

**CRANIAL MORPHOLOGY OF A PRIMITIVE DINOCEPHALIAN FROM THE  
MADUMABISA MUDSTONE FORMATION, ZIMBABWE.**

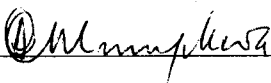
**Darlington Munyikwa**

A dissertation submitted to the Faculty of Science, University of Witwatersrand,  
Johannesburg, in fulfilment of the requirements for the degree of Master of Science.

Johannesburg 2001

**DECLARATION**

I declare that this dissertation is my own, unaided work except where it is indicated in the text. This dissertation is submitted for the degree of Master of Science at the University of Witwatersrand, Johannesburg. It has not been submitted before for any degree or any other qualification at any other university.

 \_\_\_\_\_

(Signature of candidate)

24 day of MAY 2001.

**ABSTRACT**

Dinocephalians form an important part of the Upper Permian therapsid faunas of South Africa and Russia, and have also recently been reported from China and Brazil, and even more recently a diverse dinocephalian fauna has been described from Zimbabwe. This thesis reports a new primitive tapinocephalid dinocephalian, NHMB1556, from the Upper Madumabisa Mudstone Formation in Zimbabwe. NHMB1556 is considered to be closely related to *Avenantia* and it possesses primitive tapinocephalid characters, but is more derived than *Tapinocaninus*, the most primitive tapinocephalid dinocephalian known. NHMB1556 is distinguished from other tapinocephalines by having a groove on the squamosal below its dorsal contact with the parietal, a low squamosal-parietal suture on the posterior border of the temporal fenestra, a vomer which extends posteroventrally and forms the anterior margin of the interpterygoidal vacuity and basisphenoid, which is semi-circular anteroventrally.

**TO MY CHILDREN**

## ACKNOWLEDGEMENTS

My most sincere thanks go to my supervisors Prof. B.S. Rubidge and Dr. M.A. Raath for assisting me in selecting the appropriate project for study under the prevailing circumstances and for directing me throughout the entire program of study. I am very grateful to my supervisors for their constructive comments, encouragement, and moral and material support. Their scholarship, academic reputation, and love of the subject were constant sources of inspiration to me.

I am very grateful to the South Africa Museum (SAM) for allowing me unlimited access to their collection. Great thanks go to the SAM staff in the Division of Earth Sciences, particularly Dr R.M.H. Smith and S. Kaal, for assisting me in the collection and for their hospitality during my two visits.

The assistance and encouragement received from the staff at the Bernard Price Institute for Palaeontological Research (BPI) are greatly appreciated. Dr. S.P. Modesto and Dr. R. J. Damiani were very helpful with the phylogenetic analysis and guidance in preparation of descriptive figures.

I am indebted to the Board Members and the Directorate of National Museums and Monuments of Zimbabwe (NMMZ) for granting me study leave enabling me to visit the

BPI and SAM. I would like also to thank NMMZ staff Messrs L. Ngwenya, L. Zondo and M. Zondo for their assistance during the preparation of the specimen.

I am also thankful to Mr T. Gumbi, a former employee of the Wankie Colliery Company, for bringing to the attention of Natural History Museum, Bulawayo (NHMB), the discovery of the Hwange beds that bear the therapsid fossils. The Wankie Colliery Company made it possible for us to carry out the research by granting us unconditional access to the fossil sites as well as their kind co-operation and hospitality during our visits. All efforts by several geologists and palaeontologists, including Dr. J. Lepper, B. Barber, Prof. G. Bond, Dr M.A. Raath, Prof. B.S. Rubidge, to unravel the geology and palaeontology of the Madumabisa Mudstones at Hwange, are greatly appreciated.

NMMZ, John Wakeford Scholarship Trust and myself jointly sponsored the study program. I am therefore indebted to the two funding institutions for without their financial support I could not have been able to complete the study program. I would like also to thank Prof. Bruce S. Rubidge for securing funds for my accommodation during my last visit at BPI and to attend the Palaeontological Society of Southern Africa Conference, Pretoria.

Last, but not least, I would like to thank my family for graciously releasing me from most of my daily responsibilities in my quest for a higher education. Their tolerance and

support are greatly appreciated. I am dedicating my thesis to my two children, Tariro Clarity and Taridzai Brian.

## TABLE OF CONTENTS

DECLARATION		ii
ABSTRACT		iii
ACKNOWLEDGEMENTS		v
LIST OF TABLES		x
LIST OF FIGURES		x
LIST OF APPENDIXES		xi
ABBREVIATIONS USED IN THE FIGURES		xii
<b>1</b>	<b>INTRODUCTION</b>	<b>1</b>
	1.1 Therapsid origins	1
	1.2 Historical review of the dinocephalian taxonomy	4
<b>2</b>	<b>GEOLOGICAL BACKGROUND TO THE STUDY AREA</b>	<b>18</b>
	2.1 Dwyka	20
	2.2 Ecca	20
	2.3 Madumabisa Mudstone	22



<b>3</b>	<b>MATERIALS AND METHODS</b>	26
	3.1 Materials	26
	3.2 Methods	28
	3.2.1 Specimen preparation	28
	3.2.2 Phylogenetic analysis	30
<b>4</b>	<b>DESCRIPTION OF SKULL</b>	33
	4.1 Skull roof	34
	4.2 Occiput	42
	4.3 Palate	46
	4.4 Braincase	50
<b>5</b>	<b>DISCUSSION</b>	52
<b>6</b>	<b>PHYLOGENETIC ANALYSIS</b>	58
<b>7</b>	<b>CONCLUSION</b>	62
<b>8</b>	<b>REFERENCES</b>	64

**TABLES**

Table 1.	Characteristic features of dinocephalian families	8
Table 2.	Characters of the subfamilies of the Tapinocephalidae	9
Table 3	Classification of the Dinocephalia	10
Table 4.	Characters of the tribes of the Tapinocephalinae	13

**ILLUSTRATIONS**

Figure 1.	Cladogram of the families of the Dinocephalia	11
Figure 2.	Cladogram of the main groups of the Dinocephalia	12
Figure 3.	Cladograms of the Dinocephalia with the inclusion of the Stracocephalidae and illustrating Anteosauridae as the most basal group	15
Figure 4.	Locality map of the study area	19
Figure 5.	Stratigraphic section showing the horizon of dinocephalian fossils	21

Figure 6.	Some of the better preserved dinocephalian fossils from Hwange	29
Figure 7.	Dorsal view of NHMB1556	35
Figure 8.	Lateral view of NHMB1556	37
Figure 9.	Occipital view of NHMB1556	43
Figure 10.	Ventral view of NHMB1556	47
Figure 11.	Cladogram illustrating interrelationships of dinocephalian genera	60

## APPENDIXES

Appendix 1. List of characters used in the cladistic analysis

Appendix 2. Character matrix

**ABBREVIATIONS USED IN THE TEXT FIGURES**

boc	basioccipital
bs	basisphenoid
eam	external auditory meatus
ect	ectopterygoid
f	frontal
fjug	foramen jugularis
fmag	foramen magnum
fo	fenestra ovalis
iptv	interpterygoidal vacuity
j	jugal
lpt	lateral process of pterygoid
mx	maxilla
n	nasal
op	opisthotic
p	parietal
pal	palatine
pf	pineal foramen

pm	premaxilla
po	postorbital
pof	postfrontal
pp	postparietal
prf	prefrontal
prt	prootic
ptf	posttemporal fenestra
q	quadrate
qj	quadratojugal
sq	squamosal
t	tabular
vo	vomer

## CHAPTER 1: INTRODUCTION

### 1.1 THERAPSID ORIGINS

The Dinocephalia, together with the clades Biarmosuchia, Eotitanosuchia, Anomodontia (including Dicynodontia), Gorgonopsia, Therocephalia and Cynodontia constitute the Therapsida (Hopson 1991; Hopson and Barghusen 1986; Hotton 1991; Kemp 1988). Therapsids are considered to have arisen from sphenacodont “pelycosaurs” during the early Late Permian and to be the lineage leading to mammals (Hopson 1967, 1991; Hopson and Barghusen 1986; Kemp 1982; Kermack and Kermack 1984; Rowe 1988; Sidor and Hopson 1998). A great deal of research on therapsid origin, diversification and biogeography has been undertaken and their remains have been found on every continent (Anderson and Cruickshank 1978; Colbert 1986; Hopson 1991; Hopson and Barghusen 1986; Kemp 1982, 1988; King 1988; Olson 1986; Parrish, Parrish and Ziegler 1986; Romer 1970; Sigogneau-Russell 1989).

Biarmosuchids and eotitanosuchids are considered to be the most basal therapsids (Hopson 1991; Hopson and Barghusen 1986; Kemp 1988). Most of the advanced therapsids have a wide distribution and have a well-preserved fossil record. In contrast, the basal therapsids have a limited distribution and a poor fossil record and hence their evolutionary history is vague as compared with their descendants.

The earliest therapsid faunas include biarmosuchids, eotitanosuchids, dinocephalians, non-

dicynodont anomodonts, gorgonopsians and therocephalians, and are known only from South Africa (Boonstra 1963a, 1963b, 1969; Brinkman 1981; King 1988; Modesto, Rubidge and Welman 1999; Modesto and Rubidge 2000; Rubidge, Kitching and van den Heever 1983; Rubidge and Hopson 1990, 1996; Rubidge 1991, 1994), Russia (Ivakhnenko 1994, 1996; Olson 1962; Sigogneau and Chudinov 1972) China (Cheng and Li 1997; Li, Rubidge and Cheng 1996), Zimbabwe (Bond 1973; Boonstra 1946) and Brazil (Langer 1998). Olson (1962, 1986) gave a detailed account of the Late Permian terrestrial vertebrates of the San Angelo Formation of the United States of America in which he erected the therapsid infraorders Eotheriodontia and Eutheriodontia of the suborder Theriodontia, Eodinocephalia and Eudinocephalia of the suborder Dinocephalia, and Venjukovioidea of the suborder Anomodontia. Parrish *et al.* (1986) recognised Olson's early therapsids from North America but because of poor preservation he doubted their taxonomic affinities. Recent examination by Sidor and Hopson (1995) has confirmed their "pelycosaurian" status.

Dinocephalians, anomodonts, gorgonopsians and therocephalians have been found in the Lower Beaufort Group of South Africa (Boonstra 1963a, 1963b, 1969, 1971; Brinkman 1981; King 1988; Kitching 1977; Modesto *et al.* 1999; Rubidge 1987, 1988, 1991, 1994 1995; Rubidge and Hopson 1990, 1996; Rubidge *et al.* 1983; Smith and Keyser 1995). In addition to dinocephalians, anomodonts, gorgonopsians and therocephalians, eotitanosuchids have been recognised in the Russian Ocher (Zone I) and Ishevo (Zone II) deposits (Anderson and Cruickshank 1978; Chudinov 1965; Hopson and Barghusen 1986; King 1988; Olson 1962; Parrish *et al.* 1986; Sigogneau and Chudinov 1972). Biarmosuchids and

dinocephalians have been found in China, and only the latter have been recognised in Zimbabwe and Brazil (Bond 1973; Boonstra 1946; Cheng and Li 1997, Langer 1998; Lepper, Raath and Rubidge 2000; Li *et al.* 1996; Macgregor 1946). In each of these countries (South Africa, Russia, China, Zimbabwe and Brazil), dinocephalians are an important element of early therapsid faunas. They dominated their contemporaries in body size and taxonomic diversity (Boonstra 1963a, b).

Dinocephalians and non-dicynodont anomodonts (venjukovioids and “dromasaurs”) are important taxa in tracing the evolutionary history of early therapsids because they have a restricted stratigraphic range, occurring only in the Kazanian and Tatarian deposits of Zone I and Zone II of Russia, and the *Eodiocynodon* and *Tapinocephalus* Assemblage Zones of South Africa, thus making them more helpful taxa for global correlation (Li *et al.* 1996). Currently the phylogeny of the Gorgonopsia and Therocephalia is not well established and these clades cannot therefore be relied upon for global correlations (van den Heever 1994; Modesto *et al.* 1999). The therapsid fauna from the Zone I of Russia was at one stage considered to be more primitive than the oldest therapsid fauna from the *Tapinocephalus* Assemblage Zone of South Africa (Boonstra 1969; Chudinov 1965; Rubidge 1993, 1995b; Sigogneau and Chudinov 1972; van den Heever and Grine 1981). The “dromasaurs” from Southern Africa and venjukovioids from Eastern Europe were previously not regarded as monophyletic and the latter group was considered more basal (Brinkman 1981, Hopson and Barghusen 1986; King 1994). Hopson and Rubidge (1990, 1996) recognised that non-dicynodont anomodonts belonged to the same clade and said that the most basal form of this



clade, *Patranomodon*, came from South Africa. Later Modesto *et al.* (1999) and Modesto and Rubidge (2000) described an even more basal form (*Anomocephalus*) from South Africa. Now with *Patranomodon* and *Anomocephalus*, the two most basal anomodonts known from South Africa, it has been proposed that anomodonts originated in Gondwana (Modesto *et al.* 1999). Southern Africa has also produced the most basal dinocephalian forms, *Australosyodon* and *Tapinocaninus*, as compared with the Russia forms *Ulemosarus* and *Syodon* (Rubidge 1991, 1993, 1994), suggesting a southern African origin for this group of therapsids as well.

## 1.2 HISTORICAL REVIEW OF DINOCEPHALIAN TAXONOMY

Dinocephalians are an important component of the earliest therapsid faunas of the Ocher and Ishevo complexes in Russia (Chudinov 1965, 1968; King 1988; Olson 1962). They also form a large component of the therapsid faunas of the *Eodiocynodon* and *Tapinocephalus* Assemblage Zones, the lowermost and oldest biozones of the Beaufort Group in South Africa (Boonstra 1963a, 1963b, 1968, 1969; Haughton and Brink 1954, Keyser and Smith 1978; King 1988; Kitching 1977; Looock Brynard, Heard, Kitching and Rubidge 1994; Rubidge 1987, 1988, 1991, 1994, 1995a; Smith and Keyser 1995). The Xidangu Formation at Yumen, China (Cheng and Li 1997; Li *et al.* 1996), Madumabisa Mudstone Formation in the Middle Zambezi Karoo Basin, Zimbabwe (Bond 1973; Boonstra 1946; Lepper *et al.* 2000; Macgregor 1946), and Rio do Rasto Formation, Parana Basin, Brazil (Langer 1998), have also yielded dinocephalians. Although dinocephalians were among the earliest therapsids to

be collected and studied, there are still numerous uncertainties in the literature with regard to their taxonomy (King 1988; Rubidge pers. comm.).

Boonstra (1969) gave a detailed account on the earliest collection, acquisition and taxonomic classification of dinocephalians from the Karoo in the 17<sup>th</sup> century by various people including C.H. Crisbrook, F. De Klerk, A.G. Bain, R. Broom, R. Owen, H.G. Seeley, L.D. Boonstra, H.W. Oakley and others. Among the earliest dinocephalian material from the *Tapinocephalus* Assemblage Zone, Owen (1879) and Seeley (1892) figured *Tapinocephalus atherstonei*, *Titanosuchus ferox* and *Delphinognathus conocephalus*. Seeley (1888, 1889) discussed and figured the Russian forms *Deuterosaurus* and *Rhopalodon*, and placed them into the suborder Deuterosauria. The suborder Dinocephalia was eventually erected in 1894 by Seeley for the genera *Delphinognathus* and *Tapinocephalus*, and was considered to belong to the order Anomodontia.

Broom (1903) placed *Titanosuchus* into the family Titanosuchidae of the order Therocephalia, excluding *Delphinognathus* and *Tapinocephalus* arguing that they were imperfectly known. *Deuterosaurus* and *Rhopalodon* of the family Deuterosauridae were also included by Broom (1903) in the order Therocephalia.

Broom (1905, 1910, 1911) later placed *Delphinognathus*, *Tapinocephalus*, *Titanosuchus*, *Scapanodon*, *Pelosuchus*, *Archaeosuchus* and *Gorgonops* into the Dinocephalia. The Russian forms *Deuterosaurus* and *Rhopalodon* were also considered likely to belong to the Dinocephalia,

although they were imperfectly known. They were later allied to dinocephalian therapsids by Watson (1914).

In 1923 Broom divided the Dinocephalia into two suborders, Tapinocephalia and Titanosuchia. In South Africa the family Tapinocephalidae was later further subdivided by Gregory (1926) into the subfamilies Moschopinae (including the allied genera *Delphinognathus*, *Moschops*, *Moschognathus*, *Taurops*, *Pnigalin* and *Lamiasaurus*), and Tapinocephalinae (including *Tapinocephalus*, *Mormosaurus* and *Struthiocephalus*).

Haughton (1929) established the name *Styracocephalus platyrhynchus* and placed it within the new suborder Styracocephalia. According to Haughton (1929), *Styracocephalus* possessed both gorgonopsian and dinocephalian characters, and also retained primitive ancestral features. Broom (1932) considered *Styracocephalus* to have affinities with the Gorgonopsia and referred it to the Burnetiamorpha, a classification adopted by Romer in 1956.

Boonstra (1936a) subdivided the suborder Tapinocephalia, which then consisted of thirteen genera into the following families:

Tapinocephalidae - *Tapinocephalus*, *Taurops*, *Keratocephalus*

Moschopidae - *Delphinognathus*, *Moschops*, *Criocephalus*, *Moschognathus*, *Pnigalin*,  
 ?*Lamiasaurus*

Mormosauridae - *Mormosaurus*, *Taurocephalus*, *Struthiocephalus*

Moschosauridae - *Moschosaurus*

Boonstra (1936b) reiterated that Titanosuchia and Tapinocephalia were two suborders of the Dinocephalia, which diverged from each other at a stage represented more or less by the two forms *Moschosaurus* (tapinocephalid) and *Rhopalodon* (titanosuchid). Taxonomic identification keys were provided by Boonstra (1953b) for the Dinocephalia, Titanosuchia and Tapinocephalia.

