UNIVERSITY OF CAPE TOWN
IYUNIVESITHI YASEKAPA • UNIVERSITEIT VAN KAAPSTAD

DEPARTMENT OF BOTANY

BOT4000W

HONOURS IN BOTANY

COLD CASE FILES: PALAEOFORENSIC AND TAPHONOMIC STUDY OF THE MAMAFURA DICYNODONT FROM THE END-PERMIAN

Plagiarism Declaration

1. I know that plagiarism is wrong. Plagiarism is to use another's work and to pretend that it is one's own.
2. I have used the Harvard Convention for citation and referencing. Each significant contribution to and quotation in this report from the work or works of other people has been attributed and has been cited and referenced.
3. This report is my own work
4. I have not allowed and will not allow anyone to copy my work with the intension of passing it as his or her own work.

Student no: FRDNIC008

Surname: Fordyce, Nicholas

Date: 27 September 2010

Supervisors: Anusuya Chinsamy-Turan; Roger Smith

This project aims to determine what happened moments before death through to the fossilisation of the 'Mamafura' dicynodont fossil at the Iziko Museum.

Abstract

Dicynodonts were non-mammalian herbivorous therapsids (mammal-like reptiles) that flourished world-wide during the Permian and Triassic Periods. They are nowhere more abundant than in the rock strata of the Karoo basin in South Africa. Taphonomy, the transition from biosphere to lithosphere, is of great geological and biological significance and has provided remarkable insight into palaeoenvironments. A partially articulated dicynodont that has been fossilised alongside an unidentified predator tooth shows evidence of predation and is analysed here. The dicynodont is possibly *Oudenodon grandis* and was most likely drowned after which it was scavenged from by a gorgonopsian predator, *Aelurognathus*. The fossil is important as it provides further insight into the ecology of the Late Permian and it enhances our taphonomic understanding.

Key Words

Taphonomy, Permian, canine, *Oudenodon grandis*, *Aelurognathus*, SEM, Karoo.

Contents

1) Introduction. 4
2) Geologic Setting and Sedimentology. 5
    Fossil Description. 10
3) Ecological Setting. 10
4) Materials and Methods. 13
5) Results. 14
    Identification of Mamafura. 14
6) Vertebrate Taphonomy. 24
    Bone Damage. 26
    Unidentified Tooth. 29
7) Taphonomic Assessment. 38
    Death. 38
    Scavenging. 40
    Desiccation and Burial. 41
8) Summary and Conclusions. 42
9) Acknowledgements. 42
10) References. 42
11) Appendices. 49

Introduction

In the late 19th and early 20th Centuries most palaeontological research on therapsids from the Karoo focused on taxonomic and morphological aspects (Smith *et al.* 2010). The discovery of fossils in the Beaufort Group strata by Bain in 1838 was followed by early works by Owen (1876), Broom (1907) and Haughton (1919), all of which were not very precise concerning collecting procedures. However, scientists such as Colbert (1963), Hotton (1967) and Boonstra (1969) were amongst the first to consider the mode of fossilisation and over the last two decades, research relating to therapsids has incorporated geological, stratigraphic, tectonic, taphonomic and palaeoenviornmental aspects together with the morphological, taxonomic and phylogenetic research and has resulted in a much broader understanding of the ecology of the therapsid communities from the Permian to the Jurassic (Smith *et al.* 2010).

When looking at a fossil, one is seeing the end-product of a series of events that lead to its fossilisation and preservation. This is why taphonomy or 'biostratinomy' described by Efremov (1940) as "the transition from the biosphere to the lithosphere" can be of both geological and biological/ecological significance (Smith 1993). According to Wiegelt (1927) the confluences of unusual biological and geological processes make the most substantial contributions to the fossil record. Fossils provide insight into the dynamics of catastrophic geological and ecological events and are instrumental in understanding the ecology of prehistoric systems (Thomas and Farlow 1997). In addition, the use of palaeoecological data is becoming increasingly important in conservation and reserve management (Saunders *et al.* 2008) and can provide useful insight into the present day complexity of ecosystem function.

Taphonomic studies like these, not only help to understand how fossils can be preserved the way they are, but also help to corroborate previous works and enhance our understanding of past systems. This project is a taphonomic study of a dicynodont fossil (called Mamafura), found in the Late Permian rock strata of the Karoo Basin, that exhibits signs of predation. In particular, it is a palaeo-forensic study aimed at trying to assess the events that lead to Mamafura's death and subsequent fossilisation. It is hoped this will provide some broader insight into the ecology of the Late Permian and help to explain a particularly unusual fossil find.

Geologic Setting and Sedimentology

Mamafura was found in the Late Permian Beaufort Group rock strata of the Karoo basin. The Karoo formed within the continental interior of south western Gondwana (Figure 1), just north of the Gondwanide Mountains (Smith 1993) and represents over a 100 Ma record of deposition; starting from the Late Carboniferous Dwyka (300 Ma), to the Early Jurassic Clarens Formation, the sequence was finally terminated by the Drakensberg Group Karoo flood basalts (182 Ma) (Tankard *et al.* 2009).

The basin formed under a threefold process (Tankard *et al.* 2009). Crustal uplift was followed by fault controlled subsidence and finally there were long periods of regional subsidence which were generally unaccompanied by faulting or erosion stresses (Tankard *et al.* 2009). These same processes gave rise to the Parana, Beacon and Bowen Basins (figure 1), which were all part of southern Gondwana at the time. The extensive Gondwanide Mountain chain was caused by uplift and thrusting along the subduction of the Palaeo-Pacific plate beneath the Gondwanan plate (Smith 1993). Resultant down-warping was probably the major control over subsidence of the foreland basin, up to 1000 km wide, in which clastic sediments of the Karoo Sequence accumulated (Smith 1993).

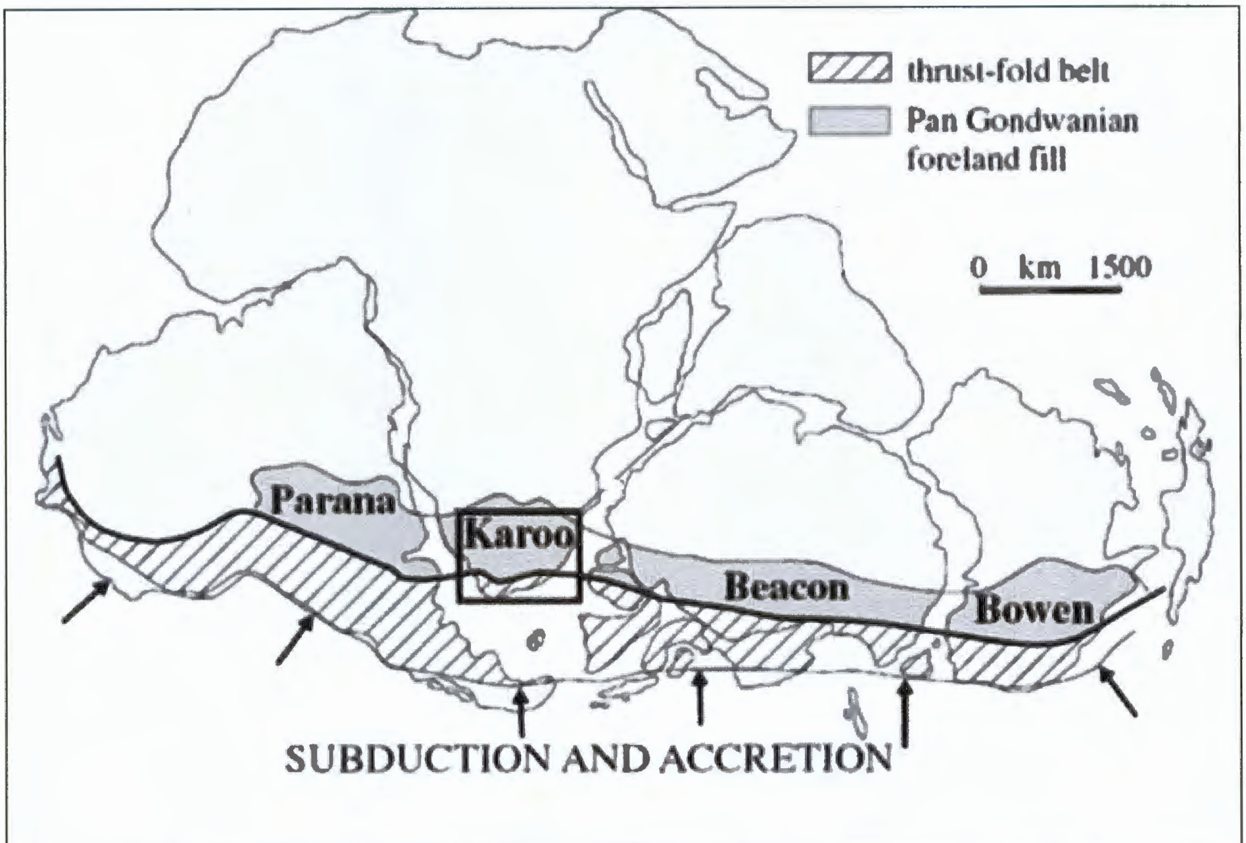


Figure 1: A reconstruction of Gondwanaland showing the proposed distributions of Karoo-aged basins and associated fold-thrust belt and subduction setting. Adapted from Catuneanu *et al.* 2000.

The Beaufort Group lies about halfway up the Karoo Sequence and comprises a 2000 metre thick fluvio-lacustrine succession of Late Permian age (Smith 1989, 1990, 1993). It is divided into the Lower Adelaide and Upper Tarkastad Subgroups (Viglietti 2009). The Adelaide Subgroup contains the Late Permian Abrahamskraal and Teekloof Formations (a 400m thick argillaceous unit in the lower part of the Beaufort succession that outcrops mainly in the Beaufort West and Fraserburg districts (Smith 1993)) in the Beaufort West area (Smith 1993; Johnson *et al.* 2006). It is dominated by mudstone with minor channel-sandstones, which were deposited by stable meandering rivers, showing low sinuosity, high sinuosity and floodplain facies associations (Turner. 1978). Evidence for these meandering rivers is present in the exhumed palaeomeanders near Reiersvlei (see figure 2), not far from Dunedin, the farm where Mamafura was discovered (figures 2 and 3).

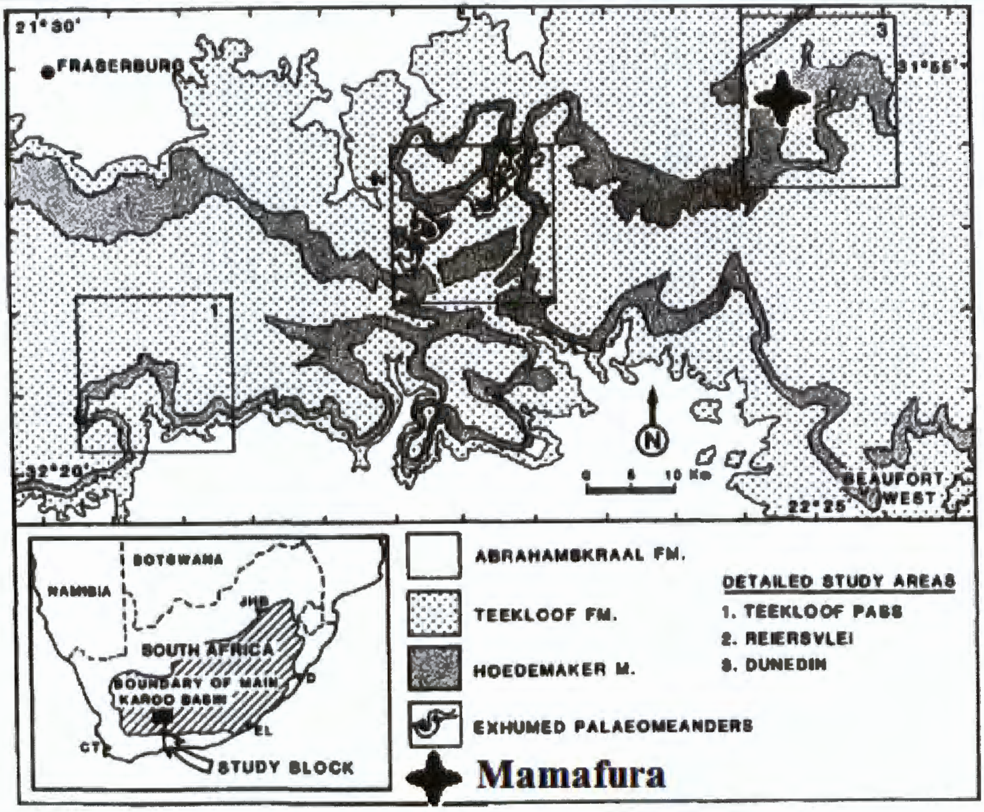


Figure 2: Lithostratigraphic map of the Hoedemaker outcrop and Teekloof Formation. Note the third study area, Dunedin, and the site where Mamafura was found marked by the black cross. An insert of South Africa showing the Karoo Basin is also included. Adapted from R. Smith (1993).

The paleontological wealth of the predominantly fluvial strata of the Late Permian Beaufort Group is perhaps its most important claim to fame. Skeletal fossils of reptiles, especially non-mammalian therapsids (commonly known as mammal-like reptiles), amphibians and freshwater fishes are well preserved in all stages of disarticulation (Smith 1993). The biostratigraphy (dating of rocks based on the presence of certain fossil species within them) of the Adelaide Subgroup consists of the *Eodicynodon, Tapinocephalus* (Abrahamskraal Formation), *Pristerognathus*, *Tropidostoma* (Teekloof Formation), *Cistecephalus,* and *Dicynodon* (Balfour Formation) assemblage zones (Rubidge 1995; Botha and Angielczyk 2007; Tankard *et al.* 2009). Mamafura comes from the *Tropidostoma* Assemblage Zone strata (figure 3).

