
PALAEONTOLOGIA

AFRICANA

ANNALS OF THE BERNARD PRICE INSTITUTE FOR
PALAEONTOLOGICAL RESEARCH
UNIVERSITY OF THE WITWATERSRAND
JOHANNESBURG

VOLUME 37, 2001

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ACKNOWLEDGEMENTS

The Bernard Price Institute for Palaeontological Research gratefully acknowledges financial support for its programmes and for publication of this journal by

THE COUNCIL'S RESEARCH COMMITTEE, UNIVERSITY OF THE WITWATERSRAND.
NATIONAL RESEARCH FOUNDATION (NRF)
PALAEO-ANTHROPOLOGY SCIENTIFIC TRUST (PAST)

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INTERPRETIVE PROBLEMS IN A SEARCH FOR MICRO-INVERTEBRATE FOSSILS FROM A NEOPROTEROZOIC LIMESTONE IN NAMIBIA

by

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ABSTRACT

Attention is focussed on a carbonate sequence in the Auros Formation of the Otavi Group in northern Namibia, where several limestone layers are found to have been phosphatised. These contain an abundance of unusual objects, some of which suggest sponge-like microfossils, whereas others superficially resemble bivalved shells. Alternatively they may be pseudofossils - the deceptive products of a phosphatisation process and subsequent diagenetic effects in the limestone. Since this deposit antedates the ca. 590 million-year-old Ghaub or Marinoan glaciation, the presence of any potential metazoan fossils is worth investigating. The objects in question are described and alternative interpretations are discussed.

KEYWORDS: Neoproterozoic, Otavi Group, microfossils, pseudofossils

INTRODUCTION

For the last few years, one of the authors (C.K.B.) has been conducting a search for micro-invertebrate fossils in Proterozoic limestones of Namibia. Many samples of limestone from the Otavi Group in the Otavi-Tsumeb-Grootfontein area were examined in thin section and as acetic acid-treated residues, but recrystallisation of the limestones in the folded Otavi Mountainland appeared to militate against the finding of well preserved microfossils there. In fact, as Martin Pickford (1995) has pointed out, virtually no fossils other than stromatolites have thus far been found in Otavi Group sediments. But, north of the Otavi Mountainland lies the flat, calcrete-covered plain of the Etosha Basin, which apparently represented a Bahamas-type carbonate platform on the Congo Craton in Late Proterozoic times. About 50 km beyond the northern border of the Otavi Mountainland outcrops, and well away from the metamorphic folded belt, some isolated hills make their appearance, through the surrounding calcrete cover, close to the Halali restcamp in the Etosha National Park. Two km east of Halali are the twin peaks of Helio Hill and when C.K.B. examined acetic acid residues of samples of a black grainstone from the base of Helio Hill, he encountered microfossil-like objects that appeared to have been phosphatised. Such objects, referred to here as 'otavias', were later found in similar limestones from the Halali Hill itself and the Halali Quarry, 2 km further west. They are considered in detail in this paper, together with shell-like objects encountered in the Halali Quarry grainstones. Although the Halali outcrops appear on the 1 : 1 000 000 Geological Map of Namibia (1980) as 'Otavi Group -

undifferentiated', it was clearly important to establish just where within the Group's stratigraphy the sequence is positioned. The outcrops were therefore examined in detail in the field by K.-H.H. and C.K.B. and samples were taken at close intervals for carbon isotope analysis and interpretation by A.R.P. and A.E.F. Comparable studies were made on the Abenab Subgroup sequence in the Kaokoveld by K.-H.H. and A.R.P., while confirmation of the presence of calcium phosphate in the microfossil-like objects from the Halali outcrops was provided by J.C. and A.J.B.

As has been pointed out by several specialists in the field of Proterozoic palaeontology who commented on the first draft of this paper, the interpretation of phosphatised objects in limestones of this age is by no means straightforward and is fraught with uncertainties. The purpose of the present paper therefore is to draw attention to, and to discuss such uncertainties in the the Halali context, with the hope that greater interpretive confidence will be possible in the future.

GEOLOGICAL CONTEXT AND CARBON ISOTOPE VALUES

As pointed out earlier (Hoffmann & Prave 1996, p. 77), "the Otavi Group is a thick succession of Neoproterozoic carbonates exposed within the Otavi Foreland fold belt of northern Namibia. It overlies predominantly coarse-grained terrigenous siliciclastic and local volcanic rocks of the Nosib Group and is overlain by fine- to coarse-grained Mulden Group siliciclastic sediments." The extent of Otavi Group outcrops in northern Namibia is shown in Figure 1, while a lithostratigraphic subdivision and correlation of the

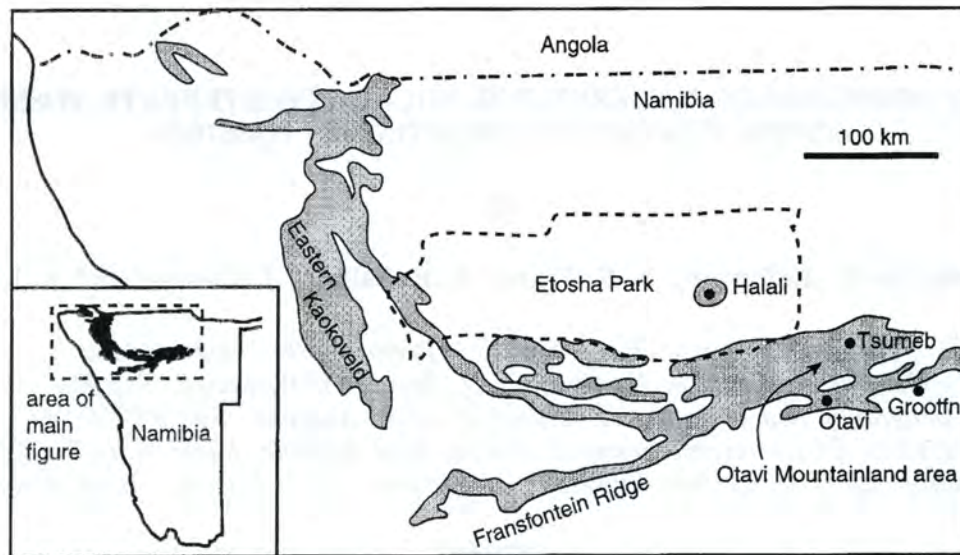


Figure 1. Map of northern Namibia showing the extent of the Otavi Group outcrops (shaded) in the Otavi Mountainland and Kaokoveld. The position of the Halali exposures, on the Etosha plain is also shown.

Eastern Kaokoveld			Otavi Mountainland		
Gp	sGp	Formation	Gp	sGp	Formation
Mulden		Upper	Mulden		Kombat
		Lower			Tschudi
Otavi	Tsumeb	Huttenberg	Otavi	Tsumeb	Huttenberg
		Elandschoek			Elandschoek
		Maieberg			Maieberg
		Keilberg			Keilberg
		△ Ghaub △			△ Ghaub △
	Abenab	Ombaatjie		Abenab	Auros
		Gruis			Gauss
		Rasthof			Berg Aukas
		△ Chuos △			△ Varianto △
	Ombambo	no formal formation subdivisions exist			
Nosib		(transitional)	Nosib		Nabis
		Nabis			

Figure 2. Simplified lithostratigraphic subdivision of Neoproterozoic rocks in northern Namibia (modified slightly from Hoffmann & Prave 1996). Triangles denote the two glaciogenic units. Gp = Group; sGp = sub-Group.

Group in the Otavi Mountainland and the eastern Kaokoveld, as was proposed by Hoffmann & Prave (1996), is given in Figure 2. Just prior to the publication of this subdivision, field studies along the Fransfontein Ridge to the east of the Otavi Mountainland, had demonstrated the presence of *two* stratigraphically and lithologically distinct glacial diamictite intervals, each succeeded by a unique cap-carbonate (Hoffmann 1994; Prave & Hoffmann 1995; Hoffmann & Prave 1996). Prior to this, a single glacial interval only, within the Otavi Group had been known for a considerable time (e.g. Le Roex 1941), but the presence of the two diamictites is now generally accepted.

Although evidence for very severe glacial conditions during Neoproterozoic time has been recognised for 37 years (Harland 1964) and the concept of a 'snowball Earth' was proposed by Kirschvink (1992) almost a decade ago, the application of the 'snowball Earth' scenario to the two glacial episodes reflected by Otavi Group diamictites is much more recent (Hoffman *et al.* 1998a, b). It postulates extreme glacial conditions, even in the equatorial regions, a cessation of continental runoff and virtual shutdown of biological activity. Such conditions would have had a dramatic effect on the evolution of early animals, whose lineages apparently go back considerably further in time on the basis of molecular evidence (Doolittle *et al.* 1996; Wray *et al.* 1996). It is therefore of interest to note that the Halali carbonate sequence with which we are concerned here is found to fall within the Auros Formation of the Abenab Subgroup, below the upper of the two glacial episodes, the Ghaub, which is thought to have occurred about 590 million years ago.

The continuity of the Halali carbonate sequence has been traced in four separate exposures. Where exposed, close to the Halali restcamp, these rocks are found to dip at a shallow angle towards the east, with the result that the oldest part of the profile outcrops in a low ridge at the Halali Quarry, 2 km west of the Halali camp, and this

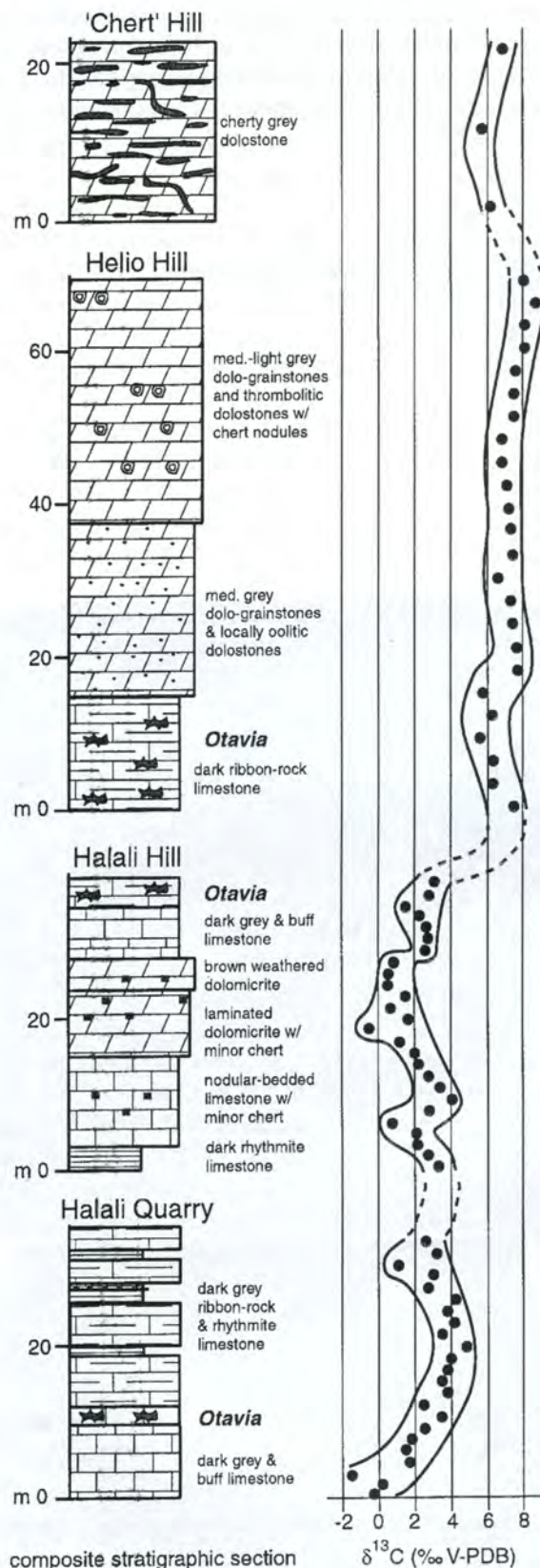


Figure 3. Composite stratigraphic section of the Otavi Group, Halali area, Etosha National Park. Each locality occurs in isolation but stratigraphic continuity is assured because the area is structurally simple and marked by shallow dips, thus the amount of stratigraphic omission between sections is minimal (no more than several metres between each section).

sequence is continued in the 40 m-thick layers of the Halali Hill, situated in the restcamp enclosure. Two kilometres to the east are the prominent twin peaks of Tweekoppies, or Helio Hill, where 60 metres of grey dolostones continue the sequence in this geographically isolated exposure of Otavi carbonates. Finally, about one km farther east is a low ridge of exposures referred to in this paper as "chert hill", which represents the stratigraphically youngest rocks reported upon here.

The lower parts of the Halali profile contain highly distinctive ribbon rocks, or nodular limestones, consisting of interfingered grey and buff layers. These outcrop again 45 km to the south, on the northern fringe of the Otavi Mountainland, just within the boundary fence of the Etosha National Park, opposite the farm Olifantslaagte. Here the ribbon rocks can be seen in stratigraphic context some distance below the Maieberg carbonate, that lies above the Ghaub diamictite elsewhere in the Otavi succession.

Lithological details of the composite Halali profile are shown in Figure 3, together with results of the carbon isotope analyses, the implications of which will now be considered.

The carbonate rocks exposed in the Halali area were measured and sampled by K.-H.H. and C.K.B. Subsequently, A.R.P., accompanied by C.K.B., field checked the sections and sample localities. A total of 77 samples was analysed for C-isotope signatures. Samples were processed following standard techniques and screening process. Samples were microdrilled (in order to minimise lithological differences, only micritic constituents were drilled) and the powders sent to the Scottish Universities Environmental Research Centre for stable isotopic analysis under the supervision of A. E. F. Approximately 1 mg of powder is loaded into a 4 ml glass tube that is sealed and heated at 70° C for 30 minutes. The sample is then placed in the Carbonate Acid Injector and a 3-way needle inserted which pumps He into the sample to purge all atmospheric gases. The He flow and vent are closed, phosphoric acid added and the sample is then allowed to react (at least 8 hours for calcite and at least 24 hours for dolomite). Once the reaction time is completed, the samples are transferred to the Gas Prep Interface Analyser linked to an AP 2003 triple-collector mass spectrometer in which the vented CO₂ is analysed. Calibrated standards are included at every run to check machine precision and reproducibility.

The resulting ¹³C trend is shown in Figure 3 and, combined with the lithofacies character of the rocks, provides convincing evidence for correlating the isolated Halali exposures to the Auros-Ombaatjie Formations (see Figure. 2) of the Otavi Group. As discussed above, the dark grey limestones that are exposed at Halali can be observed to occur subjacent to the Keilberg cap carbonate near the Etosha border fence south of Halali. In addition, the dark grey, foetid ribbon-rocks and rhythmite limestones of the Halali successions are lithologically identical to the pre-Keilberg rocks of the Ombaatjie Formation in the eastern Kaokoveld. In the

Otavi Mountainland, the rocks immediately beneath the Keilberg cap carbonate are laminated dolomicrites and dolograins, facies in every respect similar to those of the Ombaatjie Formation and Halali rocks except that they are dolomitised and recrystallised. Thus, lithostratigraphically there is good evidence to conclude that the Ombaatjie, Auros and Halali rocks are correlatives.