Romer (1956) and Watson and Romer (1956) classified dinocephalians into two suborders, Theriodontia and Anomodontia, with the corresponding infraorders, Titanosuchia and Dinocephalia. All the carnivorous forms were placed into infraorder Titanosuchia, which consisted of three families: Brithopodidae, Anteosauridae and Jonkeriidae. The infraorder Dinocephalia was restricted to herbivorous forms only and was divided into the families Deuterosauridae and Tapinocephalidae. The characters used by Romer and Watson to define Titanosuchia and Dinocephalia were either primitive therapsid attributes, or features found in both forms (carnivorous or herbivorous), or not expressed consistently throughout in each group (King 1988).

The carnivorous and herbivorous forms were later combined into the infraorder Dinocephalia of the suborder Anomodontia by Boonstra in 1963, and in South Africa the families Anteosauridae, Titanosuchidae, Styracocephalidae and Tapinocephalidae were recognised. In addition to the South African families, two families, Brithopodidae and Estemmenosuchidae, were recognised in Russia (Boonstra 1963a). In South Africa the family Tapinocephalidae was further subdivided into

subfamilies Moschosaurinae, Riebeeckosaurinae, Moschopinae, Struthiocephalinae and Tapinocephalinae (Boonstra 1963b).

Boonstra (1969) revised the classification of the dinocephalians from South Africa and recognised four families: Anteosauridae, Titanosuchidae, Tapinocephalidae and Styraocephalidae (Table 1).

**Table 1.** Characteristic features of dinocephalian families (After Boonstra 1969).

FAMILY	CHARACTERS
Anteosauridae	-Primitive carnivores with long intermeshing incisors
Titanosuchidae	-Primitive herbivores with a canine tooth. -Very strong incisor teeth with piercing talon and crushing heel. -Long series of postcanine teeth with spatulate crowns -Very little pachyostosis
Tapinocephalidae	-Advanced herbivores without a canine tooth -All teeth have a talon and heel at maturity -Upper and lower teeth of the whole battery intermesh. -Moderate to very great pachyostosis
Styraocephalidae	-Advanced herbivores with moderate canine tooth -Prominent posteriorly directed tabular bosses.

Moschosaurinae was no longer considered a subfamily of the Tapinocephalidae after *Moschosaurus* and *Struthiocephalus* were synonymised. Only four subfamilies of the Tapinocephalidae were considered valid, namely: Struthiocephalinae, Moschopinae, Tapinocephalinae and Riebeeckosaurinae (Table 2).

**Table 2.** Characteristic features of the Tapinocephalidae subfamilies (After Boonstra 1969)

<b>FAMILY</b>	<b>SUBFAMILY</b>	<b>CHARACTERS</b>
Tapinocephalidae	Struthiocephalinae	-Long fairly strong snout -Moderate pachyostosis
	Moschopinae	-Medium body size -Short snout running onto frontal in an even curve -Moderate to very great pachyostosis
	Riebeeckosaurinae	-Very long and slender snout -Narrow intertemporal region -Moderate pachyostosis
	Tapinocephalinae	-Large and massive body proportions -Moderate to short and weak snout -Either a prominent naso-frontal boss or swollen frontals -Great to very great pachyostosis

In his morphological series I and II, Boonstra (1971) considered brithopodids to be the most primitive dinocephalians, and that they gave rise to anteosaurids and titanosuchids. No descendants of anteosaurids were identified but titanosuchids were considered to have been ancestral to styracocephalids, tapinocephalids and estemmenosuchids.

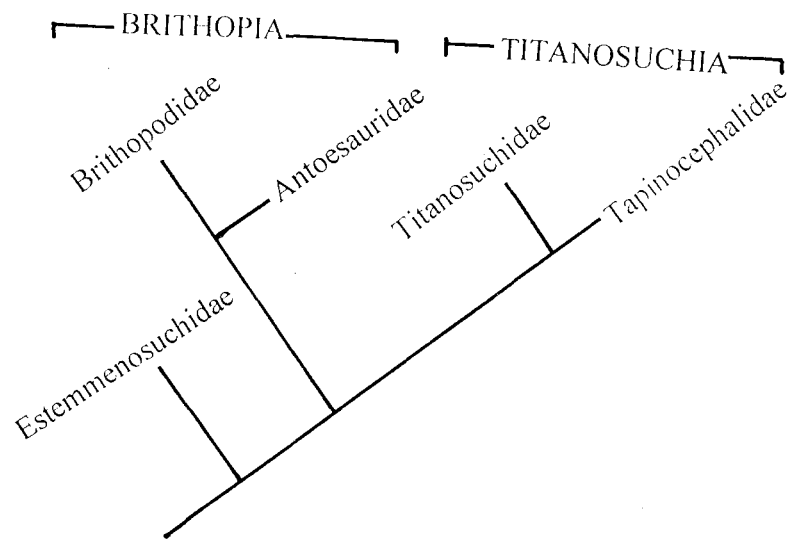
Boonstra (1972) revised the classification of the Dinocephalia, where he recognised two suborders and five families. The Dinocephalia was considered to consist of the suborders Brithopia and Titanosuchia, with the families Brithopodidae, Anteosauridae, Titanosuchidae, Tapinocephalidae, Styracocephalidae and Estemmenosuchidae (Table 3).

**Table 3.** Classification of the Dinocephalia (After Boonstra 1972).

ORDER	SUBORDER	FAMILY
Dinocephalia	Brithopia	Brithopodidae Anteosauridae
	Titanosuchia	Titanosuchidae Tapinocephalidae Styracocephalidae Estemmenosuchidae

Although Boonstra provided a framework for the systematics of the Dinocephalia, it is argued that his classification lacked cladistic analysis and that many of the characters he used to define the taxa are primitive therapsid or synapsid features. Kemp in 1982 (Figure 1) produced the first cladogram illustrating phylogenetic relationships of the Dinocephalia, but it failed to provide specific characters relating to sister groups. Kemp adopted the classification scheme of Boonstra (1972), but removed the Estemmenosuchidae from the Titanosuchia and regarded it as the most primitive family of the Dinocephalia.

In 1986 Hopson and Barghusen carried out the first full-scale cladistic analysis of the Therapsida, and three monophyletic groups were recognised: Dinocephalia, Anomodontia and Theriodontia. The Dinocephalia and Anomodontia were separated and the former was divided into two monophyletic subgroups, Anteosauria and Tapinocephalia, corresponding to the Brithopia and Titanosuchia respectively of Boonstra (1972). Because the affinities of *Styracocephalus* were uncertain, Styracocephalidae was considered to be an invalid family. The classification scheme of Hopson and Barghusen differed from that of Kemp (1982) on the position of the Estemmenosuchidae and Anteosauridae. Hopson and Barghusen



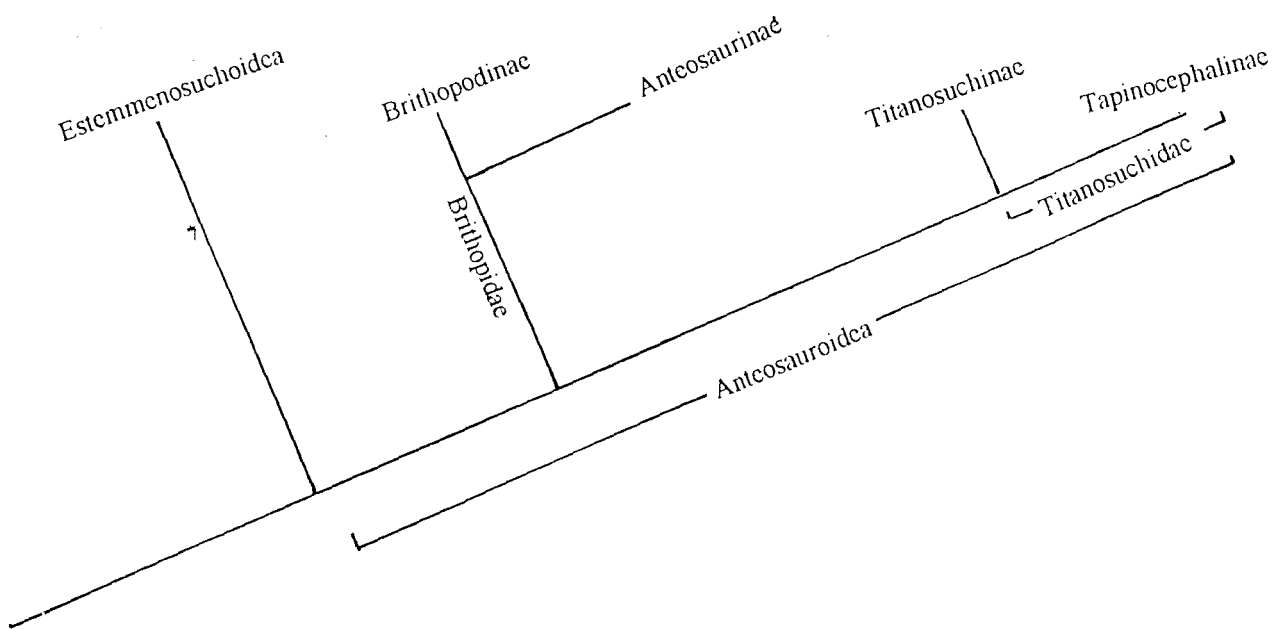
**Figure 1.** Cladogram of the families of the Dinocephalia (From Kemp 1982).

considered anteosaurids to be the most primitive whereas Kemp (1982) considered estemmenosuchids to be the plesiomorphic group.

King (1988) lamented on the lack of cladistic analysis in previous classification systems of the Dinocephalia, but she did not comment on the cladistic classification of Hopson and Barghusen (1986). As was suggested by Watson (1948), Romer (1956) and Boonstra (1969), the Dinocephalia-Dicynodontia relationship was resurrected as Anomodontia. Two superfamilies of Dinocephalia (Estemmenosuchidea and Anteosauridea) comprising of three families (Estemmenosuchidae, Brithopodidae and Titanosuchidae) were created. Because of poor preservation, *Styracocephalus* was considered to be *incertae sedis*. King (1988) considered the Brithopodidae to have the subfamilies Brithopodinae and Anteosaurinae,



whereas Titanosuchidae was split into Titanosuchinae and Tapinocephalinae (Figure 2). Tapinocephalinae was further subdivided into the tribes Struthiocephalini, Tapinocephalini and Riebeckosaurini. These corresponded with the subfamilies of Tapinocephalidae of Boonstra (1969; Table 4).



**Figure 2.** Cladogram of the main groups of the Dinocephalia (From King 1988).

King combined the subfamilies Moschopinae and Tapinocephalinae of Boonstra (1969) into the single tribe Tapinocephalini on the grounds that “pachyostosis as a character is variable within the subfamily and not a foolproof guide to relationship” (King 1988:10). In King’s analysis the genus *Struthionops* was transferred from the Struthiocephalini into Tapinocephalini.

**Table 4.** Characters of the tribes of the Tapinocephalinae (After King 1988).

TRIBE	CHARACTERS	GENERA
Struthiocephalini	-Long and fairly strong snout -Moderate pachyostosis	<i>Struthiocephalus</i> <i>Struthiocephaloides</i> <i>Taurocephalus</i>
Riebeeckosaurini	-Very long and slender snout -Narrow intertemporal region which forms a sagittal crest	<i>Riebeeckosaurus</i>
Tapinocephalini	-Medium to large body size -Moderate to short and weak snout -Naso-frontal boss or swollen frontals in some forms -Great to moderate pachyostosis	<i>Delphinognathus</i> <i>Avenantia</i> <i>Moschops</i> <i>Criocephalus</i> <i>Struthionops</i> <i>Phocosaurus</i> <i>Mormosaurus</i> <i>Keratocephalus</i> <i>Tapinocephalus</i>

Hopson and Barghusen (1986) and Hopson (1991) questioned the relationship between dinocephalians and primitive dicynodonts. Anomodontia was considered a monophyletic group consisting of Dinocephalia and Dicynodontia (Boonstra 1969; Kemp 1988; King 1988; Romer 1967; Watson 1948) on the basis of:

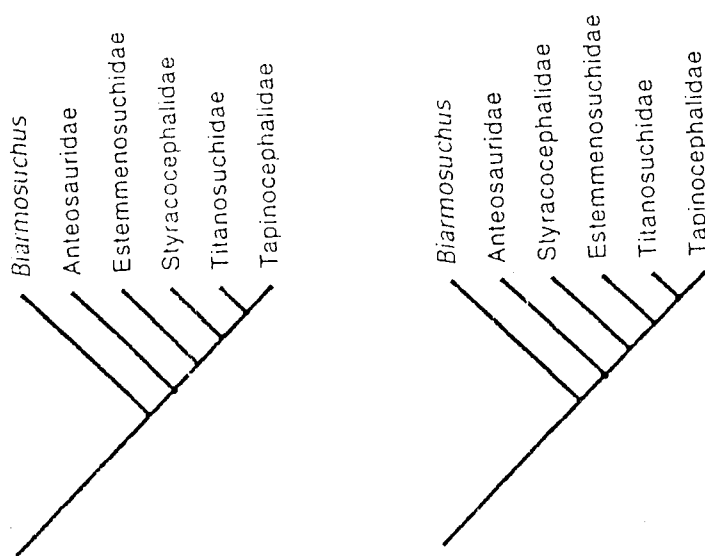
1. Loss of the coronoid bones.
2. Non-terminal nostrils and long posterior spur of premaxilla
3. Grooved or troughed palatal exposure of the vomers.

#### 4. Reduction or loss of the internal trochanter of the femur.

However coronoid bones have been reported in some dinocephalians and primitive dicynodonts and therefore character 1 is an invalid synapomorphy linking dinocephalians and dicynodonts (Boonstra 1962; Hopson and Barghusen 1986; Hopson 1991). Characters 2 and 3 were shown to be invalid since nostrils are terminal in *Estemmenosuchus* while the long spur of the premaxilla and a vomer bearing a ventral groove are primitive therapsid features (Hopson 1991). Hopson (1991) also pointed out that character 4 was convergent. The Dinocephalia and Anomodontia (Dicynodontia) therefore should be considered as separate monophyletic groups (Hopson and Barghusen 1986; Hopson 1991).

In 1997 Rubidge and van den Heever resurrected the Styracocephalidae, which was considered by Hopson and Barghusen (1986) and King (1988) as *incertae sedis*. Anteosauridae was again considered to be the basal dinocephalian group whereas Styracocephalidae was placed as the sister group of the Titanosuchidae and Tapinocephalidae (Figure 3). Kemp (1982), King (1988), Hopson and Barghusen (1986) and Rubidge and van den Heever (1997) differed on the phylogenetic position of the Estemmenosuchidae and Anteosauridae, since the first two authors considered the former family to be the most primitive while the rest proposed the latter to be the basal family. Rubidge (1991) and Li *et al.* (1996) noted the difference in the proposed positions of two families but did not discuss the issue. The phylogenetic position of the two families has no bearing on this study and therefore will not be discussed further. For this study the Anteosauridae and Tapinocephalidae will be considered as the most basal and derived dinocephalian families

respectively.



**Figure 3.** Cladograms of the Dinocephalia with the inclusion of Styraocephalidae and illustrating Anteosauridae as the most basal group (From Rubidge and van den Heever 1997).

Anteosaurid dinocephalians are found in Russia, South Africa and China. Although anteosaurids have recently been recognised in Zimbabwe from fragmentary material (Lepper *et al.* 2000), no particular anteosaurid genus has yet been described from that country. The Russian anteosaurid dinocephalians include *Archaeosyodon*, *Chthamaloporus*, *Brithopus*, *Notosyodon*, *Syodon*, *Titanophoneus*, *Doliosauriscus*, *Deuterosaurus* and *Admetophoneus* (King 1988; Olson 1962; Tschudinov 1968), and in South Africa, the Anteosauridae consists

of three genera: *Australosyodon*, *Paranteosaurus* and *Anteosaurus* (Boonstra 1954a, 1954b, 1954c, 1963a, 1963b, 1969; Haughton and Brink 1954; van den Heever and Grine 1981; King 1988; Rubidge 1994, 1995a; Smith and Keyser 1995). Two anteosaurid genera, *Sinophoneus* and *Stenocybus*, have been described from China (Cheng and Li 1997; Li *et al.* 1996).

Estemmenosuchids are found only in Russia and the four genera (*Estemmenosuchus*, *Molybodopygus*, *Anoplosuchus* and *Zopherosuchus*) have been recognised (Chudinov 1965; Hopson and Barghusen 1986; King 1988; Olson 1962).

Styracocephalid and titanosuchid dinocephalians have been reported from South Africa only. The former group is represented by single genus, *Styracocephalus* (Boonstra 1934, 1963b, 1969; Broom 1932; Haughton 1929; Haughton and Brink 1954; Rubidge and van den Heever 1997), while the latter consists of *Jonkeria* and *Titanosuchus* (Boonstra 1936b, 1953a, 1962, 1963a, 1963b, 1969; Broom 1932, Haughton and Brink 1954; van den Heever and Grine 1981; King 1988).

Tapinocephalid dinocephalians are known from Russia, South Africa and Zimbabwe. *Ulemosaurus* is the only Russian tapinocephalid (King 1988), and all the other known tapinocephalids, apart from the Zimbabwean species of *Criocephalus* (Bond 1973; Boonstra 1968, 1969; King 1988), are known only from South Africa. However the taxonomy of the Tapinocephalidae requires revision because many of the smaller and less pachyostosed forms

may, in fact, be juveniles (Boonstra 1969; King 1988; Rubidge pers. comm.).