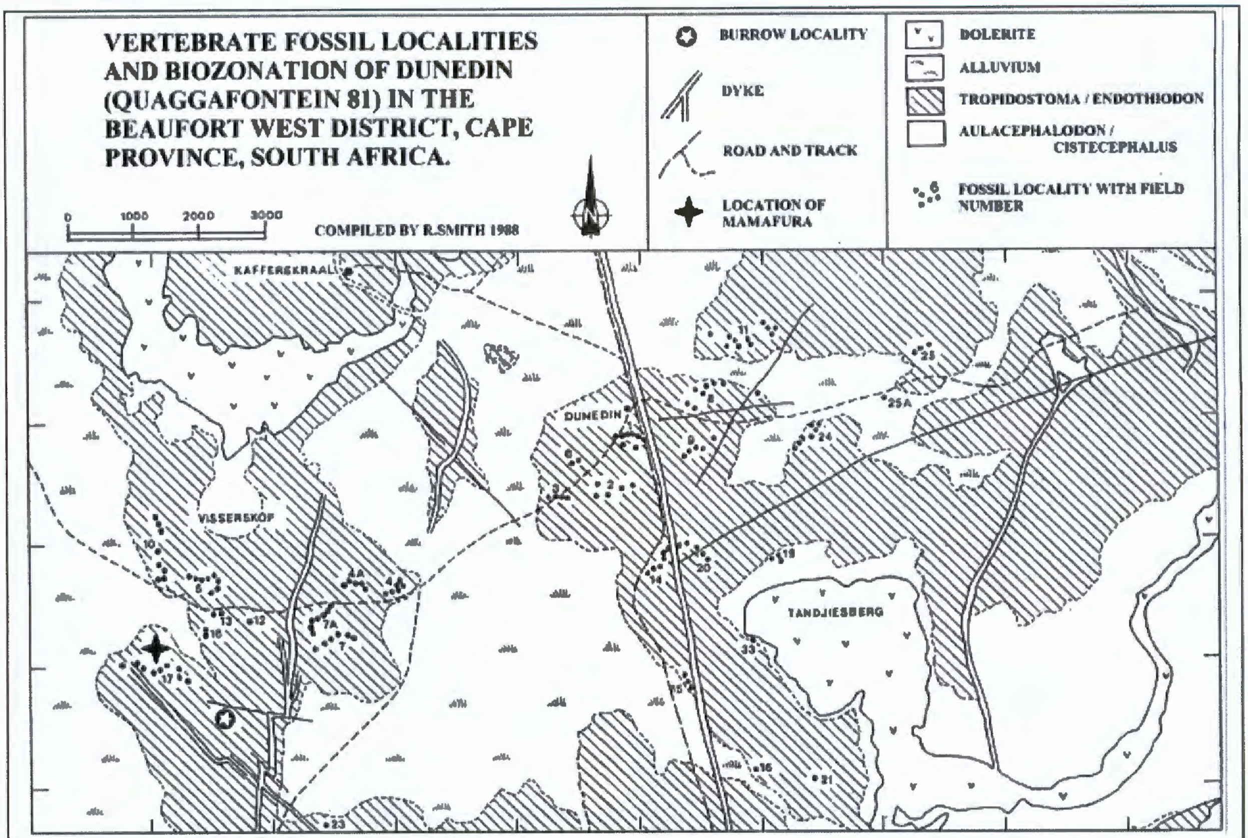


Figure 3: Mamafura and other vertebrate localities and biozonation of Dunedin (Quaggafontein 81) in the Beaufort West District, Northern Cape Province, South Africa. Adapted from Smith (1989). The coordinates for the locality are 31°59"S and 22°20"E.

Dunedin is a particularly rich fossil locality (figure 3) with a great range of fossil finds having been described from the area (Smith 1989; R. Smith 2010 *pers. comm.*). The fossil was collected by J. Nyaphuli and B. Rubidge in March of 1984 (B. Rubidge *pers. comm.* 2010). Once the fossil was uncovered a protective plaster cast was laid around it and it was taken to the Iziko South African Museum where it was prepared by Annelise Crean. The fossil was called 'Mamafura', meaning 'Old Woman', it was given the accession number SAM-PK-K06446. In 2002 it was placed on display in the museum in the Karoo Palaeontology section (See appendix 1).

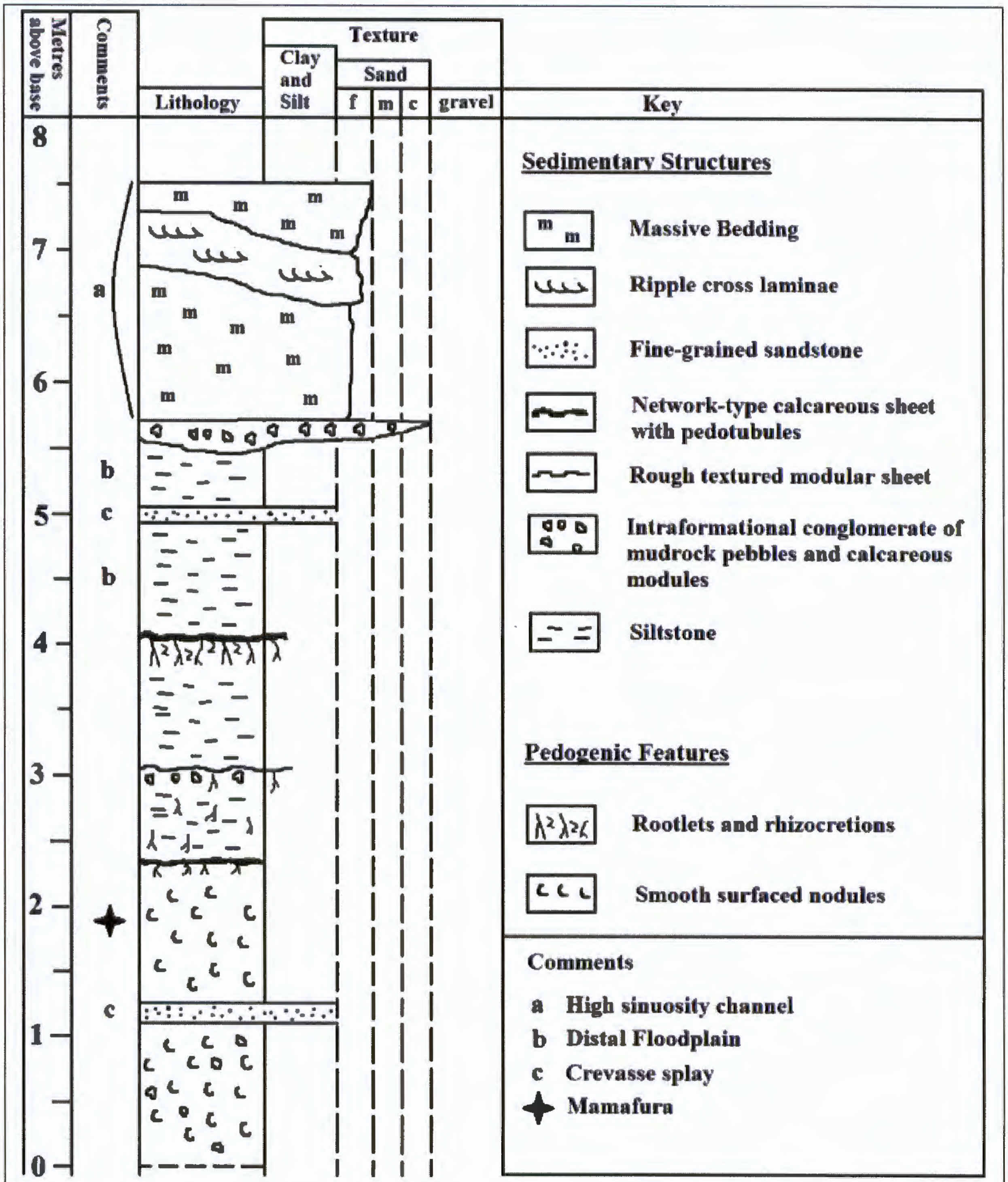


Figure 4: Sedimentological log of a section measured up from beneath the site of Mamafura's discovery through to the eroded surface. Log by N. Fordyce (2010).

As previously mentioned, Mamafura is positioned stratigraphically within the *Tropidostoma* Assemblage Zone. The fossil was embedded in flat, grey siltstones and mudstones from a floodplain facies sequence and was overtopped by palaeosols, massive bedding and ripple cross laminae (figure 4). A sequence of siltstone horizons suggest the fossil was covered by a series of seasonal flood events.

Fossil Description

Mamafura is of taphonomic interest because it exhibits both well articulated and disarticulated bones (figure 8). In particular, the head, vertebral column, ribcage and forelimbs are all articulated whilst the hind-limbs and sacral vertebrae have been disarticulated and lie scattered. Some of the hind-limb bones, specifically the femur and tibia, show some evidence of bone damage by teeth, and there is an embedded predator tooth, a canine, associated with the fossil. The head is held slightly upward, and the snout has some evidence of erosional weathering as it was the exposed part of the fossil that led to its discovery (B. Rubidge *pers. comm.* 2010). Nonetheless the snout is generally still intact. The skull has undergone some lateral compression. Some of the smaller bones, such as those associated with the feet and toes have been lost, posing an interesting taphonomic question. These characteristics make it a unique study, potentially invaluable for similar future studies.

Ecological Setting

The Permian period (300 – 250 million years ago (MYA)) was dominated by the giant supercontinent of Pangaea; a merging of Laurasia and Gondwana (McNamara 2009). During deposition of the Teekloof Formation, the southern Karoo basin was drained by three large rivers, a south-easterly, south-westerly and west-north-westerly (Cole et al., 1990). These rivers had their origins in the Gondwanide Mountains to the south (Smith 1993). The Mississippi-sized rivers meandered across a wide, flat alluvial plain before issuing into a shallow lake (Smith, 1987). Palaeopedological evidence from the Teekloof floodplain deposits suggest that a semi-arid climate prevailed in this part of the basin with mean annual temperatures between 16 and 20° C and highly seasonal rainfall of 50-70 cm/y (Smith, 1990). Palaeosol features suggest that vegetation flourished along river banks and abandoned channel furrows and consisted of *Glossopteris* trees, horsetails, ferns and clubmosses. This supported a stable terrestrial vertebrate fauna dominated by a variety of therapsid reptiles during the Late Permian (figure 5) (Smith 1993).

Figure 5: An artist's impression of the Late Permian Beaufort Group environment. It depicts the establishment of modern day ecological systems as we know them; the herbivorous *Diictodon* feeding on the *Glossopteris* family plants in a floodplain. (Artist: Cedric Hunter).

According to Smith *et al.* (2010), one of the most significant evolutionary events in the history of life on land was the development of the modern ecological structure in which terrestrial plants support a large population of herbivores, which in turn support relatively few predators (figure 5). This trophic organization was not fully developed until the Late Permian (259–251 MYA ago) of the Palaeozoic, when the vertebrate primary consumer base was largely formed by a group of therapsid synapsids ('mammal-like reptiles'); the dicynodonts (King 1981). In size they ranged from *Diictodon sesoma* (Watson 1960) with a reconstructed vertebral column length of 45.0 cm, to *Stahieckeria potens* with a length of 360.0 cm (King 1981). The fossil record indicates that herbivorous dicynodonts were not only taxonomically diverse, extraordinarily abundant and globally distributed, but also extended from the Late Permian to the Late Triassic, across the Permo-Triassic boundary (Smith *et al.* 2010). Recent work has suggested that a possible Australian dicynodont was present as recently as the Cretaceous period (Thulborn and Turner 2003).

The *Tropidostoma* Assemblage Zone, from which Mamafura was recovered, presented the fauna of the southern Karoo Basin at the time, with a series of flat, very low gradient alluvial plains some 500km wide (Smith 1987). These plains were virtually featureless except for several low ridges snaking towards the central lake (Smith 1987). The climate in the basin was becoming drier and discharge down the rivers was highly seasonal but still perennial (Smith *et al.* 2010).

The *Tropidostoma* Assemblage Zone also marked the first appearance of *Tropidostoma* and the tuskless dicynodont genera, *Oudenodon* (figure 6A) and *Rhachiocephalus* (Keyser 1975). *Diictodon* still dominated the ground level grubbing and foraging niche (figure 5). Gorgonopsians (figure 6B), large sabre-toothed reptile predators, became more abundant in response to the herbivore radiation and were larger than their main carnivorous competitors, the therocephalians (Smith *et al.* 2010). A new group of carnivores, the cynodonts, made their first appearance with *Procynosuchus* and the rare and diminutive insectivore *Charassognathus gracilis* (Botha et al. 2007).

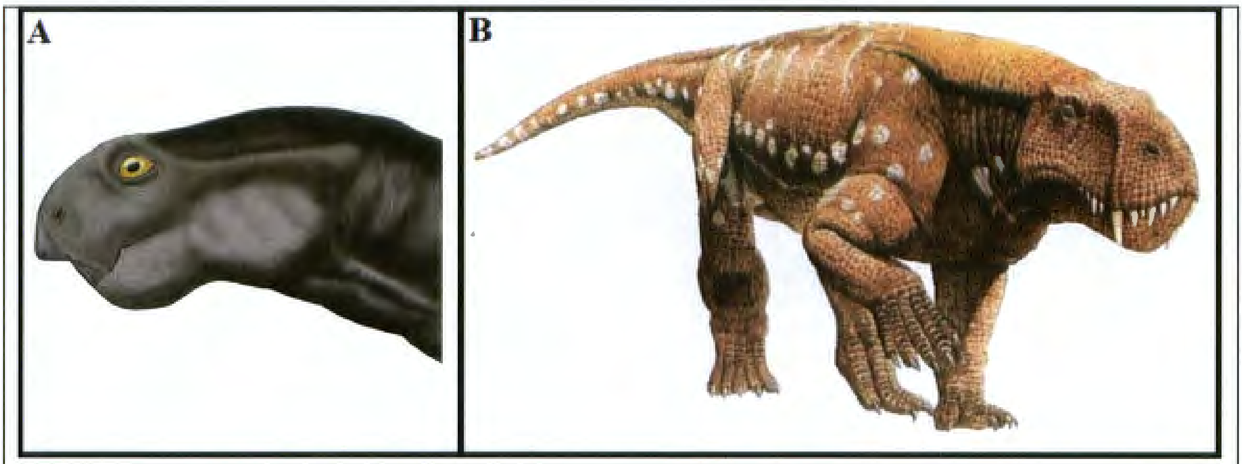


Figure 6: (A) Stylised lateral view of an *Oudenodon bainii* head (Artist: Anonymous). Note the absence of the usually ubiquitous dicynodont tusks. (B) A typical gorgonopsian, *Hipposaurus*, with a mammal-like gait and large sabre-canines (Source: Dixon 2007).

The herbivorous genera of the *Tropidostoma* Assemblage Zone included *Cistecephalus* (figure 7), *Diictodon* (figure 5), *Dicynodontoides, Emydops, Endothiodon, Oudenodon* (figure 6A), *Palemydops, Pristerodon, Rhachiocephalus* and *Tropidostoma* (Smith *et al.* 2010). The specimen count for *Tropidostoma* zone herbivores reveals the dominance of small, long bodied dicynodonts, mainly *Diictodon*, *Pristerodon* and *Emydops* with only a few medium-sized forms (*Tropidostoma* and *Oudenodon*) and even fewer large bodied taxa (*Endothiodon* and *Rhachiocephalus*) (Smith *et al.* 2010).

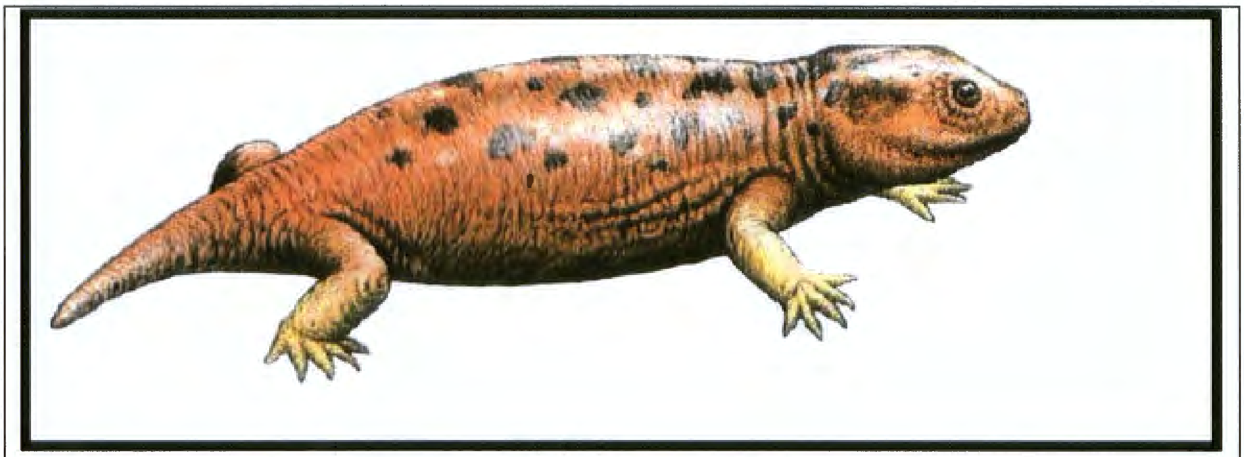


Figure 7: *Cistecephalus* had a typical burrowing body plan with stout digging limbs (Source: Dixon 2007).