This inference is corroborated by the ^{13}C data. The limestones exposed in the Halali Quarry and Halali Hill localities display a sharp rise from initially slightly negative values to mostly +2 to +4 values; several singular excursions to around 0 punctuate this trend. In the overlying Helio Hill and Chert Hill sections the ^{13}C values rise to +8 and remain uniform through the entirety of the exposed succession. Note that this rise is not attributable to dolomitisation because it initially occurs in the dark grey ribbon-rock limestones in the lower 15 m of the Helio Hill section (these limestones are identical to the underlying ones in the Halali Hill and Quarry sections). This overall trend (sharp rise from slightly negative to moderately positive and then uniformly +8) mirrors that known from the Ombaatjie Formation in the eastern Kaokoveld (e.g. Hoffman *et al.* 1988; Prave, Hoffmann & Fallick unpub. data) and the Auros Formation in the Otavi Mountainland (Prave, Hoffmann & Fallick unpub. data). Thus, the combined lithostratigraphic and chemostratigraphic data for the Halali rocks indicates that these, and any microfossils that they might contain, are pre-Ghaub glaciation in age.

EVIDENCE OF PHOSPHATISATION

As mentioned above, acetic acid dissolution of dark grey grainstone from the base of the Helio Hill revealed objects that superficially appeared to have been phosphatised. Examples of these objects, in the form of sponge-like 'Otavias' and shell-like 'Halalias', were mounted on SEM stubs and subjected to an EDS process (Energy-dispersive Spectrometry), linked to a JEOL 5800LV Scanning Electron Microscope at the University of Pretoria's Electron Microscopy Unit, by two of the authors, J.C. and A.J.B. As a control, the same procedure was carried out on an Early Cambrian 'small shelly' tubular fossil, dissolved from a sample of Ajax Limestone from the Aroona area of South Australia. The phosphatisation of such fossils has been documented by Bengtson *et al.* (1990). The elemental composition of the three samples mentioned here is shown in Figure 4 a - c, from which it can be seen that the peaks for Calcium and Phosphorus are virtually identical for the three samples. These results are taken to indicate that the two kinds of Halali objects, be they micro- or pseudo-fossils, have been preserved as calcium phosphate. At the same time it should be emphasised that the heights of peaks for any particular element are not a reliable indicator of its actual abundance in the sample being investigated, though the presence of the particular element is documented beyond doubt.

It should be mentioned that this is not the first time that calcium phosphate has been demonstrated in Otavi Group carbonates. In his study of carbonates hosting the Tsumeb ore-body, Hughes (1987) remarked on the presence of calcium phosphate being present both as cryptocrystalline collophane and as crystalline apatite.

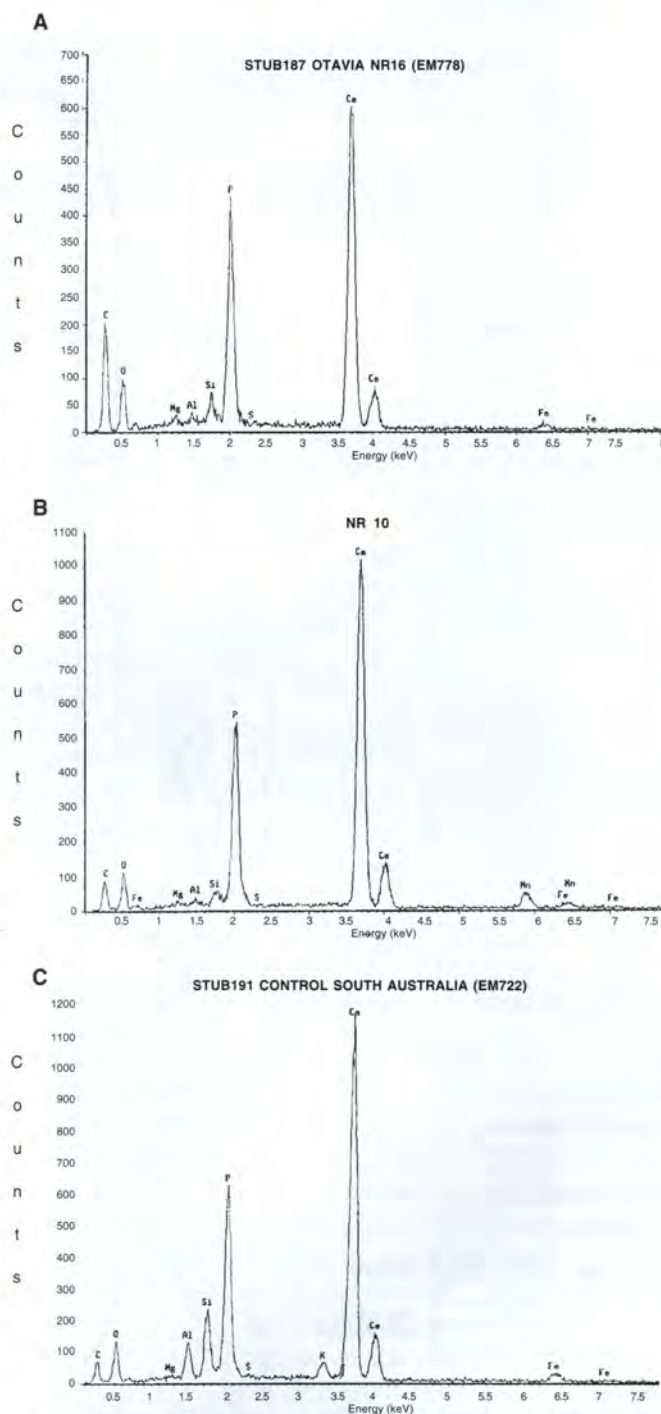


Figure 4. Energy-dispersive spectrometry diagrams documenting the occurrence of elements in samples of: A. The outer envelope of an 'Otavia' specimen from the Halali Quarry section; B. A 'Halalia' shell from the same horizon and C. A control sample, consisting of a 'small shelly' phosphatised tube fossil from the Early Cambrian Ajax Limestone, Aroona, South Australia. It will be seen that Calcium and Phosphorus are represented in a comparable manner in each of the samples by this technique.

PHOSPHATIC "OTAVIA" OBJECTS WITH A SPONGE-LIKE APPEARANCE

For convenience, the objects discussed here are referred to informally as 'otavias', although no formal taxonomic designation is provided at this stage. In the Halali sequence, otavias have been found in three layers of black/grey foetid grainstones – in the Halali Quarry section, at the top of the Halali Hill and within the lowermost few metres of the Helio Hill sequence. They are extremely common in the Quarry section, less so on the Halali Hill and rare at Helio Hill, where the enclosing matrix has been partially dolomitised. In size, otavias vary from 300 micrometers to 3.5 mm in maximum dimension, with the largest specimens occurring in the Quarry section. From here a sample of 200 otavias were individually measured, as well as 90 from the Halali Hill. The greatest dimensions of these specimens were recorded after the individual objects had been manipulated under water over a micrometer scale with the aid of a stereo microscope. Most otavias from the

Quarry section are 500-600 micrometers in their greatest dimension, while those from Halali Hill are typically 300-400 micrometers in length.

As shown in Figure 5, there is a good deal of variation in shape of otavia specimens, though they all share some features in common. When viewed as isolated objects sorted from acetic acid residues under a stereo microscope and then imaged with a scanning electron microscope (in this case, a Hitachi 510 at the Transvaal Museum), each otavia appears as a hollow bag, with one to five comparatively large openings, typically on raised, volcano-like mounds. These penetrate the phosphatic outer wall and lead directly into the internal cavity. The wall is also pierced by numerous smaller openings that generally lead into a "peripheral labyrinth" (for want of a better term), shown in Figure 6. This system of irregularly interlinked spaces is present beneath some parts of the outer wall and is variable in its extent; it also has connections with the internal cavity.

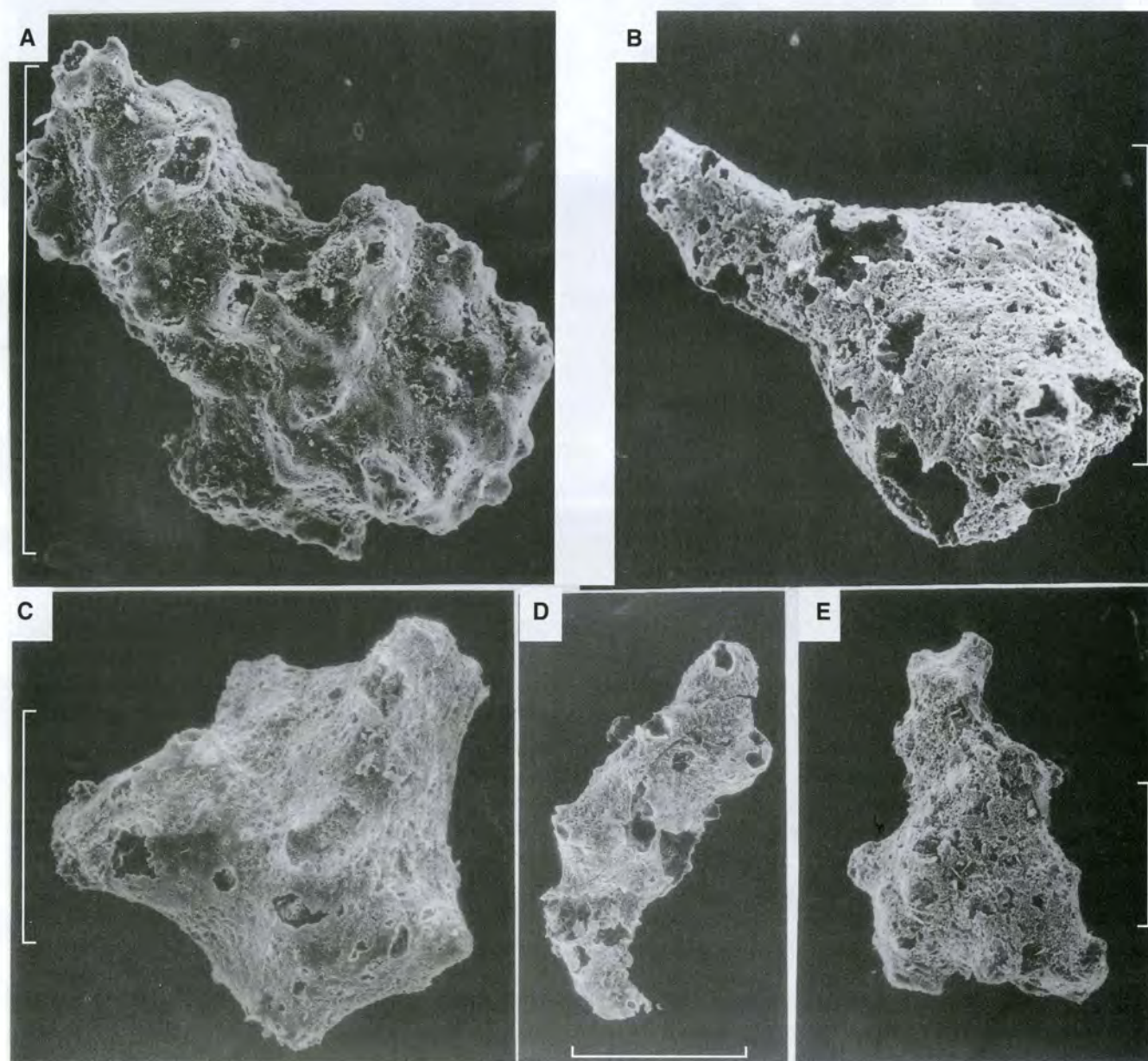


Figure 5. SEM images of 'otavia' objects recovered from acetic acid residues of Otavi limestone; A and B are from the base of Helio Hill, the others come from the Halali Quarry section. All scale bars represent 200 micrometres.

In thin sections, as shown in Figure 7, the outer envelope and peripheral labyrinth typically appear dark, or almost opaque; the walls of these structures are composed of calcium phosphate in an amorphous or cryptocrystalline form. Thin sections show the interior of the otavia structure to be filled with crystalline calcium carbonate, very similar to that of the surrounding matrix, which can perhaps best be described as a sparite.

In view of the superficial similarity in appearance of these objects to small sponges, special attention has been given to the outer walls for the possible presence

of spicules, characteristic of many later sponges. Elongate crystals do occur occasionally in the walls, but they are not convincing as spicules and are more likely to be inorganic with a diagenetic origin.

In an earlier draft of this paper, one of the authors (C.K.B.) attempted an interpretation of the otavia structures, suggesting that they were phosphatised fossils of small calcareous sponges (Alternative A below). The draft was sent for comment to various specialists on Proterozoic palaeontology and valuable comments were received from Stefan Bengtson, Andrew Knoll and Bruce Runnegar, necessitating a

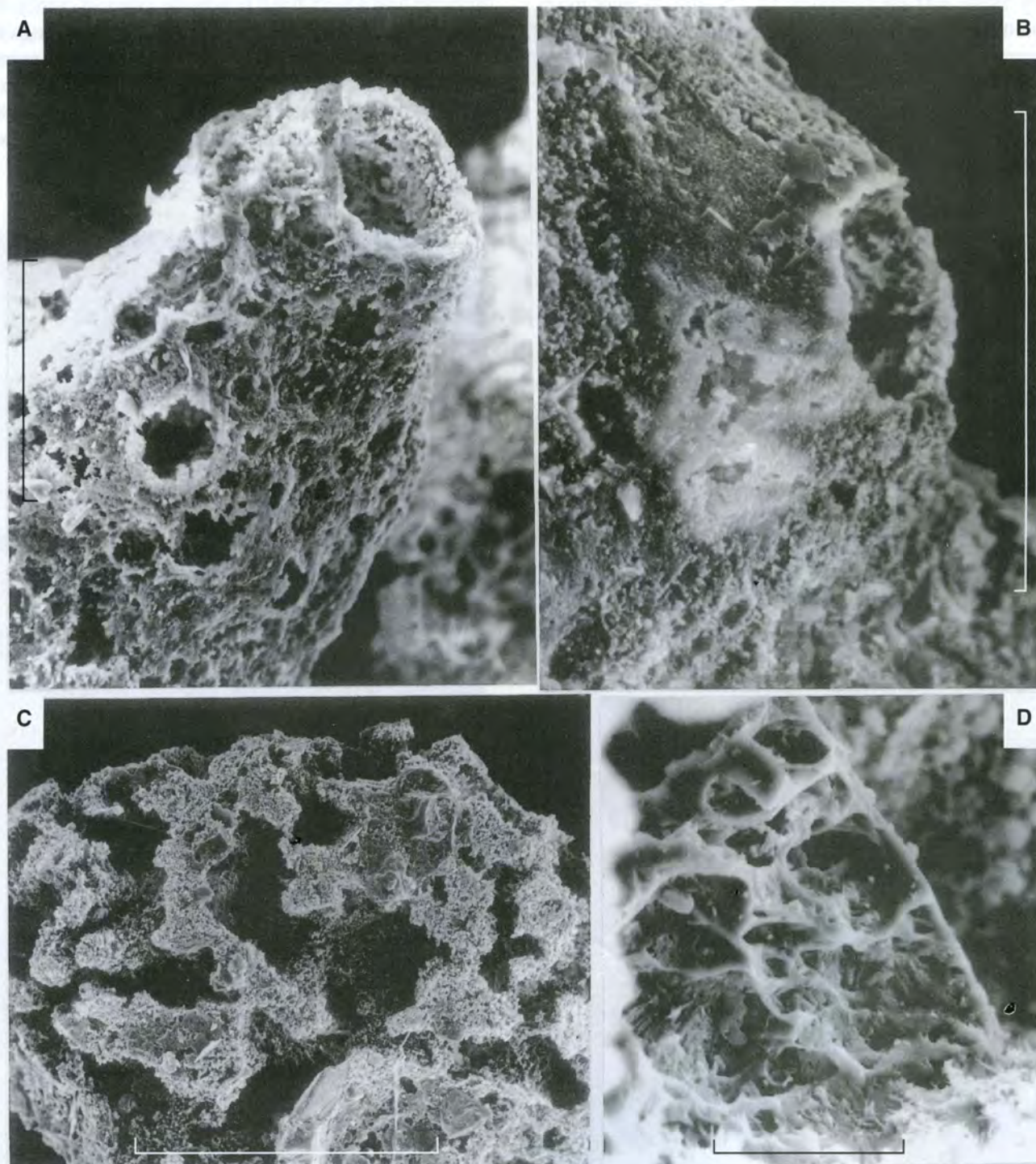


Figure 6. SEM images of 'otavia' objects from the Halali sequence. A & B show detail of openings through the outer envelope on raised eminences; scale bars each represent 50 micrometres. C & D show detail of the 'peripheral labyrinth', where the outer envelope has been removed; the scale bar for C represents 200 micrometres; that for D is 20 micrometres.

revision of some of the proposals made in the draft. These are taken into account in Alternative B, to be presented shortly, while a third possibility is expressed in Alternative C. Studies will continue on the otavias from the Halali sequence and a more firmly based interpretation may be possible in the future.

