen was not collected. In these weathered sections, the hard outer bone has been removed in places, exposing the spongy inner bone on the limb bones, and sections of the skull have a pitted appearance. It was found in association with Facies 4i pedogenic nodules. The bone is a white colour with some reddening present.

### **Fossil 7 (Taphonomic class B)**

Fossil 7 (Field number: RS-380) is a *L. declivis* specimen from the Facies 3 deposits shown in the panel section. This fossil was collected but never accessioned. It is preserved in near complete articulation, entombed within a large black weathering nodule (~2 m across). The bone is a deep black, as is typical of fossils found within these large nodule encasings.

Fossil: 6

Taphonomic Class: C



**Figure 5.11:** *Lystrosaurus declivis* partial skeleton (Field No: RS-378) as present on the panel section outcrop. This fossil was not collected. Note the weathered appearance of the bone surface.

#### **Fossils 8 and 9 (Taphonomic class A)**

Fossils 8 and 9 will be described together as they were found in close proximity within Facies 4 green siltstone laterally equivalent to immediately above the +13 m single story sandstone that caps the panel section. These two *Lystrosaurus* individuals are of special interest as they are fully articulated (tail and phalanges included) *L.murrayi* individuals (Figure: 5.12 and 5.13). Other *L.murrayi* specimens have also been found in the field area by R. Smith and his field team.

Fossils 8 and 9 are preserved dorsal up with all four legs splayed out. They are both facing the same direction one about 2 m behind the other and curiously not very excessively encrusted in micritic peri-mineralization which uniquely allowed the bones to be seen clearly prior to preparation. Preliminary investigation suggests that one of these specimens preserves a dimpled skin impression over its dorsal surface which may account for its mummified appearance and high degree of articulation (R. Smith pers. comm, 2011). *L. murrayi* is relatively abundant in the study area, and most of the specimens are preserved as isolated complete skeletons, rather than being preserved in bonebeds.

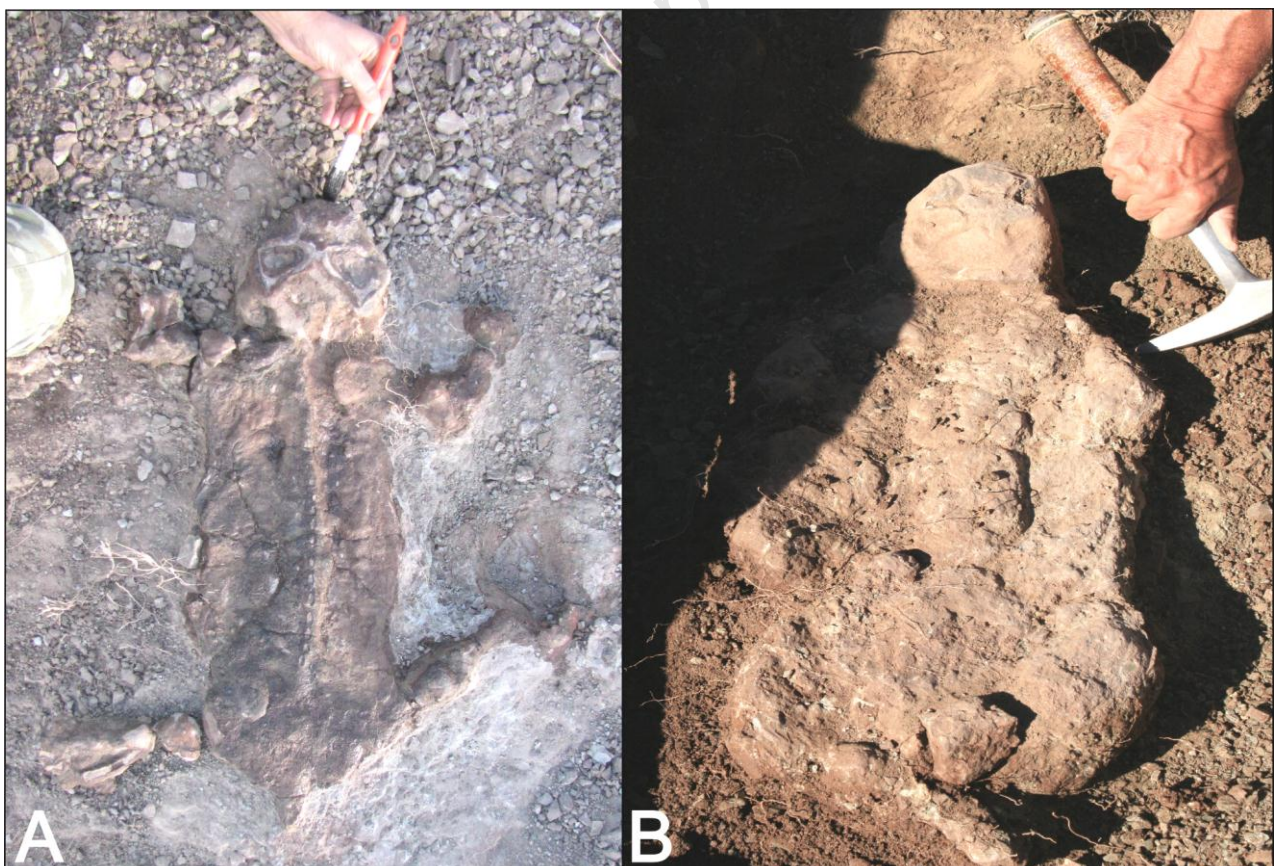
University of Cape Town

**Fossils: 8 and 9**

**Taphonomic Class: A**



**Figure 5.12:** Fossil 8 (SAM-PK-K10971) and 9 (SAM-PK-K10975) as found *in situ* by Derik Wolvaart (in photograph) and Zaituna Erasmus. These two complete fossils were found in curiously close proximity to one another.



**Figures 5.13:** (A) and (B) show the high degree of preservation of (A) Fossil 8 (SAM-PK-K10971) and (B) Fossil 9 (SAM-PK-K10975). Note the high visibility of limbs and even tail vertebrae in Fossil 8, whereas Fossil 9 is more encrusted in micritic peri-mineralization so this detail is not as obvious. Hammer and paint brush are 32 cm and 18 cm long respectively.

### **Fossil 10 (Taphonomic class I)**

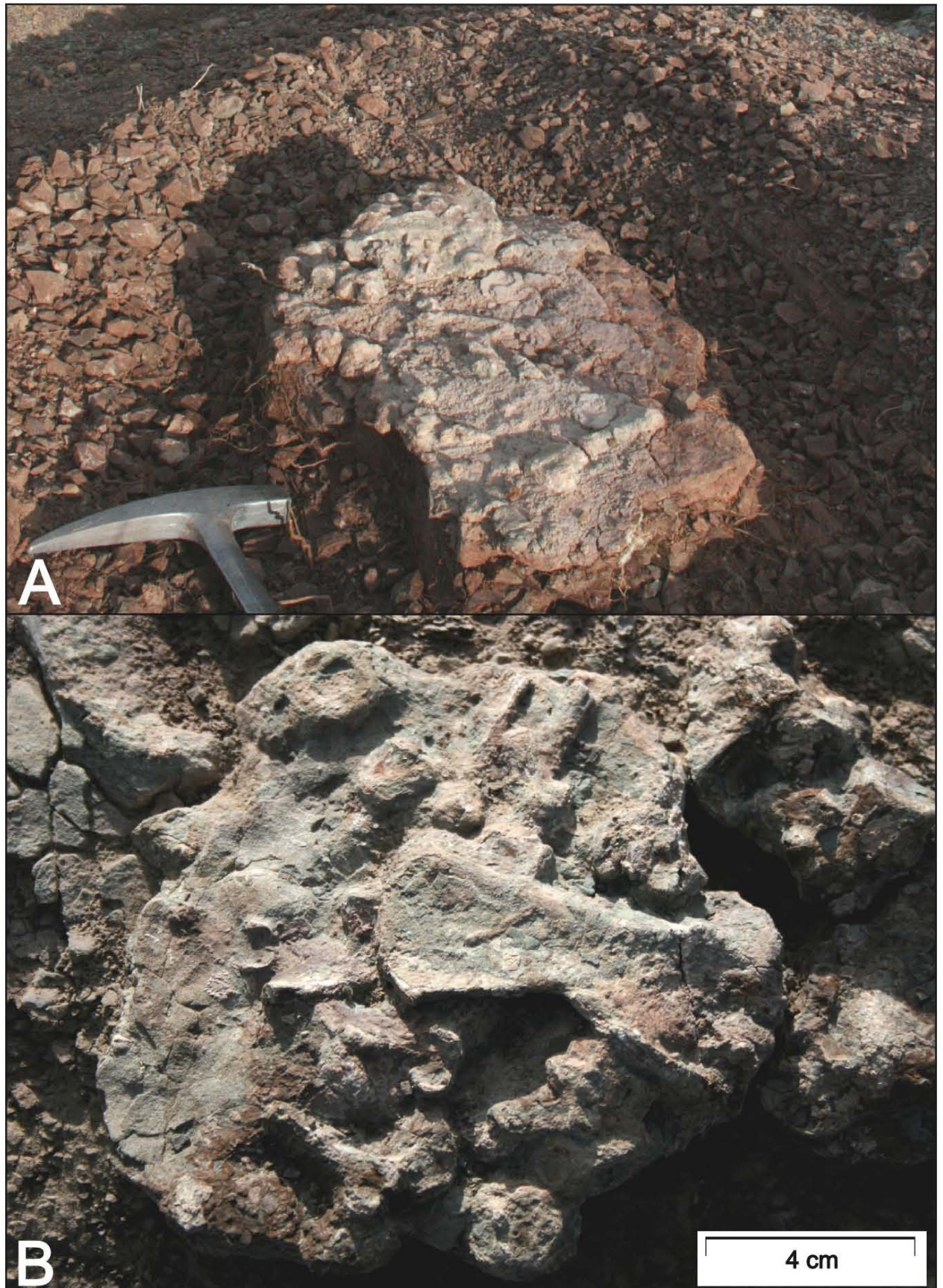
This specimen has a field number (RS-379) but no accession number as it was not collected. The fossil consists of a melange of post cranial material. The bones are of similar morphology to those present in the other *Lystrosaurus* vertebrate accumulations, hence it is assumed this is another *Lystrosaurus* bonebed (Figure 5.14). This fossil was found on the same horizon as the Claasens bonebed so potentially it is another bonebed from this same period of time and of great interest to this study.

### **Other Fossil Taxa**

Apart from the bonebeds, many other fossil taxa were encountered in the study area. They included an array of other species such as amphibians *Lydekkerina* and *Micropholis*, procolophonid *Procolophon*, cynodont *Galesaurus*, therocephalian *Regisaurus*, and finally the archosauromorph *Prolacerta*. The taphonomy of *Prolacerta* and the *Lydekkerina* specimens found on the vertical log will now be briefly described.

Fossil: 10

Taphonomic Class: I



**Figure 5.14:** (A) Fossil (Field number: RS-379) showing similar taphonomic style to *Lystrosaurus* bonebeds described on the panel section. This fossil was located on same horizon as the Claasens bonebed. (B) Closer inspection the fossil shows disarticulated post cranial material jumbled on top one another but all cemented together by micritic peri-mineralization. Hammer head is 16.5 cm long.

### **Fossil 11: Archosauromorph Remains (Taphonomic class I)**

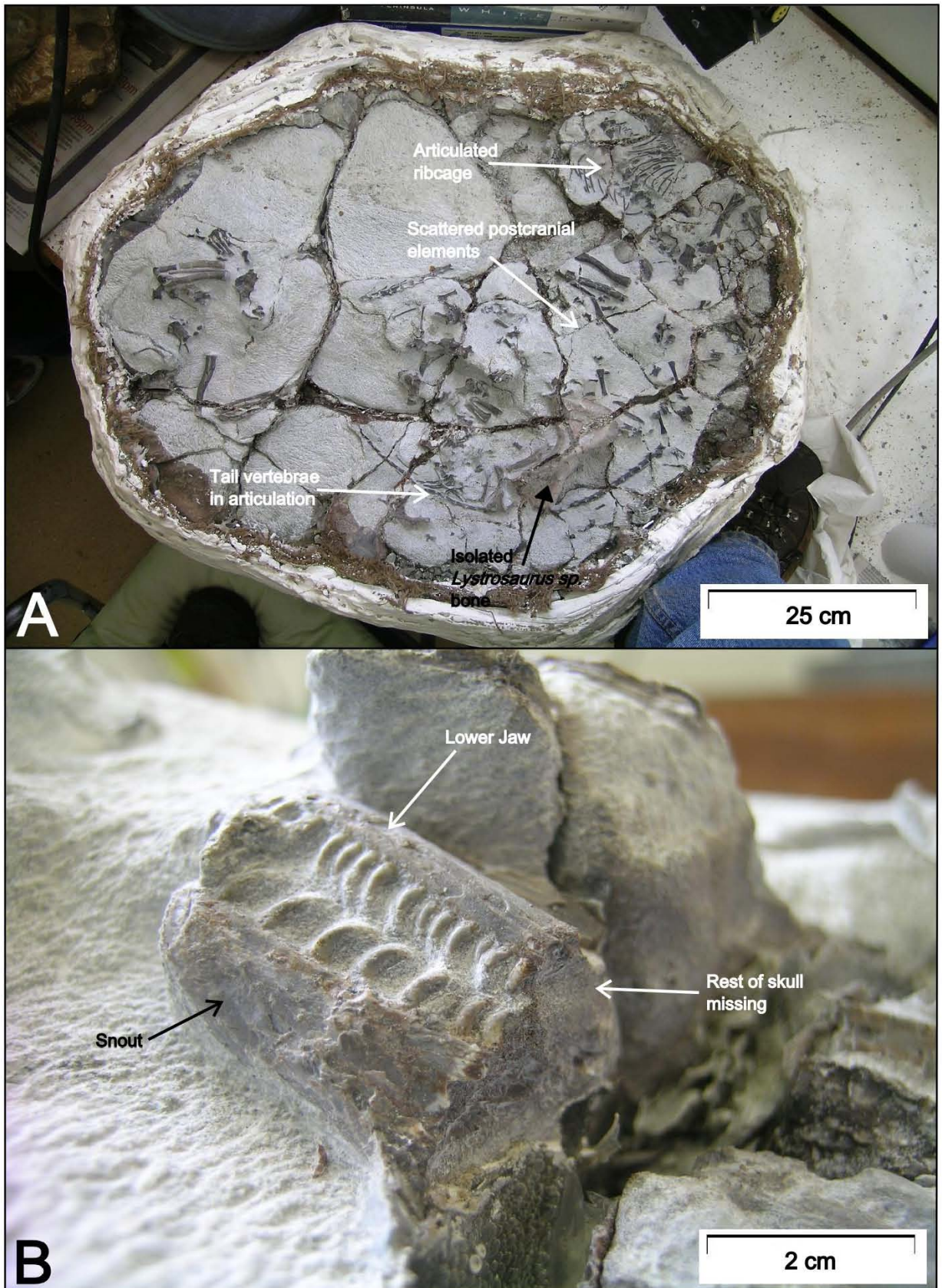
This fossil (Accession number: SAM-PK-K10620) was found on the panel section outcrop in 2008. It was located within Facies 3 sandy siltstone entombed within a large Facies 3 black weathering nodule (Figure 5.15). It has been assigned class I as the fossil consists of mainly disarticulated elements, and there are two animals present due to the presence of a single bone believed to belong to *Lystrosaurus sp.* The only articulated elements are minor vertebral sections, ribs, and some limb bones, which is markedly similar to observations from the *Lystrosaurus* bonebeds in the study area. Other bonebeds of *Prolacerta* have been found in the field area within Facies 3 large back weathering nodules. It is believed they consist of juvenile animals and this is another intriguing taphonomic problem in the field area.