The herbivores of the *Tropidostoma* zone were exposed to a wide range of carnivores belonging to either the gorgonopsians or therocephalians. The gorgonopsians included *Aelurognathus, Cynarioides, Cyonosaurus, Galerhinus, Gorgonops, Lycaenops,* and *Scymnognathus*. The therocephalians included *Choerosaurus, Hofmeyeria, Ictidosuchoides, Ictidosuchops, Ictidosuchus,* and *Scaloposaurus* (Smith *et al.* 2010).

"Of the 2716 identified specimens from this biozone, 2629 are herbivorous and 86 are carnivorous, meaning that 97% of the faunal assemblage of the *Tropidostoma* Assemblage Zone is herbivorous and 3% carnivorous- a ratio of 32:1 (Nicolas and Rubidge 2009; Sidor and Smith 2007)" (Smith *et al.* 2010, pg 12).

Materials and Methods

Taphonomic investigation of Mamafura involved three main components; the identification of Mamafura, the analysis of the bone damage and the identification of the predator tooth associated with Mamafura.

Generally, the most distinctive feature of dicynodonts is their skulls (K. Angielczyk *pers. comm.* 2010). Thus, the identification of Mamafura focused on skull features. The skull how?

length of Mamafura was compared with all the measured skull lengths of the *Oudenodon, Tropidostoma* and *Rhachiocephalus* specimens in the collections at the Iziko South African Museum. Other distinctive features such as snout shape, nasal bosses and pineal bosses were also compared with all the specimens and photographs were taken to make comparisons.

Tooth damaged was captured photographically where possible and casts of the tooth impressions were taken using dental cement. The casts were plated in gold in an argon gas vacuum and were then analysed under the Scanning Electron Microscope (SEM) where possible.

Similarly, the unidentified tooth associated with Mamafura was compared with the teeth of all known genera of the gorgonopsians and therocephalians at the time. In particular, tooth shape and tooth serrations were compared. Casts of the teeth that most closely matched the unidentified tooth were compared with a cast of the unidentified tooth. Casts were analysed under the SEM and photos of tooth serrations were taken.

Results

Identification of 'Mamafura'

Dicynodonts were a highly successful and extremely diverse group of Palaeozoic herbivore tetrapods (Rubidge and Sidor 2001; Sullivan *et al.* 2002; Angielczyk 2004; Angielczyk *et al.* 2009). They were equipped with keratinous beaks, and frequently had large, neomorphic tusks (Sullivan *et al.* 2002; Angielczyk 2004)). Nonetheless, tuskless genera did exist and included *Oudenodon* and *Rhachiocephalus* (Keyser 1975). Tuskless *Tropidostoma* specimens have also been reported (Botha and Angielczyk 2007; see figure 12E). In some genera, such as *Diictodon*, tuskless individuals are as equally abundant as tusked individuals and have since been shown to represent sexually dimorphic genders (see Sullivan *et al.* 2002). This is, however, in contrast with the majority of tusk bearing dicynodonts, where tusks are present in both genders, and appear to have been used in digging, as in the case of *Lystrosaurus* (Cluver 1971). The absence of tusks in Mamafura (figure 8) is therefore, the first distinctive characteristic in determining its identity.

not resul

Figure 8: Partially articulated skeleton of Mamafura, SAM-PK-K06446. Note the well articulated skull, forelimbs, ribcage and vertebral column and the disarticulated hind-limbs. (Photo: N. Fordyce 2010).

As stated above, Mamafura was found in the *Tropidostoma* Assemblage Zone (figure 3) of the Beaufort Group (Appendix 1). Previous work by Rubidge (1995) suggested that the only tuskless genera of dicynodonts in the *Tropidostoma* Assemblage Zone included *Tropidostoma* and *Rhachiocephalus* with *Oudenodon* only emerging from the beginning of the *Cistecephalus* Assemblage Zone (figure 9A). However, whilst *Oudenodon bainii* is commonly reported from the *Cistecephalus* and *Dicynodon* assemblage zones of South Africa (Rubidge 1995), it has, more recently, been recovered from the underlying *Tropidostoma* Assemblage Zone (Botha and Angielczyk 2007; Smith *et al.* 2010 (figure 9B)). Because *Oudenodon Bainii* specimens have been collected at *Tropidostoma* Assemblage Zone localities in the Karoo Basin of South Africa, the first appearance of *Oudenodon bainii* can no longer be used to define the base of the *Cistecephalus* Assemblage Zone.

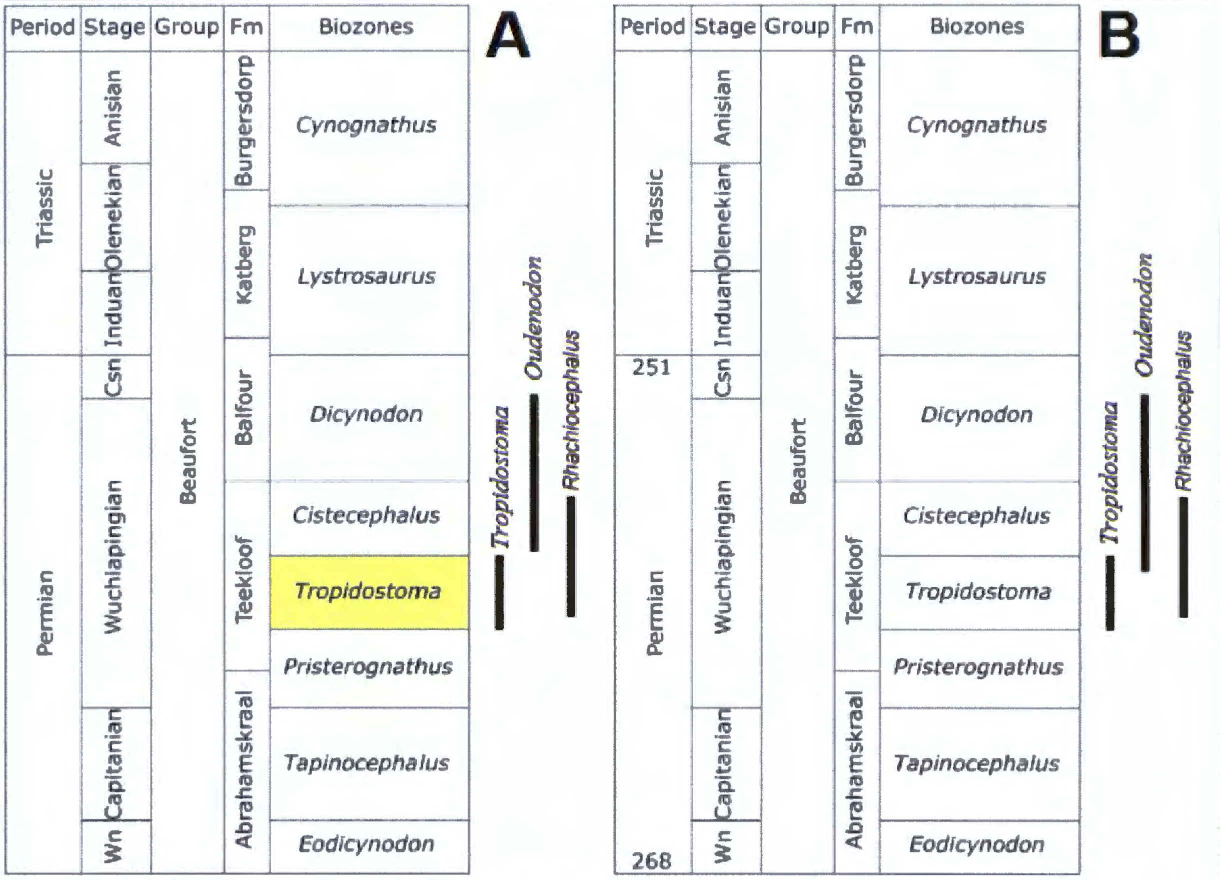


Figure 9: Biostratigraphy of the Karoo Basin showing the relevant assemblage zones and the ranges (black lines) of *Oudenodon*, *Tropidostoma* and *Rhachiocephalus* as defined by Rubidge (1995) (A) and then Botha and Angielczyk (2007) and Smith *et al.* (in press) (B). The *Tropidostoma* Assemblage Zone is highlighted in A. Adapted from Rubidge (1995) and Botha and Angielczyk (2007).

Determining the differences between *Rhachiocephalus, Tropidostoma* and *Oudenodon* are therefore important in determining the identity of Mamafura. The dicynodonts *Oudenodon bainii* and *Tropidostoma microtrema* are remarkably similar in most aspects of their morphology (figures 11 and 12). They show a great deal of overlap in their cranial and postcranial morphology, as well as growth patterns as indicated by bone histology (Botha and Angielczyk 2007). The most obvious distinguishing feature between *Oudenodon bainii* and *Tropidostoma microtrema* is the presence of tusks and / or postcanine teeth in *Tropidostoma microtrema* (figure 12B and 12D) and their absence in *Oudenodon bainii* (Botha and Angielczyk 2007) (figure 11). However, some specimens of *Tropidostoma microtrema* lack tusks or postcanine teeth (Keyser 1975; Botha and Angielczyk 2007; figure 12E) making the identification of *Oudenodon*/*Tropidostoma*-like specimens more complicated. Keyser (1975) suggests that *Oudenodon bainii* has a more blade-like ventral edge on the vomer and a flatter intertemporal region with straighter postorbitals than *Tropidostoma microtrema*. However, these differences are only useful for determining the identity of well preserved specimens. In the case of Mamafura, where lateral compression of the skull has taken place (see figures 10A and 16A), these differences are unreliable and compromised.

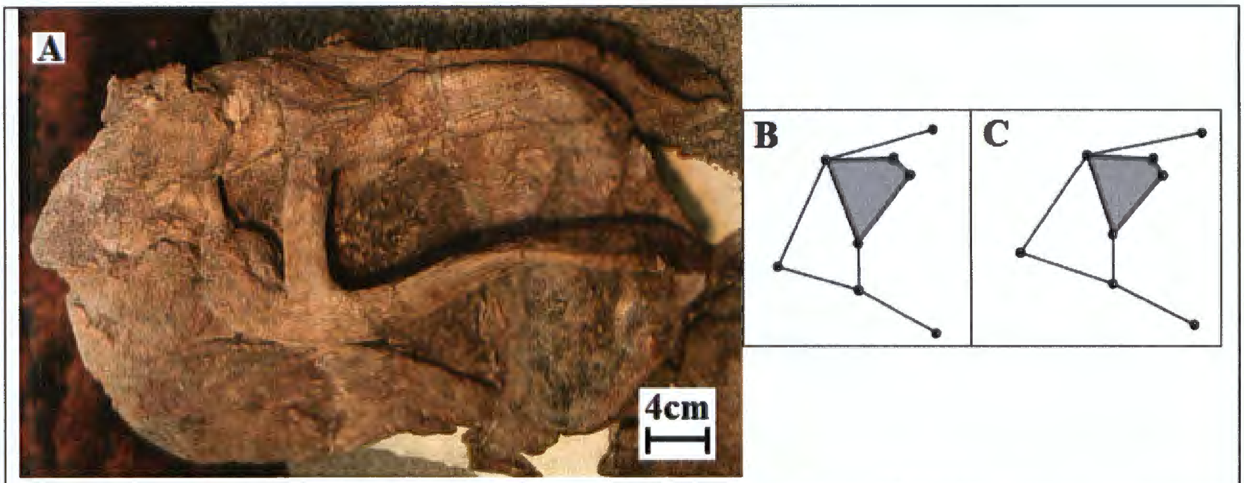


Figure 10: Lateral view of the skull of Mamafura (A) and stylized mean left lateral views of dicynodont snouts, *Oudenodon bainii* (B) and *Tropidostoma microtrema* (C) derived from a standardised geometric morphological dataset (adapted from Botha and Angielczyk 2007). (Photo (A): L. Wattrus 2010).

Botha and Angielczyk (2007) provide a geometric snout model for both *Tropidostoma microtrema* and *Oudenodon bainii* which uses eight geometric points to derive the mean snout shape. The geometric morphometric analysis demonstrated that *Tropidostoma microretrema* has a lower, longer snout and smaller external naris when compared with *Oudenodon bainii*. According to Botha and Angielczyk's model (2007), the steep angle of Mamafura's snout (figure 10A) is similar to the stylised angle of the *Oudenodon bainii* snout (figure 10B) suggesting it is *Oudenodon*-like (K. Angielczyk 2010, *pers. comm.*). In contrast, the stylised view of the *Tropidostoma microtrema* snout (figure 10C) suggests it is not as steep as both the 'mean' *Oudenodon bainii* snout and Mamafura's snout. The absence of tusks and post-canine teeth coupled with the steep snout provides strong evidence to suggest that Mamafura is more *Oudenodon*-like than *Tropidostoma*-like.

Figure 11: Lateral views of *Oudenodon bainii* skull specimens. Note the absence of tusks but the presence of nasal bosses (indicated by the black arrows) (A - SAM-PK-K11113, B - SAM-PK-K02364, C – SAM-PK-K03727, D – SAM-PK-K07254). (Photos: N. Fordyce 2010).