Alternative A

This interpretation assumes that an otavia existed originally as a multicellular sponge-like organism in the form of a hollow bag, the organic walls of which were penetrated by one or several larger openings, typically 25 - 200 micrometers in diameter and usually situated on raised eminences. These connected directly with the

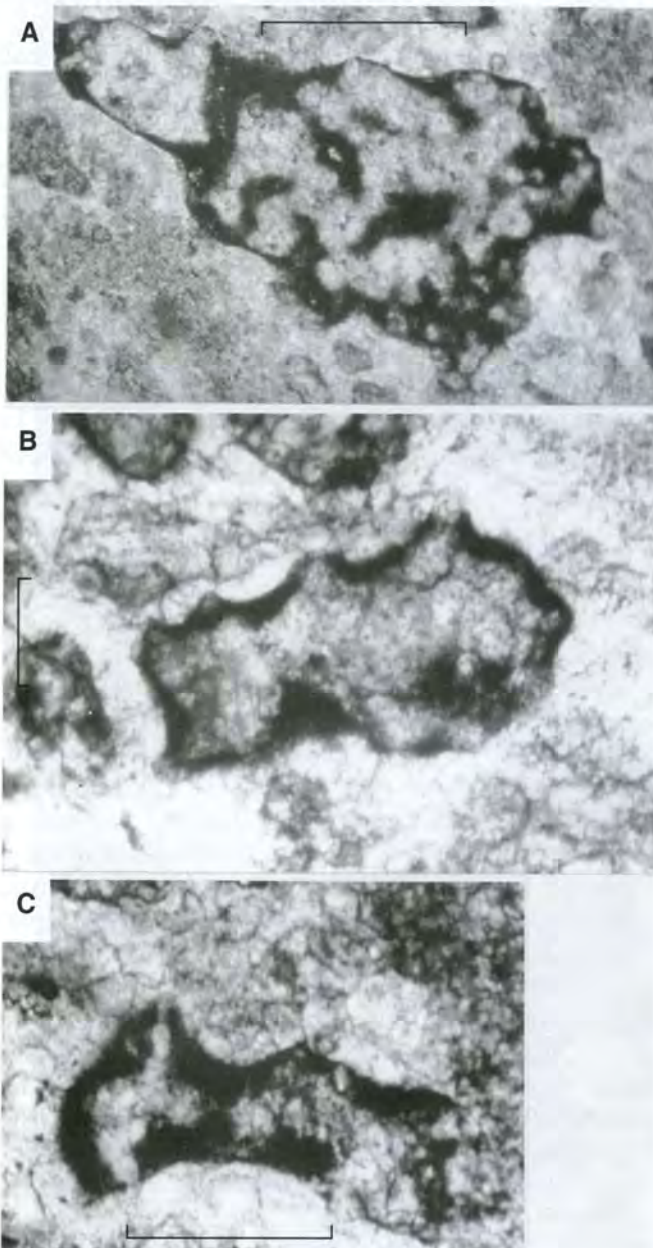


Figure 7. Thin sections of three 'otavia' objects. The black areas represent the extent of the 'peripheral labyrinths', which may fill depressions among composite microphytolite grains, according to one interpretive alternative. See text for details. Scale bars represent the following. A: 1 mm; B: 200 micrometres; C: 500 micrometres.

internal cavity and would have been the equivalent of the exhalent oscula of later sponges. Numerous smaller holes in the outer wall, representing incurrent pores or ostia, typically led into an irregular 'peripheral labyrinth' of interlinked chambers of variable extent, within some parts of the outer wall. These chambers in turn had connections with the internal cavity and could be interpreted as the paragastric cavities of sponges, in which flagellated collar cells were originally housed.

In his comment on this interpretation, Bruce Runnegar has reservations about the 'peripheral labyrinth' being of organic origin. He writes (pers. comm.): "The meshwork of phosphate is sponge-like but it is also the sort of structure one might expect to find in phosphate nodules formed inorganically". This is an observation that clearly needs to be taken seriously.

Another reservation, expressed by Stefan Bengtson (pers. comm.), is that the overall size of the otavias is too small for these to have functioned properly as sponges. In particular, he points out that there are critical lower limits for the size of incurrent pores or ostia, if these are to function effectively as the entry points of water streams carrying potential food items. He observes (pers. comm.): "The force necessary to pump water through a tube is inversely proportional to the 4th(!) Power of its diameter (the Hagen-Poiseuille equation). In other words, resistance increases dramatically with diminishing size, and a 2 micrometer tube needs $5^4=625$ times as much pressure as a 10 micrometer one to maintain the same flow, and $5^8 \approx 400,00$ times as much as a 50 micrometer one. Sponges are basically suspension feeders, and ostia this small (ie. about 10 microns across) would exclude most suspended cellular material from entering the system. Inhalent canals are typically lined with choanocytes, which are about 5-10 microns apart in diameter. Ostia down to 2 microns in diameter would be out of proportion with even the smallest inhalent canals."

Another reservation, expressed both by Bengtson and Knoll (pers. comm.), concerns the conclusion inherent in this interpretation, that the interior of the otavia "bag" was, in fact, empty prior to fossilisation. Bengtson suggests that the phosphatic 'skin' might have surrounded a solid structure. He writes (pers. comm.): "Looking at your thin sections and SEMs, I rather have the impression of irregular galleries of calcium carbonate that have been enveloped in calcium phosphate, and that the protruding necks with the "oscula" are places where the enveloped calcium carbonate has been sticking out".

This comment leads naturally to the consideration of 'microphytolites', central to Alternative B, a matter raised by Knoll and clearly critical to the understanding of Proterozoic objects of this kind.

Alternative B

In their paper on Late Proterozoic sediments from Spitsbergen, Swett & Knoll (1985 p. 341) provide the following information about microphytolites: "In the Soviet palaeontological literature the term

"microphytolite" is used to embrace a wide variety of carbonate grain morphologies ranging from fine sand to gravel in size and exhibiting highly variable shapes and internal structures. Morphologies that fall within this group include ooids, small oncolites, grapestones, algal lumps, and other, more problematic intraclasts; some have been assigned Linnean binomials and used in biostratigraphy (e.g., Raaben and Zabrodin 1972)". They point out that microphytolites are known in various upper Proterozoic carbonates from many parts of the world and, although they do occur occasionally in modern carbonate environments, they are not common there. The reason for this is that, in a microphytolite, a variety of irregular grains is held together by a bacterial and/or algal film and, in the contemporary context, such a film tends to be consumed by grazing metazoans, causing the individual grains to separate. The overall shape of a composite microphytolite aggregate can be very irregular with projections and deep embayments in connection with which Swett & Knoll (1985) remarked: "As viewed in thin section, external shapes may be extremely elongate (L:W > 20:1) or compact (L:W ~ 1:1)".

It is of interest to note that microphytolite grains provide some information of the turbulence of the water in which they formed. Where water movement is sufficient to regularly roll carbonate grains around on the sea floor, oolitic or pisolitic grainstones can develop. In conditions of intermediate turbulence, microphytolites might well form, where the composite grains are occasionally moved, but not with sufficient regularity to acquire oolitic coatings. Finally, in tranquil aqueous environments, continuous microbial mats can develop to cover the sea floor, incorporating any microphytolites that may happen to be there. Adolf Seilacher (eg. 1999) has stressed the importance of biomats to the existence of the unusual 'Ediacaran' fauna that dominated shallow marine environments during terminal Neoproterozoic times. Such biomats disappeared with the advent of abundant surface-feeding and burrowing metazoans in Cambrian times.

Alternative B postulates that an otavia is essentially no more than a microphytolite that has acquired a phosphatic coating. Deep embayments between individual grains were originally filled with adhering bacteria, cyanobacteria or other algae and their substance was phosphatised at the time that the phosphatic envelope developed. The entire otavia structure is therefore biological only in the sense that calcium phosphate replaced the slime which served as the 'glue' for the component microphytolitic grains. Large openings in the phosphatic envelope were places where parts of grains protruded; small openings represented nothing more than defects in the envelope's continuity.

Alternative C

This interpretation takes into account the very considerable role that microphytolites played in Neoproterozoic grainstones and acknowledges that these were very likely the nuclei upon which otavia

structures were built. However, in Alternative C it is speculated that the deep embayments, present in some of the microphytolite complex structures, could well have been the ideal microhabitats that promoted the evolution of the first encrusting proto-sponges. These rather loosely coordinated 'multicellular' organisms must have started as social choanoflagellates, such as still may be found in contemporary habitats, and it is suggested that these could have thrived in the deep recesses among microphytolite grains. Selective pressures may have favoured those colonies that increased their 'multicellular' tendency, promoting a coordinated flow of water, with its food particles, past the food-gathering collar cells. This would have involved the development of an outer envelope with incurrent and excurrent openings and a series of interlinked chambers in which flagellated cells were housed.

Close examination of otavia structure suggests that some of the large openings, on their raised mounds, are not simply places where microphytolite grains protruded, or where the phosphatic envelope was defective, but were biological structures. This possibility will be considered further in the future as the research project proceeds.

OIDS WITH PHOSPHATIC RIMS AND THE GENESIS OF 'HALALIA' SHELLS

In the otavia-rich grainstone of the Halali Quarry section, complete ooids occasionally occur, typically 3 - 4 mm in diameter. These have laminated outer shells of calcium phosphate, a situation that has been described elsewhere previously, as, for instance, in Lower Cambrian sediments of Spitsbergen (Swett & Crowder 1982). As complete spheroids, however, they are rare in the Halali grainstones, when compared to the relatively common pieces of broken ooids such as those shown in Figure 8A, B. These pieces consist of an outer, often laminated shell of calcium phosphate, around the remains of the micritic 'ball' that the shell enclosed. Very frequently the pieces of outer shell have separated completely from their original cores and these phosphatic shell pieces are seen in abundance in some layers of the grainstone. In thin section, the micritic interiors of the ooids typically appear dark or opaque. What caused the ooids to break up is debatable, but there are indications that the pellet-like micritic cores of some ooids have been partially removed by diagenetic dissolution causing pieces of the outer shells to collapse inwards upon themselves. Results of this process can be seen in thin sections of oolites (Figure 9A) from the Ombaatjie Formation in the eastern Kaokoveld, of approximately equivalent age to the Halali carbonates. As shown in Figure 9B, pieces of the outer shells remain in various degrees of apposition to one another, even though the fine-grained filling has been partially removed. In the thin sections and acetic acid residues from the Halali Quarry grainstone it is not unusual to see shell pieces in bivalve-like apposition, as shown in Figure 8C, D and these are referred to (by C.K.B.) as halalias. Initially it was thought that some of these could have