### **Fossil 12: Cynodont Remains (Taphonomic class C)**

Cynodont remains are common on Donald 207 found classed as either Taphonomic class A,B, or C, often in burrow deposits (Abdala et al., 2006). *Galesaurus* fossils are the most common cynodonts in the study area, but *Thrinaxodon* is also fairly common. However during this study, only one cynodont skull was found and classed as Taphonomic class C. It is named Fossil 12 in the study but has been accessioned at Iziko South African Museum (SAM-PK-K10973) (Figure: 5.16). Fossil 12 was found +12.5m on the Donald 207 log within a Facies 3 black-weathering nodule. Upon first collection, it was thought have been an amphibian, however preparation revealed a cynodont skull identified by R. Smith (pers. comm, 2012) as *Galesaurus sp.* The skull roof has been crushed from the pineal opening to the snout. The end of the snout is also missing but the lower jaw is in articulation.

Fossil: 11

Taphonomic Class: I



**Figure 5.15:** The disarticulated remains of the archosauromorph *Prolacerta* from the panel section area. It was found in close proximity to Fossil 7 and was encased within a large Facies 3 black weathering nodule. **(A)** The black colour of the bone and elements of articulated and disarticulated skeleton which show similarity to the *Lystrosaurus* bonebeds; and also other isolated bones including a single bone believed to belong to *Lystrosaurus* sp. (arrowed). **(B)** Taphonomically interesting features such as the tip of the snout with both top and lower jaw in articulation but rest of skull completely gone are believed to reflect scavenging of the carcass by carnivores prior to its burial.

Source: R. Smith (2009).

Fossil: 12

Taphonomic Class: C



**Figure 5.16:** (A) Photograph of the cynodont skull (*Galesaurus sp.*) found on the + 12.5 m on the vertical section (Field number: RS-568). Note the complete encasement within a small Facies 3 nodule. (B) Prepared skull of *Galesaurus* (SAM-PK-K10973) at Iziko South African Museum, Cape Town. Labels show position of the parietal (p), canine (c), and dentary (d).

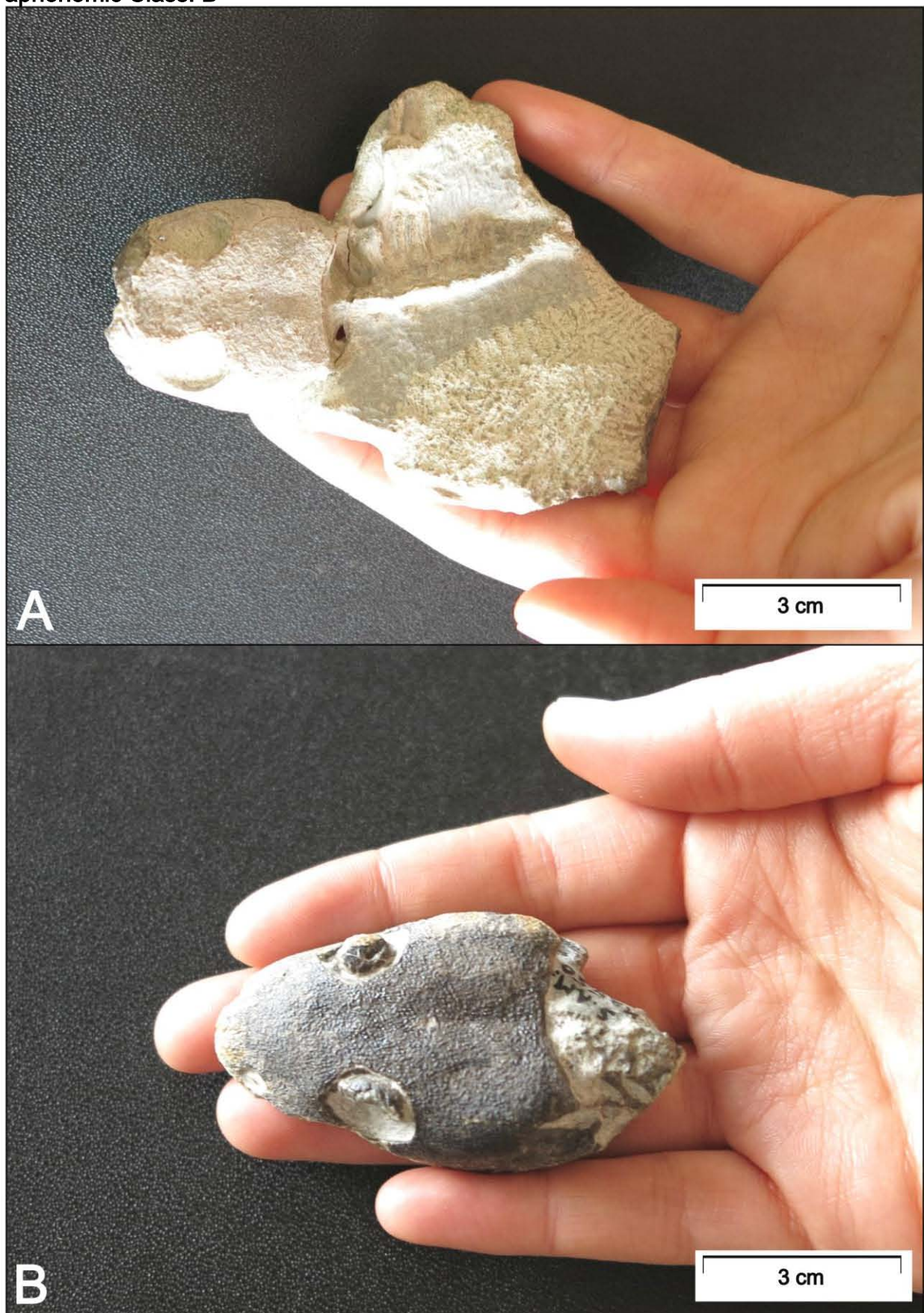
### Fossil 13: Amphibian Remains (Taphonomic class B)

Many small skeletal fragments of amphibians are found in the study area, but most commonly as isolated skulls preserved in small nodules with lower jaw in articulation. Evidence of the presence of an amphibian skull within the nodule is often small teeth protruding from the concretion. Amphibian teeth are quite distinctive as the enamel making up the main shaft of the tooth has labyrinthodont infolding.

In the study area itself the most common amphibian has been observed to be *Micropholis* (Figure: 5.17), although *Lydekkerina* has been found before on Heldemoed 667 Farm by Anneliese Crean (SAM-PK-K8010). In the study area, a *Micropholis stowi* (SAM-PK-K8550) was identified by Annelise Crean (1996), and during this study a *Micropholis sp.* (SAM-PK-K10966) was found by Roger Smith (2011) named Fossil 13 in the study. This specimen was unidentifiable to species level as its entire snout was broken off.

Fossil: 13

Taphonomic Class: B



**Figure 5.17:** Photographs of (A) *Micropholis sp.* (SAM-PK-K10966) and (B) *Micropholis stowi* (SAM-PK-K 8550) found on Donald 207. Both were found encased within Facies 3 black-weathering nodules. (A) In association is a partial articulated skeleton that includes half the vertebral column and right arm. (B) Only cervical vertebrae associated.

## **Ichnofossil Finds: Burrows**

Two large ichnofossils were logged on the vertical section (Figure: 5.18). Many burrow fills have been found on Donald 207, and although hard to identify, burrows typically are recognized in palaeosols where the burrow fill contrasts with the host strata. Burrows can be filled by any lithology, thus they cannot always be recognized in this manner. Key features to look for when identifying burrows in the field are whether the structure cross-cuts bedding planes, distinctive circular, U-shaped or elliptical diameters, linings and exterior margins, visible scratch marks and even rarely fossil remains (Groenewald et al., 2001; Miller et al., 2010).

The two burrows show many of these observations (except fossil remains) with ~15 cm and 45 cm diameters (horizontal) respectively and preserved lengths are ~1.5 m and 3 m respectively. True lengths are unknown because the smaller burrow (~15 cm) was not fully excavated and the larger burrow (~45 cm) appears eroded (entrance or terminal end). Both burrows have an inclined ramp moving away from the entrance that inclines at approximately  $14^{\circ}$ . The larger burrow shows an elliptical shape in cross section and interestingly 2/3 of the way down, the burrow ramp changes direction at a  $90^{\circ}$  and becomes a near horizontal tunnel. The smaller burrow is circular in cross section, bifurcates an obtuse angle into chambers that have a ramp of nearly  $14^{\circ}$ . Ridges and furrows on the burrow surface are interpreted as scratch marks. The ridges rise from ventral to dorsal parts of the burrow, much in the way Sidor et al. (2010) describes scratch marks on Antarctic Triassic tetrapod burrows. The smaller burrow contains Facies 4 infill. Thin section comparison of the infill of the larger burrow indicates that it best matches Facies 3. This suggests the infilling may have been the result of crevasse-splay deposition.



**Figure 5.18:** Ichnofossils believed to represent burrows of Triassic therapsid fauna. **(A)** The burrows range in morphologies and sizes from 12 cm across with scratch marks preserved, even bifurcating tunnels. Source: R. Smith, 2008. **(B)** Larger burrows are also present in the study area, up to 30 cm in tunnel diameter, but no scratch marks preserved. Both burrow types have a ramp that dips approximately  $14^\circ$  and are infilled by sandy siltstone, but rarely mudstone and siltstone filled burrows are found. Hammer 32 cm long.; Source: R. Smith, 2010.

Based on size, it is believed by R. Smith (pers. comm, 2011) that the small burrow was made by a cynodont and the larger burrow by possibly the dicynodont *Lystrosaurus*.

There is growing evidence of underground burrowing behaviour in several tetrapods at various time intervals in the Karoo succession (Abdala et al., 2006). These include the Late Permian dicynodont *Diictodon* (Smith, 1987), the cynodonts *Thrinaxodon* (Damiani et al., 2003) and *Trirachodon* (Groenewald et al., 2001) from the Early Triassic, whose complete skeletons were found within burrow casts. Detailed preservation of the hyoid (tongue bone) and stapes (ear bones) in many cynodont fossils supports their frequent habitation in burrows (F. Abdala pers. comm, 2011). Burrows have been found on the same facies (Facies 4) as the bonebeds (Smith and Botha (2005) and Abdala et al., (2006). It is generally accepted that most dicynodonts (including *Lystrosaurus*), parareptiles such as procolophonids, and cynodonts were fossorial or at least habitual burrowers due to fossil evidence and studies done on front feet and claws (Smith and Botha, 2005). Fossilized remains of *Lystrosaurus* and *Procolophon* were also found in at least four different burrow types from the *Lystrosaurus* Assemblage Zone (Groenewald, 1991; Botha-Brink and Modesto, 2010). Anatomical studies show skeletal adaptations for burrowing in the diminutive dicynodont *Cistecephalus* (Cluver, 1978) and in *Procolophon* (de Braga, 2003). Millet et al. (2001) and Hasiotis et al. (2004) have described similar ichnofossils from Triassic and Jurassic continental deposits in Antarctica.