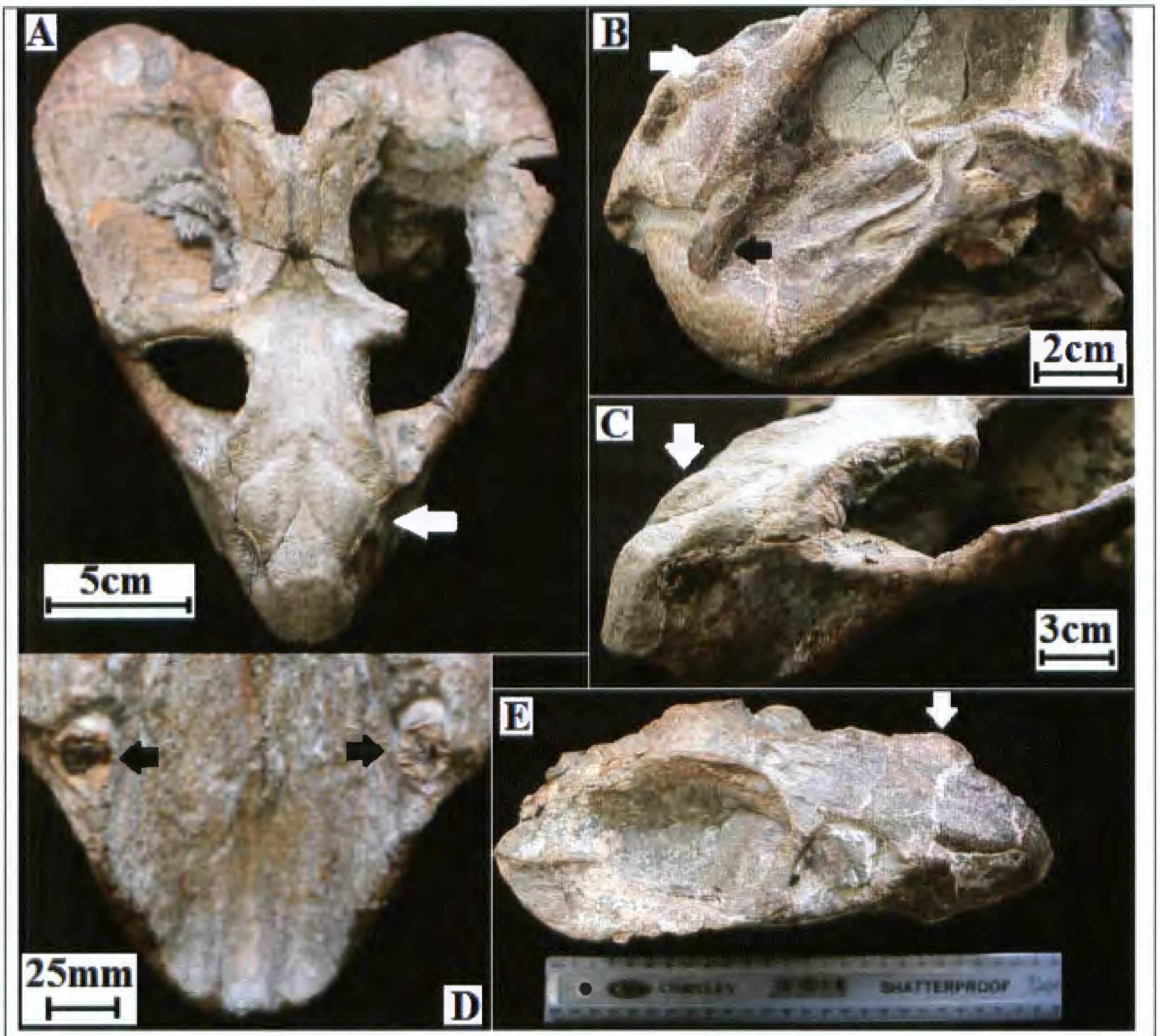


Figure 12: (A) Dorsal view of a *Tropidostoma* skull (SAM-PK-K08603) with clear nasal bosses. (B) Lateral view of the tusk of a *Tropidostoma* specimen (SAM-PK-K09960b) with nasal bosses. (C) Lateral view of the nasal bosses of SAM-PK-K08603. (D) Ventral view of the tusks of SAM-PK-K08603. (E) Lateral view of a tuskless specimen of *Tropidostoma* with nasal bosses (SAM-PK-K09960a). Note that the nasal bosses have been indicated with white arrows whilst the tusks have been indicated with black arrows. (Photos: L. Wattrus 2010)

In the past a number of *Oudenodon* species have been described across Africa (Keyser 1975). *Oudenodon bainii* was first described by Owen in 1860. Similarly, Boonstra (1938) described a new species of *Oudenodon*, *Oudenodon luangwensis*. *Oudenodon* species have also been recorded from Zambia, Tanzania and Malawi. However, Botha and

Angielczyk (2007) suggest these are all synonyms for *Oudenodon bainii.* The snout shapes of all these *Oudenodon* specimens fall within the geometric parameters defined by Botha and Angielczyk's model (2007). Hence they stress a single, fairly widely spread species (*Oudenodon bainii*) across southern Africa (J. Botha *pers. comm.* 2010). However, they also make reference to another species of *Oudenodon*, *Oudenodon grandis* which was first described as *Dicynodon grandis* by Haughton (1919) and may be distinct from *Oudenodon bainii*. I will make reference to this species later on.

Previous studies on dicynodonts, such as the study by Sullivan *et al.* (2002) on *Diictodon,* have shown that in some species there is evidence of sexual dimorphism. In showing that *Tropidostoma microtrema* and *Oudenodon bainii* were distinct species and not sexually dimorphic members of the same species, Botha and Angielczyk (2007) highlighted the differences in size between *Tropidostoma microtrema* and *Oudenodon bainii.* They emphasized that in species with sexually dimorphic traits, the gender with a sexually dimorphic trait (such as tusks) is most commonly the larger of the two genders. In the case of *Tropidostoma microtrema* and *Oudenodon bainii,* the former posses tusks but appears to have been the smaller of the two (figure 15). I chose then to analyse where Mamafura fitted in within the two species based on skull length.

Over 160 skull specimens of *Oudenodon bainii* were measured and included in the analysis. These specimens give a very accurate indication of the range of skull sizes within *Oudenodon* as the histogram (figure 13A) shows a classic normal distribution curve. The mean skull length was determined to be 180.3mm. Similarly, *Tropidostoma microtrema* skull specimens were distributed normally (the figure is not included though, see figure 14 for an example) and the mean skull length was determined to be 160.5mm. Rather surprisingly, these values are someway short of the measurement of Mamafura's skull (440mm). When included in the *Oudenodon bainii* curve, Mamafura is shown to be a significant outlier, being over 100mm larger than the largest *Oudenodon bainii* skull (figure 13B).

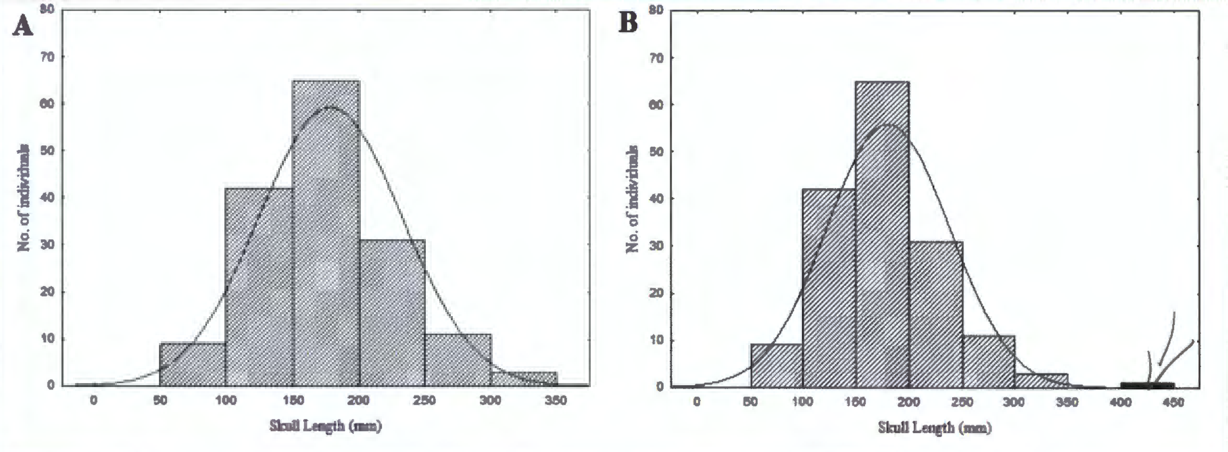
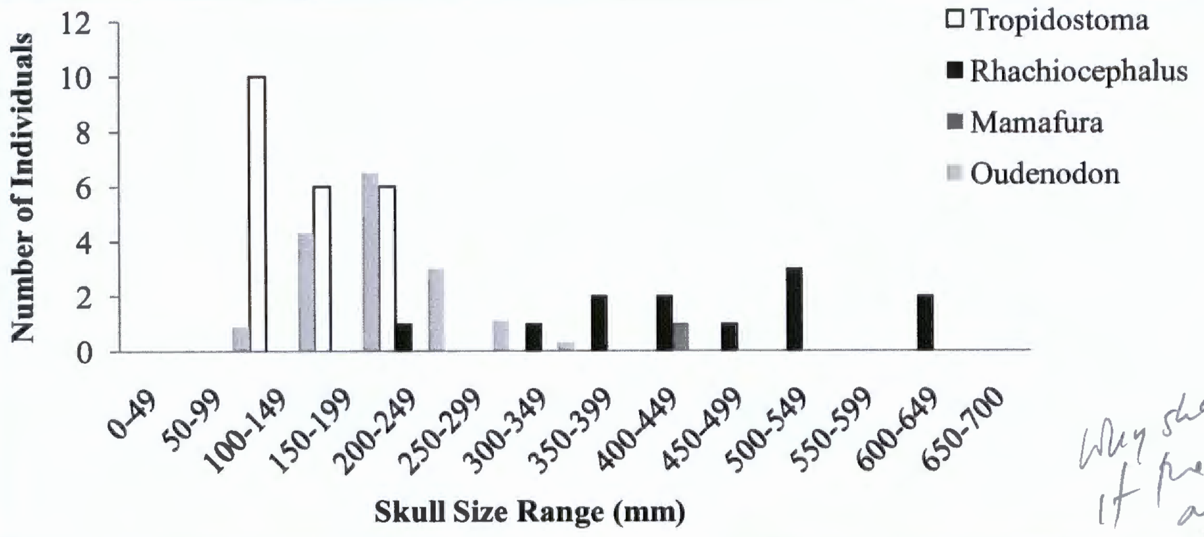


Figure 13: Histograms depicting (A) the abundance of *Oudenodon bainii* specimens for each of the skull length bin ranges (K-S d=.07931, p> .20; Lilliefors p<.05) and (B) the abundance of *Oudenodon bainii* specimens for each of the skull length bin ranges (columns) with Mamafura included (black column) (K-S d=.08504, p<.20 ; Lilliefors p<.01).

?

The significant discrepancy between the size distribution of the *Oudenodon bainii* skulls and the skull of Mamafura make it highly unlikely that Mamafura is an *Oudenodon bainii* specimen. It is possible that the lateral compression of Mamafura's skull, shown in figure 10A, may have distorted the skull length, however, the extent of any distortion is not enough to explain the 100mm plus difference between it and the largest *Oudenodon bainii* skull. The same logic applies to the even smaller, tusked *Tropidostoma microtrema.*

The evidence shown in figure 13 suggests that Mamafura is more *Rhachiocephalus*-like. *Oudenodon* and *Rhachiocephalus* are remarkably similar in morphology (figures 11 and 15) and size is often used to differentiate between the two (K. Angielczyk *pers. comm.* 2010). When comparing the skull size of Mamafura to the skull size distribution of *Rhachiocephalus*, it appears that Mamafura fits well within *Rhachiocephalus* (figure 14).



Why show fig 13 if the data are here

Figure 14: A histogram depicting the number of individuals of *Tropidostoma, Rhachiocephalus and Oudenodon* per bin range. Note that the bin ranges are respective skull length measures. The skull length of Mamafura is included (in the dark grey column) to show where it fits in along the distribution. The number of individuals per bin range for *Oudenodon* has been divided by 10 to make the columns of the other genera (which are less abundant in the collections) more noticeable.

Just use a 2nd axis!

However, *Rhachiocephalus* is best distinguished from *Oudenodon* by the presence of a large pineal boss and pineal foramen (figures 15E and F) (K. Angielczyk *pers. comm.* 2010). Furthermore, *Rhachiocephalus*, *Oudenodon* and *Tropidostoma* all have fairly large nasal bosses (see figures 11, 12A, 12B, 12C, 12E and 15D). Both these features are absent in Mamafura (Figures 10A and 16A). This has lead K. Angielczyk (*pers. comm.* 2010) to consider reclassifying Mamafura (originally classified as *Rhachiocephalus*) as *Oudenodon grandis*, although he is yet to publish this. This suggestion has been made on the basis of Mamafura being a large, tuskless dicynodont with an absence of facial bosses.

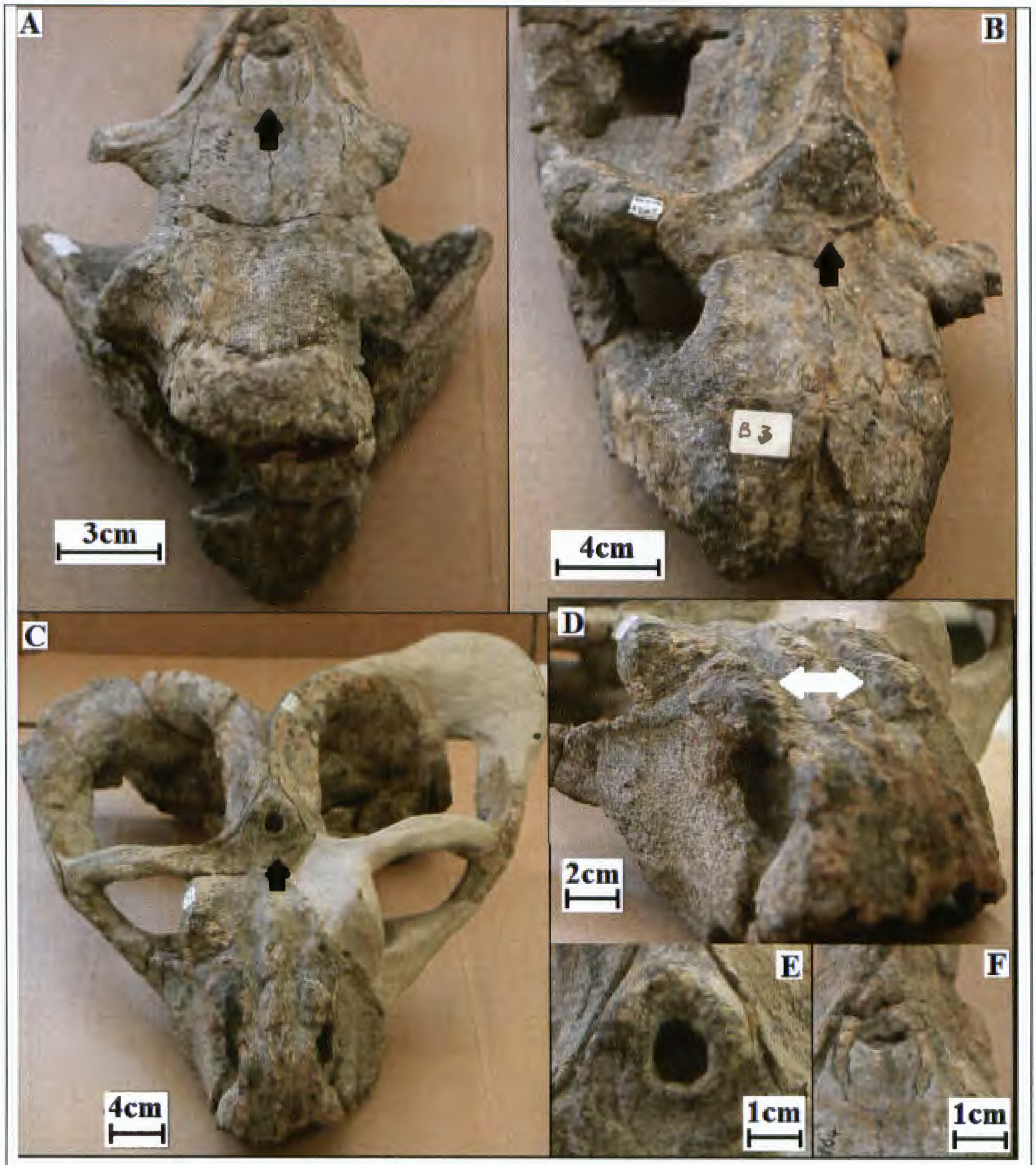


Figure 15: Dorsal views of *Rhachiocephalus* skull specimens (A – SAM-PK-K05864, B – SAM-PK-K07147, C – SAM-PK-K01393). Note the presence of large nasal bosses (D) and pineal bosses (E and F). Where appropriate nasal bosses have been indicated with white arrows whilst pineal bosses are indicated by black arrows. (Photos: L. Wattrus 2010).