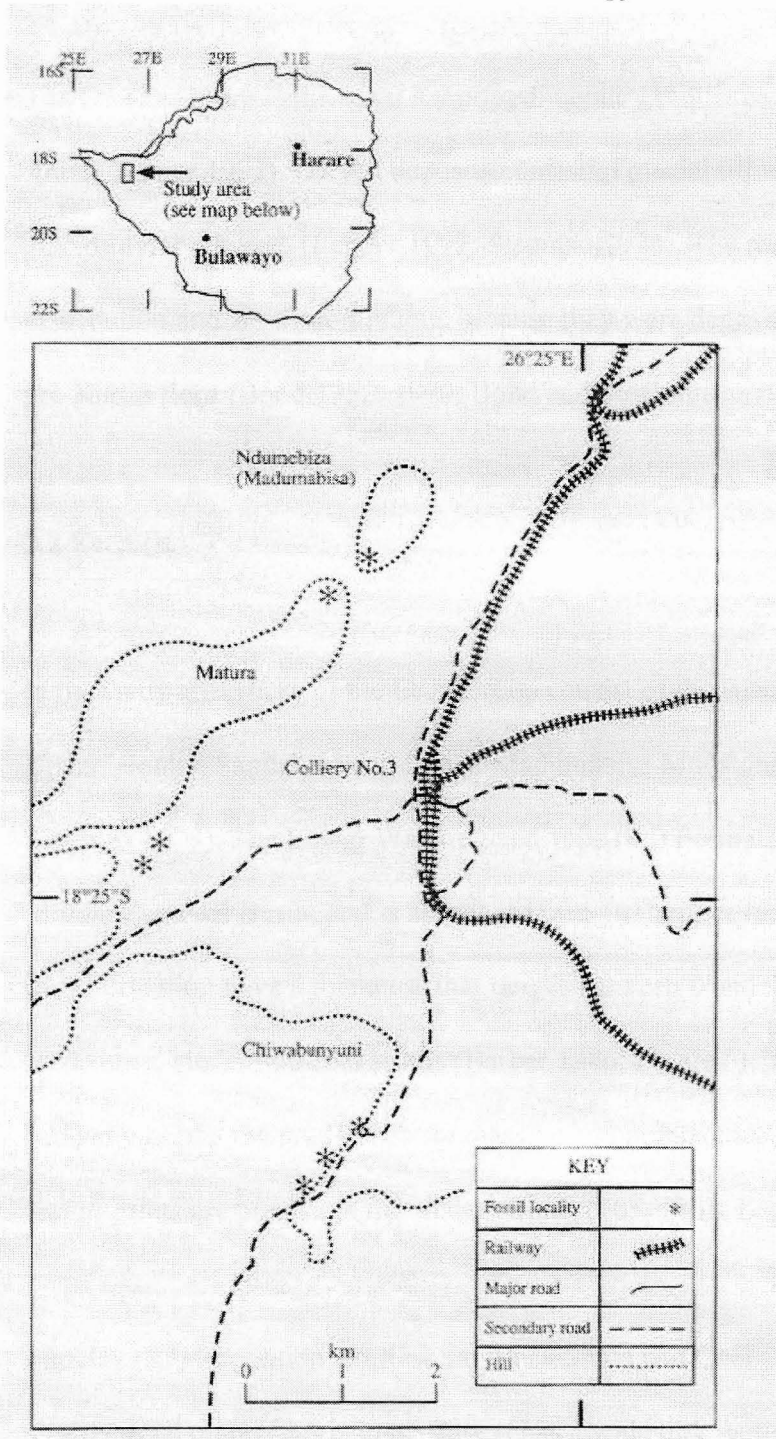
A relatively diverse dinocephalian fauna has recently been recognised at Hwange, Zimbabwe, and this includes anteosaurids and tapinocephalids (Lepper *et al.* 2000). So far *Criocephalus* is the only named and described tapinocephalid genus and comes from Gunyanka's Kraal, Zimbabwe (Bond 1973; Boonstra 1946, 1968, 1969). The holotype of *Criocephalus* is missing and its description is limited to a few sentences and scant illustrations of the braincase (Boonstra 1968; King 1988).

As a result of recent fieldwork, new tapinocephalid material from Zimbabwe is available and warrants description. The new dinocephalian material is of great importance as it may ultimately lead to biostratigraphic subdivision of the lithologically homogeneous Madumabisa Mudstone Formation and constrain the ages of the dinocephalian-bearing units. In addition, the dinocephalian fossils from Zimbabwe will contribute to greater understanding of the biogeographic distribution of the earliest therapsid faunas.

## CHAPTER 2: GEOLOGICAL BACKGROUND TO THE STUDY AREA

The study area is located in the northwest of Zimbabwe (Figure 4), and lies in the Middle Zambezi Karoo Basin. In Zimbabwe, Karoo sediments were deposited in the Zambezi and Sabi-Limpopo basins which were located northwest and southeast of a major watershed which is believed to have been parallel to but 80 km southeast of the present watershed (Stagman 1978). The Zambezi Karoo Basin is divided into the Middle Zambezi Basin stretching from Victoria Falls to Lake Kariba, and the Lower Zambezi Basin extending from Lake Kariba into Mozambique. Correlations between sediments of the two major basins and within each basin, are difficult because each basin had several depocentres which differ in lithology and succession units. A prominent erosional contact, however, divides the basins into the Upper and Lower Karoo (Lepper 1992; Stagman 1978).

Lower Karoo sediments and Escarpment Grit, a basal member of the Upper Karoo, are preserved in the study area. The rocks of the Lower Karoo sediments present are the Dwyka, Eccca and Madumabisa Mudstone (Lepper *et al.* 2000). The basal Dwyka glacial beds are overlain by the Eccca, which in turn underlies the Madumabisa Mudstone. An unconformity exists between the Madumabisa Mudstone and the Escarpment Grit. The latter unit is not completely preserved as the basal section is present capping the Madumabisa Mudstone on hilltops.



**Figure 4.** Locality map of study area showing fossil sites (From Lepper *et al.* 2000).



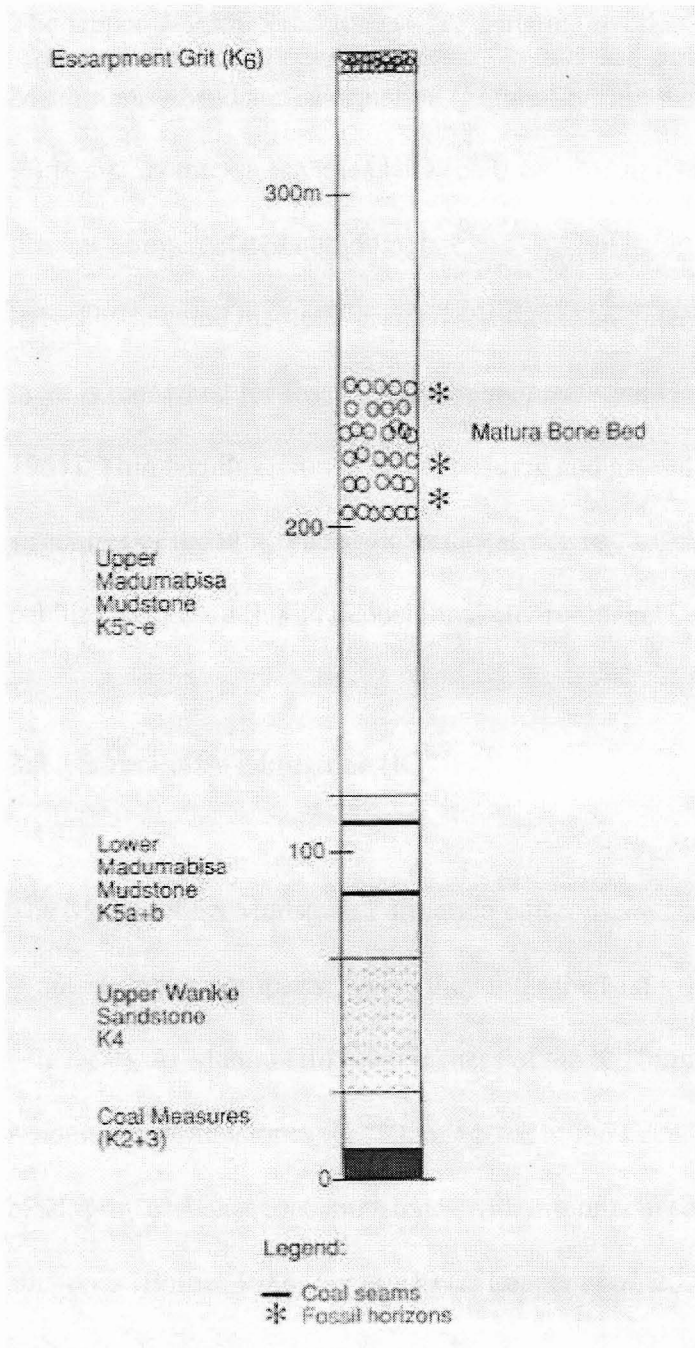
## 2.1 Dwyka (K<sup>0</sup>)

The Dwyka Group is the basal Karoo sedimentary sequence and lies uncoformably on Archaean strata (Lepper 1992). Dwyka deposits consist of glacial tillites, glaciolacustrine varvites and glaciofluvial outwash (Lepper 1992; Stagman 1978). The rocks of this Group have a patchy distribution and are discontinuous because they were deposited in valleys and depressions on the pre-Karoo floor (Bond 1952, 1970; Bond and Stockmayer 1967; Lepper 1992).

## 2.2 Eccca (K<sup>1-4</sup>)

In the study area rocks of the Eccca Group consist of the Black Shale and Coal Group, Fireclay, Upper Wankie Sandstone and Lower Madumabisa Mudstone (Lepper 1992; Lepper *et al.* 2000; Stagman 1978). The Lower Wankie Sandstone (K<sup>1</sup>) Formation is widely distributed in the Middle Zambezi Basin, and is absent at Hwange (Lepper 1992). Black Shale and Coal Group (K<sup>2</sup>) Formation have a thickness that ranges between 0 and 90 m and consists of carbonaceous mudstones, shales and coal seams (Barber 1986; Figure 5). The shales are laminated to thick bedded whereas the mudstones are massive and homogeneous. *Glossopteris* and *Gangamopteris* leaf imprints are present in the shales (Bond 1965, 1968, Lacey 1961).

Fireclay (K<sup>3</sup>) Formation overlies the Black Shale and Coal Group Formation, and it is regarded as a regional marker horizon because it has a wide distribution throughout the basin (Lepper 1992). It is silica and aluminium rich and is considered to be a lacustrine deposit or kaolinised ash bed resulting from acid volcanism (Lepper 1992).



**Figure 5.** Stratigraphic section at the Matura Hill, showing the horizon of dinocephalian fossils (From Lepper *et al.* 2000).

The Upper Wankie Sandstone (K<sup>4</sup>) Formation overlies the Fireclay and in turn underlies the Madumabisa Mudstone Formation (Figure 5). This succession is predominantly coarse-grained to gritty and its thickness varies between 0 and 100 m (Barber 1986; Lepper 1992). Pebbles are also present as intercalated conglomerate beds or lenses, as well as matrix-supported individuals. Thin lenses of fine and medium-grained sediments are interbedded in the succession, and the former layer is renowned for fossils of *Gangamopteris* and *Glossopteris* (Bond 1973; Lacey 1959, 1961). Thin bedding, trough cross-bedding and graded bedding are the predominant sedimentary structures of the unit. The sedimentary structures, together with the coarse-grained sediments and pebbles, suggest a fluvial depositional environment (Lepper 1992).

### 2.3 Madumabisa Mudstone (K<sup>5a-c</sup>)

The Madumabisa Mudstone Formation outcrops are best preserved in the western areas of the Wankie Colliery property, where they form the Matura and Madumabisa (Ndumebiza) Hills (Figure 4). At Matura Hill the thickness of the K<sup>5a-c</sup> unit is 270.82 m (Barber 1986). The Lower Madumabisa Mudstones (K<sup>5a+b</sup>), relegated to the Ecça Group, is 52.14 m thick and consists of black-grey carbonaceous mudstones with minor coal seams, dark black-grey mudstones and siltstones (Barber 1986; Lepper 1992; Lepper *et al.* 2000; Figure 5). The formation is thin bedded to massive, and the mudstones are massive and homogeneous, being characterised by conchoidal, spherical and blocky to shardy disintegration (Lepper 1992). The sediments of this succession were deposited in a quiet lacustrine environment (Lepper 1992).

A gradational contact exists between the Upper and Lower Madumabisa Mudstone, and is considered to be at a point of last occurrence of the dark-grey carbonaceous mudstones and the first appearance of limestones. Beside colour variation and presence or absence of calcareous nodules, the K<sup>5c</sup>, K<sup>5d</sup> and K<sup>5e</sup> units of the Upper Madumabisa Mudstones are indistinguishable. The mudstones in all units are massive and homogeneous without any internal structure, and are considered to have been deposited in a lacustrine environment (Lepper 1992).

The Upper Madumabisa Mudstone Formation (K<sup>5c-e</sup>) is assigned to the Beaufort Group, and consists of light green, greenish-grey to brownish-grey and reddish brown sandy limestones, mottled green to greenish-grey calcareous and non calcareous mudstones (Barber 1986; Lepper 1992; Lepper *et al.* 2000). Rocks of the Upper Madumabisa Mudstones are intercalated with beds of dark grey calcareous siltstones and calcareous fine-grained sandstones (Barber 1986; Lepper 1992; Lepper *et al.* 2000). Sandstones found mainly at the base of the siltstone layer, have a limited lateral extent and in some places have a well developed channel-lag deposit (Matura Bone Bed) at the base (Figure 5). The thickness and the stratigraphic range of the conglomerate layer (channel-lag deposit) vary between 1 and 2 m, and 800 and 840 m respectively. Mudstone intraclasts, bone fragments and wood are present in the conglomerate layer.

Therapsid fossil remains, including the tapinocephalid dinocephalian described in this dissertation, are present in the channel-lag deposit (Matura Bone Bed) at various localities. The sites, which have yielded vertebrate fossils in the study area are presented in Figure 4. Because of the high-energy in-channel, nature of the depositional environment, skeletons are disarticulated

and many of the bones were damaged prior to deposition. In addition many of the bones have been weathered out of the channel-lag and have been transported down the slopes (Lepper *et al.* 2000). As a result of both pre- and post-fossilisation damage to which these bones have been exposed, associations between different bone elements are difficult to establish.

Elsewhere in the Middle Zambezi Basin, the Upper Madumabisa Mudstones have yielded therapsid, fish, amphibian, arthropod, plant and mollusc fossil remains (Bond 1965, 1973; Bond *et al* 1970; Boonstra 1946; Macgregor 1946; NHMB records). *Criocephalus gunyankaensis*, the only described dinocephalian genus from Zimbabwe, was recovered from the K<sup>5c</sup> unit at Gunyanka's Kraal, Binga District (18°09'S, 27°50'E) (Boonstra 1946, 1968). As a result of this discovery the K<sup>5c</sup> unit was correlated with the *Tapinocephalus* Assemblage Zone of the main Karoo Basin in South Africa (Bond 1973). The overlying K<sup>5d</sup> unit at Chirisa (17°26'44"S, 28°20'E), Chidoma Hill (17°35'S, 28°27'E) and Sengwa Mine (17°36'20"S, 28°22'15"E), all in the Gokwe District, have yielded the following therapsids: *Endothiodon*, *Prorubidgea*, *Dicynodon*, *Synostocephalus*, *Eurychororhinus*, *Tropidostoma*, *Cryptocynodon* as well as other therocephalian and gorgonopsian species (Bond 1973; NHMB records). *Cryptocynodon* and *Eurychororhinus* have subsequently been considered *incertae sedis* (Cluver and King 1983; King 1988). The therapsid genera found at Chirisa, Chidoma Hill and Sengwa Mine have been recorded from the *Pristerognathus*, *Tropidostoma*, *Cistecephalus* and *Dicynodon* Assemblage Zones of the Beaufort Group in South Africa.

At this stage it is difficult to correlate the sites that have yielded vertebrate fossils in Zimbabwe

with biozones in South Africa, as collecting has been haphazard and sporadic. Such an exercise is beyond the scope of this project, but should be the subject of future investigation. As a result the stratigraphic relationship between the Hwange fossil beds and other “Beaufort” fossil sites in Zimbabwe could not be adequately addressed at this stage. However, based on the presence of dinocephalian therapsids, the Hwange and Gunyanka’s Kraal sites can be correlated together and the rest appear to be younger.

## CHAPTER 3: MATERIALS AND METHODS

### 3.1 Material

Therapsids were first discovered in the Madumabisa Mudstones at Hwange in 1985, during routine coal exploration by Mr T Gumbi of the Wankie Colliery Company. Subsequent studies undertaken by T Gumbi in 1985-87, and by Raath, Plowes and Barber in 1985 and 1986, recorded a number of sites in addition of those found earlier. The fossil bed was brought to the attention of the Palaeontology Department at the Natural History Museum, Bulawayo, (NHMB), which is the only institution with the mandate to preserve palaeontological heritage in Zimbabwe. Messrs R. Matora and E. Lendwaba, the then curators, visited the study area in 1988. Rubidge and Lepper were also at the study area in 1997.

As a result of the fieldwork undertaken at Hwange, a large number of therapsid fossil remains, including the specimen described below, were collected and repositated at NHMB. Emphasis was placed on collecting loose surface material that was considered vulnerable to erosion. The collection includes disarticulated skeletons with postcranial material being the most abundant, but because skulls are generally the most diagnostic part of the skeleton they are the only elements used in this study.

The collection has been partially prepared at NHMB, and each individual bone element allocated a separate registration number regardless of its locality and association with other parts. As a result, in excess of 600 specimens have been catalogued (NHMB1407-2003, NHMB2143-2146). The number

of catalogued entries could have been reduced if it were feasible to assign one number to all elements associated with an individual animal, a task that is not possible because of the disarticulated and scattered preservation of the bones.

Of all the therapsid material collected from Hwange, only dinocephalians have been positively identified. The dinocephalian specimens present in the collection at the NHMB are:

#### Anteosauridae

NHMB2141 – Portion of the left maxilla bearing a large canine and the first postcanine (Lepper *et al.* 2000; Figure 6a).

#### Tapinocephalidae

NHMB1556 – The best-preserved skull in the collection and the subject of this dissertation (Figures 7, 8, 9, 10). Both the snout and lower jaw are missing. The right lateral side was compressed during fossilisation and as a result the whole side is deformed. The ventral side was modified by abrasion after burial and is also poorly preserved. The dorsal and occipital regions are intact but have been greatly weathered.