#### 5.4. Interpretation

Observations can now rule out the following means of formation for the *Lystrosaurus* bonebeds. 1) The sudden death of the *Lystrosaurus* comprising the bonebeds did not result in their immediate burial. This is because when animals die in a sudden event that may bury them, such as a mass drowning, fire, or volcanic eruption, more articulation is preserved. Individuals present may also be representative of the population profile, as young and old animals are killed together. This was recorded in a Late Eocene *Brontothere* bonebed found in Wyoming, USA where the partially articulated skeletons of 25 horse-sized animals at all stages of growth were found together in an area of less than 100 m<sup>2</sup> (Dixon, 2007). The deposits in which the *Brontotheres* were found consisted of river-channel deposits showing signs of rapid deposition, as if by a flash flood. The interpretation is that they were a family herd overwhelmed by a sudden flash flood upon crossing a river (Dixon, 2007). The *Lystrosaurus* bonebed is not in a channel deposit but within a floodplain sequence and thus these individuals probably did not meet the same fate. The bonebed is also not the result of a fire or volcanic eruption as there is no evidence for this in the surrounding bedrock (charcoal, ash etc).

2) The bonebeds are not predator accumulations of any sort as no evidence of carnivory was found on the bones and no bone-rich faeces or regurgitations (Rogers et al., 2007) were found associated with the bonebed. Predators will not single out one species or age group to predate on (although young, old and sick are more often targeted) so a predator assemblage normally consists of an array of different species

and age groups (Rogers et al., 2007). This is why it is deduced that the bonebeds represent behavioural aggregation of animals.

Observations do support two hypotheses of formation: 1) Cold-induced aggregation and 2) Dry spell waterhole congregation. Both of these hypotheses still support the formation or identification of drought-formed vertebrate accumulations or bonebeds (Smith and Botha, 2005) as both could be interpreted as reactions to extreme conditions that compliment drought. Research done by Shipman (1975) identifying the three phases of drought in the geologic record and a case study by Rogers (1991) on three Upper Cretaceous dinosaur bonebeds in the Two Medicine Formation, Montana discuss observations that often parallel ones seen in the *Lystrosaurus* bonebeds. Weigelt (1989) discusses taphonomic modes of desiccated carcasses that could explain bone orientation and articulation seen in the bonebeds. The possibility of the *Lystrosaurus* occupying burrows or dens to escape adverse dry conditions also supports this. However, the shapes of the bonebeds are different to that of a burrow fill as they occupy shallow depressions, showing an oblong to elongate shape. Nevertheless, this may mean the animals congregated not in a burrow but in some protected alcove or depression. This protected congregation spot may have been surrounded by dense vegetation, even if the climate was seasonally dry.

## Cold-Induced Aggregation

It possible outside influence, such as sudden cold, caused the sub-adult *Lystrosaurus* to aggregate not long before their death. Due to the high latitude and land locked position of the earliest Triassic Karoo Basin (Faure et al., 1995) it is very likely that animals needed to cope with not only seasonal cessation of rainfall, but also seasonal drops in temperature. If a semi-arid climate was also present animals may have had to cope with daily drops in temperature. Although therapsids were clearly adapted for living in strongly seasonal high latitude biomes (Kemp, 2011) it is believed their physiology was not that of a fully endothermic animal. It is possible when seasonal drops in temperature occurred, certain species required other means to keep warm (thermoregulate) to retain daytime activities in the colder seasons.

Many modern reptiles have evolved cold-induced or winter aggregation behaviour such as garter snakes (Aleksiuk, 1977), marine iguanas (White, 1973), geckos (Cooper et al., 1985), lizards (Graves and Duvall, 1995) and tree lizards (Ernst et al., 1999). This behaviour allowed these species to reduce rate of cooling whenever temperatures begin to decrease (Aleksiuk, 1997), to protect themselves from the elements (Stamps, 1988) and allow for natural foraging and feeding during winter months when daytime temperatures allowed (Ernst et al., 1999). Modern semi-arid environments are characterised by exaggerated temperature changes between day and night and many modern desert reptiles have evolved to cope well with these temperature fluctuations by either burrowing, shelter sharing (Bridgeman Cowles and Mitchill Bogert, 2006). Thus, it is also possible that the *Lystrosaurus* were coming together at night in a safe location as a means to endure the cooler night

temperatures. Aggregation in modern reptiles has thermoregulatory significance (Aleksiuk, 1977) which means aggregation in ancient reptiles must have had similar benefits. Due to their smaller size (and larger surface-to-volume ratio) compared to adults of their species, sub-adult *Lystrosaurus* may have found it more difficult to thermoregulate. As a result, young *Lystrosaurus* may have formed bands of individuals during the cooler seasons as a means to help them to thermoregulate and continue their activities on the earliest Triassic floodplains throughout the year. However, there may have been times when young *Lystrosaurus* were taken by surprise by extreme conditions and succumbed.

Weigelt (1989) studied many death assemblages of modern animals (mainly domestic livestock) that formed in the surrounds of Houston Texas, USA during strongly seasonal fluctuations in temperature and rainfall reminiscent of tropical seasonality. In Texas, warmer southerly and easterly winds prevail in conjunction with summer dry spells. During winter months however, severe storms accompanied by icy northerly winds called northers are expected. In the years 1925-26, a winter storm was observed by Weigelt (1989) in the Houston area that followed a prolonged drought that weakened animals in the summer.

Accounts by Theodore Kirchhoff, a prominent geographer at the time describes the icy norther breaking as short rainstorms but they do not last long as the dry winds quickly suck up any moisture encountered (Weigelt, 1989). Following the norther is a considerable and often sudden drop in temperature, as much as a 20° drop within a few hours and dryness of the air makes the change even more noticeable. For free ranging livestock these storms are especially devastating. Thousands of heads of

livestock, weak from lack of food in the previous drought, huddle feebly on southern fence boundaries and succumb. In the spring, their bleached bones lie strewn across the prairie among fresh green shoots (Weigelt, 1989).

Behrensmeyer and Miller (2012) refer to an extract from Charles Darwin's *Voyage of the Beagle* (1860) where he describes mass mortalities of guanacos (undomesticated llamas) which he believed were overwhelmed by sudden snow storms. Many of the animals had crawled, before their dying, beneath and amongst bushes. It is not hard to imagine similar scenarios for the *Lystrosaurus* comprising the bonebeds. They may have been surprised by especially severe cold conditions and died in their futile attempts to mitigate exposure by aggregating together in a confined area. Isotope data from the previous chapter suggests that these adverse conditions may have been prolonged cold as well as prolonged dry periods so Weigelt's (1989) and Darwin's (1860) observations strike a compelling parallel with the *Lystrosaurus* bonebeds. If the animals had been weakened by lack of food in a previous drought, they may have not had the ability to survive cooler spells as effectively. Ernst et al. (1999) observed during their studies on tree lizards that extreme cold spells caused the cessation of feeding altogether, and sometimes the lizards did not survive the winter as a result.

Many of the Permian and Triassic tetrapods that lived in the Karoo Basin show evidence for aggregation behaviour and shelter sharing (Smith, 1987; Smith and Evans, 1996; Abdala et al., 2006). However, since the *Lystrosaurus* from the bonebeds have been proven not to belong to the same family group or brood, this is

the first time in the Karoo Basin that above ground non-brood aggregation for a therapsid genus has possibly been identified. Whether it was for seasonal or daily drops in temperature, evidence supports the serious consideration for cold-induced aggregation of sub-adult *Lystrosaurus*.

### **Dry Spell Waterhole Congregation**

Another theory has been the congregation of the sub-adult *Lystrosaurus* around drying waterholes during prolonged drought. Rogers (1991) and Shipman (1975) both discuss the species-selective nature of drought-induced mortality. They elaborate on age-specific mortality during drought as reflecting the heightened susceptibility of immature animals to water stress, which complements Weigelt's (1989) comments on young animal's performance under stress.

In modern animals we can observe how drought affects different species in different ways. Animals respond to drought according to the frequency with which they need to drink water (Shipman, 1975). This means that more mobile animals, which do not require water daily, may migrate out of a drought-afflicted area until conditions improve. Up until the end of the 19th century the mass migration of hundreds of thousands of springbok during drought conditions in the Karoo was quite a spectacle. Drought forces more water-dependant species to congregate along remaining waterways or water sources regardless of their normal habitat preferences or behaviour, forming unnatural congregations around water holes (Shipman, 1975). This could imply *L. declivis* sub-adults may have lead a seasonally semi-aquatic lifestyle suggested by Broom (1907).

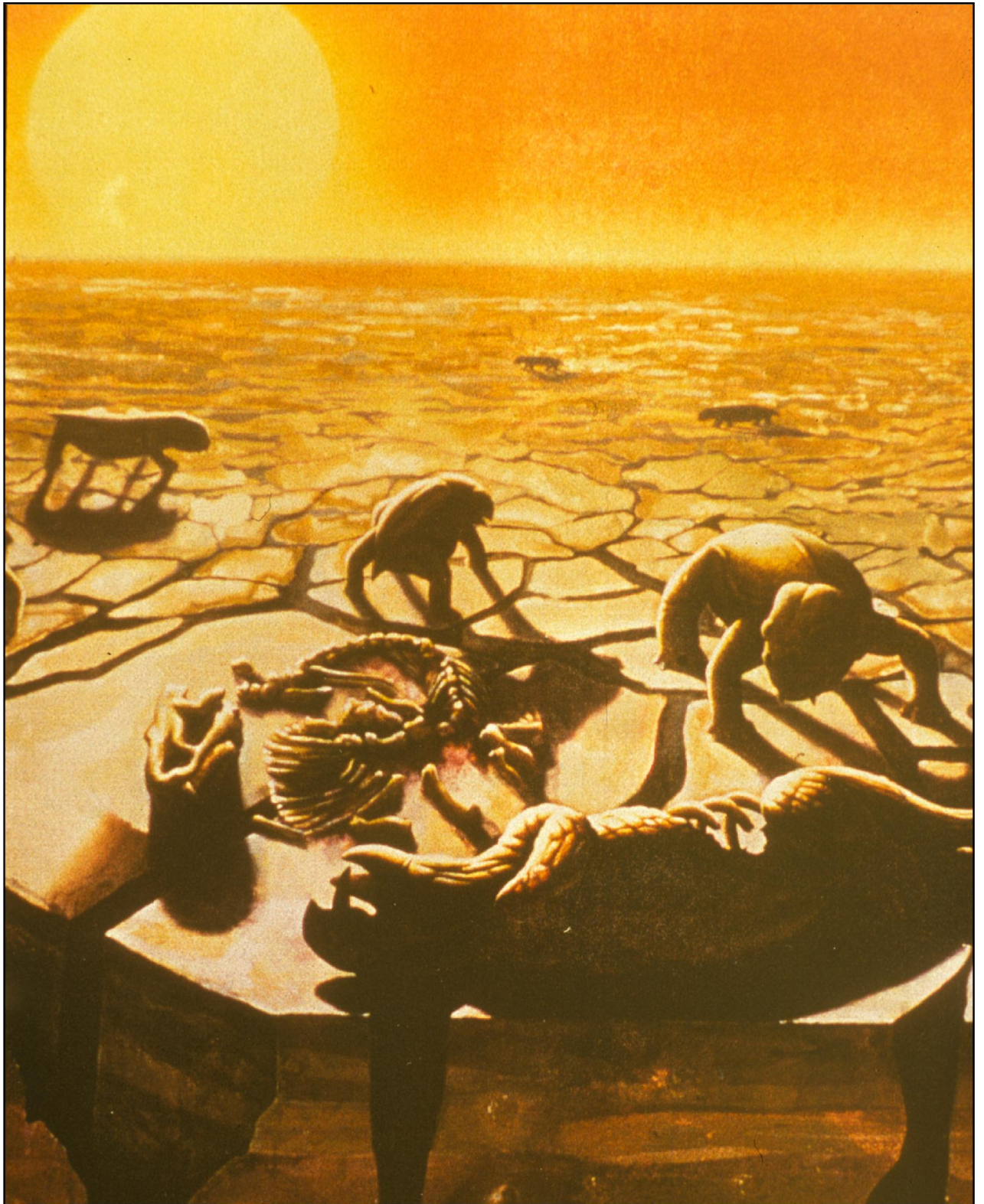
From work conducted on animal carcasses in the Amboseli National Park, Kenya after a drought gripped the area Behrensmeyer (1978) noted that bonebeds do not just form on the surface, there needs to be a spatial concentrating mechanism such as a water or food source, and these congregations of animals tend to be biased toward drought-stricken herbivores. Behrensmeyer (1978) also noted once extreme drought had set in, there were almost no juvenile animals in the population as they had died within the pre-drought phases. This supports drought event sequences laid out previously by Shipman (1975).

Dudley et al. (2001) observed the accumulation of elephant carcasses near groundwater seep basins in Hwange National Park, Zimbabwe during monitoring of drought-related mortality between the years 1993 and 1995. What they discovered was that elephants did not leave their home ranges in search of forage or water during severe droughts, and as the dry season progressed, elephants dug craters and tunnels into the ground with feet, tusks, and trunks to access subsurface water in dry riverbeds. These tunnels extended as much as 2 m below surface, and when the water level dropped below the level to which trunks of juvenile elephants could reach, juvenile elephants would suffer greatly and die of dehydration (Dudley et al., 2001).

This may have been the case with the young *L. declivis* in the bonebeds. They may have not been able to migrate out their home ranges and congregated along the drying waterholes and riverbeds before the area was gripped by a prolonged drought. Shipman (1975) has evidence that animals are more prone to dying of starvation rather than thirst in these situations, due to the large congregations of animals rapidly

consuming all the vegetation within the periphery of the water sources. Unable to venture far from the waterways because of their need to drink daily, the animals slowly starved (Figure: 5.19). Juvenile and sub-adult animals succumbed at a faster rate as adult animals were most able to wander further in search of food and could handle the extreme conditions, which may have also been extreme cold. This also explains the formation of the *Lystrosaurus* accumulations consisting of only one animal as they may represent a single drought-afflicted animal that died on the floodplain, maybe in its individual attempt to find food or water. The Claasens bonebed with its dense accumulation of bones and apparent intimate association of individuals prior to and during death, is however more difficult to explain using this hypothesis.