Oudenodon grandis was originally named Dicynodon grandis (figure 16B) by Haughton (1919) (Botha and Angielczyk 2007). Haughton (1919) described *Oudenodon grandis* as follows “A complete skull and lower jaw obtained on the farm Dunedin (the same location as Mamafura), Beaufort West, seems to belong to a new species. It is somewhat crushed laterally, and the sutures do not show very clearly-the specimen presumably being an old individual." No other specimens of *Oudenodon grandis* have been recorded at the SAM, BPI or National Museum in Bloemfontein. There are also no recorded specimens from the Rubidge Collection (B. Rubidge *pers. comm.* 2010). This has prompted G. King to make SAM-PK-K02679 (Haughton's *grandis*) an x-Type of *Rhachiocephalus*. However, K. Angielczyk (*pers. comm.* 2010) remains convinced that *Oudenodon grandis* is a distinct species, possibly frequently identified as *Rhachiocephalus* or genuinely underrepresented in the fossil record. The true identity of Mamafura, for now however, remains unresolved, although it is clear that it is neither *Oudenodon bainii* nor is it *Rhachiocephalus*. It is most likely *Oudenodon grandis*.

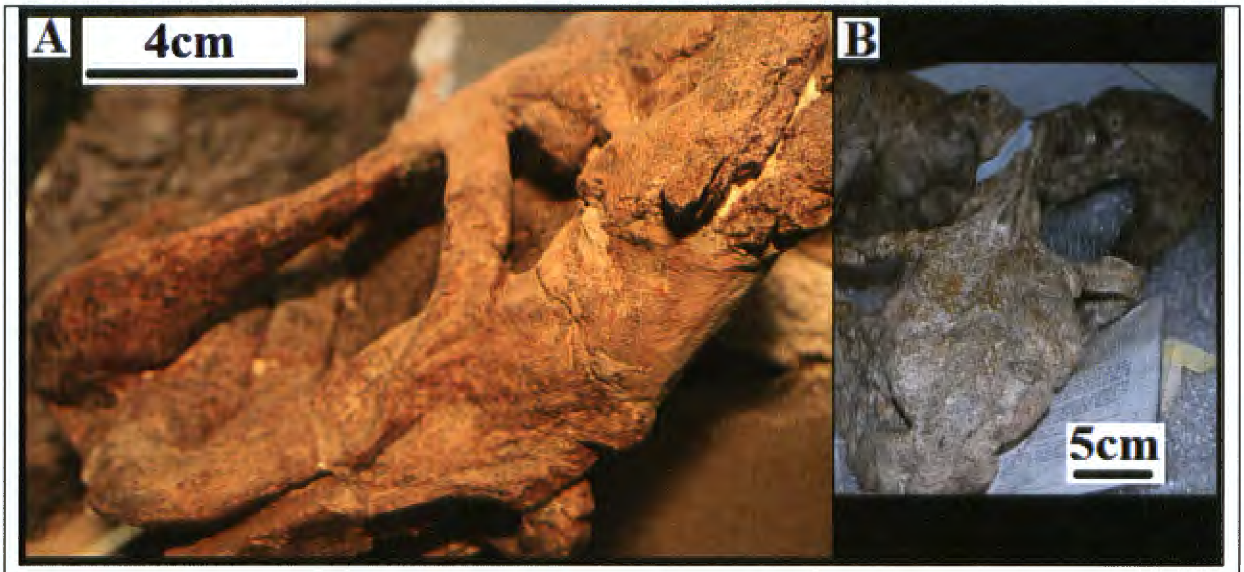


Figure 16: Dorsal views of (A) Mamafura's skull and (B) the skull of *Dicynodon grandis* (Haughton 1919) (SAM-PK-K02679). Note the absence of a pineal boss and nasal bosses in (A) and the absence of a pineal boss in (B). (Photos: N. Fordyce 2010).

Vertebrate Taphonomy

The Dunedin exposure clearly demonstrates that the transitional strata between proximal and distal floodplain facies (figures 3 and 4) are the most fossiliferous of all the inter-channel facies in this area (Smith 1993). This is interpreted as being primarily indicative of an "optimal burial environment" for the preservation of small and medium-sized dicynodonts (Smith 1990; 1993) such as Diictodon, Oudenodon and *Tropidostoma*. The relative abundance of dicynodonts in these strata suggest not only "optimal burial environment", but also a strong association and concentration of these animals with water bodies. The strip of floodplain bordering the axial flood-basin playas appears to have had the optimal balance between bone accumulation and bone burial mechanisms (Smith 1993). The floodplain accretion rates were fast enough to bury bones before they disintegrated through sun exposure and weathering, whilst the flow velocities were low enough to avoid entrainment (Smith 1993). Species died by any number of causes (old age, drought, predation etc.) and subsequent inundation by sheet flows effectively buried the embedded skeletons where they lay (R. Smith *pers. comm.* 2010). Thus there is an abundance of vertebrate fossils in the transitional strata between proximal and distal floodplain facies of the Hoedemaker member (figures 2 and 3).

Smith (1993) recognises 6 taphonomic pathways which can be used to describe the mode of fossilisation in the Karoo strata. (1) Disarticulated skeletons become embedded at site of death and are buried by vertically accreted alluvium. (2) Articulated and disarticulated skeletons become preserved in under-ground burrows. This is a particularly common taphonomic pathway for burrowers like *Diictodon*. (3) Articulated, disarticulated and transported small postcranial elements accumulate in embayments of the low-stand lake margin. (4) Carcasses of animals that died in the channel furrow and then become disarticulated during transport downstream. (5) Previously buried bone is re-exposed the by undercutting of river banks by streams. (6) Carcasses of animals accumulate around waterholes, swales and chute channels. The partially articulated nature of Mamafura along with the associated predator tooth embedded with it, makes this taphonomic study particularly unique but also valuable for understanding how possible predator action might have influenced the way the bones became fossilised, as well as providing insight into how Mamafura died, and enhancing our knowledge of the ecology of the Late Permian.

The first and most obvious observation when looking at Mamafura (Figure 8) is the rather bizarre disarticulation of the sacral vertebrae and hind-limbs and the near perfect articulation of the rest of the body. The other distinct observation is the absence of any other species, barring the tooth. If the site where Mamafura ultimately underwent fossilisation had been one that had accumulated bones by slowing the flow of water and causing the heavier bones to settle out of the flow, one might expect to see other bones from other species and an arrangement of bones based on their size, with heavier, larger bones separated from the smaller, lighter bones. Certainly one would also expect to see a greater extent of disarticulation of Mamafura. Added to that the rather puzzling question – why would the depression accumulate a tooth but lose other larger and heavier bones such as those associated with the toes and feet of Mamafura?

The current hypothesis for the death and fossilisation of Mamafura held by Roger Smith (*pers. comm.* 2010) is that Mamafura drowned, and was later scavenged before eventually being covered by a series of flood events. This taphonomic analysis will assess to what extent this hypothesis might be plausible.

Bone Damage

The first investigation of Mamafura looked at any bone damage that could be attributed to predator activity. This included any broken bones or damage to the bones caused by tooth marks. Damage was recorded on at least two of the ribs where large, round, porous calluses could be seen (Figure 17). The calluses indicate two things; firstly, Mamafura was involved in some traumatic event that resulted in it breaking at least two ribs. Secondly, the round smooth textures of the calluses indicate that the ribs had successfully healed and that Mamafura had survived for a fairly substantial period of time afterwards (A. Chinsamy-Turan *pers. comm.* 2010). The calluses, along with the fairly substantial size of the animal and the overall texture of the bones, also suggest that it was an adult. It is reasonable to conclude that the broken ribs played no role in the death of the animal and they do not provide any evidence to support or refute the idea that the animal was hunted or scavenged.

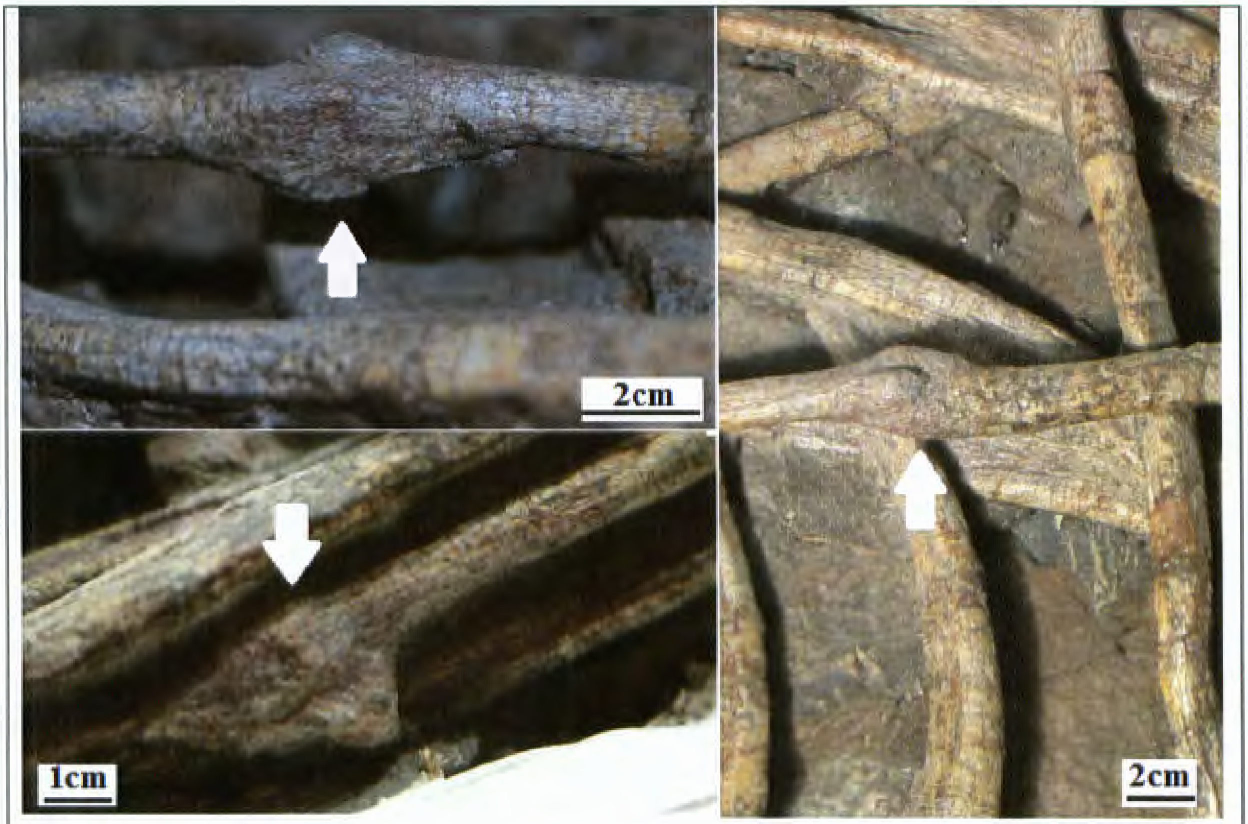


Figure 17: Calluses on some of the ribs of Mamafura. Note the well rounded, smooth nature of the calluses which are indicated by white arrows. (Photos: Nick Fordyce 2010).

The damage to the ribs could have been caused by any number of things but are most probably the result of either a fall, head butting during mating season or an attempted predator attack (R. Smith *pers. comm.* 2010). Other bone damage was observed in the form of tooth marks and tooth indentations. Two tooth scratches were recorded on the left (disarticulated) femur (figure 18). It is difficult to speculate which teeth may have caused these scratches as no obvious serrations could be seen from the SEM image (figure 18B). What is interesting to observe, is the angle of the scratches on the femur. The scratches are not parallel, but rather run in slightly different directions (see the magnified image in figure 18A). This might indicate that the scratches were created by two separate biting actions rather than by two neighbouring teeth.

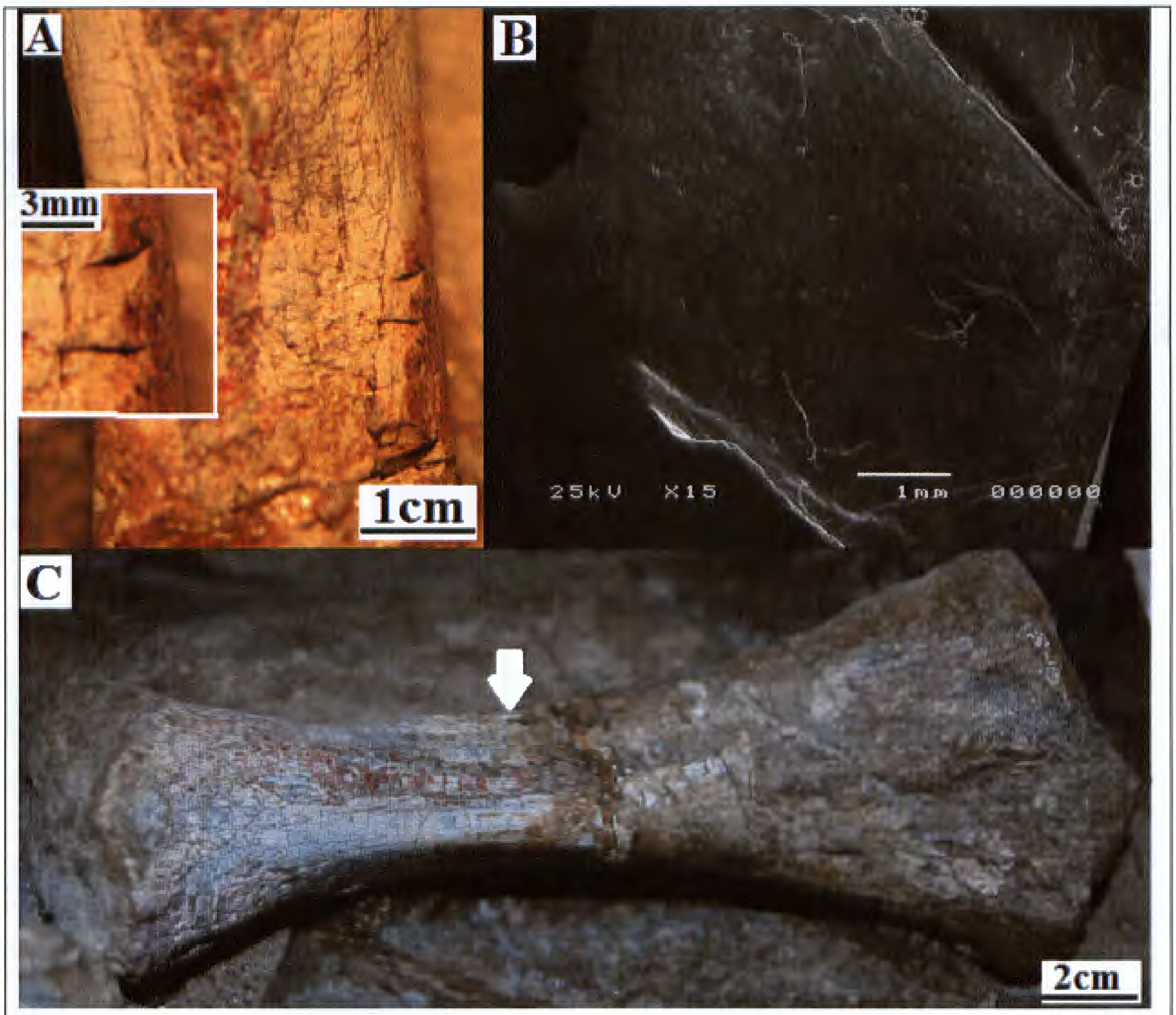


Figure 18: Two tooth scratches on the surface of the femur (A), an SEM image of the impressions (B) and the position of the scratches (although not visible) on the femur indicated by the white arrow (C). Note the sharp, white edge of the cast indicative of a tooth impression in (B). (Photos: (A and C) L. Wattrus 2010; (B) D. Ohland 2010).