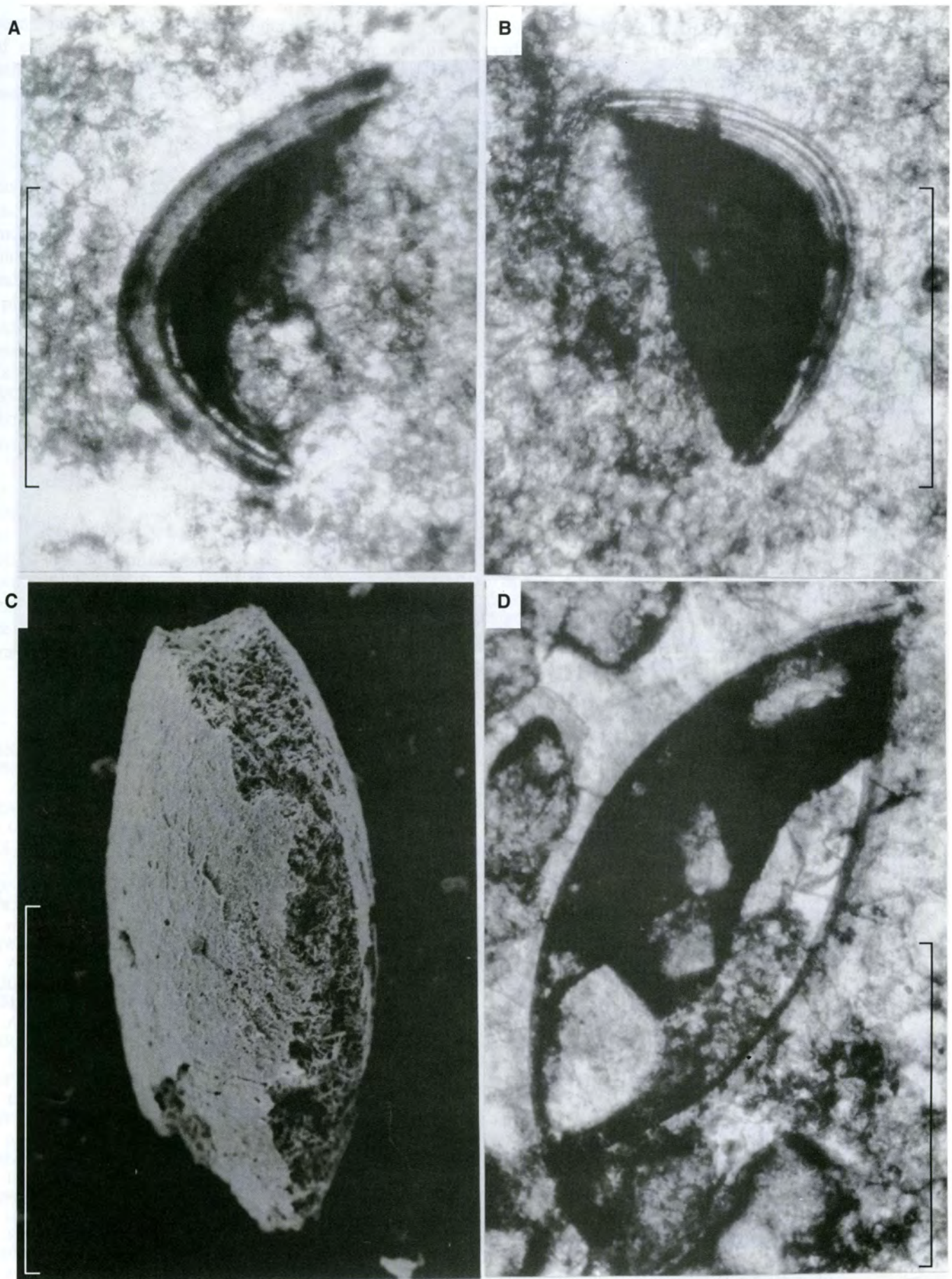
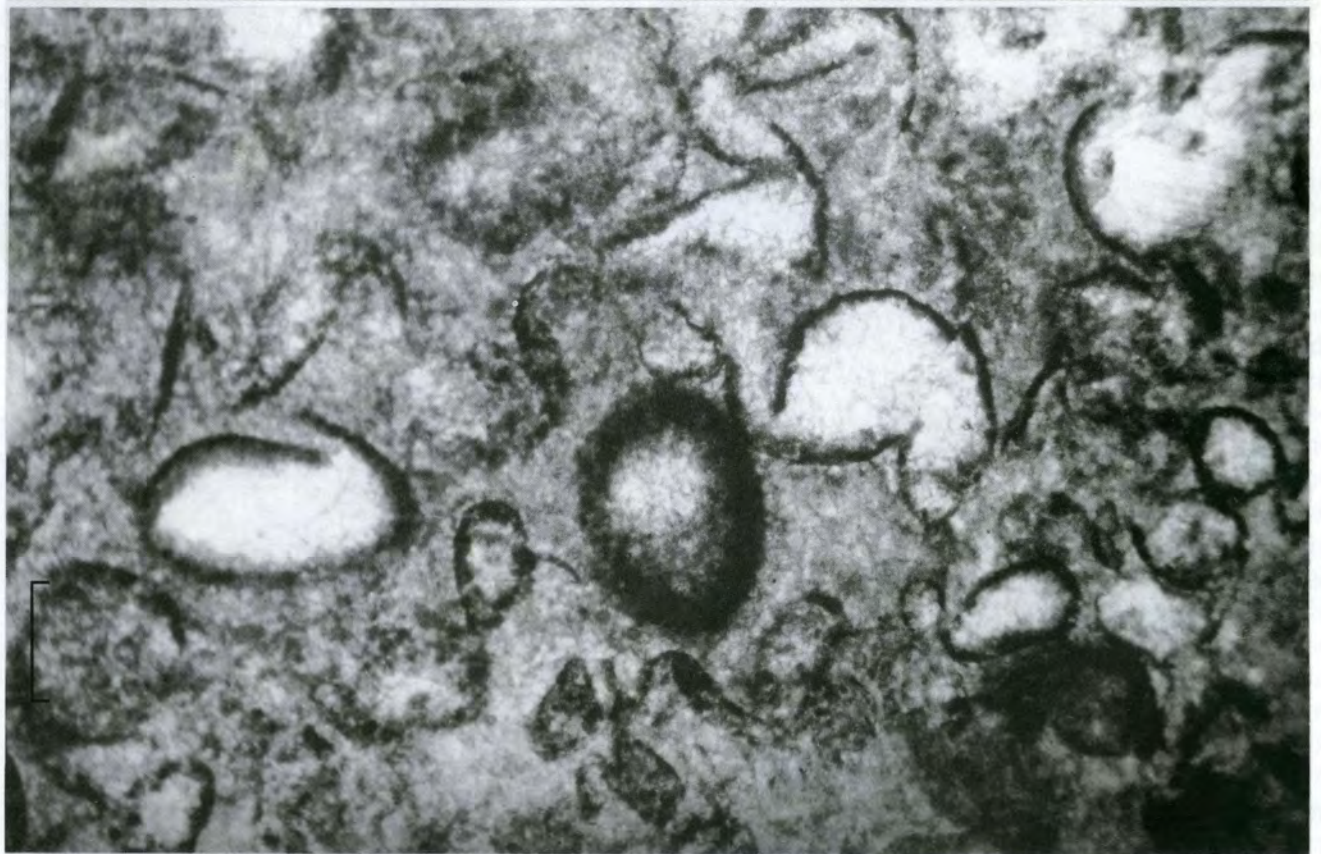
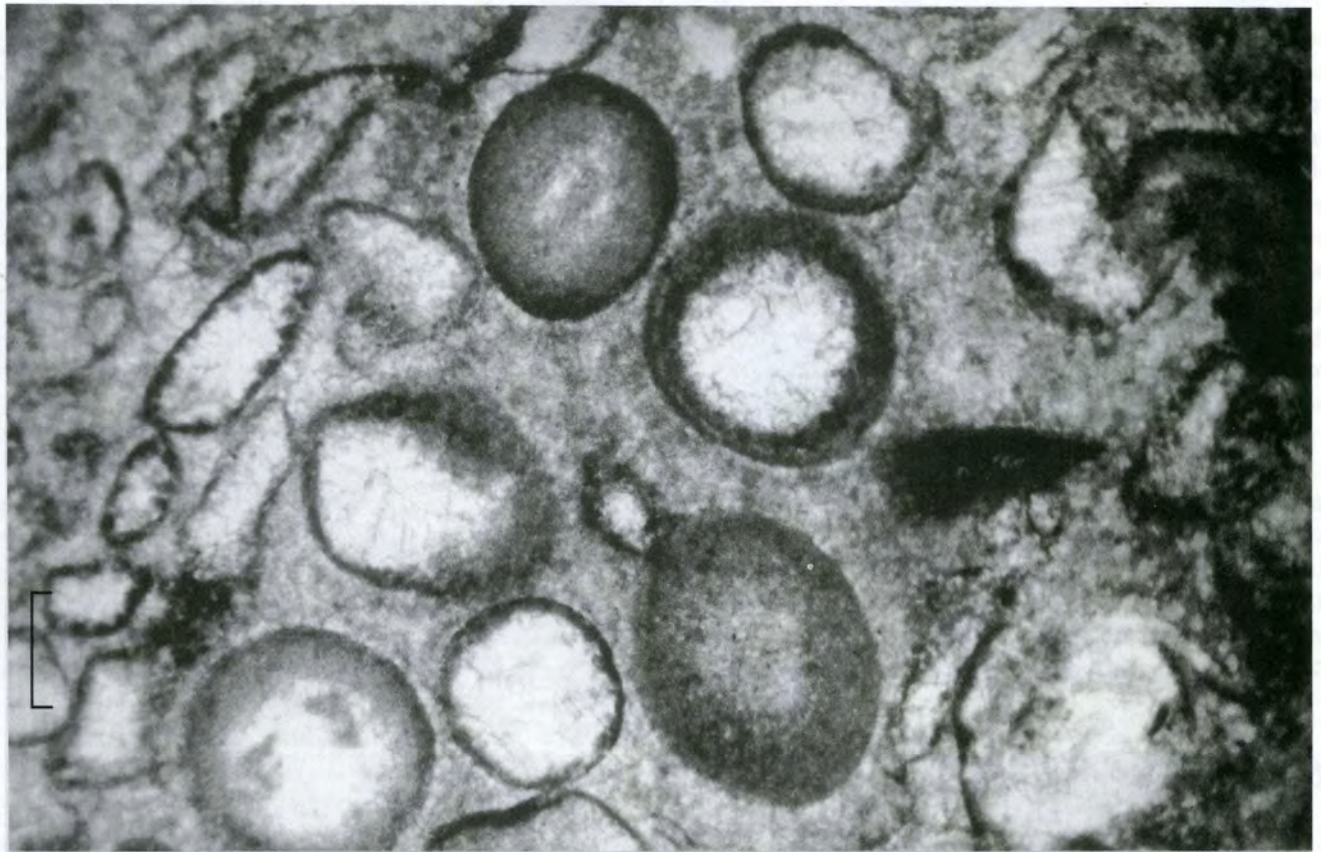


Figure 8.

A & B: Pieces of broken ooid from the Halali Quarry section. Notice the laminated external shell of calcium phosphate and the dense micritic interior. Scale bars each represent 500 micrometres. C & D: collapsed ooids from the Halali Quarry section, showing a deceptive bivalve-like condition of 'halalia' shells. C is a SEM image showing the apposition of two shell pieces with remnants of their adhering interiors, while D shows two apposed shell pieces in thin section. Scale bars each represent 500 micrometres.

A**B****Figure 9**

A& B: Thin sections of oolitic limestone from the Ombaatjie Formation in the eastern Kaokoveld, showing complete ooids with resistant rims in A, while B shows the effects of diagenetic dissolution of the interior of ooids and resulting collapse of the exterior shells. Each scale bar represents 1mm.

been true bivalved shells of biological origin, but in view of subsequent evidence, this interpretation seems unlikely. They are more probably highly deceptive pseudofossils.

CONCLUDING COMMENTS

As mentioned above, there is a strong possibility, based on molecular evidence, that metazoan lineages go back in time beyond the Ghaub glaciation. Soft-bodied micro-invertebrates were therefore presumably present during deposition of the Aurois/Ombaatjie Formations and the best chance for their preservation is probably in a phosphatised limestone such as occurs at Halali. The superb preservation potential for embryos and algae has been amply demonstrated by Proterozoic and Early Cambrian phosphorites in China (Bengtson & Zhao 1997; Xiao *et al.* 1998; Zhang *et al.* 1998), so any phosphatic limestone from this time period is well worth investigating.

The possibility, remote as it may seem, of proto-sponge fossils being present in a pre-Ghaub limestone would imply that at least one of the sponge lineages survived the Ghaub or Marinoan 'snowball Earth' episode, to continue on a wider scale once more favourable conditions returned. Remains interpreted as being those of sponges have been well documented in the 'Ediacaran' period, following the glacial (e.g. Brasier *et al.* 1997; Collins 1999; Gehling & Rigby 1996;

Li *et al.* 1998; Dong & Knoll 1996). There is even some evidence of Ediacaran-type organisms preserved in intertillite beds of Canada (Hofmann *et al.* 1990). It has been suggested that survival during the snowball Earth glacial would have been possible in locally warmed microhabitats such as close to hydrothermal vents (Erwin 1999, Farmer 2000). But new computer simulations of the snowball Earth scenario suggest that there may, in fact, have been ice-free equatorial oceans, the presence of which would have been critical for the survival of long-standing metazoan lineages (Hyde *et al.* 2000; Runnegar 2000). Studies of the palaeontological potential of the Halali phosphatic limestones will continue in the future, in the hope that they could throw some light on the antiquity of metazoan lineages in the Namibian region.

ACKNOWLEDGEMENTS

Fieldwork on this project by C.K.B. was supported by a grant from the PAST fund in Johannesburg; this help is gratefully acknowledged. Permission to undertake fieldwork in the Etosha National Park was provided by the Park authorities. Comments received on the first draft of this paper from Stefan Bengtson, Andy Knoll and Bruce Runnegar have proved of great value. The assistance in the field of Conrad Brain and Arno Günzel is much appreciated. Laura Brain's contribution in making numerous thin sections was invaluable. A.R.P. was supported by NERC grants and he also gratefully acknowledges the Geological Survey of Namibia for additional support. We would also like to thank Bruce Rubidge for his encouragement and editorial help.

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CARBONIFEROUS PYCNOXYLIC WOODS FROM THE DWYKA GROUP OF SOUTHERN NAMIBIA

by

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ABSTRACT

Glacial deposits of the Dwyka Group between Keetmanshoop and Mariental in southern Namibia have been reinvestigated for palaeontological remains and associated tuff horizons in an attempt to accurately date the deposits. SHRIMP-based dating of juvenile zircons from these tuff horizons provide ages which cumulate in the latest Carboniferous (Gzelian). The pycnoxylic woods *Megaporoxylon scherzi* Kräusel and *Megaporoxylon kaokense* Kräusel are described in detail for the first time and are compared with similar permineralised woods from Gondwana. Based on previous fossil wood studies covering the rocks of the main Karoo Basin, these species occur only in the Dwyka and lower Ecça Groups in southern Africa and do not extend to the upper Ecça Group.

KEYWORDS: Dwyka, fossil wood, *Megaporoxylon*, Namibia

INTRODUCTION

Geological setting and general stratigraphy of the Dwyka Group

During the Carboniferous most of the southern part of Gondwana was glaciated. In the Late Carboniferous and Early Permian glaciers receded, depositing the glaciogenic sediments of the Dwyka Group (Karoo Supergroup). In southern Namibia sections of the Carboniferous, glaciogenic Dwyka Group of the Aranos Basin have been subdivided into four deglaciation sequences (DS I-IV, Bangert *et al.*, in press), which were initially recognised by Theron & Blignault (1975) and Visser (1997) in the Western Cape Province, South Africa. In southern Namibia DS I and II began with tillites and debris-rainout diamictites which are overlain by minor siltstones, sandstones and conglomerates representing sediment-gravity flow deposits and fluvio-glacial outwash. The tops of the sequences are formed by lacustrine or offshore marine shale units which are essentially dropstone-free. Of particular importance is an offshore marine mudstone-unit, up to 45 m thick, named the Ganigobis Shale Member (Martin & Wilczewski 1970), which represents the top of DS II and which is especially well exposed in the area between Tses and Ganigobis (Figure 1). This shale member contains well preserved pieces and trunks of permineralised wood some of which are described in this contribution, ashfall tuffs (Bangert *et al.* 1999, Stollhofen *et al.* 2000), concretionary nodules bearing remains of paleoniscoid fishes (Gürich 1923, Gardiner 1962, Bangert *et al.* in press) and spiral coprolites (McLachlan & Anderson, 1973, Bangert *et al.* in press), bivalves (Bangert *et al.* in press), gastropods (Dickins 1961), *Conularia* sp. (Schroeder 1908), sponge spicules and crinoid columns (Bangert *et al.* in press), as well as microbial bioherms (Grill 1997).

Juvenile, magmatic zircon grains were separated from ashfall tuff horizons of the Ganigobis Shale Member and provided ²⁰⁶Pb/²³⁸U ages of 302.0±3.0 Ma and 299.5±3 Ma (Bangert *et al.* 1999). Within the framework of available numerical time-scales the Ganigobis Shale Member relates to the Late Carboniferous and more specifically to the Kasimovian (cf. Harland *et al.* 1990) or Gzelian (Menning 1995).

Deglaciation sequence III comprises mainly proglacial tunnel mouth and debris rain-out diamictites and gravity flow sandstones which terminate with the 75 m thick Hardap Shale Member (SACS 1980). The latter is characterised by occurrences of the marine bivalve *Eurydesma mytiloides* (Heath 1972), Bryozoa and Asteroidea (Martin & Wilczewski 1970), and has been related to the Gondwana-wide *Eurydesma*-transgression (Dickins 1984). The fourth deglaciation sequence, DS IV, begins with gravity flow sandstones and dropstone-bearing mudstones which are capped by greenish, dropstone-free mudstones immediately below the base of the Ecça Group.