Since it has been deduced that very little if any transport occurred in the Claasens bonebed to bring the bones in such close proximity to one another, it is difficult to come up with a reason as to why the *Lystrosaurus* came to be so close to one another if they were indeed congregating around a waterhole. They may have been wallowing in mud of the drying waterhole, but then more articulation would have been preserved, particularly in the limb bones as the limbs would have been entrapped in the mud after death. The close association of skulls and good preservation suggests huddling in some protected area away from the sun and carnivores thus for the Claasens bonebed the waterhole congregation hypothesis may not be sufficient to explain its formation.



**Figure 5.19:** An artists' reconstruction of drought-afflicted *Lystrosaurus* in the earliest Triassic Karoo Basin. Artist: Cedric Hunter (2004).

#### 5.4.1. Other Factors in Support of Hypotheses

##### Carnivory

One would expect carnivores to capitalise on attacking these weakened animals, yet no evidence of significant carnivory is seen on the bones in the bonebed. There may indeed be some form of scavenging following death, seen as missing skeletal material. One explanation by Shipman (1975) is that carnivores often change their habits during droughts. Even scavengers that habitually consume bone revert to eating only soft tissue during drought events (Shipman, 1975). It may even be likely the carnivores were eating organs only, leaving the rest. This may be because water is required to digest food and digesting bone is a higher energy task thus requiring more water. Hyenas in Hwange National Park (Zimbabwe) were observed scavenging on elephant carcasses near groundwater seeps in the early phases of the 1994 die-off, but their presence (tracks and dung) was conspicuously absent in the latter stages of the die-off (Dudley et al., 2001). It was argued that the superabundance of carcasses at the end of the drought made it unnecessary for carnivores to leave the cover of protective vegetation or woodland (Dudley et al., 2001) and it is possible carnivores in the earliest Triassic may have behaved in a similar manner.

The result is that bones and carcasses are often left alone by scavengers during droughts, leaving skeletons rarely disturbed in this manner. Animals that died in a protected out of the way depression or burrow may have also been overlooked by carnivores. These factors may explain the lack of carnivory on the *Lystrosaurus* bonebed bones and fully articulated preservation of adult animals found in the lower

Katberg Formation. Lack of carnivory also supports the cold-induced aggregation as if the animals had congregated somewhere protected, their remains may have not been found by carnivores as either vegetation or a small depression would have concealed them from view.

### **Bone Disarticulation**

The almost complete lack of articulation in the bones of animals preserved in the bonebeds implies a significant period of time in which the carcasses lay on the surface. However, some skeletal elements did escape disarticulation (ribs, phalanges, and some vertebrae), which is quite indicative of drought. During a drought very little moisture is present in the environment, so when an animal dies desiccation of the skin and other soft tissue results and the dried tendons and skin keep the joints intact (Weigelt, 1989). This is known as mummification and is seen quite often in the dry and cold climates of the modern world. In 2004, Roger Smith found the remains of *Promoschorhynchus*, a therocephalian, in the Bethulie area where skin impressions are preserved surrounding the fossil suggesting mummification. Potential skin impressions were also noted on an *L. murrayi* specimen from the vertical log (R. Smith pers. comm, 2011). This suggests that the environment during the deposition of the Katberg Formation in the earliest Triassic was dry and possibly cold enough to mummify carcasses prior to burial.

However, this same process can result in disintegration of the skeleton in the long term. Weigelt (1989) observed that when a carcass desiccates it shrivels as soft tissue dries. These shrinking mechanisms can result in unnatural, contorted

positions, the most common being the curvature of the cervical (neck) region of the spinal column due to shrinking tendons. One can also find peculiar displacement of the spine resulting in flexed body parts (such as the legs) and complete turning of the head to the extent that it can lie flat with either its under or upper side on the ground. These unnatural positions can put stress on the skeletal elements of the carcass over long periods, resulting in eventual disintegration (Weigelt, 1989).

Behrensmeyer (1978) noted the importance of vegetation in disarticulating bone elements that preferentially grew around the carcasses of drought stricken animals after the first rains following a drought in Amboseli National Park. Although no evidence of rhizcretions is preserved, this could be one explanation for the unusual occurrence of fossils in the lower Katberg Formation with disarticulated vertebrae, yet articulated ribs (R. Smith pers. comm, 2009). *Procolophon* skeletons have been found, showing spinal curvature and adult *Lystrosaurus* showing “curled up” position and overturned skulls – all indicative of desiccation (Smith, 1995). What is still puzzling are the clustering of the *Lystrosaurus* skulls within the Claasens bonebed.

Articulated and associated ribs and vertebrae attest to the presence of carcasses at the site, supporting previous statements about clustering of animals in this area before death. If the bones were carried to the site from elsewhere by water or sheet flooding there would be more significant orientation of different skeletal elements. Significant bone loss has occurred however, but this can be explained by autochthonous processes relating to plant and animal bioturbation, as vertical and horizontal can occur (Behrensmeyer, 1978). This process would lift lighter bones

upwards and heavier skeletal elements would be grown over and bound to the soil substrate (A. Behrensmeyer pers. comm, 2012). The small jaw elements from other taxon could also have their presence explained by these kinds of processes, however if the cold hypothesis holds, these smaller animals may have been sharing a shelter with the sub-adult *Lystrosaurus* prior to death. Shelter sharing behaviour has been recorded in fossils found on Donald 207 Farm (Abdala et al., 2006).

### **Bone Weathering**

These accounts can explain the attitude of the juvenile and sub-adult *Lystrosaurus* bones, if the carcasses rested on the surface for an extended period, the bones should show some indication of weathering (cracks, splitting etc.). This is not observed to a significant extent. Behrensmeyer (1978) explains that desiccation rates between different animals (i.e. mammals and reptiles) are not yet fully understood. Springbok carcasses in the Prieska area of the Karoo have been observed by yours truly which appeared to have rested on the surface for at least two years, yet show pristine bone material. This could mean that *L. declivis* did rest on the surface for a similar period of time, just not long enough for their bones to show much desiccation stress in the hot sun. Autochthonous processes acting on the bones could again explain bone preservation as if the bones were concealed by soil and vegetation not long after the death and decay of the individuals, this would have acted to protect the bones from sun and element damage, and also from carnivores. Behrensmeyer (1978) has observed in a basin north of Kilimanjaro, outside the Great Rift Valley, that it takes up to ten to fifteen years for mammal bones to fully weather and to disintegrate in the dry climate.

## Other Vertebrate Taxon

The most intriguing are other species associated with the Claasens bonebed in the form of the small jaw fragments. These specimens may have either been later attrition following minor sheet flooding on the floodplains after a drought, as they are fragmentary. Thus it is possible they were damaged and abraded as they were transported by fluid. However, these animals may have also been shelter sharing in association with the aggregating *Lystrosaurus*. It is unlikely that they were the scavengers due to their size. More work on these small jaws may help answer these questions. There are also enigmatic observations from the other vertebrate taxa that support both hypotheses

The *Prolacerta* specimen (Fossil 11) shows much taphonomic similarity to the bonebeds in its degree of articulation etc. and even though it is preserved within a different facies (Facies 3) it does support the cold drought theory as drought afflicted animals and remains are often found in close proximity to watercourses or associated with fluvial deposits (Shipman, 1975). It is also possible that the animal died at another location and its body was washed down the river and was deposited on the riverbank during wet season flooding.

The *Micropholis* specimen (Fossil 13) was one of many amphibians (including *Lydekkerina*) logged on the same stratigraphic horizon by R. Smith. Amphibian fossils are mainly found encased in nodules but also in association with *Lystrosaurus*. A fossil at the Bernard Price Institute (BPI) (University of

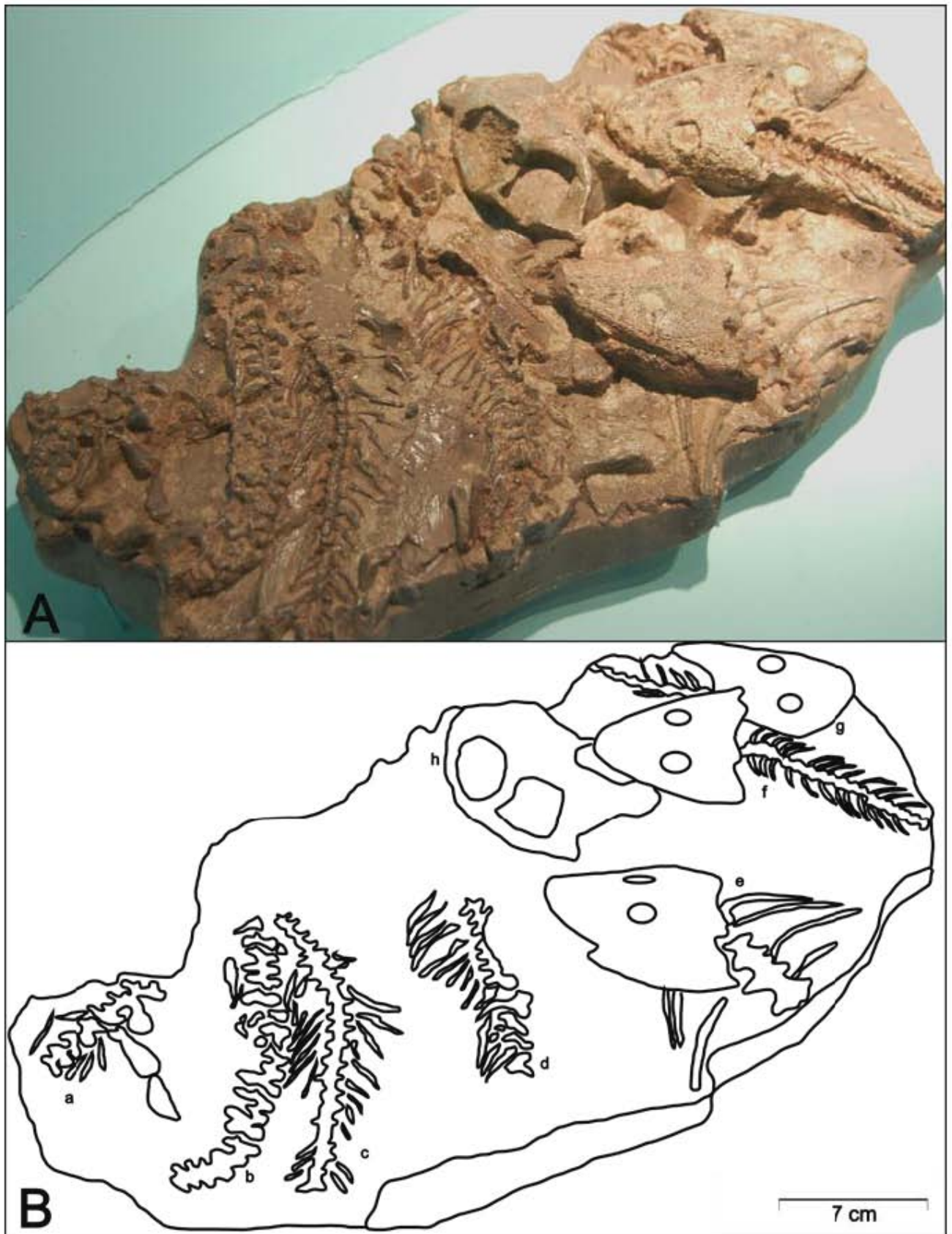
Witwatersrand) consists of the remains of an unidentified *Lystrosaurus* species in association with up to six articulated *Lydekkerina* and invertebrate burrows (accession number: KR21/4C: 5030). The fossil came from a locality in the Kwa-Zulu Natal area named Ndanyana Hills (Hartebeespruit) within Lower Triassic rocks of the Katberg Formation. Although this particular fossil was not prepared out, another very similar specimen showing several *Lydekkerina* skeletons and skulls all orientated toward a *Lystrosaurus* skeleton is also present in the BPI collections (BPI/1/3900) (Figure: 5.20). It is accepted that *Lydekkerina* was a dominantly aquatic animal as the species belonged to an extinct family of amphibians known as the Stereospondyls. This amphibian family was typified by the presence lateral lines around the lips of their eye sockets and pits within the bone of the skull. These housed canals that allowed the animal to detect minute water pressure changes in its environment.

Many fossil remains of *Lydekkerina* have been found on Donald 207 Farm, and although one may not intuitively think amphibians would be associated with semi-arid conditions, Shishkin and Rubidge (2000) argue that all the common Triassic amphibians are small compared to the amphibians of the Late Permian which is thus consistent with increased aridity in the earliest Triassic. Amphibians have also been recorded in the Triassic Fremouw Formation Antarctica (Cosgriff and Hammer, 1984), higher latitude than the earliest Triassic Karoo Basin.

How might amphibians have coped in dry and cold conditions? They may have aestivated or they may have buried themselves in the bottom of muddy depressions

waiting out the dry and cold spells (Hembree et al., 2005). The presence of these amphibians in the field area supports a monsoonal climate that was transitional from seasonally wet (cold) to dry (warm) or vice versa. It is likely these animals did not fare well in prolonged droughts and would have eventually succumbed. When flash floods ensued after the droughts, their remains were likely washed away by the floods and this may explain the scattered amphibian remains within Facies 3 nodules on Donald 207 Farm. Figure 5.20 could represent drought-stricken amphibians that died because of a prolonged drought, surrounding the body of a previous drought victim, the *Lystrosaurus* that succumbed during the initial drying.