NHMB2002 – Posterior portion of a skull roof plus two badly damaged skull fragments. The preorbital region has been lost, and the ventral, occipital and left lateral sides are damaged.

NHMB2146 – Dorsal portion of a tapinocephalid skull roof with pachyostosed postorbital bars (Lepper *et al.* 2000).



NHMB2142 – Anterior portion of the lower jaw with a pair of incisor teeth. All the teeth have a prominent heel and talon and the jaw belongs either to a tapinocephalid or a titanosuchid (Lepper *et al.* 2000; Figure 6b).

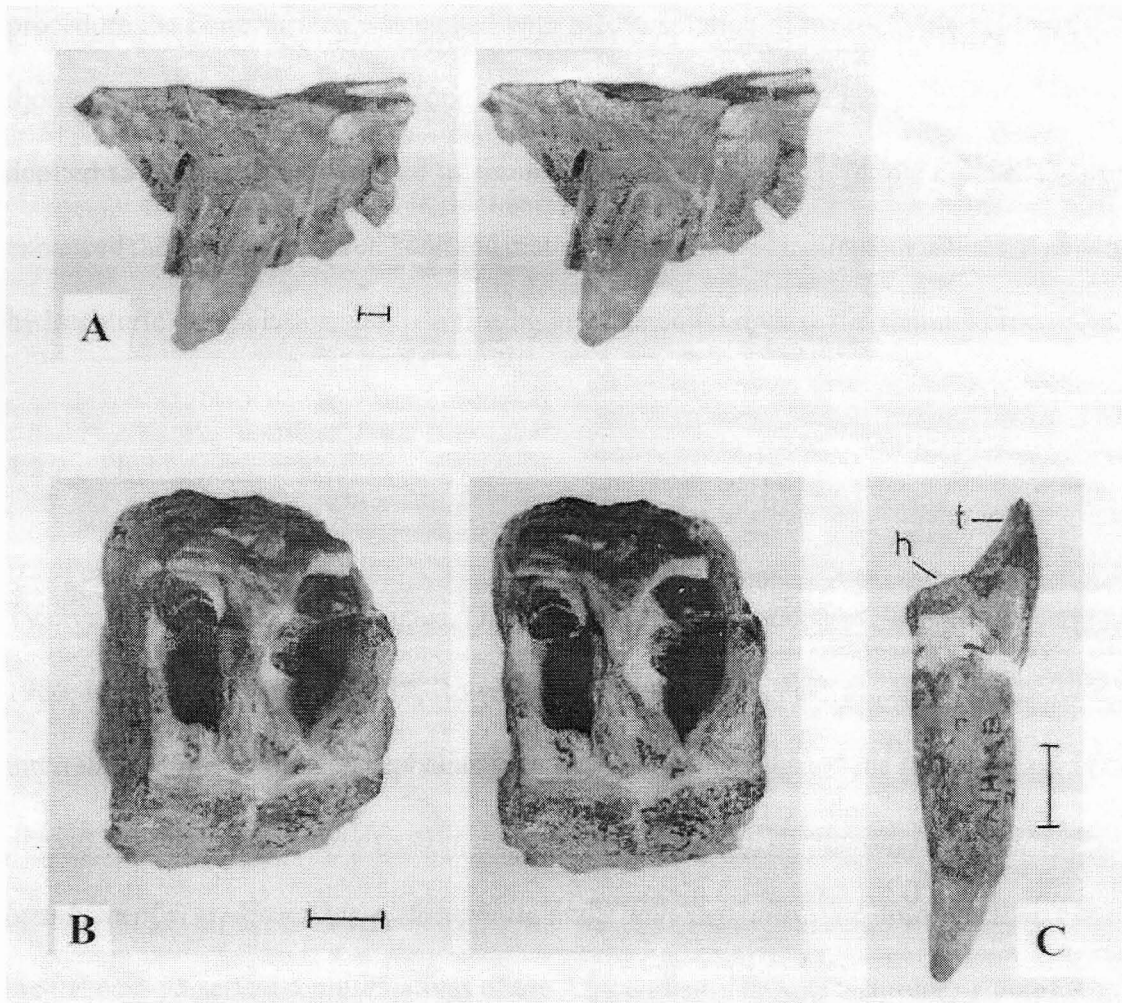
NHMB2143 – A complete incisor tooth with a talon, heel and root of a tapinocephalid or titanosuchid dinocephalian (Lepper *et al.* 2000; Figure 6c).

## 3.2 Methods

### 3.2.1 Specimen Preparation

NHMB1556, which consists of an incomplete dinocephalian skull, was prepared using air and electric powered engravers, hammer, chisel and punches following the method described by Rixon (1976). The air-powered engraver (pneumatic tool) has a hard conical stylus fitted with a tungsten-tip, which removes the matrix from the bone. The pneumatic tool operates with a reciprocal motion of the stylus and the rate of matrix removal is controlled by adjusting the amount of air, which in turn controls the number of reciprocal motions per unit time. For best results the stylus was held at an angle on or near the edge of the specimen being prepared rather than digging a hole in the centre of the matrix. A hammer, chisel and punches were used in the depressions where there was excess matrix to a point that the air and electric engraver could not produce satisfactory results, particularly in the temporal fenestra and orbit. During preparation, ethanol was used to wet the specimen in order to help to distinguish between bone and matrix, while *Trinepon 6* was used as an adhesive to repair

breaks.



**Figure 6.** Photographs of some the better preserved dinocephalian fossils from Hwange. **A**, left maxilla of an anteosaurid dinocephalian specimen NHMB2141 (stereopair); **B**, tapinocephalid specimen NHMB2142 showing dorsal view of anterior portion of lower jaw (stereopair), **C**, tapinocephalid or titanosuchid incisor tooth specimen NHMB2143. Abbreviations: t - talon; h - heel. Scale bars = 1 cm. (From Lepper *et al.* 2000).

Because of lack of definition between bone and matrix, it was found necessary to stain the bone in order to make the sutures stand out more clearly (Rubidge and van den Heever 1997). For this procedure the bone surface was etched with a 10% solution of hydrochloric acid and then rinsed thoroughly in running water. A solution of Alizarin Red S in 4% potassium hydroxide was then applied to the fossil and resulted in fossil bone assuming a deep purple colour. This procedure enhanced the contrast between bone and matrix, and facilitated tracing out sutures. Applying a weak hydrochloric acid solution and then rinsing in water could reverse the staining process.

### 3.2.2 Phylogenetic analysis

Twelve genera of the Biarmosuchia, Dinocephalia and Gorgonopsia (Hopson and Barghusen 1986; Hopson 1991; Kemp 1988; Rowe 1988) were used in a cladistic analysis. Because the interrelationships of the dinocephalian taxa were being investigated the following genera were used as the ingroup: *Australosyodon*, *Jonkeria*, NHMB1556, *Avenantia*, *Riebeeckosaurus*, *Struthiocephalus*, *Moschops*, *Criocephalus* and *Tapinocephalus*. The dinocephalian genera used are the best-preserved representatives of the African families Anteosauridae, Titanosuchidae and Tapinocephalidae (Boonstra 1969). *Styracocephalus*, the only described genus of the Styracocephalidae, was not considered for the analysis because it is poorly preserved (Hopson and Barghusen 1986; King 1988; Rubidge and van den Heever 1997). *Biarmosuchus*, the most basal therapsid (Hopson and Barghusen 1986; Hopson 1991) was used as an outgroup.

Characters were derived from specimen examination and from the literature. As indicated, only

cranial characters were utilised because “it is the only portion of the skeleton that is adequately known in most groups and it is the portion with which we have the greatest familiarity” (Hopson and Barghusen 1986:84).

Specimens were examined at the South African Museum (SAM), Cape Town, and Bernard Price Institute for Palaeontological Research (BPI), Johannesburg. Although all the specimens under consideration were examined, there were some limitations because in some cases preparation was incomplete while other specimens were poorly preserved. In some specimens, the lower jaw, dentition, braincases, snout and occipital regions were either missing or poorly preserved.

Characters were coded according to Wiley *et al* (1991) as:

- 0 primitive state
- 1 derived state
- 2 more derived
- 3 most derived
- ? not preserved or where figures and descriptions were inadequate to allow confident coding

Twenty-six morphological characters were produced and a data matrix consisting of twelve taxa was constructed (Appendix 1, 2). The characters were subjected to a maximum parsimony analysis using PAUP 3.1.1 (Wiley *et al* 1991). Heuristic search algorithm and strict consensus were then applied. Character fitness and strength of the

hypotheses were tested by MacClade 3.07 and decay analysis respectively.

**CHAPTER 4: DESCRIPTION OF SKULL NHMB 1556**

Of all the tapinocephalid dinocephalian skulls in the collection at the NHMB, specimen NHMB 1556 is the most complete and best preserved, and is in fact the most complete dinocephalian skull so far collected from Zimbabwe. NHMB1556 was therefore chosen for description and study because there is a stronger possibility to be able to compare it meaningfully with dinocephalians from other countries.

The skull is almost complete lacking only the lower jaw and anterior tips of the snout and palate. Because of lateral compression, the right lateral side and left palatal region have been crushed medially to the extent that no skull part could be recognised. Although the braincase was preserved, it was badly damaged such that most of sutures could not be distinguished. Post fossilisation cracks are present on the occipital and left lateral sides, indicating that the specimen was exposed for a long period before it was collected.

The shape of the cranial roof of NHMB1556 resembles those of the advanced tapinocephalid dinocephalians in that the intertemporal region is moderately wide and the posterodorsal portion of the skull roof is moderately pachyostosed. Because of the pachyostosis, weathering, deformation and abrasion, the sutures and surface features are not readily apparent, but as a result of staining and careful study it has been possible to trace some of these.

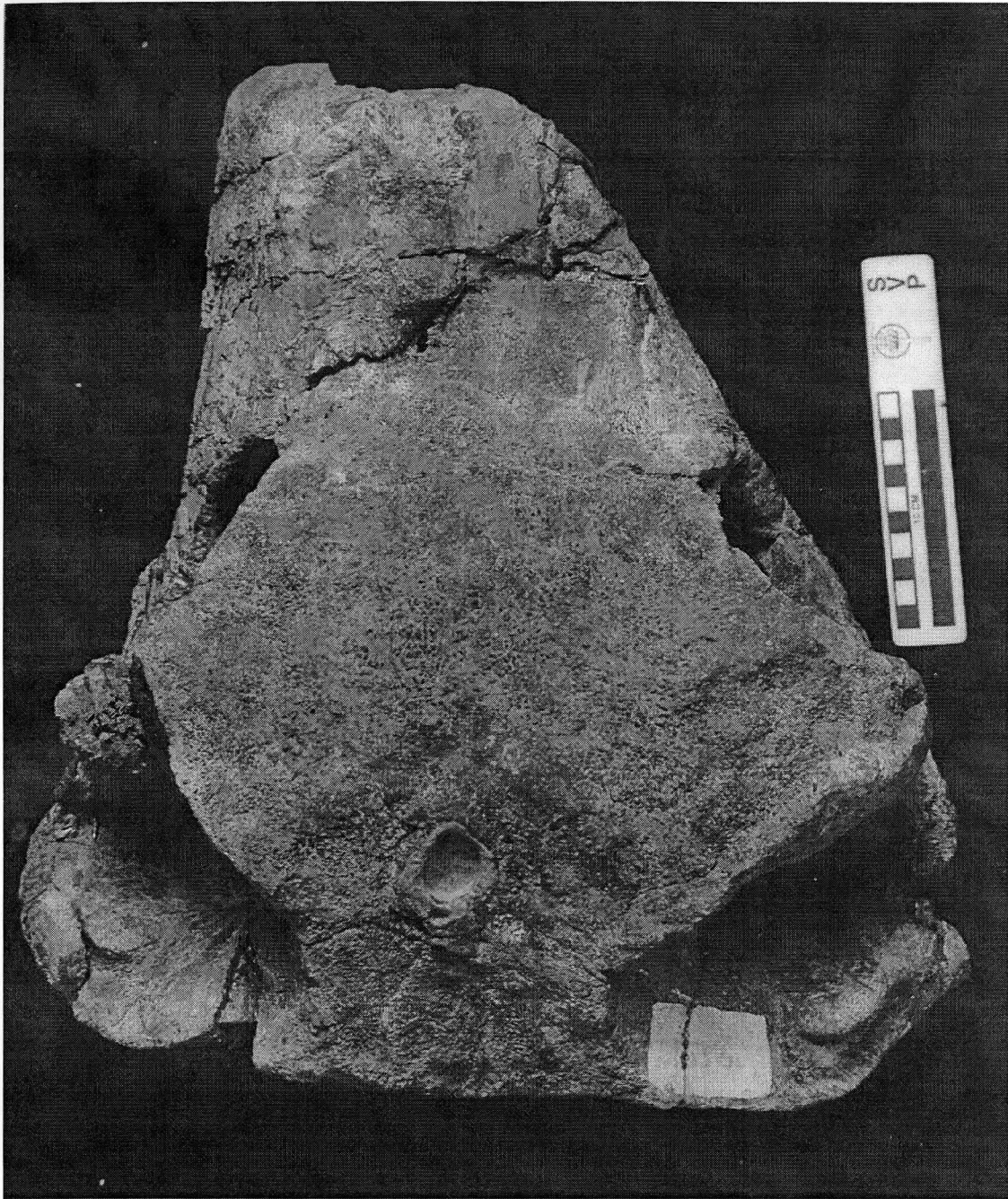
#### 4.1 Skull roof

The anterior portion of the snout that includes the septomaxilla and external nares is missing and the posterior parts of the premaxilla, nasal and maxilla are the only bones preserved in the preorbital region (Figure 7). Only the posterior-most part of the premaxilla is preserved and this is present as a thin pointed wedge extending down the midline between the nasals. This wedge pinches out posteriorly at a point in front of the orbit and at the same level where the maxilla, prefrontal and nasal meet, but it does not reach the frontal, just as in other tapinocephalid dinocephalians (Boonstra 1969).

The nasal extends as a relatively thin bone down the midline of the snout (Figure 7). On the anteromedial side, it is in contact with the premaxilla whereas laterally it forms a long sutural contact with the maxilla anteromedially and the prefrontal posteromedially. Posterodorsally it has a short anteromedially pointed suture with the frontal on the midline. From its posterior suture with the frontal, the nasal surface slopes gently anteriorly and then levels off on the snout, thereby defining a gentle slope on the cranial-facial transition.

Because of erosion the surface texture of the maxilla could not be determined with certainty, although it was probably smooth. In lateral view, the maxilla forms most of the preorbital region of the skull (Figure 8). Dorsally, it has a long lateral contact with the nasal and it meets the prefrontal and jugal posteriorly just in front of the orbit. Posterodorsally, it sends a short, thin and tapering lappet between the nasal and prefrontal. The suture between the maxilla and lachrymal could not be

determined.