Lithology and fossil content of the fossil wood sites

The fragment of permineralised wood (BP/16/935) described here was found at the Brukkaros River about 400 km S of Windhoek and about 23 km NNW of Tses (No. 1 in Figure 1). The outcrop is located downstream along the Brukkaros River about 2 km SW of the bridge of the B1 road which crosses the Brukkaros River (Figure 1). Stratigraphically the outcrop lies within the upper part of the Ganigobis Shale Member (DS II, Dwyka Group). The up to 5 m high outcrops of the river cuttings have exposed black massive mudstones with interbedded sandy and calcareous horizons which are intruded by five carbonatite dykes. Abruptly lenticular

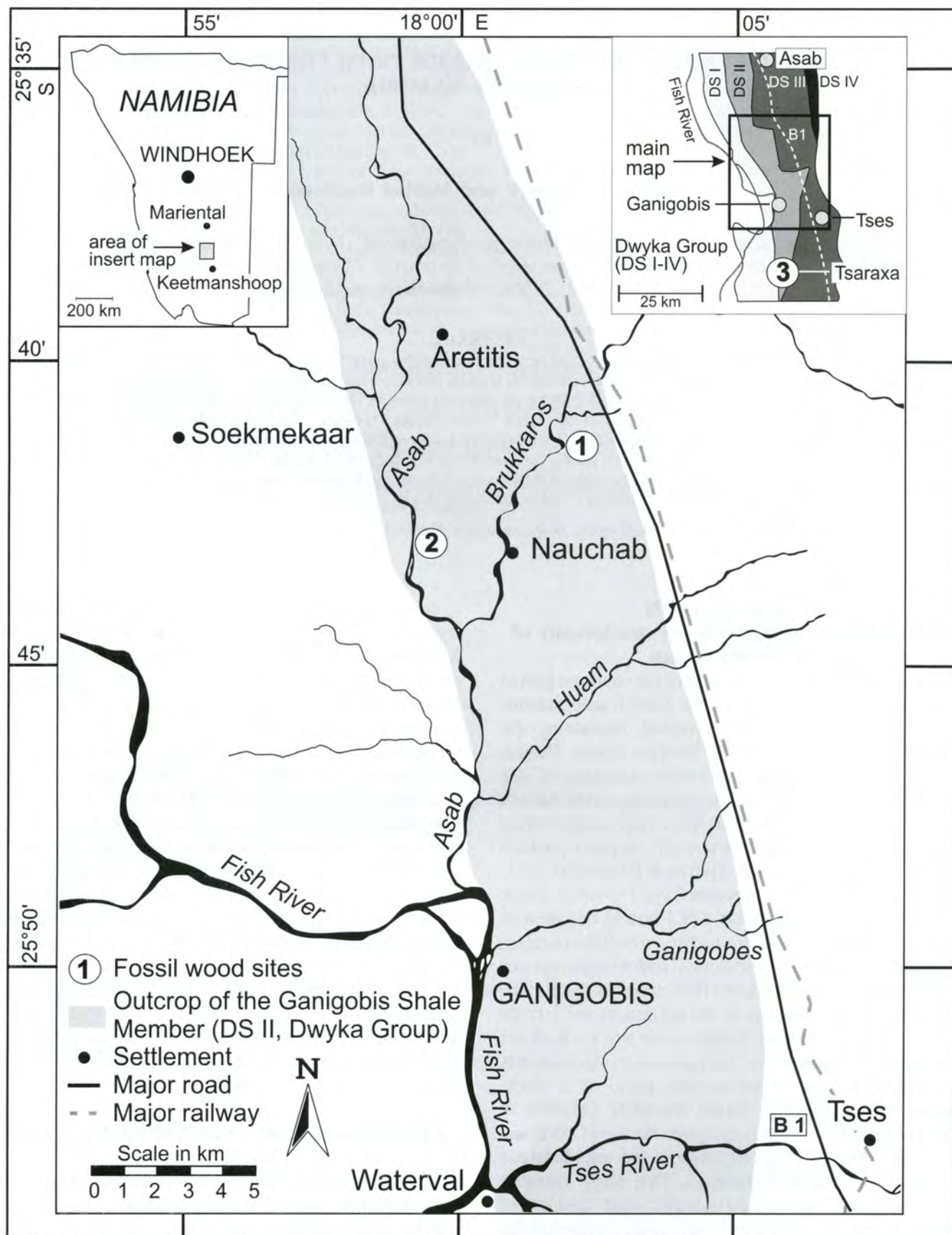


Figure 1. Detailed location map of the type area of the Ganigobis Shale Member in the vicinity of Ganigobis and Tses, southern Namibia, showing the location of the described outcrops.

calcareous sandstone bodies up to 3 m long and 60 cm thick are commonly exposed along the river cuttings. A bentonitic tuff horizon is exposed at the top of the river cuttings of the Brukkaros River (VIIIa, cf. Bangert *et al.* in press). The outcrop extends from the river cuttings (25°41.24' S, 18°01.54' E) to a few tens of metres to the east (25°41.26' S, 18° 01.88' E) where flat mounds of nodular siltstones which have diameters of 4–5 m, heights of up to 1.5 m, are exposed. The mounds are covered by round to elongate nodules of brownish-grey massive micrite, which probably represent microbial bioherms (cf. Bangert *et al.* in press).

The following fossils and ichnofossils were detected within the outcrop (cf. Bangert *et al.* in press):

- a single example of *Conularia* sp. (cf. Schroeder 1908),
- numerous shells of *Peruvispira vipersdorfensis* Dickins (1961),
- disrupted boundstone samples with column ossicles of crinoids and small sponge spicules,
- spiral and anvil-like permineralised coprolites (cf. McLachlan & Anderson 1973)
- trace fossils such as *Planolites montanus*, *Planolites* sp. and other indeterminable traces.

Permineralised fossil wood was found *in situ* on the tops of the mounds. The wood was not preserved as complete trunks but as isolated fragments of less than 10 cm in diameter. One especially well preserved sample of completely silicified wood displaying 1–7 mm thick annual growth rings is described in this contribution (BP/16/935, Figures 2–5).

The second described fragment of permineralised wood (BP/16/746) was found at the Asab River about 22 km NW of Tses and 5.5 km SW (25°43.04' S, 17°59.08' E) of the previously described outcrop (No. 2, Figure 1). Stratigraphically, the outcrop lies within the lower part of the Ganigobis Shale Member (DS II, Dwyka Group) which contains abundant concretionary mudstone nodules bearing remains of paleoniscoid fishes and spiral coprolites (cf. Bangert *et al.* in press). The outcrop is also a river cutting which extends a few hundred metres along the western side of the Asab River. The outcrop is dominated by monotonous mudstones sporadically including irregular mudstone concretions (some horizontally aligned) lacking fossils. Four bentonitic tuff horizons occur in the lower part of the outcrop. The described sample of wood was found *in situ* within the lower part of the outcrop.

A third piece of permineralised wood (BP/16/547) was discovered at the Wasser River, near the farm Tsaraxa, about 27.5 km SW of Tses (26°02.55' S, 17°57.20' E, No. 3 in Figure 1). This site is the southernmost outcrop of the lower part of the Ganigobis Shale Member with its characteristic dropstone-free facies changing southwards into shales containing varying amounts of dropstones (cf. Bangert *et al.* in press). Outcrops of the black, massive and dropstone-free mudstones occur in the river cutting of the Wasser

River. In this outcrop area three bentonitic tuff horizons were detected, which can be correlated to those located to the north but no other fossils were discovered. The described sample of permineralised wood was collected by Hermann Grill in the outcrop area.

Previously described fossil woods from Namibia

Fossil wood is fairly abundant within deposits of the Karoo Supergroup in Namibia but has seldom been described in detail (Pickford 1995). Descriptions were given by Kräusel (Kräusel & Range 1928, Kräusel 1956a, b), who erected several new genera of pycnoxylic woods with well-preserved primary vasculature and piths. It is the secondary xylem amongst gymnosperm woods that is most frequently preserved. This has led to the development of a dual nomenclatural system. There is a large number of genera for woods with only secondary xylem (woods without a pith = homoxylous, or woods where the pith has simply not been preserved). A separate group of genera incorporates wood with intact primary xylem, pith and secondary xylem (pycnoxylic woods = dense and massive with secondary xylem more abundant, as in tree-like conifers; manoxylic = loose, soft and scanty with the pith more abundant, as in pteridosperms). Pith is generally considered to be the most important feature and woods preserving this tissue are segregated into two groups. Homocellular piths have only parenchymatous tissue whereas heterocellular piths have sclereids, secretory cells, or secretory canals within the parenchymatous tissue. The shape of the pith, cylindrical or variously lobed, is another feature of taxonomic significance.

Lower Gondwanan woods can be divided into five types based on the tracheid pit and spiral thickening arrangements in the secondary wood (Lepekhina 1972, Pant & Singh 1987). Thus two specimens with the same secondary xylem but only one having a pith, are placed in different taxa. This is essential because they could belong to different plant groups. Affinities of the woods have been discussed by various authors, but there is little consensus (cf. Kräusel *et al.* 1961, Lepekhina 1972, Pant & Singh 1987). Homoxylous woods have recently been described from the younger formations of the Karoo Basin (Bamford 1999).

The pycnoxylic woods from Namibia and their characteristics are summarised in Table 1. Table 2 shows a comparison of *Megaporoxylon*-type woods described in the literature. In this paper a newly discovered specimen of *Megaporoxylon scherzi* is described because it is particularly well preserved and well dated. Two less well preserved specimens of *Megaporoxylon kaokense* are also described. Polished thin sections were made of all of the silicified woods in the following orientations: transverse section, radial longitudinal section and tangential longitudinal section. The sections were mounted on petrographic slides, ground and polished to a thickness of approximately 25–30 µm, studied and photographed under a Zeiss Axioskop microscope.

DESCRIPTION OF WOOD

Megaporoxylon scherzi Kräusel 1956b.

Specimen No: BB27 and Slide No: BP/16/935

Locality: Brukkaros River, about 23 km NNW of Tses, 25°41.26' S, 18°01.88' E (No. 1: Figure 1)

Stratigraphy: Ganigobis Shale Member, DS II, Dwyka Group, Karoo Supergroup

Collector: Berthold Bangert

Figures: 2-8

Description

The wood is silicified, yellow and brown, and measures 9x5x6 cm. The pith is only a few centimetres in diameter and heterocellular with cells containing a dark substance (secretory cells?) scattered within the parenchymatous pith. The primary xylem lobes are very small and endarch (Figures 2, 3). In longitudinal section the protoxylem tracheids exhibit typical annular or helical thickening (Figure 4). The growth rings are very clearly seen, varying in width from 1-7 mm, with an average of 4.6 mm (Figure 5). Latewood comprises one tenth to one quarter of each ring and ends abruptly at the beginning of the earlywood. The transition from earlywood to latewood is gradual. There are usually 20-30 rows of latewood cells. In transverse section the tracheids of the secondary xylem are square to polygonal and thin walled (wall between two adjacent cells is 5µm wide) in the earlywood, and only slightly thicker in the latewood (7.5µm). The earlywood mean tangential diameter is 35µm (range 25-42µm) and mean radial diameter is 36µm (range 25-47µm). The latewood mean tangential diameter is 29µm (range 25-35µm) and mean radial diameter is 12µm (range 7-22µm). Bordered pitting on the radial walls of the tracheids is araucarian, predominantly uniseriate and contiguous (90%), slightly flattened, but also biseriate and alternate, and rarely uniseriate and separate (Figure 6). In the earlywood the mean diameter of the pits is 12.5µm, and 10µm in the latewood. The pit apertures are mostly 5µm wide and round but some areas show the cross-like structure of elongated pits of adjacent cells overlapping at right angles, particularly in the narrow latewood tracheids (Figure 7).

The rays are uniseriate and low, 2-10-15 (minimum, mean, maximum) cells high, with thin, unpitted walls. The cross-field pits are oopores: large, simple, oval to fusiform and obliquely orientated, the single pit (very rarely two) filling most of the field (Figure 8). In the earlywood they are on average 37 µm long and 15 µm wide, orientated in the same direction. The latewood cross-field pits are orientated in the opposite direction and are smaller, but because the field is also smaller, they occupy most of the field. These pits are 20 µm long and 5 µm wide, and also without a border. No resin canals, resin or axial parenchyma were seen within the secondary xylem.

Identification

This wood is the same as *Megaporoxylon scherzi* described by Kräusel (1956b) from the upper Dwyka beds (now considered to be the Lower Ecca Group) of the Karoo Supergroup near Mariental. He did not give measurements of the cells or pits but said that the cross-field pits of *M. kaokense* were up to three times as high as the tracheid pits. In *M. scherzi* (Kräusel 1956b) the cross-field pits were very similar to those of *M. kaokense* (Kräusel 1956a) but were oval and slanting, not round. *M. zellei* has slightly shorter oopores (Kräusel 1956b).

Megaporoxylon kaokense Kräusel 1956a

(1) Specimen No: BB28, and slide No: BP/16/746

Locality: Asab River, about 22 km NW of Tses, 25°43.04' S, 17°59.08' E (No. 2: Figure 1)

Stratigraphy: Ganigobis Shale Member, DS II, Dwyka Group, Karoo Supergroup

Collector: Berthold Bangert

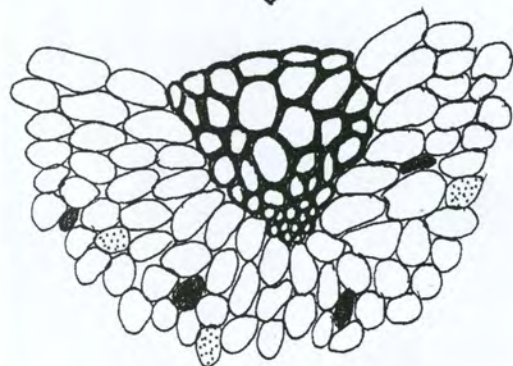
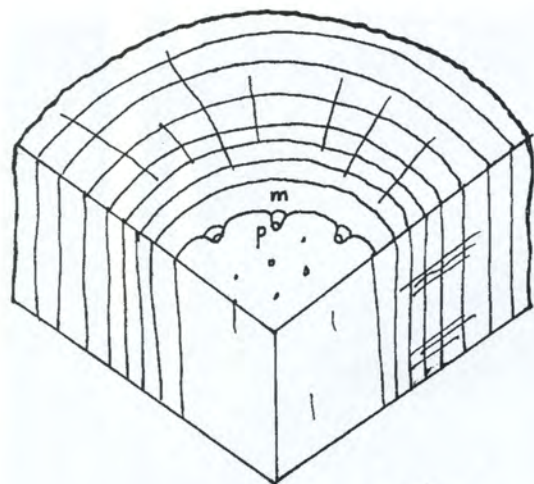
Figures: 9-12

Description

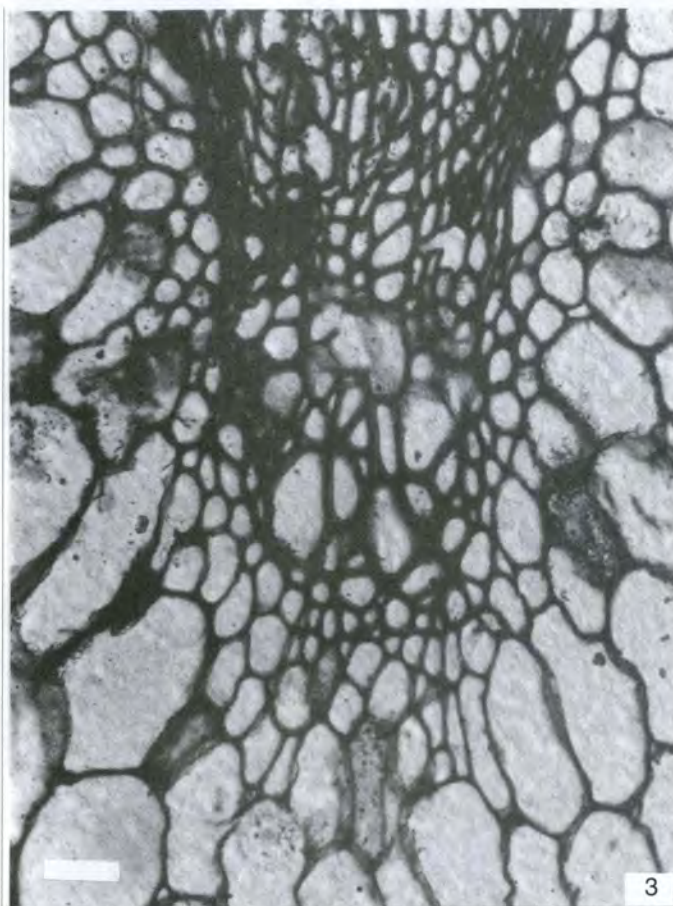
The specimen BP/16/746 is grey, laterally compressed with longitudinal grooves, but has surprisingly well preserved secondary xylem. The pith is heterocellular with secretory cells scattered between the parenchyma cells. Diameter of the pith is unknown. The primary xylem is in lobes extending into the pith and is endarch (Figure 9). In longitudinal section these protoxylem tracheids have close spiral thickening. The metaxylem tracheids have alternate biseriate pitting.