University of Cape Town



**Figure 5.20:** (A) BPI/1/3900 is a fossil showing the remains of eight individuals (one *Lystrosaurus* and seven *Lydekkerina*). (B) A simplified sketch showing positions of individuals with a letter making up the multi-individual accumulation: (a-g), *Lydekkerina*; (h), *Lystrosaurus*.

## **Ichnofossils and Drought Adaptation**

Fossorial and semi-fossorial behaviour is common in modern tetrapods living in semi-arid ecosystems because of the temperature fluctuations that occur in these environments (Kinlaw, 1999). This is because the microclimate created in a burrow is much milder and fluctuates less markedly than surface temperatures due to the burrows subsurface air volume and circulation and burrow-wall surface area (Vaughn, 1961; Martin and Bennet, 1977; Lynch, 1980; Meyer, 1999). Burrowing to the water table may have helped animals keep cool when daytime temperatures rose and warm at night when temperatures dropped (Hasiotis et al., 2007). Although rare in the fossil record, evidence of extinct species use of burrows as aestivation chambers, shelter and shelter sharing, and for raising young have been found (Smith, 1987; Groenewald et al., 2001; Hembree et al., 2005; Abdala et al., 2006). This means burrows may have had a complex array of uses to different tetrapod taxa (even to search for water in dry riverbeds, (Dudley et al., 2001), but their main objective seems to have been their use as refuges from climatic extremes as well as day and night time temperature changes. In vertebrate taxa, these extremes are usually in relation to temperature fluctuations (heat or cold) (Miller et al., 2001; Hasiotis et al., 2007).

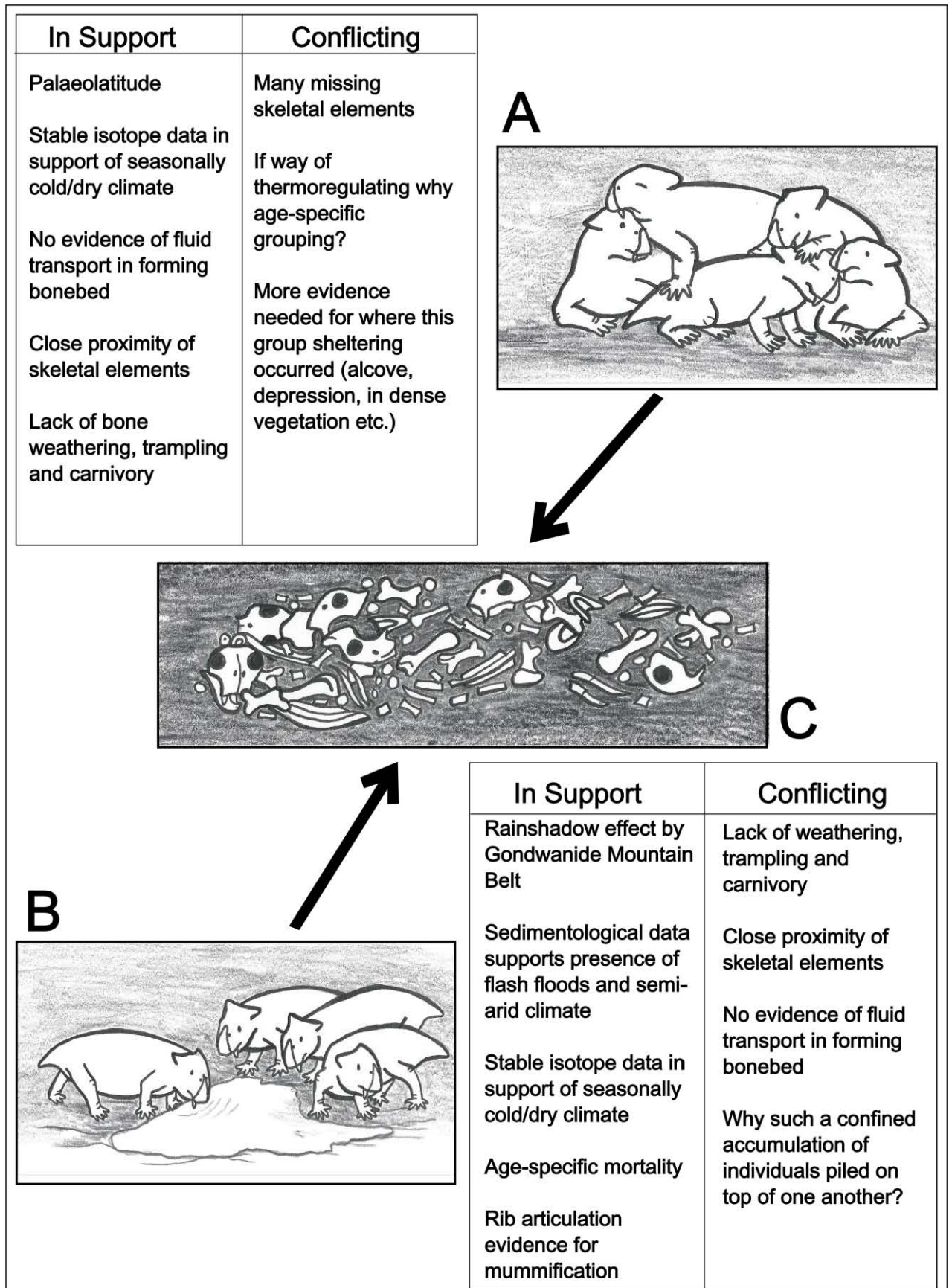
South Africa's reasonably high latitudinal position and presence of carbonate nodules within the Beaufort Group supports the model for a strongly seasonal climate for the Late Permian-Early Triassic Karoo Basin (Smith, 1990, 1993, 1995). Burrows found in earliest Triassic Antarctic rocks show marked similarity to burrows from the Karoo Basin (Sidor et al., 2001; Hasiotis et al., 2004). These burrows coincide with the

sudden appearance of tetrapod remains in the Triassic Fremouw Formation and it is possible that this reflects climatic changes occurring in southern Gondwana, allowing animals to inhabit the higher latitudes by use of burrows to cope with seasonal fluctuations in temperature and light regime (Sidor et al., 2001). Burrowing adaptations inherited from latest Permian relatives were also allowing earliest Triassic animals to mitigate stresses caused cooler and drier periods. Thus, burrows greatly support the presence of a dry environment, as animals may have needed use burrows to hibernate or aestivate within, to protect their soft-shelled eggs and/or young from the elements in brood chambers, or merely to escape from daily surface temperature extremes.

Work done by Abdala et al. (2006) on shelter sharing in burrows shows that many animals may have not been able to construct their own burrows, but would have used burrows made by other animals (cynodonts, dicynodonts, procolophonids etc.) showing mutual tolerance of different species existed such that both could benefit from the burrow and escape climatic extremes. Burrowing adaptations, although seen in other amphibian, reptile, and bird lineages, has a long history in early non-mammalian synapsid evolution (Damiani et al., 2003). It was most likely a key adaptation that helped some therapsid species survive the End-Permian mass extinction event; and thrive in the strongly seasonal climate of the earliest Triassic.

### 5.5. Taphonomic Pathway for *Lystrosaurus* Bonebeds

Taphonomic assessment of the Claasens bonebed and other bonebeds present in the study area suggests two possible origins for their formation; however they do not contradict the hypothesis of a semi-arid setting for the deaths of these animals. The following taphonomic-pathway diagram is based on observations and data collected from the fossil bonebeds (Figure: 5.21). The diagram is representative of two possible formation for the Claasens bonebed however, the possible processes in support or in conflict with evidence preserved in the Claasens bonebed can be applied to the other smaller *Lystrosaurus* bonebeds and accumulations found on Donald 207. The taphonomic diagram as a result also shows where more evidence needs to be collected in order to come to a serious consensus for either scenario that may have caused an accumulation like the Claasens bonebed to form.



**Figure 5.21:** Taphonomic pathways diagram depicts two possible origins for the *Lystrosaurus* bonebeds found on Donald 207 Farm. (A) Cold-induced aggregation and (B) Dry spell waterhole congregation. (C) A sketch of the Claasens bonebed. Each theory of formation has an associated table showing evidence in support and in conflict with preserved evidence.