**Figure 7.** Dorsal view of NHMB1556. Scale bar =10 cm



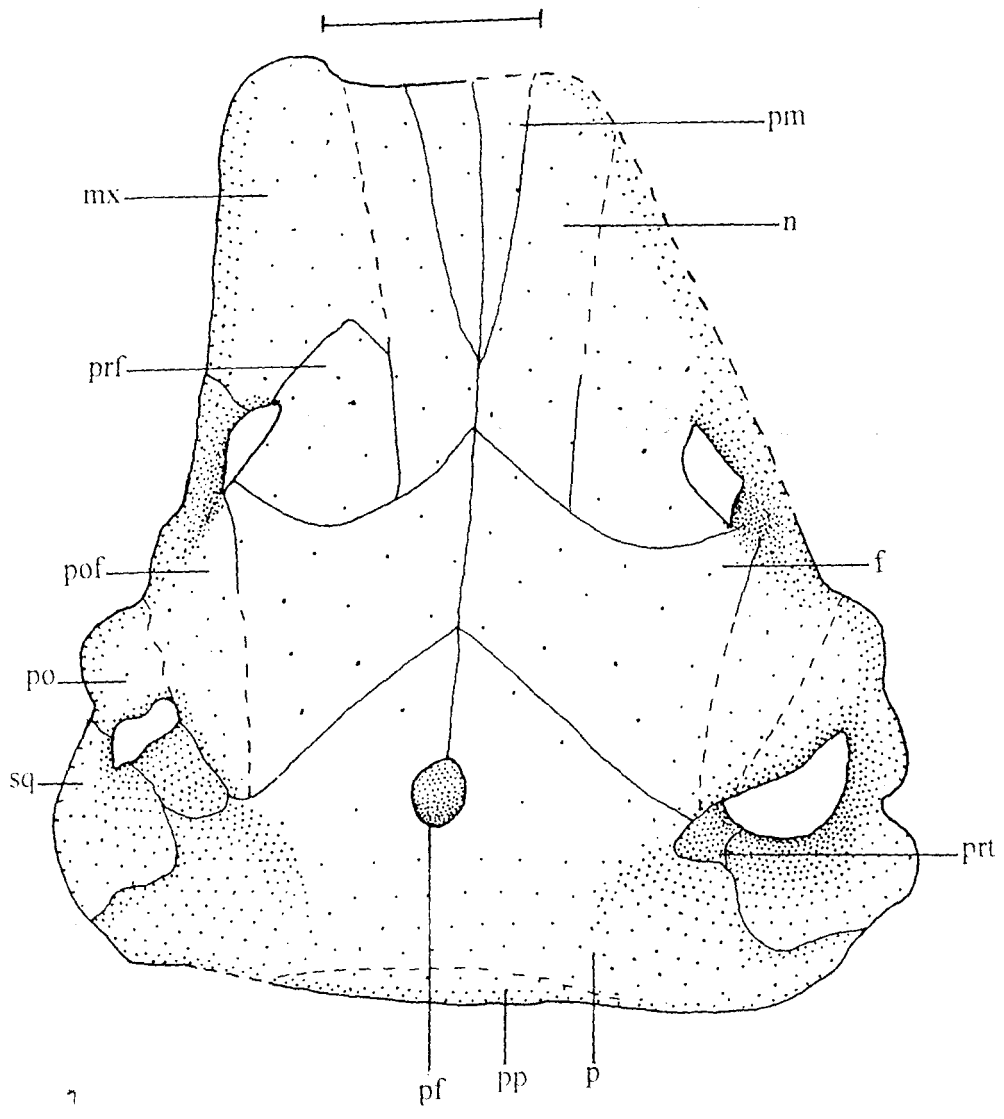
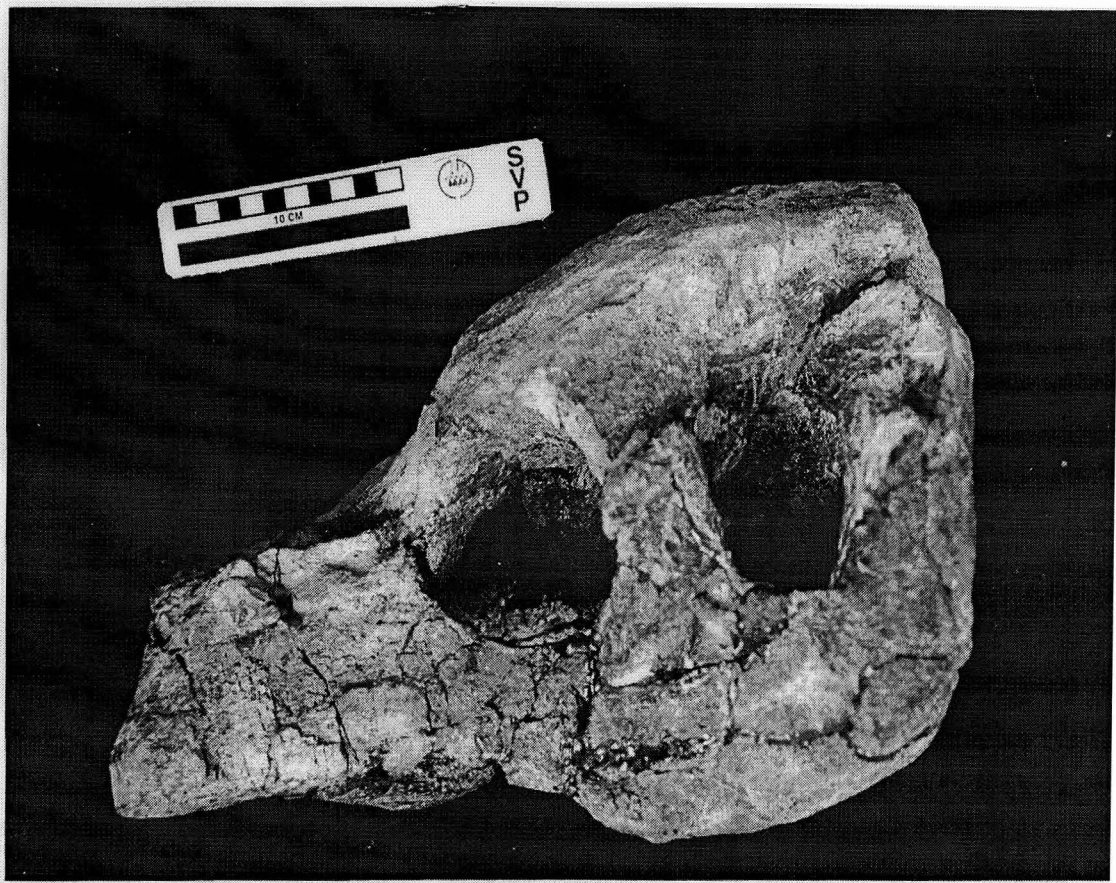


Figure 7. Dorsal view of NIIMB1556. Scale bar =10 cm. See page xii for abbreviations.



**Figure 8.** Lateral view of NHMB1556. Scale bar =10 cm.

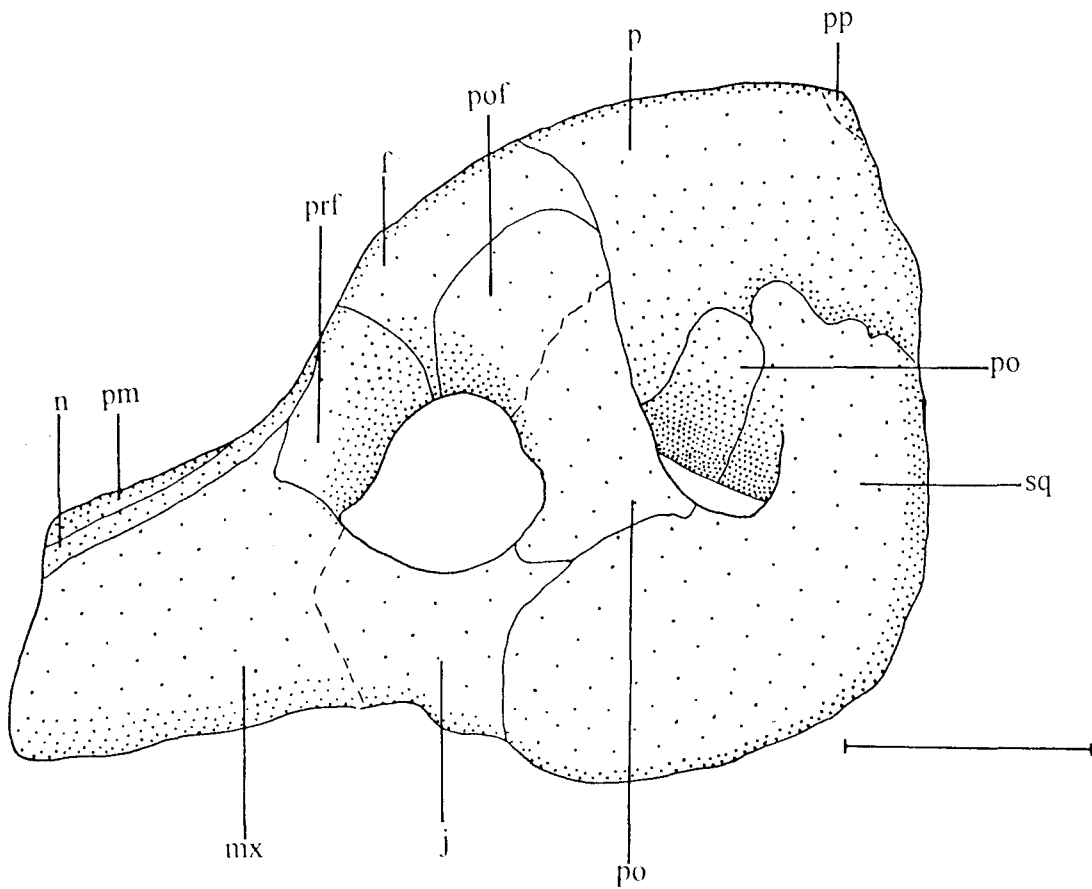


Figure 8. Lateral view of NHMB1556. Scale bar =10 cm. See page xii for abbreviations.

The prefrontal is a relatively large bone that makes up at least half of the dorsal border of the orbit (Figure 8). It is in contact with the nasal on its medial side and forms a curved suture with the frontal posteriorly from the centre of the dorsal border of the orbit. From the anterior margin of the orbit, the prefrontal extends anteriorly for short a distance to contact the maxilla and terminates in a blunt point. The suture with the lachrymal could not be determined with the result that it was not possible to ascertain the relationship between the prefrontal and lachrymal.

The frontal and parietal constitute most of the skull roof in dorsal view (Figure 7). The frontal has an almost rectangular exposure on the skull roof, and together with its mate form a flat dorsal surface between the orbit and temporal fenestra. Anteriorly it forms an anteromedially pointed suture with the nasal on the midline. This suture continues laterally to the orbital margin in a semi-circle so that the prefrontal forms a rounded contact with the frontal. Dorsolaterally, most of the contact between the frontal and postfrontal is not clear but the former bone cuts off the latter from the rim of the temporal fenestra. A thin tongue of the frontal enters the dorsal border of the orbit and excludes the prefrontal from contact with the postfrontal. Posterodorsally, the frontal forms a posteromedially pointed suture with the parietal on the midline and it does not reach the pineal foramen.

The parietal is a complex bone that forms the greater part of the intertemporal region including the posterior edge of the skull roof (Figure 7, 8). Anterodorsally it forms an anteromedially pointed suture with the frontal on the midline. From the anteriormost point on the midline, the two arms of the parietal form an almost flat surface, which slopes gently posterodorsally. As a result of weathering, the suture between the parietal and postparietal is not clear (Figure 7). Anteroventrally

the parietal meets the postorbital and postfrontal, and posteroventrally it underlies the squamosal. The parietal therefore is the dominant bone on the border of the temporal fenestra as it makes up more than half of the dorsal and posterodorsal margins. A pineal foramen is situated in the centre of the parietal just in front of the posterodorsal margin of the temporal fenestra (Figure 7). As a result of erosion on its rim it is not possible to ascertain whether it was situated on a ridge or boss as in *Avenantia* and *Delphinognathus* (Boonstra 1957, 1969; King 1988).

Although the sutures of the postfrontal are not clear, it appears to meet the frontal dorsally, postorbital ventrally and to have a short contact on the parietal posteriorly. It also contributes to the posterodorsal border of the orbit, but the extent is uncertain as the suture with the postorbital could not be ascertained.

The postorbital is a relatively thin bone when compared with other tapinocephalid genera (Boonstra 1969; King 1988; Rubidge 1991), and it forms the posterior and anterior border of the orbit and temporal fenestra respectively (Figure 8). This bone extends almost vertically between the orbit and the temporal fenestra, and thins dorsoventrally. The dorsal section of the left postorbital was lost after fossilisation and its relationship with the postfrontal cannot be established. The right postorbital is the only bone that was not distorted by compression in that region and it meets the postfrontal in an almost horizontal suture half way up the postorbital bar. Posterodorsally it meets the parietal on the dorsal margin of the temporal fenestra and ventrally it extends slightly below the orbit where it forms an anterodorsally curved suture with the squamosal and jugal (Figure 8).

The squamosal is a complex bone that forms the ventral, posterior and posterodorsal border of the temporal fenestra (Figure 8). A unique feature of specimen NHMB 1556 is the presence of a groove on the squamosal immediately below its dorsal suture with the parietal. The groove is curved dorsoventrally and it extends into the temporal fenestra from the posterior edge of the cranial roof. From the anteroventral edge of the temporal fenestra the squamosal extends for almost 75% of the postorbital bar before it meets the jugal in a vertical suture (Figure 8).

As a result of weathering, the anteroventral suture of the jugal with the maxilla could not be established with certainty. There are indications that it forms a short broad lappet anteromedially (Figure 8). Posteromedially it sends a short thin lappet along the suture between postorbital and squamosal. From the tip of the lappet, the jugal meets the postorbital dorsomedially up to the ventral margin of the orbit, and the squamosal ventromedially down to the lateral edge of the skull. The jugal makes up the entire ventral border of the orbit. Because the lachrymal could not be identified the relationship between the jugal and the former could not be determined.

The temporal fenestra is relatively large as compared with that of most advanced tapinocephalid dinocephalians, where it has been secondarily reduced by pachyostosis (Boonstra 1969,1971; Kemp 1982). The fenestra is spherical with the dorsoventral diameter slightly larger than the anteroposterior diameter. As a result of a relatively large temporal fenestra, the intertemporal region is narrow. The squamosal, parietal and postorbital provide a large area for muscle attachment of the adductor jaw musculature when compared with the corresponding bones of most other tapinocephalid dinocephalians.

## 4.2 Occiput

The section on the right side of the occiput consisting of the squamosal, quadrate and opisthotic is not preserved. As preserved the occipital plate is roughly semi-circular and is twice as broad as high (Figure 9). As in most tapinocephalid dinocephalians, the dorsal edge of the occipital plate lies further posteriorly than the ventral edge and as a result the occipital plate slopes anteroventrally. The sutures between bones at the centre of the occiput are indistinguishable, as is the situation in most other tapinocephalid dinocephalians, but in this specimen the problem is compounded by the intensive erosion suffered by the occipital region.

The squamosal and parietal have been described in the skull roof section but as both bones are partly visible in the occipital view (Figure 9), they are briefly described here. The squamosal and parietal meet in a zig-zag suture and contribute equally to the lateral edge of the occiput. A thin and shallow, dorsoventrally oriented triangular external auditory meatus is situated in the lower part of the squamosal extending dorsally as far as the region above the posttemporal fenestra. Ventrally the squamosal is in contact with the lateral and dorsal surface of the quadrate, but its relationship with the quadratojugal could not be established as the latter is not preserved. The squamosal meets the opisthotic ventromedially and the tabular dorsomedially. Together with the opisthotic, quadrate and basioccipital, the squamosal forms the ventral edge of the occipital plate.



**Figure 9.** Occipital view of NHMB1556. Scale bar = 10 cm



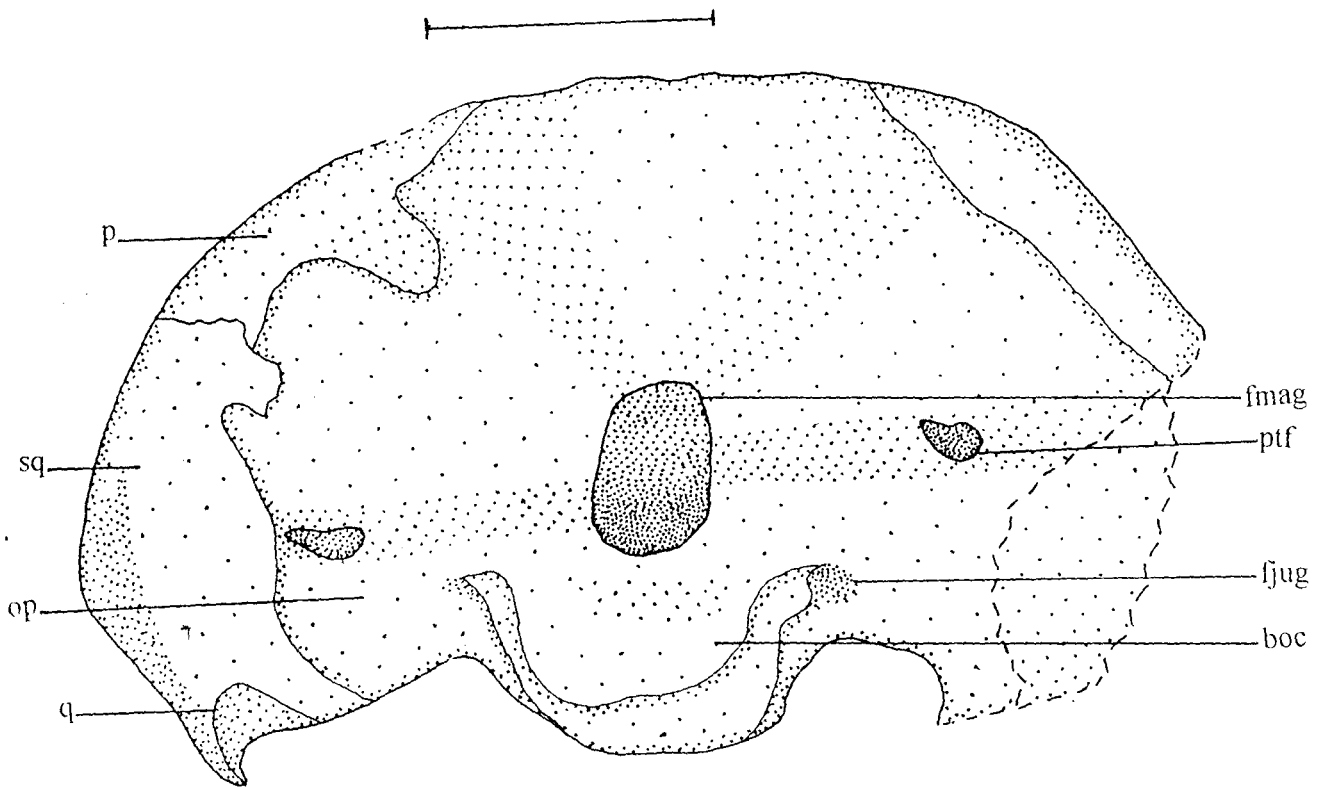


Figure 9. Occipital view of NIMB1556. Scale bar = 10 cm. See page xii for abbreviations.

From its ventral suture with the squamosal the parietal forms the dorsolateral edge of the occiput. As a result of extensive erosion its relationship with other bones other than the squamosal could not be established. The only determinable sutures of the tabular are those between it and the squamosal ventromedially and parietal dorsomedially, and as a result its relationship with other bones could not be established. A posttemporal fenestra lies on the tabular along its ventral suture with the opisthotic medial to the squamosal.

The basioccipital is relatively large as compared to other tapinocephalid dinocephalians (Boonstra 1969). It is more visible in the palatal region and described more fully later.