In the secondary xylem the growth rings are on average 1 mm wide and have less latewood, only 2-3 rows, than the specimen described above (BP/16/935). Tracheids are squarish in transverse section and have a dark substance in the lumina which is likely to be an artefact of preservation (Figure 9). The earlywood tracheid mean tangential diameter is 35 µm (range 25-45µm) and mean radial diameter is 33 µm (range 27-45µm). The growth rings are narrow (<1 mm) near the pith. The latewood is made up of 2-3 rows of radially compressed tracheids. The latewood tracheid mean tangential diameter is 33µm (range 20-40µm) and mean radial diameter is 12 µm (range 10-18µm). Adjacent cell walls are 7-10µm thick. Tracheid bordered pitting is clear in some areas (Figure 11). These pits are uniseriate or biseriate and alternate, contiguous and slightly flattened. Their diameter is 12-15µm. There are approximately equal proportions of uniseriate and biseriate pitting.

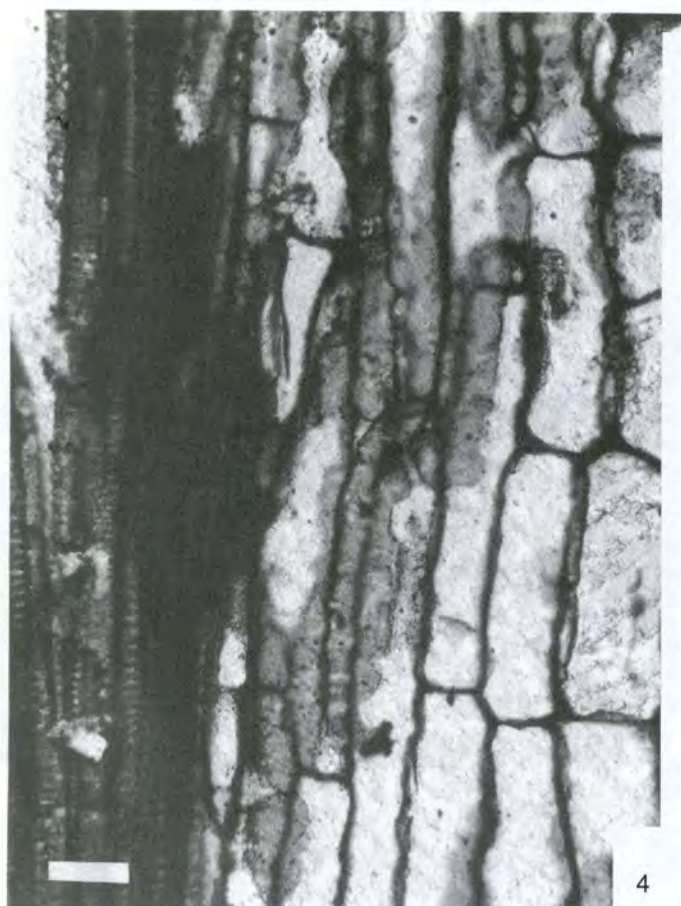
The rays are low, 1-5-12 cells high, exclusively uniseriate and relatively rare (Figure 10). The cross-field pits are large, completely filling the field, simple and almost round, 17.5µm x 17.5µm (Figure 12). No resin or resin canals occur in the secondary xylem.



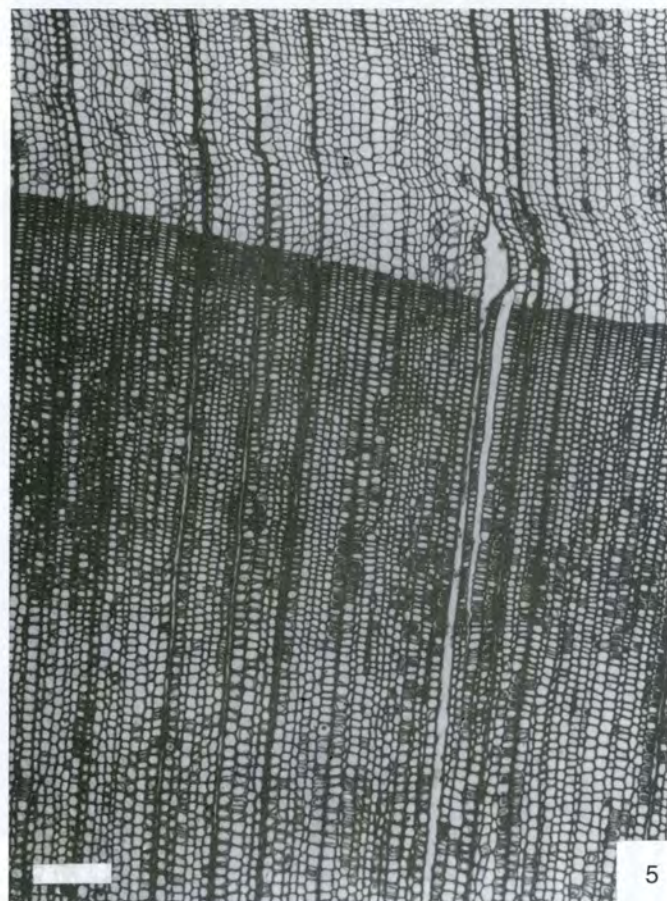
2



3

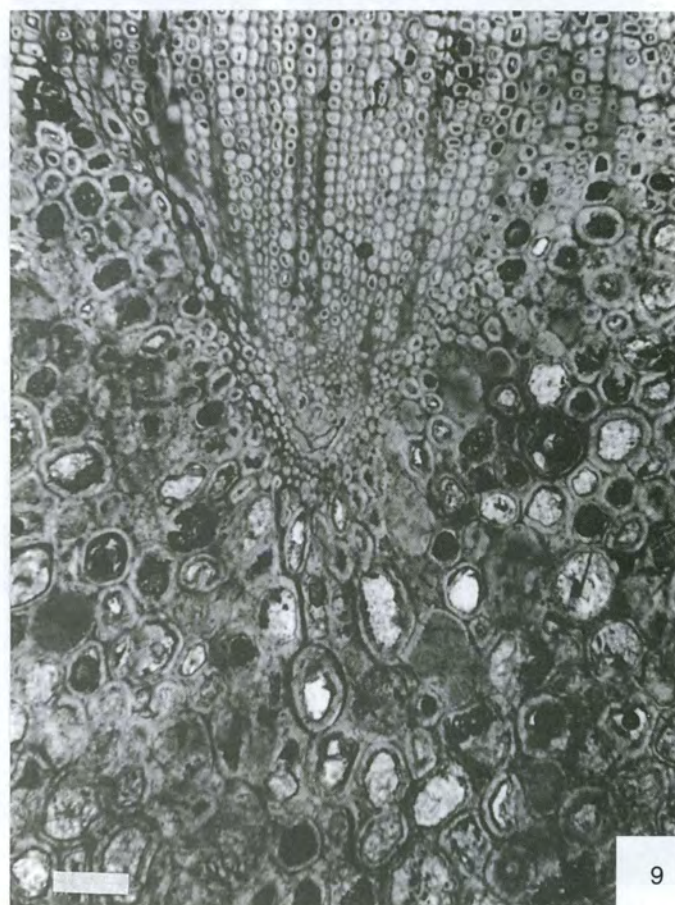


4

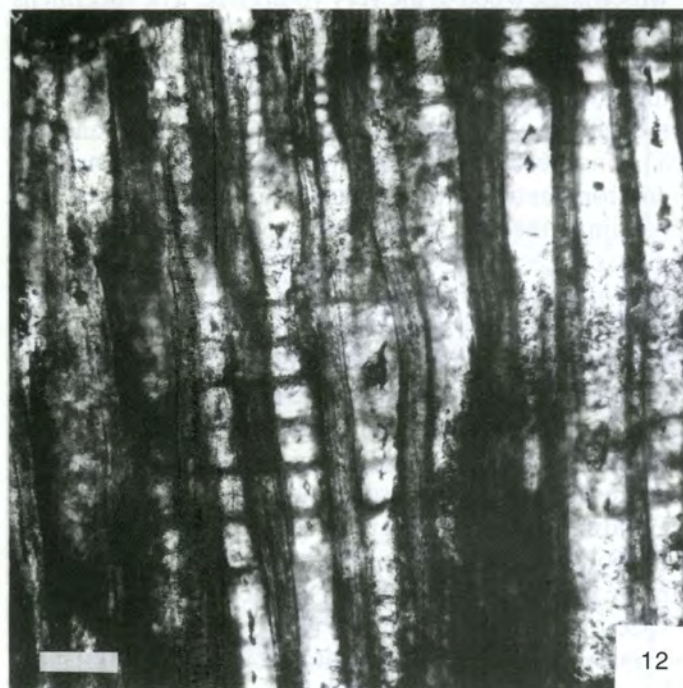
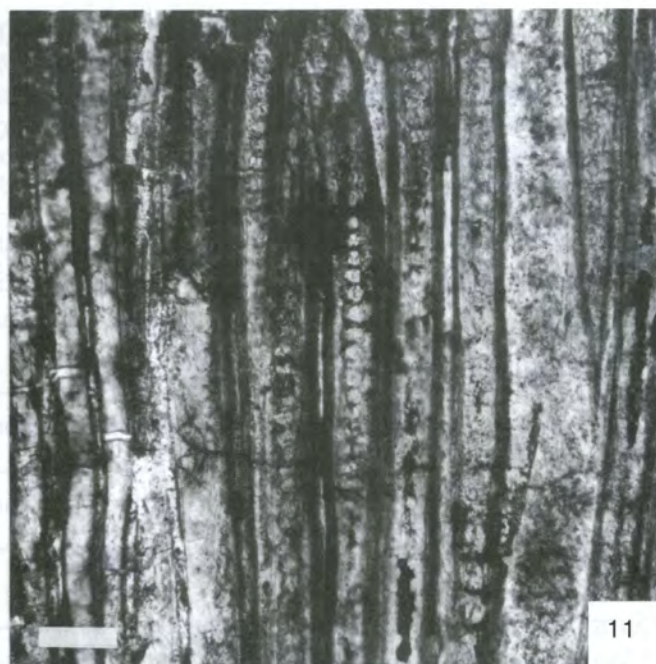


5

Figures 2-5. *Megaporoxylon scherzi* Kräusel, BP/16/935; 2: Diagram of specimen showing growth rings in secondary xylem and endarch primary xylem: metaxylem (m, large thick-walled cells), and protoxylem (p, cluster of small thick-walled cells) which is nearer the pith (large thin-walled cells, some with resiniferous contents); 3: Transverse section (TS) of specimen BP/16/935 showing the primary xylem lobe: (secondary xylem above photograph), metaxylem (large central cells), small protoxylem cells just below and large pith cells. Scale bar = 60 μm ; 4: Radial longitudinal section (RLS). Protoxylem tracheids have helical and annular thickenings (left), pith cells on the right. Scale bar = 40 μm ; 5: (TS). Earlywood tracheids with thin walls in upper part and thicker walled latewood tracheids below. Scale bar = 350 μm .



Figures 6-8: *Megaporoxylon scherzi*, BP/16/935; 6: (RLS). Uni- and biseriate bordered pitting on radial walls of earlywood tracheids. Scale bar = 20 μm ; 7: (RLS). Uniseriate pits on radial walls of latewood tracheids. Scale bar = 40 μm ; 8: (RLS). Crossfield pitting. Oopores in the earlywood are oval oblique. Scale bar = 40 μm . 9: *Megaporoxylon kaokense* Kräusel BP/16/746. TS showing secondary xylem (top), primary xylem lobe and pith with dark cells below. Scale bar = 175 μm .



Figures 10-13: *Megaporoxylon kaokense* BP/16/746; 10: Tangential longitudinal section (TLS) showing low rays, uniseriate and 3-5 cells high. Scale bar = 40 μm . 11: (RLS). Bordered pits on the radial walls of the tracheids are uniseriate and contiguous. Scale bar = 60 μm . 12: (RLS). Cross-field pits are round oopores, filling the field. Scale bar = 60 μm . 13: BP/16/547, *Megaporoxylon kaokense* (Ganigobis Shale Member). (RLS). Cross-field pits are large round oopores, filling the field. Scale = 20 μm .

(2) Specimen and slide number: BP/16/547

Locality: Wasser River, near the farm Tsaraxa, about 27.5 km SW of Tses, 26°02.55' S, 17°57.20' E (Figure 1 insert).

Stratigraphy: Ganigobis Shale Member, DS II, Dwyka Group, Karoo Supergroup

Collector: Hermann Grill

Figure: 13

Description

This specimen is grey-black, measured 9 x 9 x 4.5 cm, has growth rings 1–2 mm wide and was from a trunk with a diameter greater than 50 cm. No pith was preserved, only secondary xylem. The earlywood tracheid mean tangential diameter is 26 µm (range 20–30 µm) and the radial diameter is 24 µm (range 20–30 µm). For the latewood the mean tangential diameter is 25 µm (range 23–27 µm) and mean radial diameter is 13 µm (range 10–15 µm). Bordered pitting occurs only on the radial walls of the tracheids and is 1–2 seriate, alternate, contiguous or rarely separate, with a diameter of 10 µm. The rays are low and uniseriate, 2–5–8 cells high and rare. Cross-field pits are large, simple, round to oval and fill the cross-field, 17.5 µm by 17.5 µm (Figure 13).

Identification

These specimens are conspecific with woods assigned to *Megaporoxyton kaokense* Kräusel (1956a) from the Tsarabis Formation (Lower Ecça Group, formerly Upper Dwyka) in the southern Kaokoveld. They are very similar to the specimen of *M. scherzi*, described above, except that the cross-field pits are more rounded, rather than elliptic and oblique. Only single pits were seen but there were very few cross-field pits visible altogether.