Another tooth impression was observed in the form of a large indentation on the left (disarticulated) tibia (figure 19). It appears that during the action of biting, the bone was punctured rather than scratched or fractured. The large size of the indentation meant it was not possible to view the impression under the SEM. The cast also revealed no evidence of serrations when viewed under the light microscope, but nonetheless the impression has been attributed to a predator tooth owing to the sheer depth of the indentation.

Figure 19: Tooth indentation on the tibia (A) and the cast of the impression (B). The white arrow indicates the position of the indentation on the tibia. (Photos: N. Fordyce 2010).

Fossil bones that bear tooth marks can provide insight into the ecology, behaviour, and functional morphology of the organisms that produced them and the systems they lived in (Erickson and Olson 1996). These bones can be useful in revealing the identity of extinct predators and scavengers and their feeding preferences, and the methods they used to dispatch and consume their prey (Erickson and Olson 1996). Perhaps more important though, is that they can provide invaluable taphonomic information for determining the sequence of events before death through to eventual fossilisation of the bones. In the case of Mamafura, the bone impressions suggest that the carcass was fed on, specifically from the left rear. This suggests that Mamafura may well have ended up laying dead on its right side. It also suggests that the predators favoured feeding from the rear first, a characteristic observed in modern day predators like lions and hyenas (Thomas and Farlow 1997).

Unidentified tooth

Predation of Mamafura is backed up by the presence of an unidentified, isolated tooth which was associated with the fossil (figure 20). Whilst, no clear serrations could be found on the bones with tooth marks, it seems likely that the presence of this tooth is not coincidental. The absence of any other fossil material from other species prevents this from being a bonebed and suggests the tooth was deposited there at the same time as Mamafura. In light of this, it provides a very key piece of evidence to try and understand what happened just before Mamafura's burial.

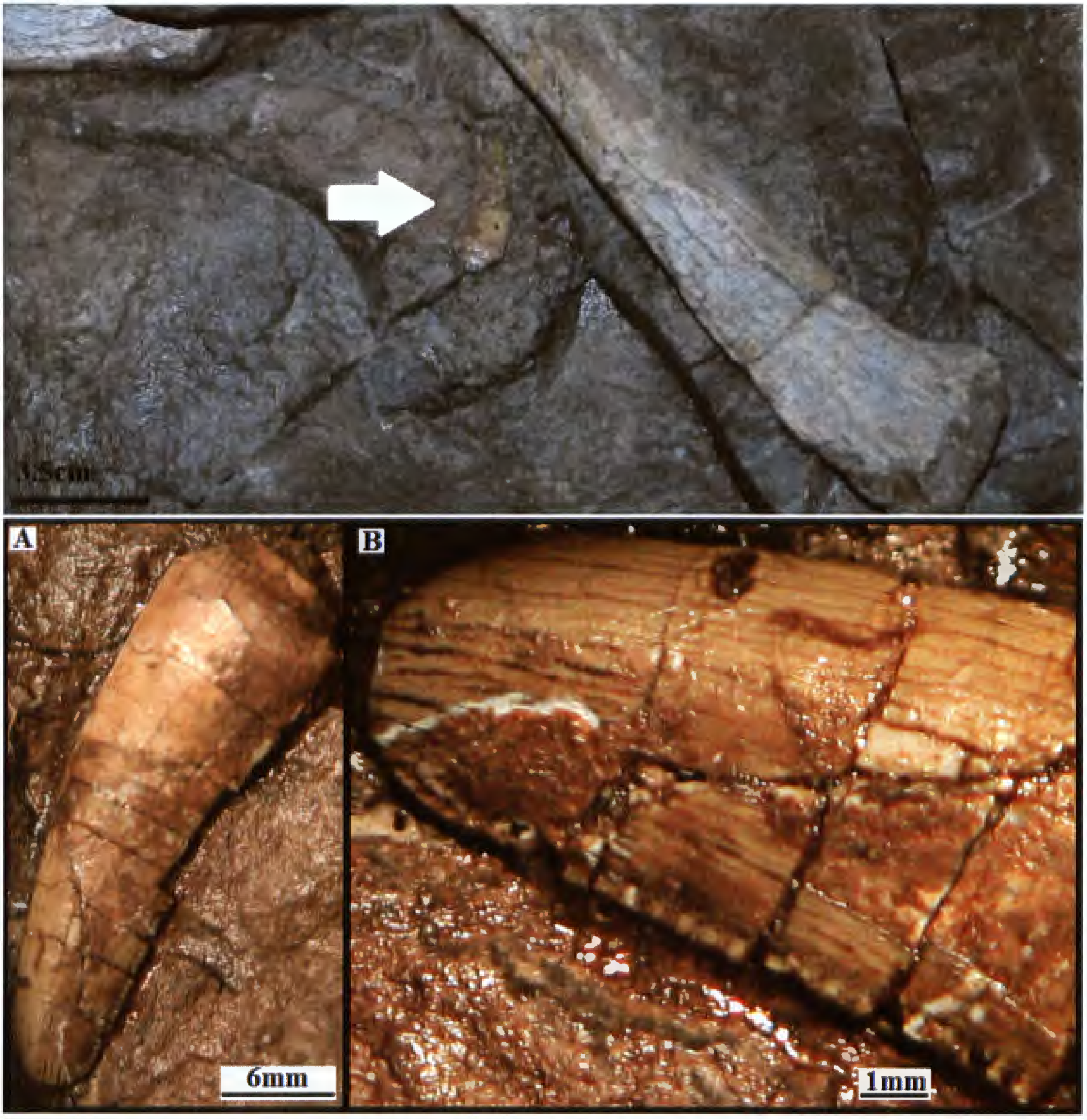


Figure 20: Unidentified tooth associated with Mamafura. Note the square serrations on the ventral side in (B). The white arrow indicates the position of the tooth within the mudrock and alongside the fibula. (Photos: L. Wattrus 2010).

The *Tropidostoma* Assemblage Zone has a wide range of both therocephalian and gorgonopsian predators (Smith *et al.* 2010). Nonetheless, previous studies have shown that it is possible to identify the species to which a tooth or even a tooth fragment belongs (Erickson and Olson 1996; Ray and Chinsamy 2002). Smith *et al.* (2010) suggest that the gorgonopsians included *Aelurognathus, Cynarioides, Cyonosaurus, Galerhinus, Gorgonops, Lycaenops,* and *Scymnognathus* whilst the therocephalians included *Choerosaurus, Hofmeyeria, Ictidosuchoides, Ictidosuchops, Ictidosuchus,* and *Scaloposaurus.* Where possible, specimens from all the aforementioned genera were investigated in an attempt to identify the tooth embedded with Mamafura. The therocephalians were well represented in the collections but only a fragment type specimen of *Choerosaurus* was available and it was not useful in a tooth analysis.

Figure 21: Skull and tooth images of (A) *Ictidosuchoides* (SAM-PK-K08659), (B) *Scalopsaurus constrictus* (SAM-PK-K10403), (C) *Hofmeyeria* (SAM-PK-K10525), (D) *Scalopsaurus* (SAM-PK-K10382). (Photos: N. Fordyce 2010).

The therocephalians canines did not appear to be particularly similar to the tooth embedded with Mamafura. For the most part they were very small species possessing small needle-like teeth. *Scalopsaurus* (figure 21C and 21D) and *Ictidosuchops* (Figure 22A) were particularly tiny, ruling them out as the 'culprits' immediately. *Hofmeryeria* (figure 21D), *Ictidosuchoides* (Figure 21A) and *Ictidosuchoidea* (figure 22C) were slightly larger but still not large enough to match the unidentified tooth. The shape and length of their canines were also in no way similar to the unidentified tooth. *Ictidosuchus* (figure 22B) was perhaps the closest match to the unidentified tooth but still was not an adequate match as it had a canine with exaggerated curvature when compared with the unidentified tooth. The width at the base of the tooth was also much narrower than that of the unidentified tooth. These characteristics, according to Erickson and Olson (1996) can be significant in determining which species a tooth belongs to. In addition, the absence of obvious serrations made any match even more unlikely as serrations have been used very successfully in the past to identify the 'owner' of a tooth (Ray and Chinsamy 2002).

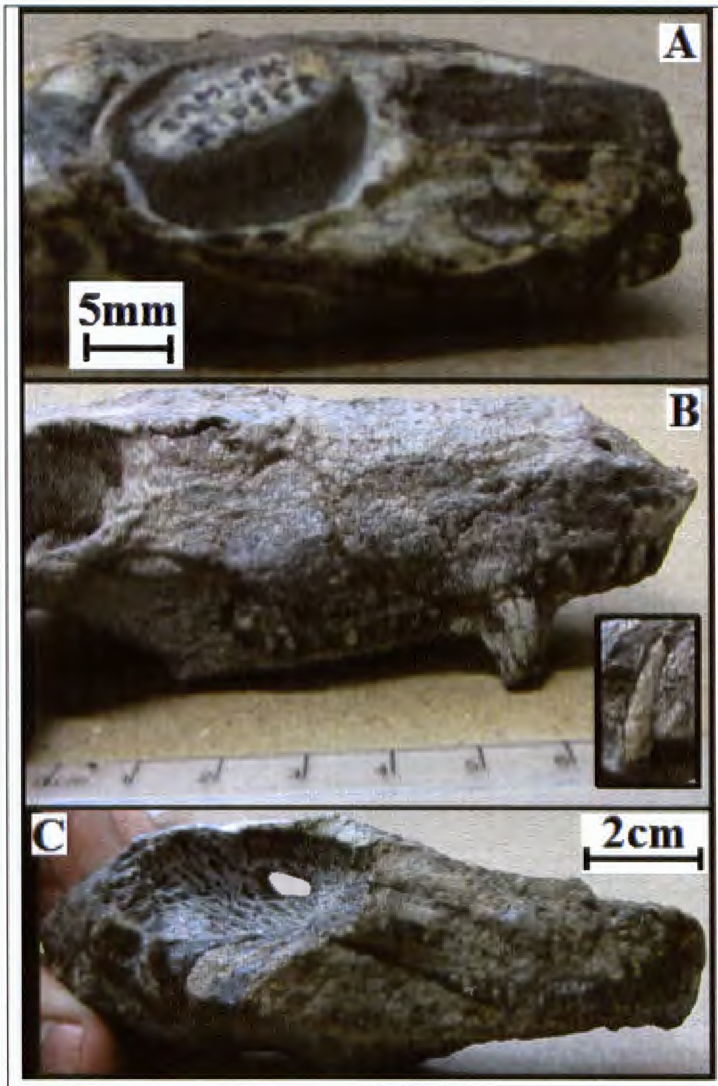


Figure 22: Skull and tooth view of (A) *Ictidosuchops intermedius* (SAM-PK-K10558), (B) *Ictidosuchus primaevus* (SAM-PK-K10650), (C) *Ictidosuchoidea* (SAM-PK-K07441). (Photos: N. Fordyce 2010).

The absence of any suitable therocephalian 'culprits' implies that the larger gorgonopsians are responsible. However, my analysis of both *Lycaenops* and *Scymnognathus* suggested neither of them could be responsible either. Whilst *Scymnognathus* was very large and probably capable of bringing down a dicynodont the size of Mamafura, its teeth were very unlike the one embedded with Mamafura. *Scymnognathus* has wide, rounded and straight teeth (figure 23A); quite dissimilar to the unidentified tooth. The absence of serrations on the teeth of the *Scymnognathus* specimens is also a distinctive feature. Similarly, tooth moulds from *Lycaenops* revealed no serrations and the curvature of the teeth from the investigated specimens (figure 23B and 23C) are far more exaggerated than the unidentified tooth.

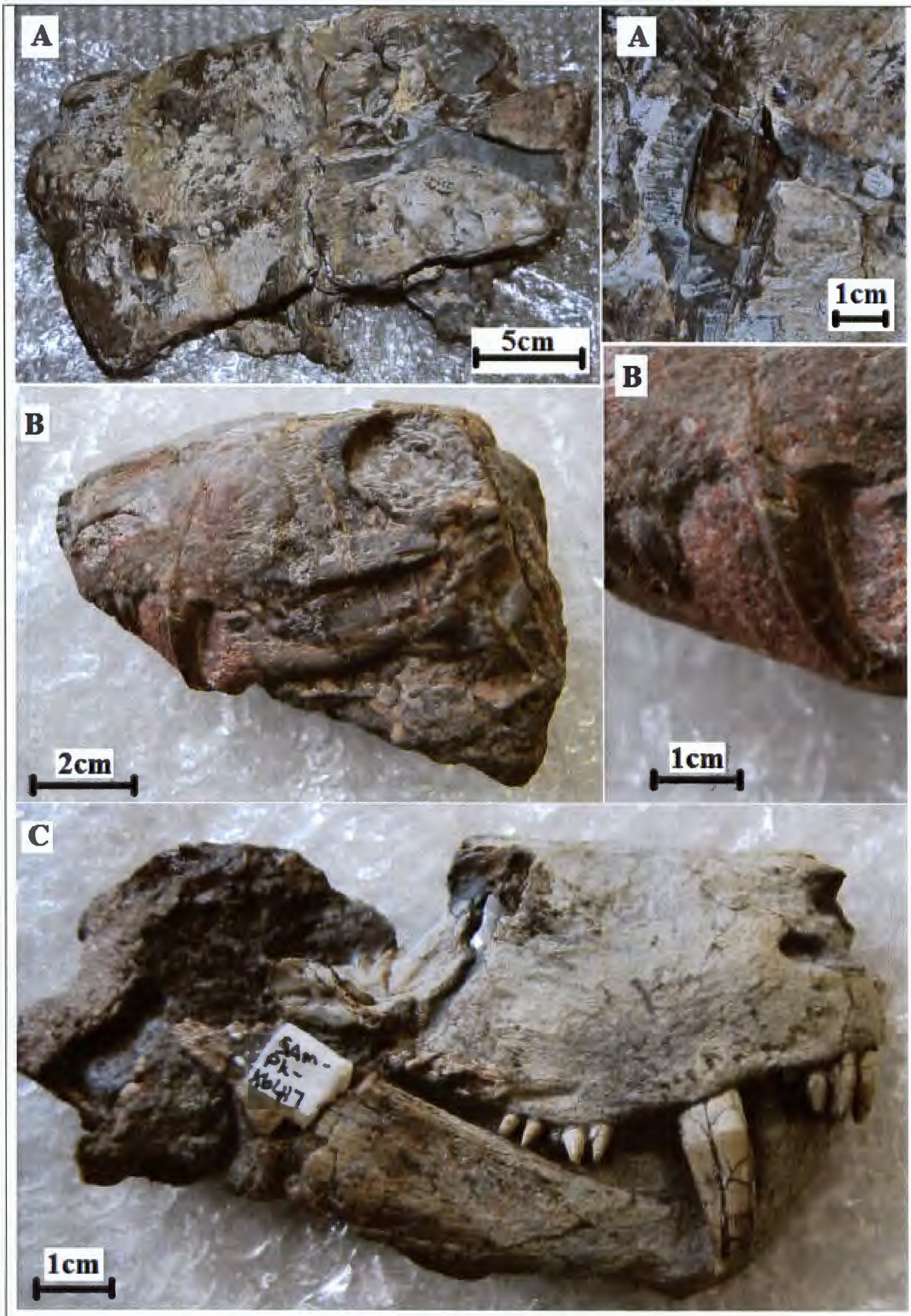


Figure 23: Skull and canine views of (A) *Scymnognathus tigriceps* (SAM-PK-K02342), (B) *Lycaenops* (SAM-PK-K06835) and (C) *Lycaenops* (SAM-PK-K06417). (Photos: N. Fordyce 2010

The curvature, length and width at base of the unidentified tooth appears to be most like the canines of *Cyonosaurus* (figures 24A, 24B and 24C) and *Aelurognathus* (figures 24D and 24E). The tip of the unidentified tooth appears to have broken off during the predators lifetime and then became smooth and rounded (figure 20). Similar patterns of 'wear and tear' can be seen in the *Cyonosaurus* specimen in figure 24A and in the *Aelurognathus* specimen in figure 24E.