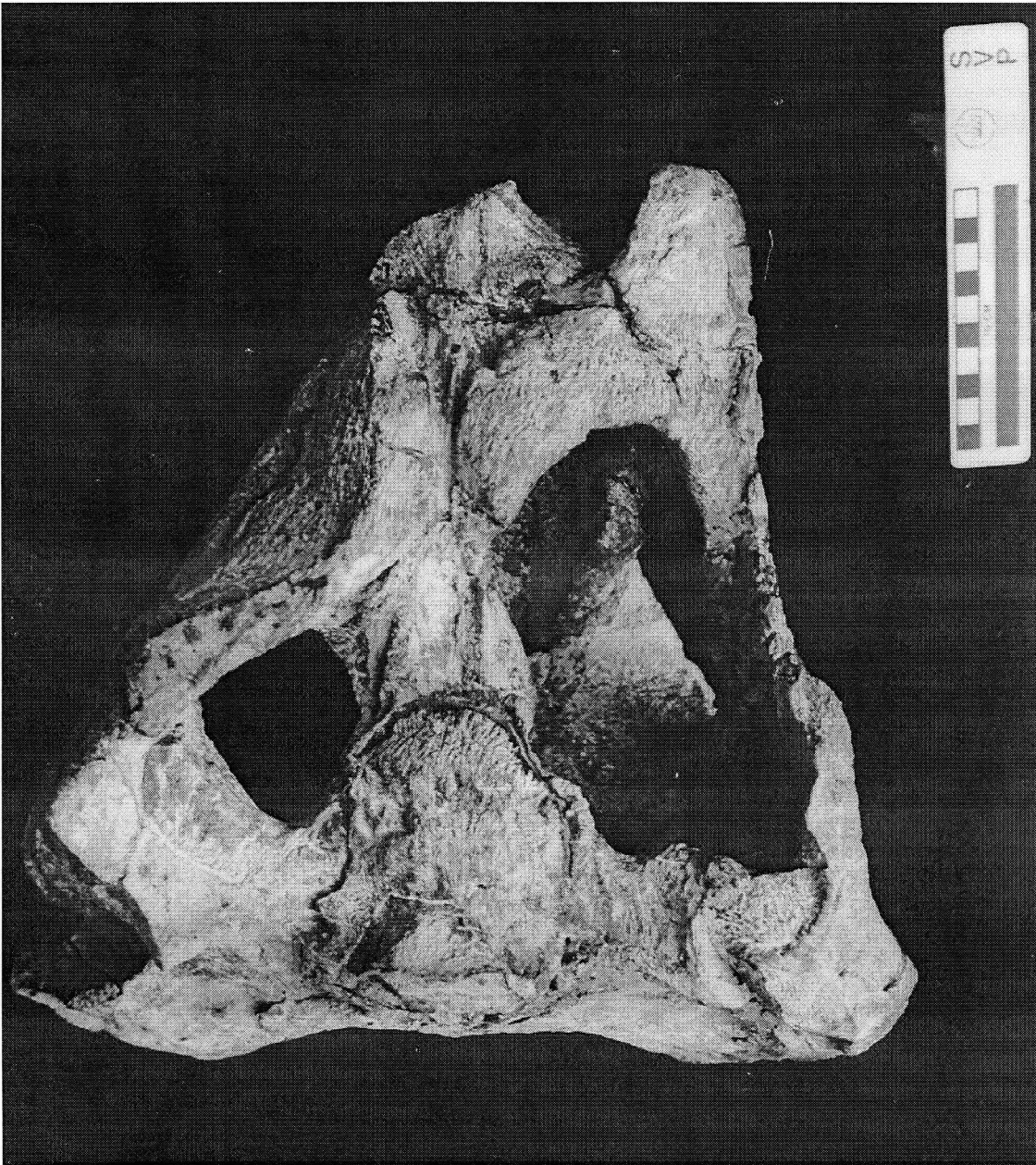
The sutures of the opisthotic, basioccipital, exoccipital, supraoccipital, paroccipital and postparietal are indeterminable and therefore the relationship of each bone with others could not be established. Although the sutures of the bones occupying the centre of the occipital plate are indeterminable, ridges and depressions are prominent. A median ridge runs dorsoventrally from the dorsal edge of the occipital plate until it meets the foramen magnum. On either side of the ventrally oriented central ridge, which extends from the dorsal occipital edge to the foramen magnum, is a triangular depression oriented transversely from the dorsolateral occipital edge to the foramen magnum. A second ridge, broader than the central one, extends transversely from the dorsolateral edge of the parietal down to the foramen magnum. Ventral to the second ridge lies a shallow depression oriented horizontally and extending from the ventrolateral side of the squamosal to the foramen magnum.

### 4.3 Palate

The anterior tip of the palate medial to the internal naris is not preserved and the anteroventral parts present are the incomplete maxilla, palatine and vomer (Figure 10). The vomers are paired elongated and flattened bones separated by a suture on the longitudinal ridge extending the entire length of the preserved section down the midline. Each vomer forms the medial and posterior border of the internal naris, and continues posteriorly from the posterior margin of the internal naris down to the interpterygoidal vacuity, underlying the palatine and pterygoid respectively in the process (Figure 10). Posteriorly the vomer forms the anterior margin of the interpterygoidal vacuity whereas in most other tapinocephalid dinocephalians it does not meet the interpterygoidal vacuity as its posterior suture with the pterygoid lies anterior to the interpterygoidal vacuity (Boonstra 1936, 1957, 1969; Rubidge 1991).

The left palatine is crushed such that it was not possible to ascertain its relationship with other bones. The right palatine is a complex bone, which is in contact with the vomer, maxilla, pterygoid and ectopterygoid. From its posteroventral suture with the pterygoid and ectopterygoid, the palatine extends forward along the medial surface of the maxilla to form the lateral border of the internal naris (Figure 10). It continues posteriorly from the posteroventral margin of the internal naris until it meets the pterygoid medially where it ventrally overlies the vomer. A raised surface is present on the posteroventral region of the palatine towards the midline of the palate, indicating that a palatine boss may once have been present but because of the extent of bone erosion it is impossible to ascertain

whether the raised surface was dentigerous. Palatine bosses are present in all described dinocephalians but in tapinocephalid dinocephalians palatine teeth have been found only in *Struthiocephalus* and *Tapinocanius* (Boonstra 1936, 1953, 1957; Rubidge 1991).



**Figure 10.** Ventral view of NHMB1556. Scale bar =10 cm.

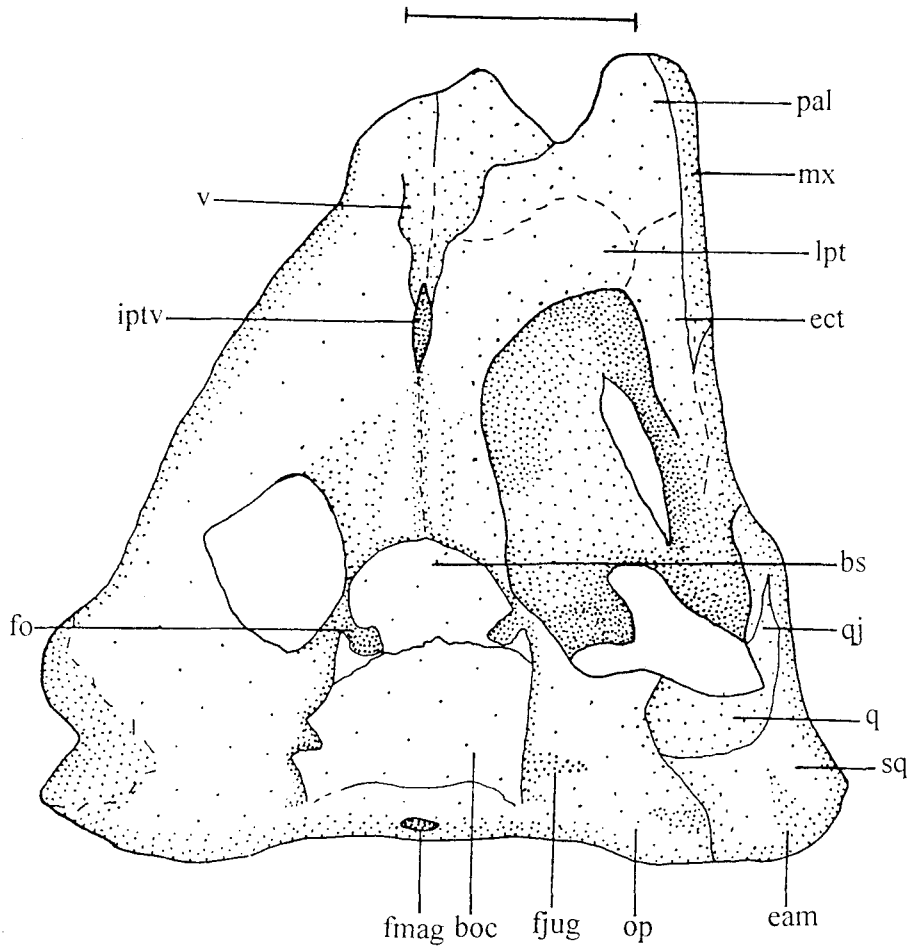


Figure 10. Ventral view of NHMB1556. Scale bar = 10 cm. See page xii for abbreviations.

The maxilla has been described under the skull roof, but a small portion of it is preserved in the ventral region (Figure 10). It is in lateral contact with the palatine anteromedially and ectopterygoid posteromedially. Its posteroventral relationship with other bones could not be determined although it ends in sharp point, medial to the ectopterygoid.

The ectopterygoid is a small bone bounded anteroventrally by the palatine and laterally by the pterygoid and maxilla towards the centre and lateral margin of the palate respectively (Figure 10). Its posteroventral suture is indeterminable and as a result its relationship with the jugal could not be established.

The left pterygoid is crushed with the result that its configuration and relationship with other bones is indeterminable. The anterior process of the right pterygoid meets the palatine just in front of a raised surface. The lateral flange of the pterygoid stretches transversely across the palate to meet the ectopterygoid anterolaterally. The suture between the pterygoid and ectopterygoid is not clear but it appears that the former bone forms the entire lateral contact of the latter. The quadrate ramus of the pterygoid was not preserved and, as a result of weathering the surface features of the pterygoid posterior to the lateral process are indeterminable. A moderately wide interpterygoidal vacuity is present on the anteroventral midline of the palate and it extends anteriorly into the vomer. Posteroventrally, the pterygoid has a curved anteroventral and lateral suture with the basisphenoid.

#### 4.4 Braincase

The ventral surface of the basicranium has been damaged and much of the original bone surface has been removed. The basisphenoid is a relatively large semi-circular bone, and it meets the pterygoid laterally and anteroventrally and the basioccipital posteriorly (Figure 10). A prominent transverse suture behind the posterior border of the fenestra ovalis marks the contact of the basisphenoid with basioccipital (Figure 10).

The spherical fenestra ovalis lies on the posterolateral side of the basisphenoid medial to the ventral orbital foramen (Figure 10). From the margin of the basisphenoid, the fenestra ovalis extends obliquely posteriorly to the posteroventral suture of the basisphenoid. As a result the basisphenoid forms more than half of the margin of the fenestra ovalis, the basioccipital forming the remaining portion.

The basioccipital forms the ventral portion of the occipital condyle from where it extends anteroventrally to meet the basisphenoid in a transverse suture half way along the fenestra ovalis (Figure 10). Its lateral relationship with other bones could not be established. A foramen jugularis is present on the posterolateral side of the basioccipital and it is orientated laterally.

Because of weathering the detailed relationship of the opisthotic, prootic, paroccipital and supraoccipital could not be discerned. From its lateral contact with the basioccipital, however, the opisthotic can be seen to extend transversely to meet the squamosal posterolaterally and

quadrate anterolaterally. Its relationship with the quadrate ramus of the pterygoid could not be established because the latter bone was not preserved. Anteroventrally the opisthotic meets the pterygoid medial to the fenestra ovalis.

The sutures of the bones that enclose the posterior wall of the braincase are not discernible. The basioccipital forms most of the ventral margin of the foramen magnum. The exoccipital, paroccipital, and opisthotic contribute to the ventral and lateral borders of the foramen magnum but the level of contribution of each bone could not be established with certainty because of weathering.

In lateral view, the postorbital obscures most of the lateral region of the braincase and little of the interorbital region is seen through the orbit. In the absence of parasagittal and sagittal sections, very little of the lateral and dorsal sections of the braincase is exposed. The portion exposed through the orbit has been damaged to an extent that most of the sutures cannot be observed. The bones that could be identified are the epipterygoid, sphenoidal complex, pterygoid, opisthotic and prootic. The epipterygoid descends probably from the orbitosphenoid to meet the pterygoid and basisphenoid above the fenestra ovalis. It meets the prootic dorsolaterally and the opisthotic ventrolaterally. It also meets the pterygoid ventrally and the frontal dorsally. The sutures of the bones of the sphenoid complex parasphenoid, presphenoid and septosphenoid could not be distinguished. According to Boonstra (1968), sphenoidal sutures of dinocephalian therapsids close at maturity and since this suture could not be distinguished it is probable that NHMB 1556 was a mature animal when it died.



**CHAPTER 5: DISCUSSION**

Several classification schemes of the Dinocephalia have been proposed but those of Boonstra (1969, 1972) and King (1988) have been considered to be the most useful for this study. King's (1988) classification scheme differs from other schemes (Boonstra 1963a,b, 1969, 1972; Hopson and Barghusen 1986; Kemp 1982) in the rank of taxa and number of families, subfamilies and tribes. The other schemes recognised five families (Anteosauridae including Brithopodidae, Estemmenosuchidae, Titanosuchidae, Styracocephalidae and Tapinocephalidae) and four tapinocephaline subfamilies (Struthiocephalinae, Moschopinae, Riebeeckosaurinae and Tapinocephalinae), but King (1988) considered three families (Estemmenosuchidae, Brithopodidae and Titanosuchidae), four subfamilies (Brithopodinae, Anteosaurinae, Titanosuchinae and Tapinocephalinae) and three tapinocephaline tribes (Struthiocephalini, Riebeeckosaurini and Tapinocephalini). While the classification scheme of King (1988) considered as invalid the families Tapinocephalidae and Styracocephalidae, and subfamily Moschopinae, and also reduced the rank of Boonstra's (1969) subfamilies to tribe, it retained most of the characters used by Boonstra (1969) to identify the taxa. Although King's (1988) classification is the most recent, Boonstra's (1969, 1972) classification schemes are the most preferred for this study because the former is considered to be restrictive. In this dissertation the Tapinocephalidae is therefore considered to have four subfamilies, namely: Struthiocephalinae, Moschopinae, Riebeeckosaurinae and Tapinocephalinae.

As was pointed out in Chapter 1, the identification of dinocephalian families (Boonstra 1963b, 1969, 1972; Hopson and Barghusen 1986; Kemp 1982; King 1988) is based on:

1. Presence and size of heels on the incisor and postcanine teeth
2. Presence or absence of canine tooth.
3. Intermeshing of teeth.
4. Degree of pachyostosis
5. Anteroventral rotation of occiput

Teeth and snout are not preserved in the Zimbabwean specimen and therefore characters 1 to 4 could not be tested.

As NHMB1556 has a relatively wide intertemporal region, moderately pachyostosed posterodorsal portion of skull roof and a pronounced anteroventral rotation of the occiput, it is considered to be a tapinocephalid dinocephalian (Boonstra 1969; Hopson and Barghusen 1986).

Boonstra (1969; Table 2) subdivided the Tapinocephalidae into four subfamilies

(Struthiocephalinae, Moschopinae, Riebeeckosaurinae and Tapinocephalinae) based on:

1. length of snout
2. size of skull
3. degree of pachyostosis
4. width of intertemporal region

As the snout of NHMB1556 is not preserved, no deductions could be derived from the first character. According to Boonstra (1969:33) "size of skull is a function of age and also sex".

Similarly, pachyostosis as a character is variable within the subfamilies depending on age, normal or morbid physiological processes, and possibly sex (Boonstra 1957, 1969; King 1988). It

therefore follows that characters 2 and 3 cannot be reliably used.

The subfamily Riebeeckosaurinae is characterised by a narrow intertemporal (Boonstra 1969; King 1988; Table 2,4), while all the others have a wide intertemporal region. As specimen NHMB1556 has a relatively broad intertemporal region it is not considered to be a riebeeckosaurine.

For the remaining tapinocephalid subfamilies (Struthiocephalinae, Moschopinae and Tapinocephalinae), characters in the literature (Boonstra 1969; Hopson and Barghusen 1986; King 1988) are not of use in order to assign NHMB1556 a subfamily. Comparisons were therefore carried out between NHMB1556 and tapinocephalid dinocephalians in the South African Museum, Bernard Price Institute (Palaeontology) and National Museum in Bloemfontein, the only South African institutions which keep dinocephalian holotypes.

*Tapinocaninus*, the most primitive tapinocephaline (Rubidge 1991), whose subfamily was not specified in the original description, was also considered in the comparative analysis. More recently, Ivachnenko (2000) has included *Tapinocaninus* together with *Ulemosaurus* in the family Ulemosauridae.

As in *Avenantia*, *Delphinognathus* and *Keratocephalus*, the pineal foramen of NHMB1556 is anteriorly situated. This area is weathered in NHMB1556, but in *Delphinognathus* and *Avenantia* the boss or ridge is so prominent (Boonstra 1957, 1969; King 1988) that one would expect to see a remnant in the Zimbabwean specimen if such a structure was once present.

Boonstra (1971:21) stated “In the Tapinocephalidae the greatly varying pachyostotic thickening of the skull bones affects the nature of the temporal fenestra, the adductor chamber and the degree of participation of the bones forming the borders of the fenestra”. The size and shape of the temporal fenestra and the bones that form its borders are therefore of diagnostic value.

*Avenantia*, NHMB1556, *Delphinognathus* and *Struthionops* have a slender postorbital which thins dorsoventrally in the last three genera, but in other tapinocephalid genera, the postorbital is broad and massive where it occupies most of the postorbital bar. Because the postorbital and posttemporal bars of NHMB1556, *Avenantia*, *Delphinognathus* and *Struthionops* are relatively slender, the temporal fenestra of these genera has a relatively greater anteroposterior diameter than other tapinocephalines except *Tapinocaninus* (Boonstra 1953a, 1956, 1957, 1969; King 1988; Rubidge 1991). Although *Tapinocaninus* has a broad postorbital, its temporal fenestra has a relatively large anteroposterior diameter (Rubidge 1991). In addition to having a temporal fenestra with a large anteroposterior diameter, the temporal opening of NHMB1556, *Tapinocaninus*, *Avenantia*, *Delphinognathus* and *Struthionops* is dorsally situated, resulting in a narrow intertemporal region. Because of the large temporal fenestra, narrow intertemporal region and reduced pachyostosis, there is a large area for muscle attachment. According to Hopson and Barghusen (1986), tapinocephalid dinocephalians with a large area for muscle attachment and narrow intertemporal region are considered to be primitive because the large area for muscle attachment was eliminated from the temporal roof in advanced tapinocephalines as the dorsal surface became more expanded due to pachyostosis.