Comparison with other fossil woods

Kräusel (1956a, b; Kräusel & Range 1928) described 17 taxa of fossil woods from Dwyka and Ecça Group deposits in Namibia which had pith preserved (Table 1). Mostly the piths have small diameters, less than 5 cm, the primary xylem was endarch in the Dwyka woods (one exception), and mesarch in the Ecça woods, and all the secondary woods have araucarian tracheid pitting on the radial walls. Generic differences lie in the pith types and the cross-field pitting. Typical araucarian cross-field pitting is cupressoid (or narrowly bordered), but one specimen, *Dadoxylon arberi*, has small, simple pits of the *Zalasskioxylon* secondary xylem type. The other woods have secondary xylem of the *Protophylladoxylon*-type and are shown here in Table 1 as having oopores in the cross-field pit column. In his original description of *Protophylladoxylon* Kräusel (1939) described the secondary xylem as having purely araucarian tracheid pitting (slightly compressed pits, usually 2 or more seriate and alternate), but Müller-Stoll & Schultze-Motel (1989) included woods with mixed tracheid pitting (araucarian and abietinian) in this genus. The type of pitting rather than the secondary wood genera are used here to avoid

confusion. The secondary xylem of *Megaporoxyton* is the same as that of *Protophylladoxylon* Kräusel.

Maheshwari (1966) described a fourth species of *Megaporoxyton*, *M. krauseli* from the Raniganj (Upper Permian) of India, and two more species from the Permian of Antarctica (Maheshwari 1972). All six species are very similar (Table 2). The species from India and Antarctica are a little younger than the Namibian species. To the best of the authors' knowledge *Megaporoxyton* has not been described from South America but it does occur there (Da Rosa Alves, pers. comm). Kräusel & Dolianiti (1958) described several other genera shared between Brazil and Namibia (*Lobatoxylon*, *Taxopitys*), although different species characterised each area. *Protophylladoxylon* is common to both continents (Guerra-Sommer, 1977) but without a pith preserved it is difficult to determine whether the same plant is being considered. The *Protophylladoxylon* woods, i.e. those without a pith, occur in the Mesozoic rather than the Palaeozoic (Müller-Stoll & Schultze-Motel 1989), so *Megaporoxyton* and *Protophylladoxylon* are unlikely to belong to the same gymnospermous groups.

DISCUSSION

Megaporoxyton scherzi (Figure 5) has very clear growth rings and abundant latewood whereas *Megaporoxyton kaokense* has narrower latewood. In both cases the wood nearest to the pith has been studied, which is the wood of the very young tree. The specimens originate from different localities: *M. scherzi* was found in the upper part and *M. kaokense* was collected from the lower part of the Ganigobis Shale Member and so they are very unlikely to be exactly contemporaneous. The authors cannot assume that their immediate environments were the same, nor do we know for certain if the two species of wood represent different plant taxa because woods tend to be more conservative than other parts or organs of the plant. The growth rings, however, imply a seasonal environment which is to be expected due to the high latitude position of southern Gondwana during the Carboniferous and Early Permian.

The stratigraphically restricted distribution (Carboniferous - Lower Permian) of *Megaporoxyton* makes it a potentially useful biostratigraphic indicator. Gondwanan woods with piths seem to be confined to the Carboniferous and Lower Permian deposits which could be a preservational artefact but of the many intact specimens collected from the Upper Permian and Triassic of southern Africa (Bamford 1999, 2000) none has a pith. The dominant Gondwanan gymnosperms at this time were the Cordaitales, Glossopteridales and early conifers. The Cordaitales have been recorded from the Upper Carboniferous to the Upper Permian deposits with many organ genera having been assigned to this group. The cordaitalean woods *Mesoxylon* and *Cordaitoxylon* have large piths with secondary xylem of the *Araucarioxylon*-type (Trivett & Rothwell 1991). The glossopterids are predominantly a Permian group; leaves have also been found in rocks of the

TABLE 1.

Fossil woods described from Namibia by Kräusel (in Kräusel & Range 1928, first eight taxa; Kräusel 1956a,b, the rest of the taxa). All the woods have alternate pitting on the radial tracheid walls of the secondary xylem, variously described as "Araucarioxylon-type, Zaleskioxylon-type or Phyllocladoxylon-type". The main differences are in the cross-field pits which for the three preceding taxa are cupressoid, simple and ooporoid respectively. The Kaoko Formation here is equivalent to the Dwyka and lower Ecça Groups in this region. (Bp = bordered pits on tracheid walls; R = ray width).

FOSSIL WOOD	PITH TYPE	PRIMARY XYLEM	2 XYLEM: CROSS-FIELD	LOCALITY STRATIGRAPHY
<i>Medullopitys sclerotica</i>	heterogeneous sclerenchyma strands	mesarch	oopores	Keetmanshoop Ecça Group
<i>Abietopitys perforata</i>	homogeneous	mesarch	cupressoid	Keetmanshoop Ecça Group
<i>Phyllocladopitys capensis</i>	homogeneous	mesarch	oopores	Ganigobis Dwyka Group
<i>Phyllocladoxylon capense</i>	—	—	oopores	Ganigobis Dwyka Group
<i>Dadoxylon rangei</i>	homogeneous (?)	mesarch	cupressoid	Various Ecça Group
<i>Dadoxylon porosum</i>	homogeneous (?)	mesarch	cupressoid	Keetmanshoop Ecça Group
<i>Dadoxylon arberi</i>	homogeneous (?)	mesarch	simple, small, numerous	Doros crater Tsarabis Fm (Lower Ecça Group)
<i>Taxopitys africana</i>	heterogeneous secretory cells	mesarch	cupressoid spiral thickening	Doros crater Tsarabis Fm (Lower Ecça Group)
<i>Solenoxylon wissi</i>	discoid, large	endarch	cupressoid bp: 1-3	Kaokoveld Tsarabis Fm (Lower Ecça Group)
<i>Solenoxylon kurzi</i>	discoid, large	endarch	cupressoid bp: 1	Kaokoveld Tsarabis Fm (Lower Ecça Group)
<i>Solenoxylon oberholzeri</i>	discoid, large	endarch	cupressoid bp: 2-4; R: 2 ser.	Kaokoveld Tsarabis Fm (Lower Ecça Group)
<i>Lobatoxylon kaokense</i>	lobed	endarch	cupressoid	Kaokoveld Tsarabis Fm (Lower Ecça Group)
<i>Megaporoxyton kaokense</i>	heterogeneous secretory cells	endarch	oopores (round)	Kaokoveld Tsarabis Fm (Lower Ecça Group)
<i>Megaporoxyton scherzi</i>	heterogeneous secretory cells	endarch	oopores (oval, slanting)	Mariental Lower Ecça (?) Group
<i>Megaporoxyton zellei</i>	heterogeneous secretory cells	endarch	oopores shorter	Amalia Dwyka Group
<i>Kaokoxyton reunigi</i>	heterogeneous sclerenchyma	endarch	cupressoid single, small	Kaokoveld Tsarabis Fm (Lower Ecça Group)
<i>Kaokoxyton durum</i>	heterogeneous sclerenchyma	endarch	cupressoid several, smaller	Kaokoveld Tsarabis Fm (Lower Ecça Group)
<i>Phyllocladopitys martini</i>	homogeneous	mesarch	oopores bp: flattened	Mariental Lower Ecça (?) Group

TABLE 2.

Comparison of woods of *Megaporoxylon* described in the literature and in this paper. Growth rings are distinct in all of the species.

SPECIES	LOCALITY STRATIGRAPHY AUTHOR	PITH TYPE Primary xylem	TRACHEID PITS number arrangement size	CROSS-FIELD Number of pits shape size	RAYS width height (cells)
<i>Megaporoxylon kaokense</i>	Kaokoveld, Namibia Tsarabis Fm., Lower Ecca Group Kräusel 1956a	heterogeneous secretory cells endarch	mostly 1 seriate, araucarian --	1 large or 2 smaller, simple, round 3 x size tracheid pits	1 seriate 1-14
<i>M. scherzi</i>	Mariental, Namibia Lower Ecca (?) Group Kräusel 1956b	heterogeneous secretory cells endarch	mostly 1 seriate araucarian	1-2 simple, round to oval and slanting	1 seriate 1-25
<i>M. zellei</i>	Amalia, Namibia Dwyka Group Kräusel 1956b	heterogeneous secretory cells endarch	1-3 seriate araucarian --	1 large, simple, broader and not as high as in <i>M. kaokense</i>	1 seriate 1-12-18
<i>M. krauseli</i>	Raniganj, India Upper Permian Maheshwari 1966	heterogeneous secretory cells endarch ?	1-3 seriate	1-2 (-3) large, simple, round	1 seriate 1-6-23
<i>M. antarcticum</i>	Mt Weaver, Antarctica Permian Maheshwari 1972	homogeneous endarch	2-3 seriate araucarian 8-11 µm	1 large, simple, elliptical 18 x 11,5 µm	1 seriate 2-6-17
<i>M. canalosum</i>	Mercer Ridge Antarctica Permian Maheshwari 1972	heterogeneous secretory cells endarch	1-2 (-3) seriate araucarian --	1 large, simple, oval-elliptic, oblique 16x22 - 5x12 µm	1 seriate 1-4-8
BP/16/935 <i>M. scherzi</i>	Bruckaros, Namibia Ganigobis Shale Member Dwyka Group Bangert & Bamford	heterogeneous secretory cells endarch	1 (-2) seriate araucarian 10-12,5 µm	1 large or 2 smaller, simple, oval and oblique pits 20 x 5 - 37x15 µm	1 seriate 2-10-15
BP/16/746 <i>M. kaokense</i>	Ganigobis, Namibia Ganigobis Shale Member Dwyka Group Bangert & Bamford	heterogeneous secretory cells endarch	1-2 seriate araucarian 12-15 µm	1 large, round, simple pit, 17,5 µm completely fills the field	1 seriate 1-5-12
BP/16/547 <i>M. kaokense</i> ?	near Tses, Namibia Ganigobis Shale Member Dwyka Group Bangert & Bamford	unknown	1-2 seriate araucarian 10 µm	1 large, round simple pit, 30 x 25 µm, completely fills the field	1 seriate 2-5-8

Dwyka Group in the south-western main Karoo Basin (Anderson & McLachlan 1976). *Araucarioxylon* has been considered the wood type of the glossopterids (Gould & Delevoryas 1977; Pigg & Taylor 1993) but this wood type may have been produced by more than one plant group, especially as this wood type occurs after the extinction of the *Glossopteris* flora. The lack of phylogenetically informative characters currently prohibits assignment of *Megaporoxylon* woods to any gymnosperm order.

ACKNOWLEDGEMENTS

Volker Lorenz and Markus Geiger (Würzburg) helped with the field work and collecting samples of permineralised wood. Richard Lewis (BPI) and Rupert Wassermann (Würzburg) are thanked for preparing the slides. Research was funded by the German Research Foundation (DFG) and the Postgraduate Research Program "Interdisciplinary Geoscience Research in Africa". The National Monuments Council of Namibia is thanked for their permission to study the wood samples outside Namibia. Logistic support by the Geological Survey of Namibia is gratefully acknowledged. Kathleen Pigg and an anonymous reviewer are thanked for their comments.

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A NEW ACTINOPTERYGIAN FISH SPECIES FROM THE LATE PERMIAN BEAUFORT GROUP, SOUTH AFRICA

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ABSTRACT

A new genus and species of actinopterygian (ray-finned) fish, *Bethesdaichthys kitchingi*, is described from the Tatarian, Late Permian, Lower Beaufort Group of South Africa. *Bethesdaichthys* is presently known from three localities, two in the New Bethesda and one in the Victoria West districts of the Karoo region respectively. The fossils were recovered from within the Abrahamskraal Formation *Tapinocephalus* Assemblage Zone at the Victoria West locality, and from an uncertain Formation possibly closely equivalent to the Balfour Formation, within the *Dicynodon* Assemblage Zone at the New Bethesda sites. *Bethesdaichthys kitchingi* is a fusiform fish, up to approximately 300mm in total length, with the skull displaying a moderately oblique suspensorium, and a maxilla with a large sub-rectangular postorbital blade. Furthermore there is a complex of four suborbital bones adjacent to the orbit. The pectoral fin is large relative to body size and the tail is heterocercal with an elongate tapered dorsal body lobe. The anterior midflank scales in particular exhibit a distinctive dermal ornamentation consisting of numerous ganoine ridges. The phylogenetics and interrelationships of *Bethesdaichthys kitchingi* are examined. It appears to exhibit a relatively conservative morphology similar to that found in possibly related Carboniferous taxa such as the South African taxa *Australichthys* and *Willmorichthys*. *Bethesdaichthys kitchingi* is derived relative to stem-actinopterans such as the *Howqualepis* and *Mimia*, and also derived relative to southern African Palaeozoic actinopterygians such as *Mentzichthys jubbi*, and *Namaichthys schroederi*, but basal to stem-neopterygians such as *Australosomus*, *Perleidus* and *Saurichthys*.

KEYWORDS: *Bethesdaichthys*, palaeoniscid, Late Permian, Tatarian, Beaufort Group, Actinopterygii.

INTRODUCTION

A new genus and species of Late Permian actinopterygian fish is described here from the Lower Beaufort Group of South Africa, based essentially on well preserved and diagnostic skeletal elements. Taxonomically relevant actinopterygian fossil remains, in particular diagnostic skull remains, have up to now not been described from the Lower Beaufort Group, although incompletely preserved skeletal remains and isolated body scales of fossil fish have been recorded from much or most of the biostratigraphic range (see Broom 1913a, 1913b; Jubb & Gardiner 1975; Woodward 1888, 1889, 1893). Recently, Bender (2000) documented for the first time well preserved and relatively complete actinopterygian remains from the Lower Beaufort Group, tentatively describing several new species, including *Bethesdaichthys kitchingi*.

Bethesdaichthys kitchingi is an actinopterygian fish which belongs to a group of early actinopterygian taxa collectively referred to as "palaeoniscids" (Traquair 1877-1914; Gardiner 1967) or "Palaeoniscomorpha" (Lund *et al.* 1995). It is generally accepted that the palaeoniscids constitute a paraphyletic group of mostly Palaeozoic actinopterygians (Coates 1993), with a global distribution. These palaeoniscids or lower actinopterygians represent the "primitive" or basal members of the Subclass Actinopterygii (Gardiner 1973).

The sedimentary rocks of the Beaufort Group have yielded diverse and important fossils, including macro- and micro-palaeobotanical remains, vertebrate and invertebrate body fossils and traces (Hancox & Rubidge 1997). Analysis of the fossils provides information on the evolution of life in the Permo-Triassic, and has proved significant in unravelling the geological development of the Karoo Basin (Hancox & Rubidge 1997). On the basis of its uniquely large and relatively complete continental Permo-Triassic sedimentary sequence, the Beaufort Group is considered almost as a 'world stratotype' for continental Permo-Triassic age geological and palaeontological research (Smith 1990). The Beaufort Group is particularly renowned for its diversity and range of therapsid fossils, which elucidate the evolutionary transition to mammals (Broom 1932; SACS 1980). The therapsids have been utilized as a basis for an eightfold biostratigraphic subdivision of the Group (Rubidge 1995), with the Lower Beaufort Group comprising six of the eight biozones (Figure 1).