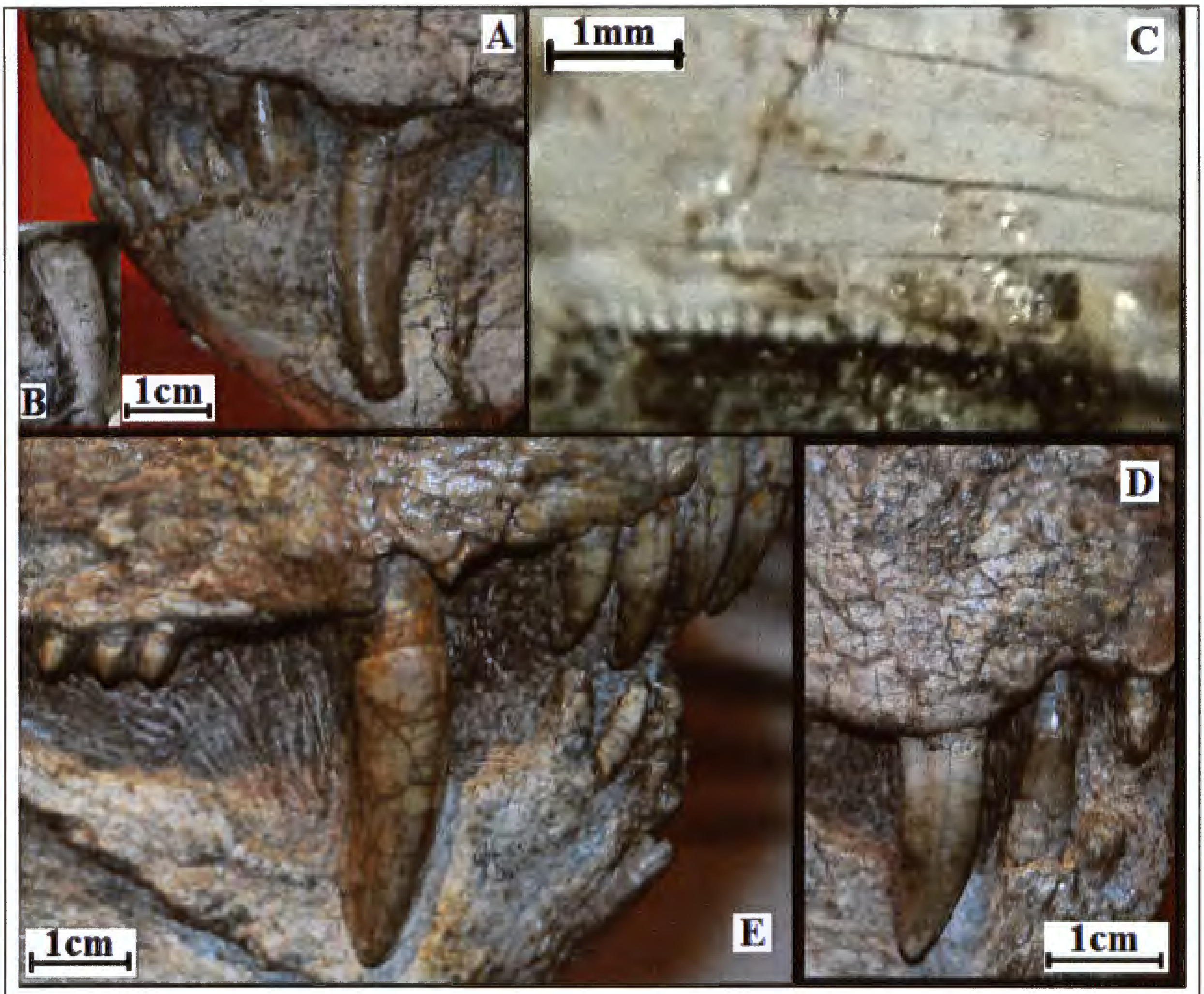
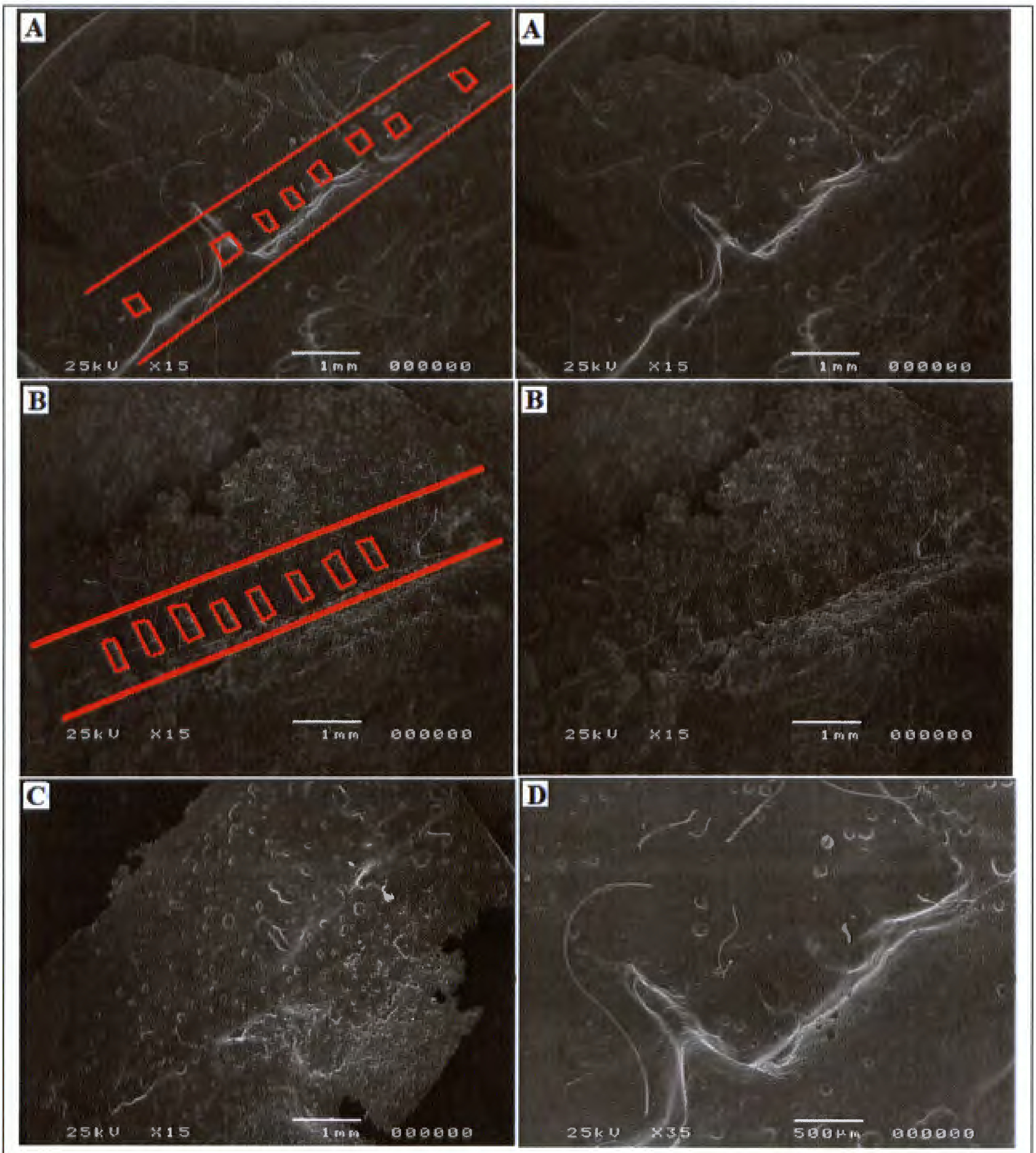


Figure 24: Lateral views of *Cyonosaurus* canines (A and B) and *Aelurognathus* canines (D and E). (C) is an image taken through a hand lens of the serrations on a *Cyonosaurus* canine. (A – SAM-PK-K10033, B – SAM-PK-K10700, C – SAM-PK-K10700, D – SAM-PK-K10034, E – SAM-PK-K10035). (Photos: L. Wattrus 2010).

The analysis of the tooth serrations suggests that the probable 'owner' of the tooth is *Aelurognathus*. The images (figure 20) and SEM images (figures 25A and 25D) of the unidentified tooth show 0.5mm square serrations. In contrast, the serrations present on the *Cyonosaurus* specimens (figure 24C) are rectangular, not square, and are much smaller at 0.2mm in size (figure 25C). Conversely, the serrations observed on the *Aelurognathus* teeth are square and are roughly 0.4-0.5mm in size (figure 25B). The combination of shape and size make for a fairly distinctive feature on the tooth and a powerful piece of evidence to suggest that the tooth belonged to a gorgonopsian from the *Aelurognathus* genus.



?!

Figure 25: SEM images of casts taken from gorgonopsian canines. (A) and (D) - the unidentified tooth embedded with Mamafura, (B) – *Aelurognathus* (SAM-PK-K10071) and (C) – *Cyonosaurus* (SAM-PK-K10700). Note: The serrations have been indicated in red in duplicated images and run from the bottom left corner diagonally to the top right corner in each image. Serrations in (C) are only just visible but can be corroborated from figure 24C. (Images: D Ohland 2010).

Taphonomic assessment

1 – Death

The evidence I have shown strongly supports the idea that a predator fed from Mamafura, particularly from the rear and the soft underbelly below the ribs. Bone damage suggests that the predator possibly removed some of the left hind-limb bones, possibly to gain further access to the softer flesh. This behaviour is observable in modern day predators such as Wild Dogs (*Lycaon pictus*) (Estes and Goddard 1967) and is indicated in figure 26C. It is also possible that the predators, having opened the carcass up, fed from the inside out, and in so doing, did not disarticulate the ribcage. There is very little evidence to show that the bones were gnawed at. There is also very little evidence from the teeth of both *Cyonosaurus* and *Aelurognathus* to suggest that they were capable of breaking bone. The sharp, pointed tips of the *Aelurognathus* and *Cyonosaurus* teeth (figures 24 and 27) suggest they were flesh eaters as opposed to bone crunchers like hyenas who have larger, more robust saw-like teeth (figures 26A and B) (Monastersky 1993; Pickrell 2002)

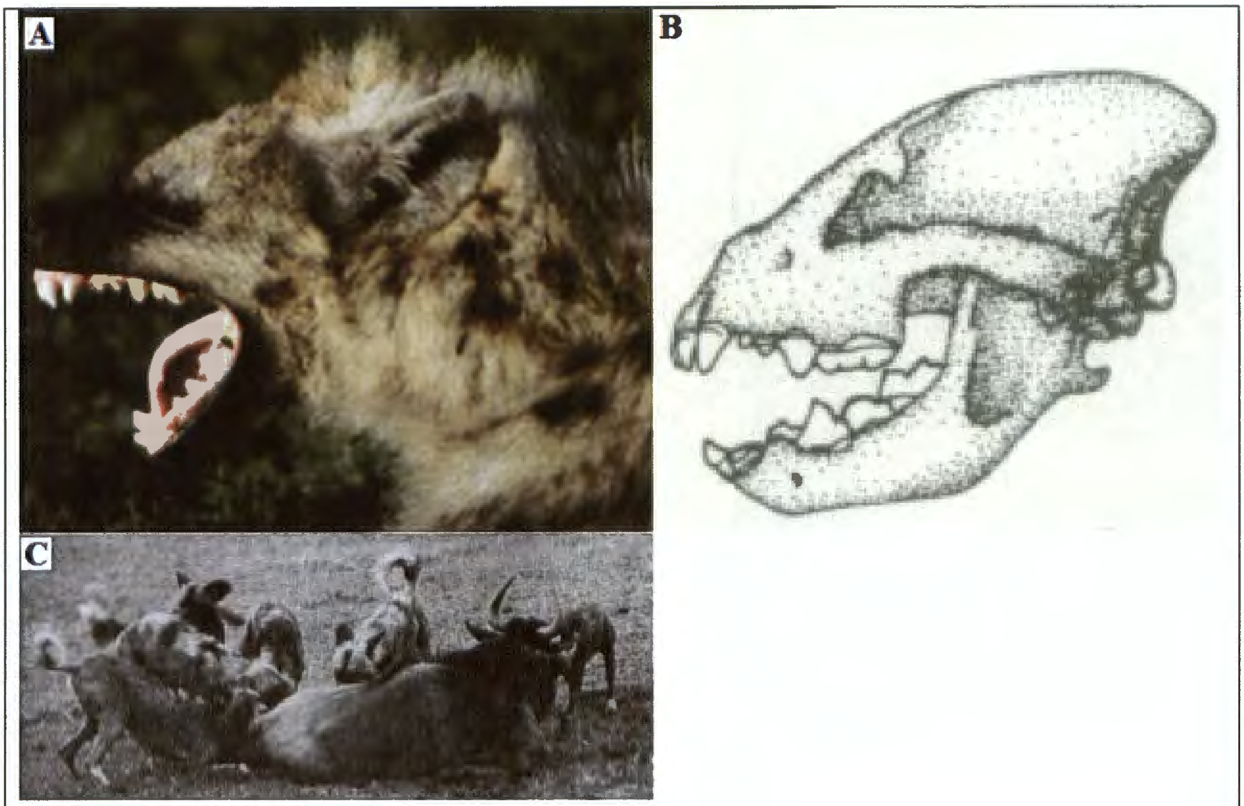


Figure 26: Spotted Hyena (*Crocuta crocuta*) jaws with large, robust, bone-crushing teeth (A and B) and a pack of Wild Dogs (*Lycaon pictus*) feeding from the rear on a Wildebeest kill (C). (Adapted from (A) Pickrell (2002), (B) Monastersky (1993) and (C) Estes and Goddard (1967)).