The degree of participation of the bones that form the posterior margin of the temporal fenestra

in NHMB1556 differs from that of other tapinocephalid dinocephalians. In NHMB1556 the suture between the squamosal and parietal medial to the posterior margin of the temporal fenestra is low as compared to other tapinocephalid dinocephalians. In *Tapinocanius* the suture is slightly higher than that of NHMB1556 but lower than that of other tapinocephalines. Because of the low contact between the squamosal and parietal in NHMB1556, the parietal occupies a large area (about 50%) of the dorsal and posterior borders of the temporal fenestra.

The squamosal of NHMB1556 is unique among all the known tapinocephalines in that it possesses a groove below its dorsal contact with the parietal. The groove extends inside the temporal fenestra from the lower squamosal-parietal suture.

As in all the described tapinocephaline genera, the occipital region of NHMB1556 slopes anteroventrally and is broader than high (Boonstra 1956, 1957; King 1988; Rubidge 1991). It is, however, more compressed laterally in *Tapinocanius*, *Moschops*, *Criocephalus* and *Tapinocephalus*, and these genera have a deeper external auditory meatus as compared to NHMB 1556.

The vomer of NHMB1556 extends posteriorly as far as the interpterygoidal vacuity but in all known tapinocephalines the two arms of the pterygoid meet on the midline above the anterior border of the interpterygoidal vacuity, thereby separating the interpterygoidal vacuity from the vomer. As in *Tapinocanius*, *Moschops*, *Criocephalus*, *Tapinocephalus*, the vomer of NHMB 1556 has a midline ridge.

The posteroventral and anteroventral region of the palatine and pterygoid respectively are on a raised surface indicating a possibility of a boss on both bones. Because of weathering it was not possible to determine whether the raised palatine surface bore teeth, as *Tapinocanius* and *Struthiocephalus* (Boonstra 1953; Rubidge 1991).

With reference to the braincase, the basisphenoid of NHMB1556 and *Tapinocanius* is almost semi-circular anteroventrally whereas it is pointed in other tapinocephalid dinocephalians (Boonstra 1936, 1953, 1955, 1957, Rubidge 1991). The shape of the basisphenoid of *Tapinocanius* and NHMB1556 is however slightly different in that in the former it is narrow and there is a depression on the anteroventral midline in the latter.

Based on these differences it appears that NHMB1556 is a new type of tapinocephalid dinocephalian and it is considered to be a primitive form because of the characters: relatively narrow intertemporal region, large area for muscle attachment and reduced pachyostosis. Differentiating features which characterise the specimen as a new genus are: squamosal possessing a groove below its dorsal contact with the parietal on the posterior border of the temporal fenestra, a low suture between the squamosal and parietal on the posterior border of the temporal fenestra, vomer forming the entire anterior border of the interpterygoidal vacuity, and a semi-circular basisphenoid with depression on the midline anteriorly. Because of the very incomplete nature of the skull it was not possible to assign NHMB1556 to a tapinocephalid subfamily, and it was also decided not to erect a new genus until better material becomes available.

**CHAPTER 6: PHYLOGENETIC ANALYSIS**

Several authors have attempted to address the phylogenetic relationships of the dinocephalian families. Boonstra (1936a) analysed the interrelationships of tapinocephalid dinocephalian families and their relationship with titanosuchid dinocephalians. In 1963b, Boonstra looked at the relationships of the different dinocephalian families, but also included the interrelationships of different genera. Several cladistic schemes have since been proposed (e.g. Kemp 1982; Hopson and Barghusen 1986; King 1988; Rubidge 1991; Rubidge and van den Heever 1997) but these have addressed only the dinocephalian families and subfamilies. Rubidge (1994) provided a hand-crafted cladogram suggesting possible relationships of various anteosaurid genera, but apart from this no phylogenetic analyses to obtain resolution within families have been undertaken.

Earlier in this dissertation (page 16) it was pointed out that it appears that there may be too many tapinocephalid genera, and that the Tapinocephalidae requires taxonomic revision. During the course of this study I have been able to recognise several well-defined tapinocephalid genera, and as it appears that specimen NHMB1556 is a new genus manifesting different characters it was decided to undertake a computer based phylogenetic analysis using PAUP 3.1.1.

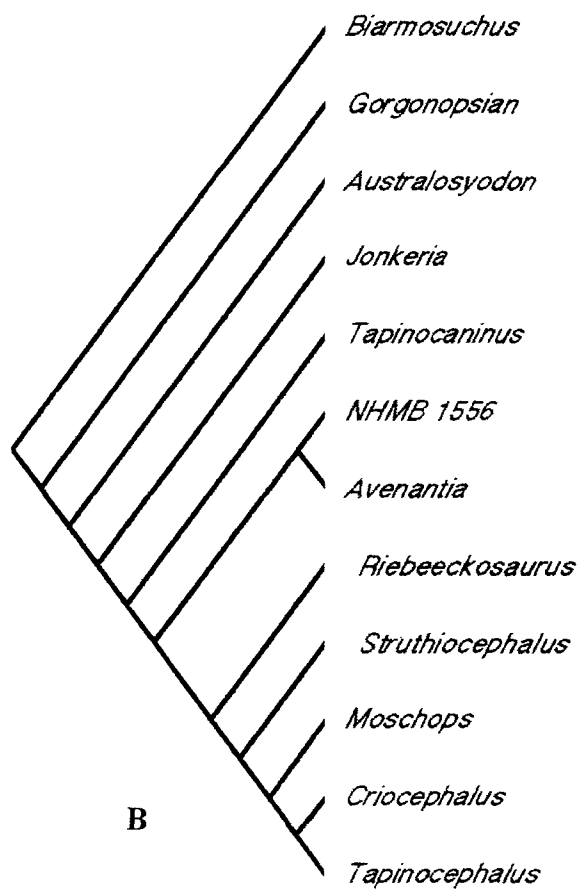
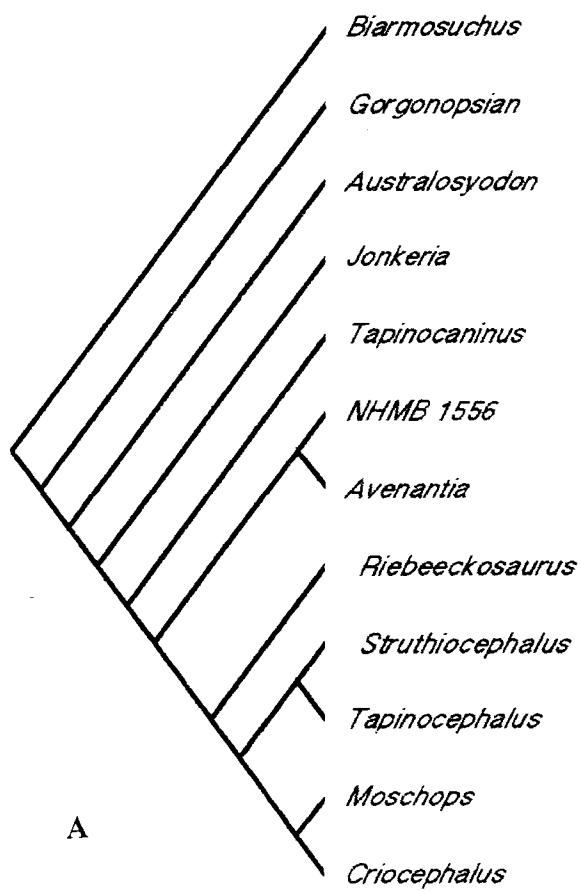
The maximum parsimony analysis recovered two trees (Figure 11a,b) with a length of 54 steps, consistency index (CI) of 0.778, CI excluding uninformative characters of 0.769, homoplasy index (HI) of 0.222, HI excluding uninformative characters of 0.231, retention index (RI) of 0.854 and a rescaled consistency index (RC) of 0.664. The strict consensus topology (Figure 11c)

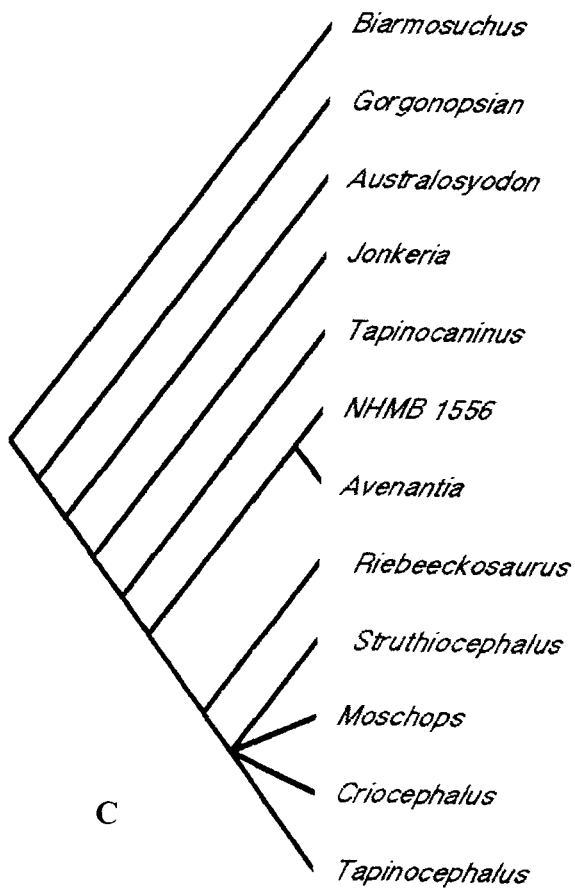
is the least preferred because there is no resolution on the phylogenetic positions of the derived taxa *Struthiocephalus*, *Moschops*, *Criocephalus* and *Tapinocephalus*.

In both trees (Figure 11a, b) NHMB1556 is closely related to *Avenantia* and both genera are considered the least derived tapinocephalid dinocephalians. All the tree topologies show that Anteosauridae and Tapinocephalidae are the most primitive and most derived dinocephalian families respectively, which agrees with literature (Boonstra 1969; Hopson and Barghusen 1986; Rubidge and van den Heever 1997). *Australosyodon* came out as the most primitive member of the Dinocephalia, but there are contrasting hypotheses on the most derived member as both *Criocephalus* and *Tapinocephalus* are jointly considered as the most derived. In regard to tapinocephalid dinocephalians, the analysis supported the view that *Tapinocaninus* is the most primitive (Rubidge 1991) and both *Criocephalus* and *Tapinocephalus* the most derived.

Tree decay analysis (Bremer 1988) indicated that the hypothesised phylogenetic positions of dinocephalians are reasonably supported, requiring at least two steps to break. The interrelationships among the tapinocephalines are however less stable, collapsing only after one step. The proposed phylogeny of the tapinocephalines can be improved with more taxa and characters. The increase in characters is largely limited by the poor state of preservation of the fossils.







**Figure 11.** Interrelationships of dinocephalian genera. **A**, first tree, **B**, second tree; **C**, consensus tree.

**CHAPTER 7: CONCLUSION**

Although the tapinocephalid *Criocephalus* has been known from Zimbabwe more than half a century (Boonstra 1946, 1968, 1969; King 1988) only very recently has the presence of a diverse dinocephalian fauna from the Madumabisa Mudstone Formation of Zimbabwe been recognised (Lepper *et al.* 2000). The recognition of a primitive tapinocephalid dinocephalian in Zimbabwe is further proof of the existence of a diverse dinocephalian fauna. Although the remains of this dinocephalian are fragmentary, further fieldwork will undoubtedly reveal more specimens and help to fill the biogeographic distribution gap, which exists between the dinocephalians of Gondwana and Laurasia.

Cladistic analysis confirmed that *Tapinocanius* is the most primitive tapinocephaline dinocephalian (Rubidge 1991), but there was no phylogenetic resolution on the advanced forms as *Criocephalus* and *Tapinocephalus* are jointly considered the most derived forms. The Zimbabwean specimen and *Avenantia* are more derived than *Tapinocanius* but possess the following primitive tapinocephaline characters: narrow intertemporal region and large surface area for muscle attachment. However NHMB1556 differs from other primitive forms in that its squamosal has a groove below its dorsal contact with the parietal on the posterior border of the temporal fenestra, the suture between the squamosal and parietal on the posterior border of the temporal is low, vomer forms the anterior margin of the interpterygoidal vacuity and the basisphenoid is semi-circular anteroventrally.

The available material strongly suggests that NHMB1556 represents a new taxon, perhaps even at generic level. Because of the incomplete nature of the skull it was however decided not to assign NMHB1556 to a tapinocephalid subfamily and was also considered undesirable to formally erect a new genus for it until more and better-preserved material becomes available.

## REFERENCES

- ANDERSON, J.M. and CRUICKSHANK, A.R.I. 1978. The biostratigraphy of the Permian and the Triassic. Part 5. A review of the classification and distribution of Permo-Triassic tetrapods. *Palaeont. afr.* **21**, 15-44.
- BARBER, B. 1986. The Madumabisa Mudstone Formation in the Matura Hill Borehole, Wankie Coal Locality. *Ann. Zimbabwe geol. Surv.* **X11**, 14-17.
- BOND, G. 1952. Evidence of glaciation in the Lower Part of the Karoo System in southern Rhodesia. *Trans. Geol. Soc. S. Afr.* **55**, 1-12.
- 1965. Some new fossil localities in the Karoo System of Rhodesia. *Arnoldia*. **2**(11), 1-4.
  - 1968. The flora of the Black Shale and Coal Group (K<sup>2</sup>) in the mid-Zambezi basin. *Arnoldia* **3**(38), 1-2.
  - 1970. Dwyka Series in Rhodesia. *Proc. Geol. Assoc.* **81**(3), 463-472.
  - 1973. The palaeontology of Rhodesia. *Bull. geol. Surv. Rhod.* **70**, 1-121.
  - and STOCKLMAYER, V.R.C. 1967. Possible ice-margin fluctuations in the Dwyka Series in Rhodesia. *Palaeogeogr., Palaeoclimatol., Palaeocol.* **3**, 433-446.
- BOONSTRA, L.D. 1934. On an aberrant gorgonopsian *Burnetia mirabilis*. *S. Afr. J. Sci.* **31**, 462-470.
- 1936a. Some features of the cranial morphology of the tapinocephalid dinocephalians. *Bull. Am. Mus. Nat. Hist.* **72**, 75-98.
  - 1936b. The cranial morphology of some titanosuchid dinocephalians. *Bull. Am. Nat. Hist.* **72**, 99-116.
  - 1946. Report on some of reptilian fossils from Gunyanka's Kraal, Bus Valley. *Trans. Rhod.*

*Sci. Ass.* **41**, 46-49.

1953a. A suggested clarification of the taxonomic status of the South African titanosaurs.

*Ann. S. Afr. Mus.* **42**, 19-28.

1953b. Cranial morphology and taxonomy of the tapinocephalid genus *Struthiocephalus*.

*Ann. S. Afr. Mus.* **42**, 32-53.

1954a. The cranial structure of the titanosaur *Anteosaurus*. *Ann. S. Afr. Mus.*

**42**, 108-148.

1954b. The smallest titanosaurid yet discovered from the Karoo. *Ann. S. Afr. Mus.*

**42**, 149-156.

1954c. *Parantecosaurus gen. nov.*: a titanosaurid reptile. *Ann. S. Afr. Mus.*

**42**, 157-159.

1955. *Struthiocephalus*: a new dinocephalian. *Ann. S. Afr. Mus.* **42**, 180-184.

1956. The skull of *Tapinocephalus* and its near relatives. *Ann. S. Afr. Mus.* **43**, 137-169.

1957. The moschopid skulls in the South African Museum. *Ann. S. Afr. Mus.* **44**, 15-38.

1962. The dentition of the titanosaurid dinocephalian. *Ann. S. Afr. Mus.* **46**, 57-112.

1963a. Early dichotomies in the therapsids. *S. Afr. J. Sci.* **59**, 176-195.

1963b. Diversity of within the South African Dinocephalia. *S. Afr. J. Sci.* **59**, 196-207.

1968. The braincase, basicranial axis and median septum in the Dinocephalia. *Ann. S. Afr.*

*Mus.* **50**(10), 195-273.

1969. The fauna of the *Tapinocephalus* Zone (Beaufort Beds of the Karoo). *Ann. S. Afr.*

*Mus.* **59**(1), 17-46.

1971. The early therapsids. *Ann. S. Afr. Mus.* **59**(2) 17-40.

- 1972. Discard the names Theriodontia and Anomodontia: A new classification of the Therapsida. *Ann. S. Afr. Mus.* **59**(11), 315-337.
- BREMER, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42**(4), 795-803.
- BRINKMAN, D. 1981. The structure and relationships of the dromasaurs (Reptilia: Therapsida). *Breviora* **465**, 1-34.
- BROOM, R. 1903. On the evidence of a new species of *Titanosuchus*. *Ann. S. Afr. Mus.* **4**, 142-143.
- 1905. On the use of the term Anomodontia. *Rec. Albany Mus.* **1**, 275-278.
  - 1910. A comparison of the Permian reptiles of North America with those of South Africa. *Bull. Am. Mus. Nat. Hist.* **28**, 197-234.
  - 1911. On some of new South African Permian reptiles. *Proc. zool. Soc. Lond.* **1911**, 1073-1082.
  - 1923. On the structure of the skull in the carnivorous dinocephalian reptiles. *Proc. zool. Soc. Lond.* **1923**, 661-684.
  - 1932. *The mammal-like reptiles of South Africa and the origin of mammals.* 376. H and G Witherby, London.
- CHENG, Z. and LI, J. 1997. A new genus of primitive dinocephalian – The third report on Late Permian Dashankou lower tetrapod fauna. *Vertebrate Palasiatica.* **35**, 35-43.
- CHUNDINOV, P.K. 1965. New facts about the fauna of the Upper Permian of the U.S.S.R. *J. Geol.* **73**, 117-130.
- 1968. A new dinocephalian from the Cisuralian region (Reptilia, Therapsida, Upper Permian). *Postilla* **121**, 1-20.