Figure 5.3 (A): Claasens bonebed overlay i

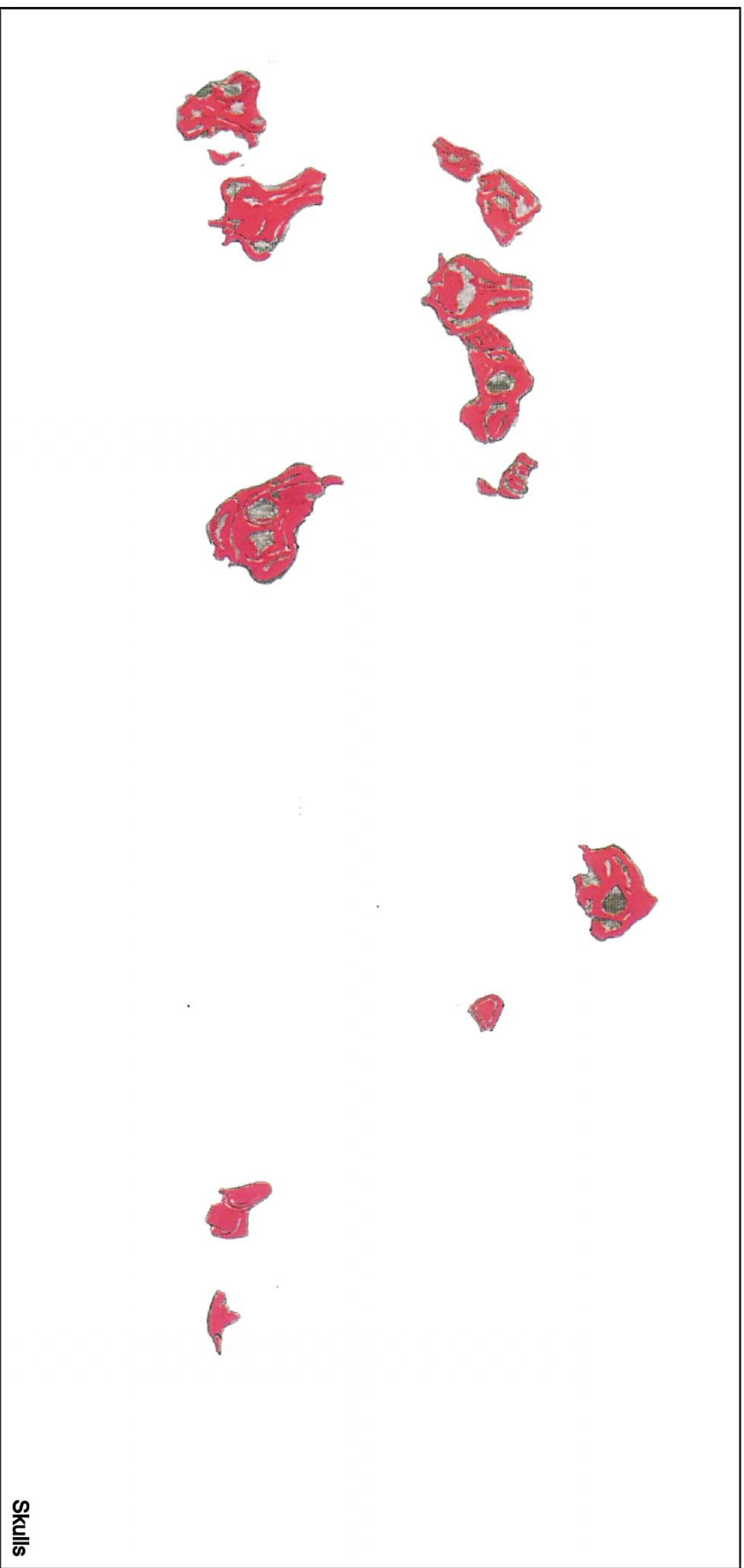


Figure 5.3 (A): Classens bonebed overlay ii



Figure 5.3 (A): Claasens bonebed overlay iii

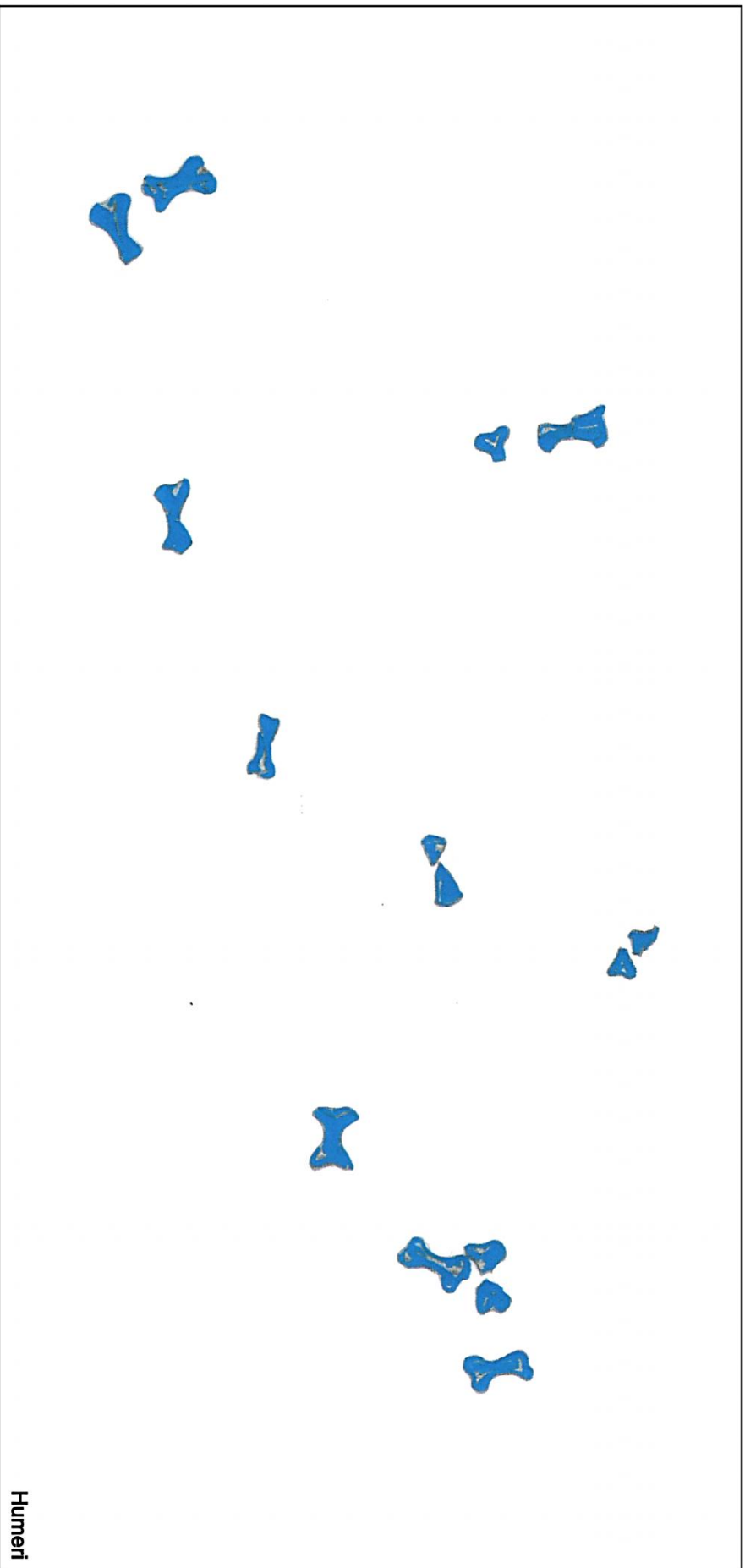


Figure 5.3 (A): Claasens bonebed overlay iv

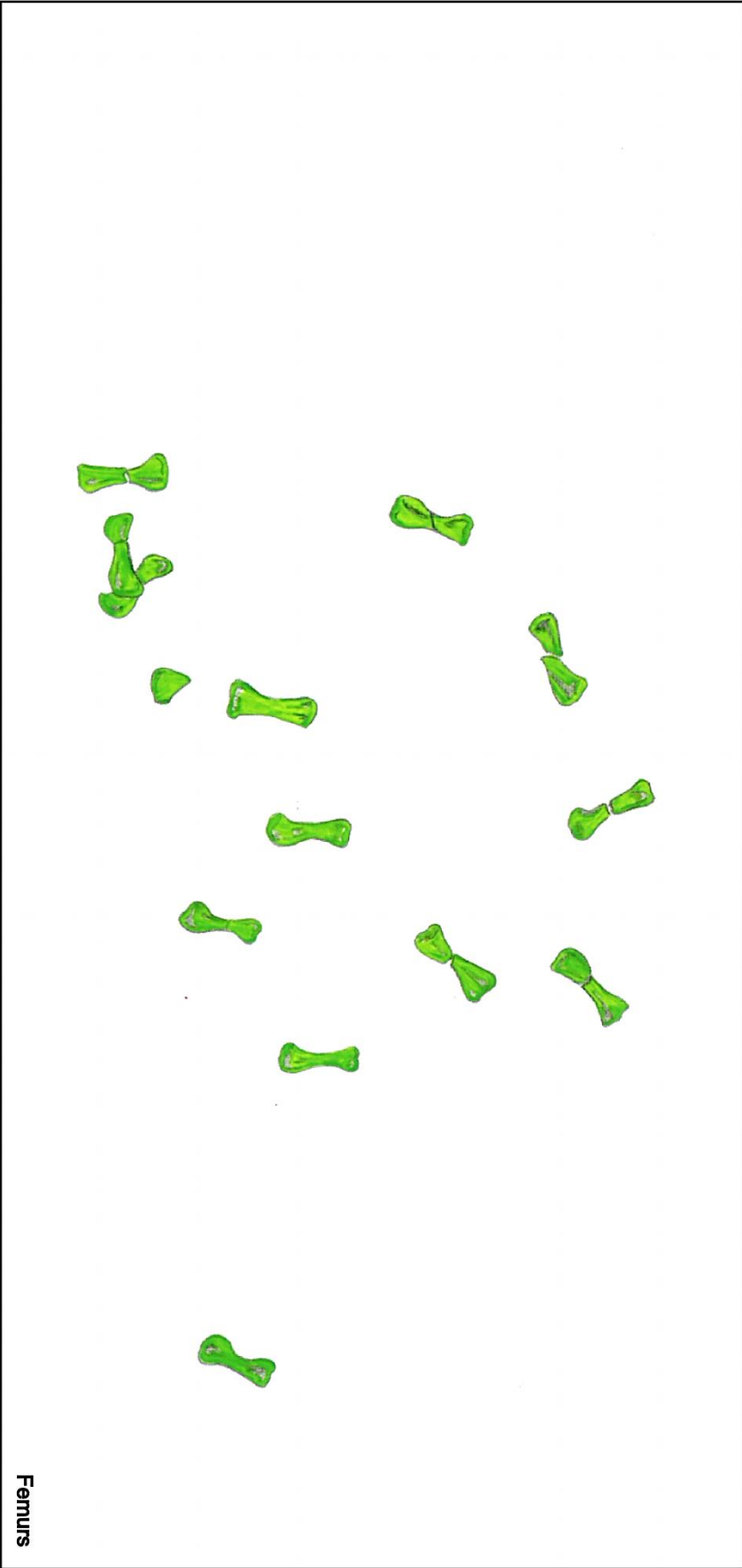
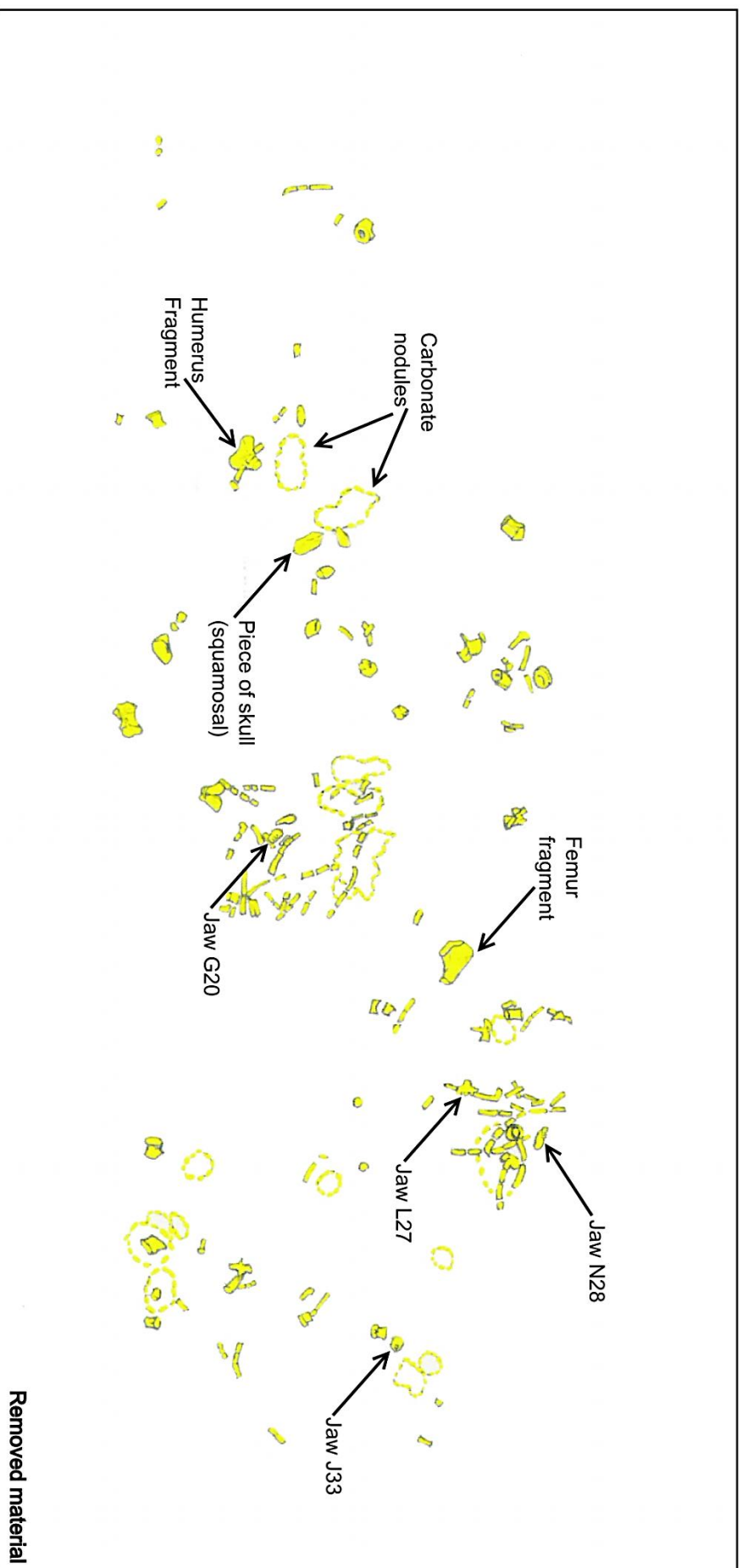


Figure 5.3 (A): Claasens bonebed overlay v



Figure 5.3 (A): Claasens bonebed overlay vi



## 6. Synthesis

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### 6.1 Discussion

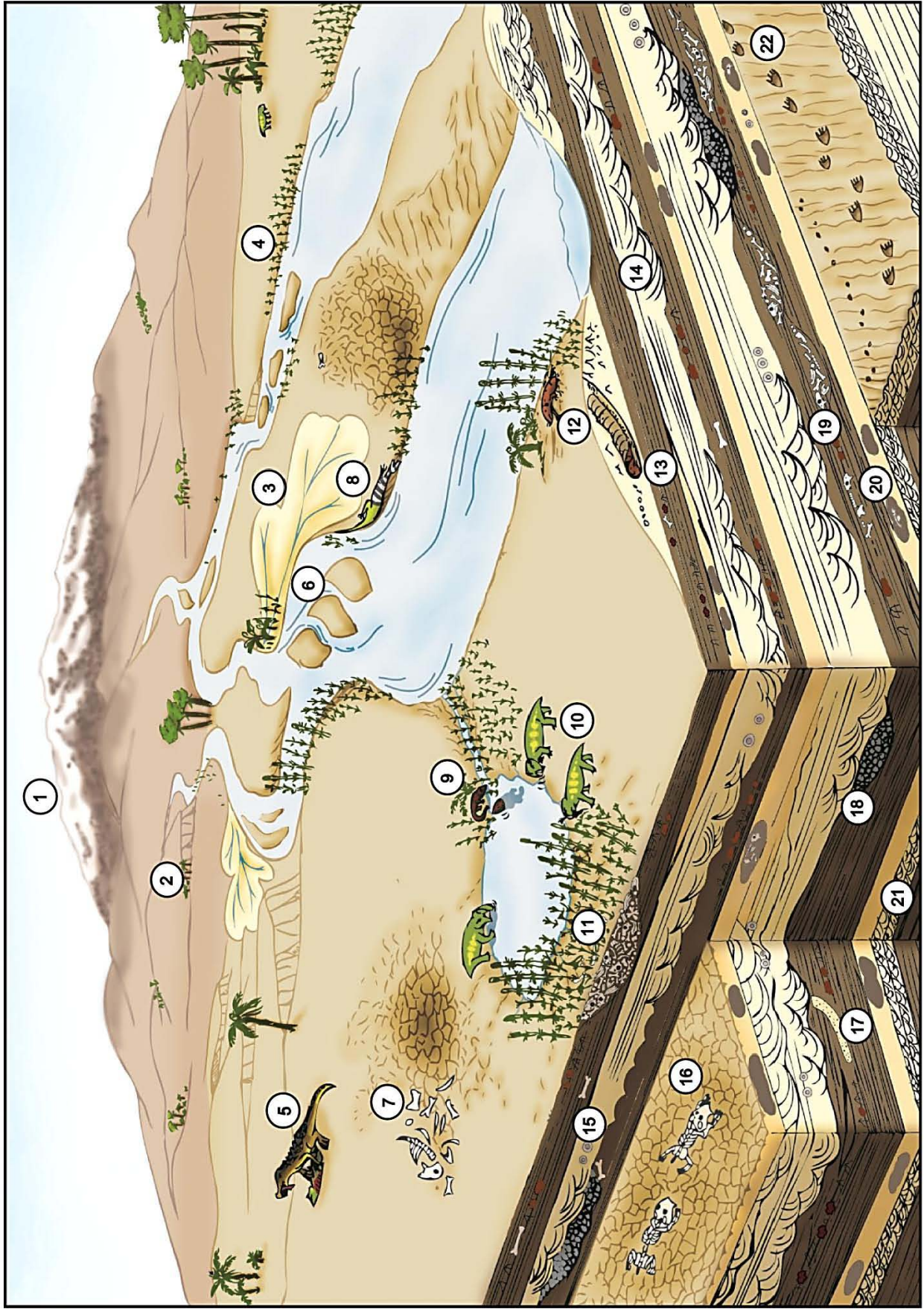
All the results and interpretations gathered during fieldwork, labwork and also from literature can now be synthesised into a palaeoenvironmental reconstruction of the earliest Triassic in the Bethulie area (Figure: 6.1). This diagram, with its numbered points of interest, will now be used as a basis for explanation of subjects discussed in this concluding chapter.