Given the size of the fully articulated *Cyonosaurus* (SAM-PK-K10428; figure 27) (similar in size to *Aelurognathus*) specimen at SAM it seems rather unlikely that they would have actively hunted a dicynodont the size of Mamafura. It is possible that *Cyonosaurus* and *Aelurognathus* were pack hunters. This would have made it more plausible for an animal the size of Mamafura to be successfully hunted. However, if this were the case one might expect to see more evidence of bone damage from the kill. The absence of any unhealed bone injuries, and the relative scarcity of bone damage, suggests this is an unlikely scenario. It seems far more plausible that Mamafura was dead and then scavenged on by the predators.

Figure 27: Articulated *Cyonosaurus* skeleton (SAM-PK-K10428). Note its small size when compared with Mamafura. (Photo: N. Fordyce 2010).

The question then remains as to how Mamafura may have died. The hypothesis held by R. Smith (*pers. comm.* 2010) is that Mamafura drowned and was then scavenged from. The final resting position of Mamafura is indicative of an animal that has drowned in a flood, floated to the surface of the water and then slowly been deposited as the water level subsides (R. Smith *pers. comm.* 2010). Seasonal flood events were common during the Late Permian (Smith 1989; 1990; 1993) and this hypothesis is supported by Smith's fourth taphonomic pathway (1993) which suggests that "Some animals that foraged on mid-channel sand-bars in the major rivers were drowned during rising floods as the islands were inundated.... As these carcasses were transported downstream they slowly disarticulated, dropping bones into the gravel lag that lined scour pools on the channel bed." In the case of Mamafura it seems as though the flood event subsided before disarticulation could occur, causing the carcass to be deposited on the river floodplain.

2 – Scavenging

Having been deposited on the floodplain it is likely that the weight of Mamafura caused it to 'dig itself in' much like a dune in a desert. Slower, subsiding water levels deposited silt around the back of Mamafura causing it to become 'anchored' on the floodplain (R. Smith *pers. comm.* 2010). Once water levels had subsided, a gorgonopsian or many gorgonopsians, probably *Aelurognathus*, moved in and scavenged from the carcass. The weight of the carcass would have prevented them from moving it in the mud, so they were most likely forced to move the hind-limb bones to get at some of the fleshy meat and innards. Similar patterns of scavenging have been found with *Lystrosaurus murrayi* (figure 28) and although they are from a different time period, it nonetheless supports the idea that the hindquarters are favoured first

Figure 28: *Lystrosaurus murrayi* specimen (SAM-PK-K8038) exhibiting signs of scavenging. Note the fully articulated skull, vertebral column and forelimbs and the disarticulated hind-limbs and sacral vertebrae. (Photo: N. Fordyce 2010)

3 – Desiccation and burial

Having been scavenged on, the carcass then lay out on the floodplain and desiccated. It is likely that at least some of the skin remained intact, especially around the ribcage. The ribs are usually one of the first sets of bones to disarticulate if not held in place (A. Morris *pers. comm.* 2010). Despite that, there is also evidence to suggest that the carcass was buried soon after death. 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. The stages are defined by easily observable criteria (cracking, flaking, skin and ligament presence, etc.). Based on the appearance of Mamafura's bones, many of which are almost pristine, it seems the bones are only at stage one of bone weathering. Stage one's criteria involve longitudinal cracks, the presence of fat, skin and/or other tissue (Behrensmeyer 1978). There are very few longitudinal cracks and, as stated above, there is evidence to support the idea that some of the skin was intact at the time of burial. Fossilisation rarely preserves soft tissue like skin so this was probably destroyed over time. Stage one is interpreted as being less than 5 years of exposure to desiccation on the floodplain.

Based on the sedimentological log (figure 4) it appears as though 3 or 4 seasonal flood events eventually buried Mamafura, causing her to become preserved. The flood events stripped her of some of her smaller bones, specifically those associated with the toes and feet (R. Smith *pers. comm.* 2010), although it is possible that these are just scattered a bit further around at the site where she was discovered.

Summary and Conclusions

The taphonomic study of the evidence of Mamafura supports the following conclusions;

1) Mamafura, a large, tuskless dicynodont with no obvious bosses, is most probably a rare species of dicynodont, *Oudenodon grandis*.
2) It's final resting position supports the hypothesis that it drowned in a flood event.
3) It was scavenged on by a gorgonopsian, most likely *Aelurognathus*.
4) Having been scavenged on, it then lay on a floodplain and briefly desiccated before being buried by a sequence of flood events.
5) Ironically, although it died in a flood, it was ultimately a series of floods that allowed its story to be brought back to life 253 million years later.

Future Directions

This project was a taphonomic study of the Mamafura fossil on display at the Iziko South African Museum (SAM). In researching and attempting to identify Mamafura (SAM-PK-K06446), it has become apparent that it matches none of the described species that it most closely resembles. The implication being that this is a new, closely related species of dicynodont, most probably the poorly described *Oudenodon grandis.* Future work is required to properly identify Mamafura and describe the distinctive features of *Oudenodon grandis.* One other specimen described as *Oudenodon grandis* is present at SAM (SAM-PK-K02679) and should be included in the analysis.

Acknowledgements

I would like to thank my supervisors, Anusuya Chinsamy-Turan and Roger Smith, for their help, dedication and enthusiasm, and for putting up with my unpredictable way of working. Thanks also to the Iziko SAM Assistant Collections Manager, Sheena Kaal, whose help and organisation made this project possible. Special thanks must also go out to Derek Ohland who provided access and assistance with the SEM and to Romala Govender who assisted with taking the casts of the tooth impressions and who gave so readily of her time. Additional thanks to Ken Angielczyk, Bruce Rubidge and Jennifer Botha for their email correspondence. I would also like to thank Laurence Wattrus, who gave of his time to help with the photography of specimens and whose photos put those I took to shame! Lastly thanks must go to the NRF, whose funding made this project possible.

References

Behrensmeyer, A. 1978. Taphonomic and ecologic information from bone weathering. *Palaeobiology,* **4**, 150-162.

Boonstra, L. D. 1938. A report of some Karoo reptiles from the Luangwa Valley, Northern Rhodesia. *Quaternary Journal of the Geological Society of London,* **94**, 371-384.

Boonstra, L. D. 1969. The fauna of the *Tapinocephalus* Zone. *Annals of the South African Museum,* **56**, 1-53.

Botha, J., Abdala, F., and Smith, R. 2007. The oldest cynodont: new clues on the origin and early diversification of the Cynodontia. *Zoological Journal of the Linnean Society,* **149**, 477-492.

Botha, J., and Angielczyk, K. D. 2007. An integrative approach to distinguishing the late Permian dicynodont species *Oudenodon bainii* and *Tropidostoma microtrema* (Therapsida: Anomodontia). *Palaeontology,* **50**, 1175-1209.

Broom, R. 1907. On the geological horizons of the vertebrate genera of the Karoo formation. *Records of the Albany Museum, Grahamstown,* **2**, 156-163.

Catuneanu, O., and Elango, H. 2000. Tectonic control on fluvial styles: The Balfour Formation of the Karoo Basin, South Africa. *Sedimentary Geology,* **140**, 291-313.

Cluver, M. A. 1971. The cranial morphology of the dicynodont genus *Lystrosaurus*. *Annals of the South African Museum,* **56**, 155–274.

Colbert, E. H. 1963. The relevance of palaeontological data concerning evidence of aridity and hot climates in past geological ages. *Proceedings NATO Palaeoclimates Conference, Newcastle University,* pp. 378-381.

Cole, D. I., Smith, R. M. H., and Wickens, H. D. E. V. 1990. Basin plain to fluvio-lacustrine deposits in the Permian Ecca and Lower Beaufort Groups of the Karoo Sequence: Guidebook Geocongress '90, Geological Society of South Africa, P02, 83 pp.

Dixon, D. 2007. The World Encyclopedia of Dinosaurs and Prehistoric Creatures. *Lorenz Books*, London, 512pp.

Efremov, J. A. 1940. Taphonomy: A new branch of palaeontology. *Pan-American Geologist*, **74**, 81-93.

Erickson, G. M., and Olson, K. H. 1996. Bite marks attributable to *Tyrannosaurs rex:* Preliminary description and implications. *Vertebrate Palaeontology,* **16**, 175-178.

Estes, R. D., and Goddard, J. 1967. Prey Selection and the hunting behaviour of the African Wild Dog. *The Journal of Wildlife Management,* **31**, 52-70.

Haughton, S. H. 1919. A review of the reptilian fauna of the Karoo system of Southern Africa. *Transactions of the Geological Society of South Africa*, **22**, 1-25.

Hotton, N. 1967. Stratigraphy and sedimentation in the Beaufort Series (Permian-Triassic), South Africa. *University of Kansas Press*, Lawrence, **5**, 390-427.

Johnson, M. R., van Vuuren, C. J., Visser, J. N. J., Cole, D. I., De, V., Wickens, H., Christie, A. D. M., Roberts, D. L., and Brandl, G. 2006. Sedimentary rocks of the Karoo Supergroup, In: *Geology of South Africa.* Geological Society of South Africa, Johannesburg, pp. 477-481.

Keyser, A. W. 1975. A re-evaluation of the cranial morphology and systematics of some tuskless Anomodontia. *Memoir of the Geological Society of South Africa,* **67**, 1-110.

McNamara, K. 2009. Permian In: *Prehistoric: The definitive visual history of life on earth,* (Eds) Guerrero, A. G., and Frances, P. 1st edn, pp: 170-193. Dorling Kindersley Limited, London.

Monastersky, R. 1993. A question of crushers. *Science News,* **144**, 397-397.

Nicolas, M. V. M., and Rubidge, B. S. 2009. Changes in Permo-Triassic tetrapod ecological representation in the Beaufort Group (Karoo Supergroup) of South Africa. *Lethaia,* **43**, 45-59.

Owen, R. 1860. On some reptilian fossils from South Africa. *Quarterly Journal of the Geological Society of London*. **16**, 49–63.

Owen, R. 1876. Descriptive and illustrated catalogue of the fossil reptilia of South Africa in the collection of the British Museum. London: British Museum (Natural History).

Pickrell, J. 2002. Rebranding the Hyena. *Science News,* **161**, 267-269.

Ray, S. and Chinsamy, A. 2002. A theropod tooth from the Late Triassic of southern Africa. *Journal of Bioscience,* **27**, 295-298.

Rubidge, B. (ed.) 1995. Biostratigraphy of the Beaufort Group (Karoo Supergroup). *Council for Geoscience*, Pretoria, 46 pp.

Rubidge, B. S., and Sidor, C. A. 2001. Evolutionary patterns among Permo-Triassic therapsids. *Annual Review of Ecology, Evolution and Systematics*, **32**, 449-480.

Saunders, K. M., Hodgson, D. A., Harrison, J., McMinn, A. 2008. Palaeoecological tools for improving the management of coastal ecosystems; a case study from Lake King (Gippsland lakes), Australia. *Journal of Palaeolimnology.* **40**, 33-47.

Sidor, C. A., and Smith, R. M. H. 2007. A second burnetiamorph therapsid from the Permian Teekloof Formation of South Africa and its associated fauna. *Journal of Vertebrate Paleontology.* **10**, 420-430.

Smith, R. M. H. 1987. Morphology and depositional history of ex-humed Permian point-bars in the south-western Karoo, South Africa: *Journal of Sedimentary Petrology*, **57**, 19-29.

Smith, R. M. H. 1989. Fluvial facies, vertebrate taphonomy and palaeosols of the Teekloof Formation (Permian) near Beaufort West, Cape Province, South Africa: unpublished Ph.D. Dissertation, University of Cape Town, 230 pp.

Smith, R. M. H. 1990. Alluvial palaeosols and pedofacies sequences in the Permian lower Beaufort of the southwestern Karoo Basin, South Africa. *Journal of Sedimentary Petrology*. **60**, 258-276.

Smith, R. M. H. 1993. Vertebrate Taphonomy of Late Permian Floodplain Deposits in the Southwestern Karoo Basin of South Africa. *Palaios*, **8**, 45-67.

Smith, R., Rubidge, B., van der Walt, M. In press. Therapsid biodiversity patterns and palaeoenvironments of the Karoo Basin, South Africa. Pp 1-55. In: The Forerunners of Mammals: Radiation, histology and biology. A. Chinsamy-Turan (Ed.). Indiana University Press.

Sullivan, C., Reisz, R. R. and Smith, R. M. H. 2002. The Permian mammal-like herbivore, *Diictodon,* the oldest known example of sexually dimorphic armament. *Proceedings of the Royal Society of London,* **270**, 173-178.

Tankard, A., Welsink, H., Aukes, P., Newton, R., and Stettler, E. 2009. Tectonic evolution of the Cape and Karoo Basins of South Africa. *Marine and Petroleum Geology*, **3**, 1-35.

Thulborn, T., and Turner, S. 2003. The last dicynodont: The Australian Cretaceous relict. *Proceedings: Biological Sciences,* **270**, 983-993.

Thomas, D. A., and Farlow, J. O. 1997. Tracking a dinosaur attack. *Scientific American,* 48-53.

Turner, B. 1978. Sedimentary patterns of uranium mineralization in the Southern Karoo (Gondwana) Basin, South Africa. In: Mial, Andrew D. (Ed). *Fluvial Sedimentology. Memoir Canadian Society for Petroleum Geologists,* **5**, 831-848.

Viglietti, P. 2009. Taphonomic study of a *Lystrosaurus* bonebed from the Lower Katberg in the southern Karoo Basin. Unpublished Honours Thesis, University of Cape Town, 66pp.

Watson, D. M. S. I960. The anomodont skeleton. *The Transactions of the Zoological Society of London*, **29**, 131-208.

Wiegelt, J. 1927. *Recent Vertebrate Carcasses and their Palaeobiological Implications.* Chicago Press, Chicago and London, 188pp.

Appendices

Appendix 1: Table of information about Mamafura

Accession No.	SAM-PK-K06446
Class	*Reptilia*
Subclass	*Synapsida*
Order	*Therapsida*
Suborder	*Dicynodontia*
Infraorder	*Pristerodontia*
Family	*Oudenodontidae*
Genus	*Oudenodon*
Species	*grandis*
Other Genus Name	*Rhachiocephalus*
Other Species Name	*Sp.*
Identifier	Ken Angielczyk
Identification Date	02/03/2010
Collector	J. Nyaphuli
Date Collected	00/03/1984
Field Number	17.8
Country	South Africa
Province	Northern Cape
District	Beaufort West
Government Farm and Number	Adjoining Quaggas Fontein 84
Latitude	31 deg 59 mins 00 secs S
Longitude	22 deg 20 mins 00 secs E
Group	Beaufort
Formation	Teekloof
Member	Hoedemaker
Assemblage Zone	*Tropidostoma*
Age	Late Permian
Preparator	Annelise Crean