- CLUVER, M.A. and KING, G.M. 1983. A reassessment of the relationships of Permian Dicynodontia (Reptilia, Therapsida) and a new classification of dicynodonts. *Ann. S. Afr. Mus.* **91**(3), 195-273.
- COLBERT, E.H. 1986. Therapsids in Pangaea and their contemporaries and competitors. 133-145. In: Hotton, N., MacLean, P.D., Roth, E.C. (eds.). *The ecology and biology of mammal-like reptiles*. Smithsonian Institution Press, Washington.
- GREGORY, W.K. 1926. The skeleton of *Moschops capensis* Broom, a dinocephalian reptile from the Permian of South Africa. *Bull. Am. Mus. Nat. Hist.* **56**, 179-251.
- HAUGHTON, S.H. 1929. On some new therapsids genera. *Ann. S. Afr. Mus.* **28**, 55-78.
- and BRINK, A. S. 1954. A bibliographical list of Reptilia from the Karoo beds of Africa. *Palaeont. afr.* **2**, 1-187.
- HOPSON, J.A. 1967. Mammal-like reptiles and the origin of mammals. *Discovery* **2**(2), 25-33.
- 1991. Systematics of the nonmammalian Synapsida and implications for patterns of evolution in synapsids. 635-692. In: Schultze H-P and Trueb L. (eds.). *Origins of higher groups of tetrapods*. Comstock Publishing Associates. London.
- and BARGHUSEN, H.R. 1986. An analysis of therapsids relationships. 83-106. In: Hotton, N., MacLean, P.D., Roth, E.C. (eds.). *The ecology and biology of mammal-like reptiles*. Smithsonian Institution Press, Washington.
- HOTTON III, N. 1991. The nature and diversity of synapsids: prologue to the origin of mammals. 598-634. In: Schultze H-P and Trueb L. (eds.). *Origins of higher groups of tetrapods*. Comstock Publishing Associates. London.
- IVACHNENKO, M.F. 1994. A new Late Permian dromasaurian (Anomodontia) from Eastern



Europe. *Palaeont. J.* **28**, 96-103.

- 1996. Primitive anomodonts, venjukovioids from the Late Permian of Eastern Europe. *Palaeontol. J.* **30**, 77-84.

- 2000. Estemmenosuchids and primitive theriodonts from the Late Permian. *Paleont. J.* **34**, 184-192

KEMP, T.S. 1982. *Mammal-like reptiles and the origin of mammals*. Academic Press. London.

- 1988. Interrelationships of the Synapsida. 1-22. In: Benton, M.J. (eds.). *The phylogeny and classification of the tetrapods. 2 Mammals*. Syst. Assoc. Spec. **35B**.

KERMACK, D.M. and KERMACK, K.A. 1984. *The evolution of mammalian characters*. Croom, Helm, London.

KEYSER, A.W. and SMITH, R.M.H. 1978. Vertebrate biozonation of the Beaufort Group with special reference to the western Karoo Basin. *Ann. geol. Surv. S. Afr.* **12**, 1-36.

KING, G.M. 1988. Anomodontia. 1-174. In: Wellnhofer, P. (ed.). *Encyclopaedia of paleoherpetology*. **17C**. Gustav Fischer Stuttgart.

- 1994. The early anomodont *Venjukovia* and the evolution of the anomodont skull. *J. Zool. Lond.* **232**, 651-673.

KITCHING, J.W. 1977. The distribution of the Karoo vertebrate fauna. *Memoirs of the Bernard Price Institute for Palaeontological Research*, Uni. Witwatersrand. 1, 1-133.

LACEY, W.S. 1959. Occurrence of preserved Glossopteridian frutifications in Rhodesia and Nyasaland. *Nature* **184**, 1592-1593.

- 1961. Studies in the Karoo floras of Rhodesia and Nyasaland. *Proc. Trans. Rhod. Sci. Assoc.* **49**, 26-53.

- LANGER, M.C. 1998. Are dinocephalians present in the Brazilian Upper Permian? *J. Afr. Earth Sci.* **27**(1A), 129-130.
- LEPPER, J. 1992. The Lower Karoo in the Mid-Zambezi Basin (Zimbabwe). *Geol. Jahrb. B.* **82**, 3-38.
- , RAATH, M.A. and RUBIDGE, B.S. 2000. A diverse dinocephalian fauna from Zimbabwe. *S. Afr. J. Sci.* **96**, 403-405.
- LI, J., RUBIDGE, B.S. and CHENG, Z. 1996. A primitive anteosaurid dinocephalian from China – implications for the distribution of early therapsid faunas. *S. Afr. J. Sci.* **92**, 252-253.
- LOOCK, J.C., BRYNARD, R.H.J., HEARD, R.G., KITCHING, J.W., and RUBIDGE, B.S. 1994. The stratigraphy of the Lower Beaufort Group in an area north of Lainsburg, South Africa. *J. Afr. Earth Sci.* **18**(3), 185-195.
- MACGREGOR, A.M. 1946. Preliminary note on the discovery of reptilian fossils in the Madumabisa shales of the Sebungwe District. *Trans. Rhod. Scient. Assoc.* **41**, 1-9.
- MODESTO, S.P., RUBIDGE, B. and WELMAN, J. 1999. The most basal anomodont therapsid and the primacy of Gondwana in the evolution of the anomodonts. *Proc. R. Soc. Lond* **B266**, 331-337.
- and RUBIDGE, B.S. 2000. A basal anomodont therapsid from the Lower Beaufort Group, Upper Permian of South Africa. *J. Vert. Paleontol.* **20**(3), 515-521.
- OLSON, E.C. 1962. Late Permian terrestrial vertebrates, USA and USSR. *Trans. Am. Phil. Soc.* **52**, 3-224.
- 1986. Relationships and ecology of the early therapsids and their predecessors. 47-60. In: Hotton, N., MacLean, P.D., Roth, E.C. (eds.). *The ecology and biology of mammal-like*

*reptiles*. Smithsonian Institution Press, Washington.

OWEN, R. 1879. Description of fragmentary indications of a huge kind of theriodont reptile (*Titanosuchus ferox* Ow.) from Beaufort West, Gouph Tract, Cape of Good Hope.

*J. geol. Soc. Lond.* **35**, 189-198.

PARRISH, J.M., PARRISH, J.T and ZIEGLER, A.M. 1986. Permian-Triassic paleogeography and paleoclimatology and implications for therapsid distribution. 109-132. In: Hotton, N., MacLean, P.D., Roth, E.C. (eds.). *The ecology and biology of mammal-like reptiles*. Smithsonian Institution Press, Washington.

RIXON, A.E. 1976. *Fossil animal remains: their preparation and conservation*. 304. Athlone Press, Uni. London.

ROMER, A.S. 1956. *Osteology of reptiles*. 772. Uni. Chicago Press.

- 1966. *Vertebrate palaeontology*. 3<sup>rd</sup> ed. 468. Uni. Chicago Press, Chicago.

- 1970. Tetrapod vertebrates and Gondwanaland. 111-124. In: Haughton S.H. (ed.). *Second Gondwana Symposium: Proceedings and papers*. Council for Scientific and Industrial Research. Pretoria.

ROWE, T. 1988. Definition, diagnosis and origin of Mammalia. *J. Vert. Palaeont.* **8**(3), 241-264.

RUBIDGE, B.S. 1987. South Africa's oldest land-living reptiles from the Ecca-Beaufort transition in the southern Karoo. *S. Afr. J. Sci.* **83**, 165-166.

- 1988. *A palaeontological and palaeoenvironmental synthesis of the Permian Ecca-Beaufort contact in the southern Karoo between Prince Albert and Rietbron, Cape Province, South Africa*. PhD. Thesis, Uni. Port Elizabeth.

- 1991. A new primitive dinocephalian mammal-like reptile from the Permian of southern

Africa. *Palaeont.* **34**, 547-559.

- 1993. New South African fossil links with the earliest mammal-like reptile (therapsid) faunas from Russia. *S. Afr. J. Sci.* **89**, 460-461.
  - 1994. *Australosyodon*, the first primitive anteosaurid dinocephalian from Upper Permian of Gondwana. *Palaeont.* **37**(3), 579-594.
  - 1995a. Biostratigraphy of the *Eodicynodon* Assemblage Zone. In: Rubidge, B.S. (ed). *Biostratigraphy of the Beaufort Group (Karoo Supergroup) South Africa*. South African Commission for Stratigraphy, Pretoria.
  - 1995b. Did mammals originate from Africa? South African fossils and Russian connection. *Sidney Haughton Memorial Lecture*. **4**. Royal Soc. South Africa, Cape Town.
  - KITCHING, J.W. and VAN DEN HEEVER J.A. 1983. First record of a theriocephalian (Therapsida: Pristerognathidae) from the Ecca of South Africa. *Navors. Nas. Mus. Bloemfontein*. **4**, 229-235.
  - and HOPSON J.A. 1990. A new anomodont therapsid from South Africa and its bearing on the ancestry of Dicynodontia. *S. Afr. J. Sci.* **86**, 43-45.
  - and HOPSON, J.A. 1996. A primitive anomodont therapsid from the base of the Beaufort Group (Upper Permian) of South Africa. *Zool. J. Linn. Soc.* **117**, 115-139.
  - and VAN DEN HEEVER, J.A. 1997. Morphology and systematic position of the dinocephalian *Styracocephalus platyrhynchus*. *Lethaia* **30**, 158-168.
- SEELEY, H.G. 1888. Research on the structure, organisation, and classification of the fossil Reptilia. Part II. On *Pareiasaurus bombidens* (Owen) and the significance of its affinities to amphibians, reptiles and mammals. *Phil. Trans. Roy. Soc.* **179**(B), 59-109.

- 1889. Research on the structure, organisation, and classification of the fossil Reptilia. Part IV. On the anomodont Reptilia and their allies. *Phil. Trans. Roy. Soc.* 180(B), 215-296.
  - 1892. On *Delphinognathus conocephalus* (Seeley) from the middle Karoo beds, Cape Colony, preserved in the South African Museum, Cape town. *Q. J. Geol. Soc. Lond.* **48**, 469-475.
  - 1894. Researches on the structure, organisation and classification of the fossil Reptilia. 1X(1). On the Therosuchia. *Phil. R. Soc.* **B185**, 987-1018.
- SIDOR, C.A. and Hopson, J.A. 1995. The taxonomic status of the Upper Permian eotheriodont therapsids of the San Angelo Formation (Guadalupian), Texas. *J. Vert. Palaeont.* **15**(3), 53A.
- and HOPSON, J.A. 1998. Ghost lineages and “mammalness”: assessing the temporal pattern of character acquisition in the Synapsida. *Paleobiol.* **24**(2), 254-273.
- SIGOGNEAU-RUSSELL, D. 1989. Theriodontia 1: Phthinosuchia, Biarmosuchia, Eotitanosuchia, Gorgonopsia. 1-123. In: Wellnhofer, P. (ed.). *Encyclopaedia of Paleoherpitology*. Gustav Fisher Verlag.
- SIGOGNEAU, D. and CHUNDINOV, P.K. 1972. Reflections on some Russian eotheriodonts (Reptilia, Synapsida, Therapsida) *Palaeoverit.* **5**, 79-109.
- SMITH, R.H.M. and KEYSER, A.W. 1995. Biostratigraphy of the *Tapinocephalus* Assemblage Zone. 6-9. In: Rubidge, B.S. (ed.). *Biostratigraphy of the Beaufort Group (Karoo Supergroup) South Africa*. South Africa Commission for Stratigraphy, Pretoria
- STAGMAN, J.G. 1978. An outline of the geology of Rhodesia. *Rhod. geol. Surv. Bull.* **80**, 1-126.
- VAN DEN HEEVER, J.A. 1994. The cranial anatomy of the early Therocephalia (Amniota: Therapsida). *Ann. Univ. Stellenbosch* **1**, 1-59.

- and GRINE F.E. 1981. Dinocephalian type material in the South African Museum (Reptilia, Therapsida). *Ann. S. Afr. Mus.* **86** (3), 73-114.

WATSON, D.M.S. 1914. The Dinocephalia, an order of mammal-like reptiles. *Proc. zool. Soc. Lond.* **1914**, 749-786.

- 1948. Dicynodon and its allies. *Proc. zool. Soc. Lond.* **118**, 823-877.

- ROMER, A.S. 1956. A classification of therapsids. *Bull. Mus. comp. Zool. Harv.* **114**, 35-98.

WILEY, E.O., SIEGEL-CAUSEY, D., BROOKS, D.R. AND FUNK, V.A. 1991.

*The complete cladistics – a primer of phylogenetic procedures.* Uni. Kansas. Special Publ. **19**, 1-157.

**APPENDIX 1. LIST OF CHARACTERS USED IN CLADISTIC ANALYSIS**

- ✓ 1. Pineal foramen situated on a boss or ridge: present (0), absent (1)
- ✓ 2. Caniniform teeth: present (0), absent (1)
- ✓ 3. Postorbital: thin (0), broad and massive (1)
- ✓ 4. Teeth intermeshing: absent (0), incisors only (1), incisors and postcanines (2)
- ✓ 5. Intertemporal region: broad (0) narrow (1), secondarily widened because of pachyostosis (2)
- ✓ 6. Anteroposterior diameter of temporal fenestra: small (0) large (1), reduced (2)
- ✓ 7. Muscle attachment area outside skull roof: absent (0), present (1), reduced (2)
- ✓ 8. Heels on teeth: absent (0), present on incisor only (1), present on incisor and postcanine (2)
- ✓ 9. Frontal participation on the dorsal orbital border: large (0), small (1), absent (2)
- ✓ 10. Pterygoid teeth: present (0), absent (1)
- ✓ 11. External auditory meatus: vertical (0), sloping anteroventrally (1), horizontal (2)
- ✓ 12. Position of the jaw articulation: behind postorbital (0), below postorbital (1), in front of postorbital (2)
- ✓ 13. Teeth on the palatine bosses: present (0), absent (1)
- ✓ 14. Vomers ventral surface: median trough (0), reduced median trough (1), flat (2) median ridge (2)
- ✓ 15. Anteroventral shape of basisphenoid: rounded (0), pointed (1)
- ✓ 16. Vomer midline suture between nares: absent (0), present (1)
- ✓ 17. Squamosal – jugal suture: below temporal fenestra (0), between orbit and temporal fenestra (1), below orbit (2)
- ✓ 18. Squamosal meeting postorbital: absent (0), present (1)

- ✓ 19. Postorbital bar formed by: postorbital and jugal (0), postorbital and postfrontal (1),  
postorbital only (2)
- ✓ 20. Parietal / frontal ratio: parietal shorter than frontal (0), parietal equal or longer than frontal (1)
- ✓ 21. Position of transverse flange of pterygoid: beneath orbit (0), in front of orbit (1)
- ✓ 22. Frontal reaching dorsal border of temporal fenestra absent (0), present (1)
- ✓ 23. Skull height relative to width: low (0), equal (1) high (2)
- ✓ 24. Snout length / cranial length ratio: snout longer than cranial roof (0), snout shorter than  
cranial roof (1) same length (2)
- ✓ 25. Interorbital width / temporal width ratio: interorbital width half of temporal roof (0),  
interorbital width more than half of temporal (1), interorbital width secondarily reduced to  
half of temporal roof (2)
- ✓ 26. Pachyostosis of postorbital: absent (0), moderate (1), great (2).



## APPENDIX 2. CHARACTER MATRIX

	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	<b>7</b>	<b>8</b>	<b>9</b>
<i>Biarmosuchus</i>	0	0	0	0	0	0	0	0	0
NHMB 1556	1	?	0	?	1	1	1	?	1
<i>Tapinocaninus</i>	1	0	1	1	1	1	1	2	1
<i>Avenantia</i>	0	1	0	2	1	1	1	2	1
<i>Struthiocephalus</i>	0	1	1	2	2	2	2	2	1
<i>Moschops</i>	1	1	1	2	2	2	2	2	1
<i>Criocephalus</i>	1	1	1	2	2	2	2	2	1
<i>Tapinocephalus</i>	1	1	1	2	2	2	2	2	2
<i>Riebeeckosaurus</i>	1	1	1	2	1	1	1	2	1
<i>Jonkeria</i>	?	0	0	1	1	1	1	1	0
<i>Australosyodon</i>	1	0	0	1	1	1	1	1	0
Gorgonopsian	0	0	0	0	0	1	1	1	0
	<b>10</b>	<b>11</b>	<b>12</b>	<b>13</b>	<b>14</b>	<b>15</b>	<b>16</b>	<b>17</b>	<b>18</b>
<i>Biarmosuchus</i>	0	0	0	0	0	0	0	0	0
NHMB 1556	?	1	1	?	2	0	1	1	1
<i>Tapinocaninus</i>	1	1	1	0	1	0	1	1	1
<i>Avenantia</i>	1	1	1	1	2	1	1	2	1
<i>Struthiocephalus</i>	1	2	2	1	2	1	1	2	1
<i>Moschops</i>	1	2	2	1	2	1	1	1	1
<i>Criocephalus</i>	1	2	2	1	2	1	1	1	1
<i>Tapinocephalus</i>	1	2	2	1	2	1	1	2	1
<i>Riebeeckosaurus</i>	1	2	?	?	?	?	1	?	?
<i>Jonkeria</i>	?	1	1	?	?	1	1	1	1
<i>Australosyodon</i>	0	1	0	0	0	1	1	0	0
Gorgonopsian	0	0	0	0	3	1	0	0	0
	<b>19</b>	<b>20</b>	<b>21</b>	<b>22</b>	<b>23</b>	<b>24</b>	<b>25</b>	<b>26</b>	
<i>Biarmosuchus</i>	0	0	0	0	0	0	0	0	
NHMB 1556	?	1	1	0	1	?	1	1	
<i>Tapinocaninus</i>	1	0	0	0	0	1	1	2	
<i>Avenantia</i>	1	1	1	0	1	0	1	1	
<i>Struthiocephalus</i>	1	1	1	0	2	0	1	2	
<i>Moschops</i>	1	1	1	0	2	1	2	2	
<i>Criocephalus</i>	1	1	1	1	2	1	2	2	
<i>Tapinocephalus</i>	1	1	1	1	2	2	2	2	
<i>Riebeeckosaurus</i>	1	?	?	1	1	0	2	2	
<i>Jonkeria</i>	1	0	0	1	1	0	0	0	
<i>Australosyodon</i>	1	0	0	0	0	0	0	0	
Gorgonopsian	2	0	0	0	0	0	2	0	