In the earliest Triassic, due the collision of Gondwana and Eurasia, the Karoo Basin of southern Gondwana had become part of the supercontinent Pangaea. The position of the Karoo Basin, at approximately 50° S (Smith et al., 1981; Faure et al., 1995) was a major influence on climate along with the orographic rain shadow effect the Gondwanide Mountains. Eight orogenic pulses caused the rise of this mountain belt according to data collected from the present day Cape Fold Belt (Hälbich and Söhnge, 1983). The rainshadow effect that the Gondwanide Mountains created effectively prevented rain-bearing frontal systems from penetrating the interior of Pangaea (Haycock et al., 1997). Many sites across the globe record vegetation die-off which may have caused the river sinuosity's to change at the End-Permian mass extinction event which shows aridification of climate was not just a local phenomenon (Michaleson, 2002; Newell et al., 2010).

This mountain belt may have been snow-capped for much of the year, thus also influencing seasonal discharge of the earliest Triassic rivers flowing into the foreland (1) (Haycock et al.,

1997). Sedimentological observations show that the rivers of the earliest Triassic were not the perennial meandering rivers of the latest Permian, but were ephemeral braided to anastomosing rivers (2) (Smith and Botha, 2005; Botha and Smith, 2006).

Although lack of planar cross-bedding shows that transverse and linguoid bar deposits were not being completely preserved (Horn et al., 2012), sedimentary structures such as trough cross-bedding, horizontal lamination (14), climbing ripples, ripple-cross lamination (21) and ripple surfaces (22) preserved within the sandstones on Donald 207 Farm show sedimentation was dominantly flood controlled. This deposition occurred during waning flow energy by migration of bars within the channel (6) (Hiller and Stavrakis, 1984; Smith, 1995; Smith and Botha, 2005; Botha and Smith, 2006; Pace et al., 2009). Where river branches were more anastomosing, deposition of levee (Moody-Stuart, 1966; Ashworth and Lewin, 2012) and/or crevasse splay deposits (Tooth, 2000; Long, 2006) (Facies 3) occurred on the proximal floodplain during flood events (Smith, 1995) (Nanson and Knighton, 1996) (3).



**Figure 6.1:** Palaeoenvironment reconstruction of the earliest Triassic lower Katberg Formation. Areas of interest in the diagram have been numbered. See overleaf for descriptions of numbered areas. Artists: P. Viglietti, G. Viglietti, (2012).

1. The Gondwanide Mountain Belt covers much of the southern periphery of the Karoo Basin. Snow may have capped the highest peaks all year round.
2. Ephemeral, braided and anastomosing rivers flow northwards into the basin from their southerly source areas in the Gondwanide Mountains.
3. Breaks in the levee of more anastomosing channels, or channel bank during flood events deposit crevasse splays on the proximal floodplains.
4. *Equisitalian* (horsetails) are the dominant vegetation on the dry floodplains and vegetation is mainly found growing in close proximity to the riverbanks.
5. The archosaur *Proterosuchus* and its prey.
6. Migrating transverse and linguoid bars.
7. Mud cracked surface and floodplain skeleton.
8. A dead archosauromorph *Prolacerta* washed downstream by flood.
9. *Lydekkerina* and/or *Micropholis*.
10. Gregarious *Lystrosaurus declivis* drinking at a floodplain pool sourced from a small leak sprung in the river levee. Their aggregation may have been caused by dry or cold conditions (or both).
11. Multiple vertebrate accumulation of *Lystrosaurus declivis*.
12. The cynodont *Galesaurus* and burrow complex.
13. Siltstone with rooted horizons (rhizocretions), invertebrate burrows, and pedogenic calcareous nodules.
14. Sandstone beds with scoured bases filled by trough cross-bedded and horizontally laminated sandstone.
15. Concentrically patterned round nodules within the sandstone beds that form in early diagenesis.
16. Preserved palaeosurface with in-filled desiccation cracks, and two complete *Lystrosaurus murrayi* skeletons. These two individuals may have died in a drought event or were overcome in a monsoonal storm.
17. Sand-filled burrow cast.
18. Clast-supported informational conglomerate preserved as a channel lag deposit associated with sandstone bed bases.
19. Multiple bone on bone accumulations of *Lystrosaurus declivis* in floodplain siltstone deposits.
20. Large diagenetic nodule with fossil preserved inside.
21. Sandstone bed top preserving ripple-cross lamination.
22. Preserved silt-draped ripple surface on top of a sandstone bed with footprints.

The scoured bases of sandstone beds, nested sandstone bodies with erosional contacts, thin interchannel deposits (Facies 3 and 4) and intraformational conglomerates (18) (Facies 5) indicate relatively frequent avulsion of river channels and lateral continuity of channel deposits (Sambrook et al., 2006; Long, 2006; Fielding et al., 2012). Sand-filled mud cracks beneath sandstone bases indicate dry spells followed by erratic and sudden flood events (Smith and Botha, 2005; Botha and Smith, 2006) (16).

Carbonate nodules present in all the facies on Donald 207 Farm support the presence of a seasonal, semi-arid climate (McPherson, 1979; Smith, 1990; Khadkikar et al., 1998; Schmid et al., 2006). Three nodule types were identified on Donald 207 Farm, one type found in Facies 4 having a pedogenic origin (Smith, 1995) (13), whereas the concentric nodule type of Facies 1 and 2 (15), and the large black-weathering nodules of Facies 3 (20) support an early diagenetic origin due to pristine preservation of fossils within (when present) and preservation of minor sedimentary structures (Johnson, 1989; Smith, 1990; 1993; Rubidge, 1995). Stable isotope analysis done on the carbonate nodule samples taken from the study area fits with data collected from Quaternary and Holocene calcretes and concretions that formed under a cool, seasonally dry climate. Modern dryland environments cope with not only strongly seasonal climatic extremes, but also fluctuating day and night time temperatures (Kinlaw, 1999).

Taphonomic observations reveal that the fauna of the earliest Triassic were subjected to more extreme environmental and climatic conditions than that of the fauna of the latest Permian (7, 16). *Lystrosaurus* (particularly *L. declivis*) (10) appears to be abundant in the

earliest Triassic as indicated by the large number of bonebeds (11, 19) found in the lower Katberg strata as well as many individual skeletons that have been logged and collected across the Karoo Basin (7, 16). Other vertebrate taxa have been found but not in nearly the same abundance as *Lystrosaurus* (5, 8, 9, 12) (Botha and Smith, 2006, 2007). The earliest Triassic Karoo Basin environment, at least in the Bethulie area of the southeast, was probably favourable for preserving *Lystrosaurus* in these accumulations. Behrensmeyer (1978) and Weigelt (1989) noted a propensity for younger and less experienced animals to fall victim to extreme conditions. This new study reveals the likelihood of behavioural aggregation of sub-adult *L. declivis* in close proximity to one another induced by dry spells and/or cold snaps during seasonal or daily temperature changes. The latter theory in particular explains the formation of the Claasens bonebed as the dry spell waterhole congregation hypothesis provides insufficient explanation to why these animals were so intimately associated.

Other fossil taxa are quite rare in the form of bonebeds, but some have been found (small *Prolacerta* bonebeds) which require further study. The multiple individual accumulation taphonomic style is noted in many other parts of the Karoo Basin during the earliest Triassic, but the occurrence of the bonebeds are not nearly as frequent as on Donald 207 Farm. It is interesting to consider why, as yet, no bonebeds of *L. murrayi* have been found. This may reflect differing behavioural or feeding strategies in the two species because *L. murrayi* specimens are also abundant on Donald 207 Farm. It is possible *L. murrayi* was more able to cope with dry and cold conditions and possibly had the ability to migrate out of the area.

Amphibians (9) and also the archosauromorph, *Prolacerta* (8) have been found as complete skeletons in Facies 3 sandy siltstone. They may represent animals that were killed either in droughts or during flood events and subsequently washed downstream to their final resting places. The many fossil remains of amphibians on Donald 207 Farm does not rule out the drought hypothesis as amphibians became significantly smaller in the Triassic than their Permian predecessors which supports aridification of climate (Shishkin and Rubidge, 2001). Amphibian presence also complements data for seasonal cold periods as these animals may have proliferated in numbers during warmer wet seasons, dying en masse when the monsoonal rainfall regime caused cooling and failed to produce rainfall in the area for extended periods.

A combination of regression, volcanism, and anoxia (Erwin, 1993), Siberian trap volcanism (Renne et al., 1995; Bowring et al., 1998) and dissociation of gas hydrates (Heydari and Hassanzadeh, 2003) are believed to have been significant events that altered global climate, culminating in the End-Permian mass extinction event and depositional environment changes across the globe (Veevers, 1994; Michaleson, 2002; Catuneanu, 2004; Smith and Botha, 2005; Erwin, 2006; Newell et al., 2010). In order to improve understanding of what occurs during and after mass extinction events we should not concentrate too much on isolated events (Weigelt, 1989). Events such as supercontinent formation, drought, floods, tectonic uplift, fluvial-style change, follow each other through time and although cause damage, if taken individually, produce effects of widely varying intensities. Our aim should be to understand the complex combinations of these events coalescing at the right time

when attempting to understand biological crises, catastrophes and extinctions in the geologic record. This is what Erwin (2006) refers to as “a tangled web of destruction”.

The End-Permian mass extinction event was indeed very significant, but what is not as well emphasised is the rapid recovery of the Karoo fauna that occurred in the earliest Triassic (Smith and Botha, 2005). Fossilisation mode may have changed across the PTB, but fossil abundance does not (Smith and Botha, 2005; Botha and Smith, 2006, 2007). This means species that survived the extinction event were already thriving, and clearly well-adapted to the redistribution of vegetation belts (i.e. the replacement of *Glossopteris* by *Dicroidium* seed ferns and *Sphenopsid* horsetails (4)) on the semi-arid floodplains of the earliest Triassic Karoo Basin (Botha and Smith, 2007). Though many of the taxa that lived in the latest Permian did not continue past the PTB, the ones that did filled the empty niches of those that did not, resulting in the rapid radiation of the recovery fauna that thrived in the new earliest Triassic environment (Smith and Botha, 2005).

The fossorial lifestyles of many of the earliest Triassic taxa may have been an adaptation for escaping the severe environmental conditions of the time period (12,17) (Groenewald et al., 2001; Damiani et al., 2003; Abdala et al., 2006; Smith and Botha, 2005; Sidor et al., 2010). Burrowing was shared by some of their Permian therapsid predecessors (Smith, 1987) that went extinct indicating that it was not the single reason for their survival, and the recovery success. Earliest Triassic taxa all shared some adaptations that allowed them to deal better with the more frequent extreme climatic events. These adaptations, as of yet, are not entirely understood. *Lystrosaurus* does not continue into the Middle Triassic Burgersdorp Formation

which overlies the Katberg Formation, so although *Lystrosaurus* did have adaptations that allowed it to survive the initial extinction, they were not adaptations that allowed it to continue to thrive in the Middle Triassic period. Their therapsid cousins the cynodonts (12) however, did have surviving ancestors that gave rise to the first mammals (Kemp, 1982; 2011). The descendants of the cynodonts managed to live in the shadow of dinosaurs and survive another two mass extinctions events at the End-Triassic and End-Cretaceous some 50 and 180 Ma later respectively. This is why studies on therapsids are relevant, as their survival and subsequent evolution is inherently linked to our own origins as mammals.

## 6.2 Conclusions

This sedimentological, geochemical, stable isotope and taphonomic study on the earliest Triassic lower Katberg Formation in the Bethulie district of the southern Karoo Basin has allowed the following conclusions to be made:

- Climatic changes across the PTB, following the formation of Pangaea and the rain shadow effect of the Gondwanide Mountain Belt, exacerbated by atmospheric disturbances (possibly due to greenhouse gas emissions from massive basaltic flooding in Siberian part of northern Pangaea, and/ or dissolution of gas hydrates), manifest as a change in fluvial style in the Karoo Basin and in other Karoo-aged Basins present on Pangaea. In the Karoo Basin, this caused an increase in massive channel-sandstones relative to inter-bedded mudstones deposited by braided and anastomosing ephemeral rivers compared to perennial meandering rivers in the Permian.

- $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values from carbonate nodules indicate a cool semi-arid climate in the earliest Triassic in agreement with stable isotope values from nodules and calcretes sampled in similar PTB sections, and are consistent with Pleistocene, and Holocene seasonally cool arid environments (Rowe and Maher, 2000; Neymark et al., 2005; Schmid et al., 2006; and Ringrose et al., 2009).
- The taphonomic study supports two hypotheses for the formation of the *Lystrosaurus* bonebeds. They are: 1) Cold-induced aggregation and 2) Dry spell waterhole congregation.
- In the Claasens bonebed, articulated ribs (held together possibly by skin) amongst disarticulated skeletal material, and lack of any specific orientation implies no transport of bones into close proximity. This means the *Lystrosaurus* died in this position very close together which can be explained by animals huddling close together. Evidence from cold-induced aggregation of modern reptiles suggests the *Lystrosaurus* may have been huddling as a means to thermoregulate.
- In the smaller bonebeds (and the Claasens bonebed), the species selective (only one species present) and the age-specific nature (sub-adult) may suggest accumulations represent congregation of *L. declivis*, around waterholes during an extended period of drought.
- Other vertebrate taxa are present in the study area but are rare and it is likely that this does not reflect the true abundance of animals, whereas the abundance of *Lystrosaurus* bonebeds (particularly of *L. declivis*) in the lower Katberg Formation reflects preferential preservation (possibly due to climate), therefore overrepresented. Thus the bonebeds are not a true reflection of their relative abundance in the living ecosystem.

- Vertebrate burrows were an adaptive strategy to escape extreme environmental conditions, (such as drought or seasonal temperature changes) and daily temperature fluctuations common in arid ecosystems. Animals were most likely utilizing these burrows to rear young and/or hibernate and were most likely a key adaptation in allowing therapsids and other fauna to thrive in the earliest Triassic Karoo Basin. The burrows, however, were not the only reason the Triassic fauna thrived and these other reasons for thriving are not entirely understood at present.

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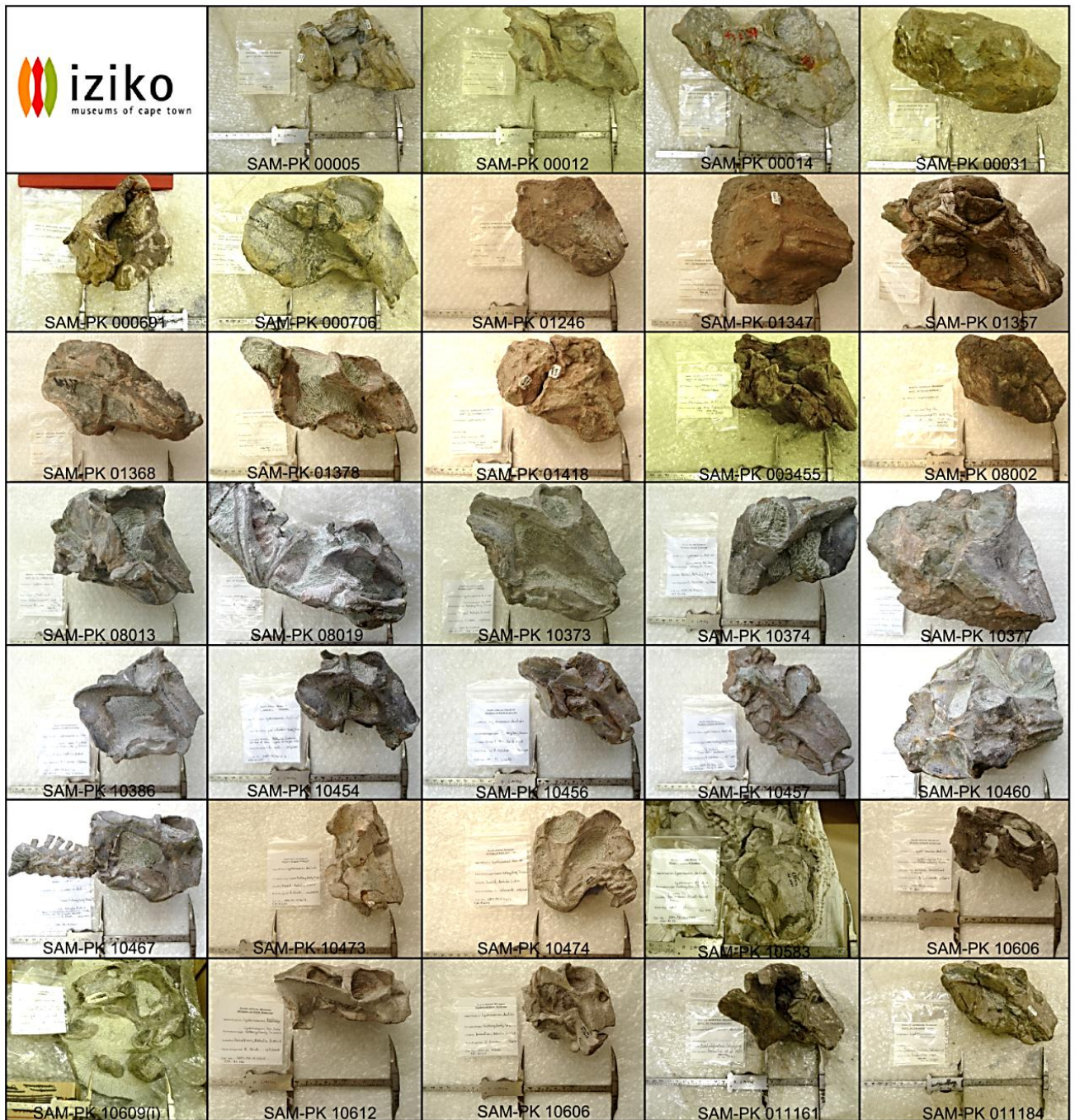
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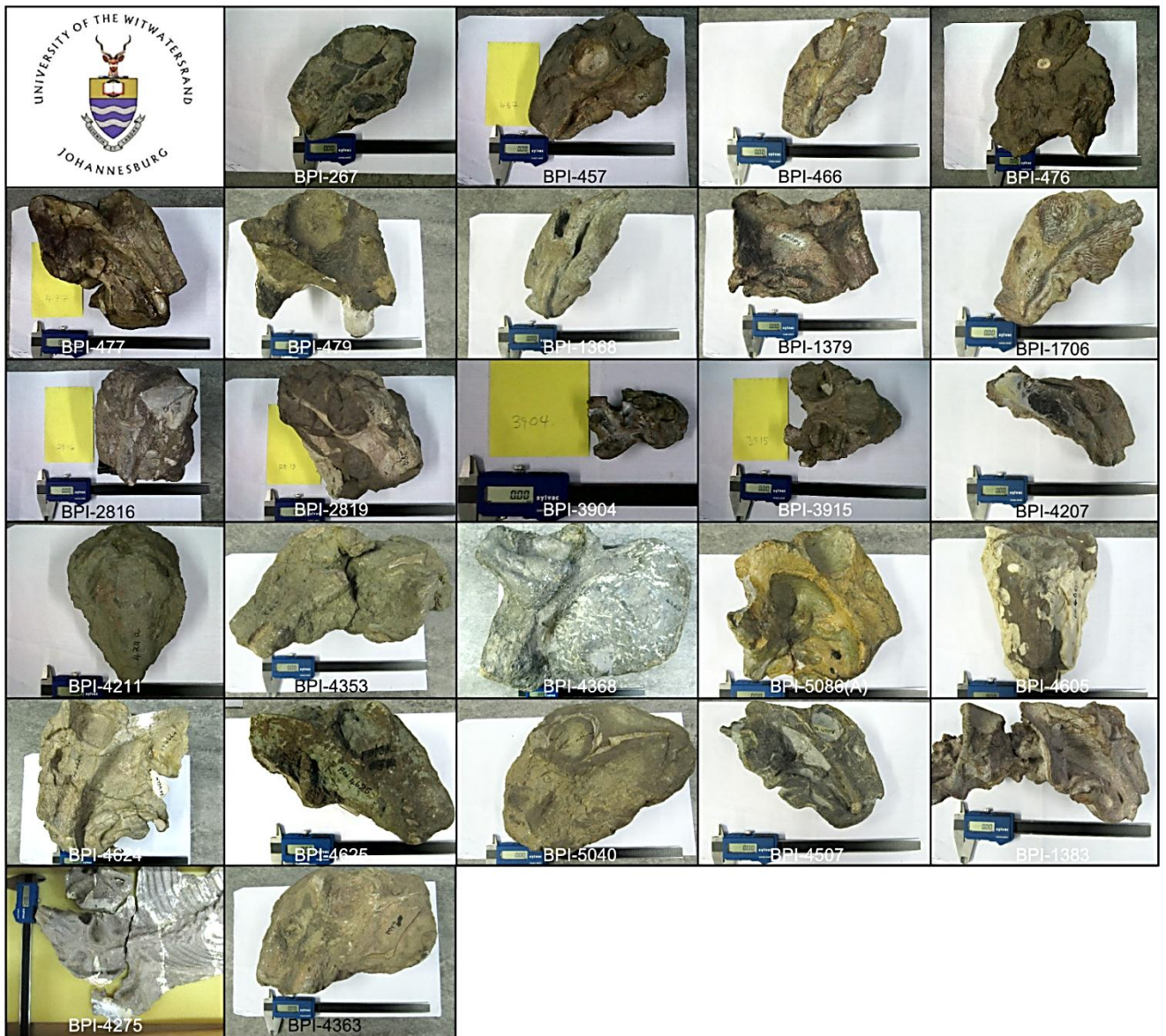


Accession Number	Store Location	Skull Length (mm)	Snout Length (mm)	Orbital Diameter (mm)	Interorbital Region (mm)	Intertemporal Region (mm)
SAM-PK-000691	D06.01	110	73	33.5	57	24
SAM-PK-000706	D06.02	227	120	64	62	45
SAM-PK-003455	D06.02	156	76	48	53	25
SAM-PK-011161	D06.03	101	71	43	54	
SAM-PK-011184	D06.04	138	74	44	56	23.5
SAM-PK-00005	D08.02	115	73.5	46	53	23
SAM-PK-00012	D08.03	156	77	45	64	26.5
SAM-PK-00014	D08.03	139	73	45	50	25
SAM-PK-00031	D08.03	155				
SAM-PK-01246	D10.02	159	78	44	55	32
SAM-PK-01347	D11.03	165	110	52	83	30
SAM-PK-01357	D11.03	201	101	58	88	34
SAM-PK-01368	D11.04	181	85	46	78	
SAM-PK-01378	D12.01	162	82	48	58	30
SAM-PK-01418	D12.03	130	60	50.5	53	25
SAM-PK-08002	D07.04	120	71	33	52	22
SAM-PK-08013	E08.01	183	93	44	82	33
SAM-PK-08019	E08.03	139	73	39	53	26
SAM-PK-08566	E05.02	150				
SAM-PK-10373	E05.02	175	96	53	60	28
SAM-PK-10374	E05.02	144	77	45	62	24
SAM-PK-10377	E05.03	250	151	75	80	55
SAM-PK-10384	E05.03	104	57	35	41	23
SAM-PK-10386	E05.04	120	70	30	57	30.5
SAM-PK-10454	E05.04	111	65	38.5	45	22
SAM-PK-10456	E05.04	113	62	33	56	22
SAM-PK-10457	E05.04	120	60	33	53	23
SAM-PK-10460	E05.04	166	87	47	70	34
SAM-PK-10467	E05.04	109	55	33.5	50	33
SAM-PK-10470	E06.01		80			
SAM-PK-10473	E06.01	143	108	46	70	
SAM-PK-10474	E06.01	107	54	34	42	21
SAM-PK-10579	E06.02		67			
SAM-PK-10583	E06.03	95	45	35	33	22
SAM-PK-10606	E06.04	103	61	43		20
SAM-PK-10609 (i)	E06.04	142	74	49	59	32
SAM-PK-10609 (ii)	E06.04	158	88	46	42	35
SAM-PK-10612	E06.05	112	60	35	56	26
SAM-PK-10616	E06.05	99	49	35	35	21
SAM-PK-10804		164	112	47	64	24
SAM-PK-10380		146	81	46	58	50
SAM-PK-10467		166	105	45	69	28
P.Ward Fossil		86	61	31	49	18
JB5		160	96	45	66	30
JB10		96	58	29	34	12
SAM-PK-?		124	74	40	44	18
Claasens 1	display	181	81	46	70	32
Claasens 2	display	141	85	40	59	29
Claasens 3	display			35	54	24
Claasens 4	display					21
Claasens 5	display	154	83	39	67	35
Claasens 6	display	156	85	41		
Claasens 7	display	125	70	40	54	25
BPI-457	KC5/M	130	68	39	57	25
BPI-476	KR19/1C	122	76	37	57	27
BPI-477	KC5/Z	145	87	46	72	24
BPI-479	KR21/3A	155	106	52	81	34
BPI-1368	KR20/3D	110	68	34	49	26
BPI-1379	KC5/Z	135	77	38	61	30
BPI-1383	KC5/Z	114	75	34	40	23
BPI-1706	KR21/3B	118	56	38	47	26
BPI-3904	KC5/Z	44	15	15	17	11
BPI-2816	KR21/5A	133	81	36	60	23
BPI-2819	KR21/2H	146	68	40	59	
BPI-3915	KR21/1F	116	55	31	45	23
BPI-4207	KR20/3D	114	67	38	46	24
BPI-4211	KR20/4F	116	68	36	56	20
BPI-4275	KC5/D	98	51	32	39	19
BPI-4343	KR21/1G	214	107	48	86	22
BPI-4353	KR21/1F	196	100	46	79	26
BPI-4368	KR21/5G	310	140	83	76	56
BPI-4507	KC5/Z	121	71	36	44.5	25
BPI-4605	KR21/4B	119	75	41	59	25
BPI-4624	KC5/Z	229	114	48	75	27
BPI-5040	KR21/3A	101	46			29
BPI-466	KC5/M	127	68	33	45	29
BPI-267	KC5/Z	127	68	37	62	29

Appendix 2: Absolute skull dimension values of *L. declivis* specimens from Iziko South African Museum (SAM-PK-K) and the Bernard Price Institute (BPI).



**Appendix 2:** *L. declivis* specimens from the Karoo Palaeontology collections at Iziko South African Museum used in the skull measurements study.



**Appendix 2:** *L. declivis* specimens used in the skull measurements study from the Karoo Palaeontology collections at the Bernard Price Institute, University of Witwatersrand, Johannesburg.