MATERIALS AND METHODS

Three laterally compressed *Bethesdaichthys* specimens were recovered from a *Tapinocephalus* Assemblage Zone locality on the farm Blourug, Victoria West district, Abrahamskraal Formation, Adelaide Subgroup, Lower Beaufort Group. These specimens were contained within a single, thin, buff-coloured, fine

STRATIGRAPHY						
			WEST OF 24°E	EAST OF 24°E	NORTHERN OFS	ASSEMBLAGE ZONE
PERMIAN	BEAUFORT GROUP	ADELAIDE SUBGROUP	TEEKLOOF F. Steenkampsvlakte M. Oukloof M. Hoedemaker M. Poortjie M. ABRAHAMSKRAAL F.	BALFOUR F.		DICYNODON
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TRIASSIC	BEAUFORT GROUP	TARKASTAD SUBGROUP	TEEKLOOF F. Steenkampsvlakte M. Oukloof M. Hoedemaker M. Poortjie M. ABRAHAMSKRAAL F.	BALFOUR F.		DICYNODON
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 Sandstone-rich Unit

Figure 1. Lithostratigraphic units and Vertebrate Assemblage Zones of the Beaufort Group (after Rubidge *et al.* 1995).

to medium grained sandstone unit, which outcrops over a lateral distance of approximately 70m, and contains numerous specimens of other early actinopterygian species. Until now the exact biostratigraphic zone of the site has been uncertain, but as skull elements of a dinocephalian therapsid were found approximately 15m below the fish site, it appears that the site falls within the *Tapinocephalus* Assemblage Zone.

A total of 15 *Bethesdaichthys* specimens were recovered from a *Dicynodon* Assemblage Zone roadside locality on the farm Wilgerbosch, New Bethesda district, Adelaide Subgroup, Lower Beaufort Group. These specimens were derived from a blue-green to green, ripple cross-laminated, silty mudstone with a mudstone veneer on the upper surface; and also from an interbedded mudstone/siltstone/fine-grained sandstone sequence, up to 13 cm thick with fossil fish found throughout the sequence. A single specimen was recovered from a site located at a reservoir also on the farm Wilgerbosch and approximately 35m stratigraphically above the roadside site; preserved in a blue-green siltstone horizon which is situated below a laminated sequence similar in form to that at the roadside site. The formational designation of the Wilgerbosch sites is uncertain (Cole *et al.* in press), but they appear to be situated in roughly the stratigraphic equivalent of the Balfour Formation (see Figure 1).

Most specimens required mechanical and chemical preparation before analysis was possible. Air scribes and an assortment of needles and probes were used initially to remove covering rock matrix, and in certain cases to finely prepare the specimen surface prior to analysis. A dilute 10% solution of acetic acid was on occasions used to soften surrounding matrix. In the case of a number of specimens, analysis was problematical because of the weathered nature of the surface bone and ganoine. In this case preparation of latex rubber casts or peels was found to reveal excellent underlying morphological detail; study and illustration of the casts was facilitated by whitening with ammonium chloride. Thin sections of scales were prepared, and studied for histological analysis using a Zeiss standard petrographic microscope with polarised light. Interpretive drawings were made using a Leica MZ6 microscope with drawing tube. Photographs were taken using a Nikon FM camera mounted on a copy stand, and for the thin sections, a Zeiss polaroid camera was used. The scanning electron micrographs were made on a Leica Stereoscan 440 at the Council for Geoscience, Pretoria. The phylogenetic analysis was carried out by using the Gardiner and Schaeffer 1989 (cladogram III) as a basis, since this is the most recent comprehensive early actinopterygian phylogenetic analysis. The relevant *Bethesdaichthys* characters were compared to those of the constituent taxa in the Gardiner and Schaeffer (1989) cladogram, thus determining the phylogenetic position of *Bethesdaichthys*. The results of the phylogenetic investigation of *Bethesdaichthys* were illustrated together with a revision of the Gardiner and Schaeffer cladogram III, in which certain nodes and taxa within the cladogram were updated.

SYSTEMATIC PALAEONTOLOGY

Class Actinopterygii Woodward 1891

Infraclass Actinopteri Cope 1871

Genus *Bethesdaichthys* gen. nov.

Derivation of name: Named after the Karoo mountain hamlet, Nieu Bethesda, which is close to the Wilgerbosch site where the first specimen of this taxon was found. Bethesda means "place of flowing waters" (Bible: John, Chap. 5: 2-4), probably appropriate to Late Permian fluvial conditions in the region of the Wilgerbosch fossil fish site. The suffix '-ichthys' is derived from the ancient Greek word for fish.

Diagnosis: A fusiform fish, approximately 300cm in total length. Skull relatively broad, with a moderately oblique suspensorium. Dermopterotic broadens anteriorly and does not suture with the nasal. Dermosphenotic is a crescent-shaped bone. Snout region consists of a small premaxilla, antorbital, narrow rostral and fairly elongate nasal. Jugal is a broad wedge-shaped bone. Maxilla has a large subrectangular postorbital blade. Dentition consists of a median row of large pointed conical teeth and an outer row of numerous smaller pointed teeth. Preopercular with almost right-angled inflexion between the wedge-shaped dorsal, and ventral limbs. There is a complex of four suborbital bones including a large triangular suborbital between the maxilla and the jugal. Opercular is broad and rectangular, subopercular approximately 2/3 of the height of the opercular with an obliquely angled ventral margin. Branchiostegal rays number nine. Distal bifurcation of the fin-rays is visible on the dorsal and caudal fins. Pectoral fin is relatively large and consists of fin-rays which are proximally jointed. Caudal fin is heterocercal with an elongate dorsal body lobe. The anterior rows of flank scales exhibit a distinctive dermal ornament, with up to 14 curved and steeply inclined dorsal ganoine ridges distinct from a series of up to 10 horizontally inclined ventral ridges. A series of enlarged ridge scales is present along most of the dorsal margin. Scale histology shows a laterally continuous, multilayered ganoine layer.

Remarks: *Bethesdaichthys* is clearly different from any of the other Beaufort Group actinopterygian taxa, based on: fewer than 12-13 branchiostegal rays, the shape of the dermosphenotic, maxilla, preopercular, and opercular in particular, and in the morphology of the suborbitals. *Bethesdaichthys* can be compared to the South African Carboniferous genus *Australichthys* on the basis of maxilla, preopercular and opercular shape and form (see Gardiner 1969), but differs with regard to the dorsal fin shape, size and form.

Type species: *Bethesdaichthys kitchingi* nov.

Derivation of the name: In honour of Mr 'Croonie' Kitching, Nieu Bethesda resident and road builder, who first discovered the Wilgerbosch fossil fish site in about 1928 while constructing a new road over part of the site.

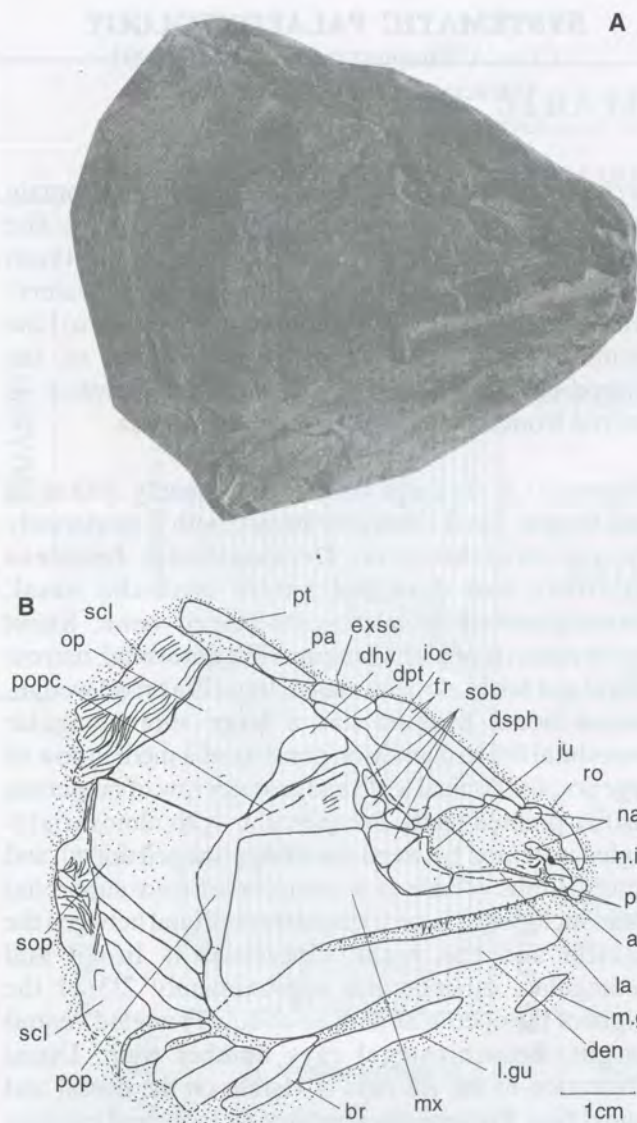


Figure 2. *Bethesdaichthys kitchingi* holotype BP/1/4373/3. A. Lateral view showing the dermal skull region. B. Camera lucida interpretation. (See p. 38 for abbreviations)

Holotype: BP/1/4373/3, in the Bernard Price Institute for Palaeontological Research (BPI), University of the Witwatersrand, Johannesburg. From the Wilgerbosch roadside locality, *Dicynodon* Assemblage Zone, Lower Beaufort Group.

Referred specimens: BP/1/4373/2, 3, 19, 110, 119, 120, 121, 122, 123, 124, 134, 138; BP/1/116, housed at the BPI Palaeontology, Johannesburg. PB/95/6; PB/96/15, housed at the Council For Geoscience, Pretoria; V101, housed at the Victoria West Museum, Victoria West; TM 20, housed at the Transvaal Museum, Pretoria.

Horizon and locality: V101 is from the Blourug locality, *Tapinocephalus* Assemblage Zone, Lower Beaufort Group. TM 20 is from the Wilgerbosch reservoir site, and the rest of the specimens from the Wilgerbosch roadside locality, *Dicynodon* Assemblage Zone, Lower Beaufort Group.

Diagnosis: As for genus.

Remarks: A total of three specimens are recorded from Victoria West, one from the Wilgerbosch reservoir site, and fifteen from the Wilgerbosch roadside locality.

DESCRIPTION

Skull Roof

The skull roof is made up of paired parietals, frontals and extrascapulars, a large dermopterotic and small dermosphenotic located on either side of the frontals. The dermal ornament over the whole of the head region is fairly robust, in the form of mixed short ridges and denticles, which are similar in shape and form to that seen in the cheek region, but more robust. Bones of the skull roof region were studied mainly in specimen BP/1/4373/3 (Figure 2).

Parietals: (Figures 2, 3). The median section of the right parietal is rather poorly preserved in BP/1/4373/3. It is rectangular and approximately one third of the frontal length. Anteriorly it sutures with the frontal and posteriorly with the extrascapulars.

Frontals: (Figures 2, 3). The right frontal is preserved in a somewhat distorted state in BP/1/4373/3. It is relatively long, and narrow although this could be an artifact of preservation. Anteriorly it sutures with the rostral and posteriorly with the parietals.

Dermopterotic: (Figures 2, 3). Most of the right dermopterotic is preserved in BP/1/4373/3. It appears broadest anteriorly and tapers posteriorly. The anterior overlap with the dermosphenotic appears smooth and almost straight vertical. It does not contact the nasal, and is fairly far removed from it. The median section of a broad sensory-line canal is present near the ventral margin.

Dermosphenotic: (Figures 2, 3). The dermosphenotic is small relative to the size of the dermopterotic. It is a narrow, crescentic bone which curves dorsally where it contacts the nasal anteriorly and the dermopterotic posteriorly, and ventrally down under the dermopterotic to form a point at its ventro-posterior extremity. The

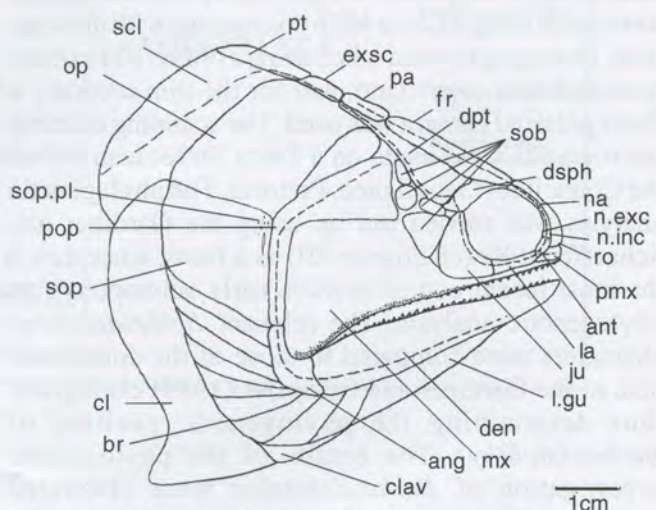


Figure 3. *Bethesdaichthys kitchingi*, restoration of the head in lateral view. (See p.38 for abbreviations)

infraorbital canal can be seen in BP/1/4373/3, close to the ventral margin.

Extrascapulars: (Figures 2, 3). The extrascapulars are not well preserved, but part of a narrow right extrascapular is preserved in BP/1/4373/3.

Snout

The snout region can be seen preserved in a distorted state in BP/1/4373/3 (Figure 2). It consists of a single median rostral, paired premaxillae, an antorbital and a nasal.

Rostral: (Figures 2, 3). The rostral abuts the frontal near the nasal/dermosphenotic suture, and evidently sutures with the premaxillae anteroventrally without being part of the jaw margin.

Premaxillae: (Figures 2, 3). Both premaxillae are preserved in specimen BP/1/4373/3. They are small almost square bones, excluded from the jaw margin, and thus do not contain teeth.

Antorbital: (Figures 2, 3). The single antorbital consists of a fairly narrow rectangular bone which contacts the lachrymal posteriorly. The antorbital contacts the nasal and rostral anteriorly, and the premaxilla anteroventrally. The large distorted opening seen on the dorsal side is part of the well developed infraorbital sensory canal system which has weathered forming a cavity.

Nasal: (Figures 2, 3). The nasal is fractured, with a posterior section in contact with the dermosphenotic broken off from an anterior section in which the incurrent and excurrent nares are visible. It is a narrow bone which is elongate relative to the rostral. It sutures with the dermosphenotic beneath the frontal.

Cheek and Infraorbitals

The cheek region in *Bethesdaichthys* is made up of a large maxillary, preopercular, jugal, lachrymal and a suborbital complex. This region is best noted in specimen number BP/1/4373/3 (Figure 2), although the dermal ornament and various morphological characters can be seen in a number of additional specimens including BP/1/4373/2 and PB/96/15. The dermal ornament consists of numerous, closely aligned, ganoine ridges and denticles (Figure 4).

Jugal: (Figures 2, 3). The jugal is a large crescentic bone which tapers dorsally and anteroventrally. The anterior and posterior margins are evenly curved to accommodate the orbit and maxilla respectively. The dorsal and ventral margins are narrow at the dermosphenotic and lachrymal contacts respectively. A broad infraorbital sensory line canal is present close to the anterior margin and bends almost at right angles in the centre of the bone.

Lachrymal: (Figures 2, 3). The lachrymal is a narrow, elongated, rectangular bone. A large infraorbital sensory line canal is visible over its length. Anteriorly it sutures with the antorbital and posteriorly with the jugal. Ventrally it sutures with the infraorbital limb of the maxilla.

Maxilla: (Figures 2, 3, 4). The maxilla consists of a large, subrectangular, fairly high postorbital blade and an equally long, slender, curved infraorbital blade which appears to form the anterior-most margin of the skull together with the premaxilla. The postorbital blade dermal ornament is well developed in PB/96/15, consisting of robust, well defined ganoine ridges.

Dentition: (Figures 2, 3, 4, 5). Although the dentition is not completely preserved, there appears to be an entire

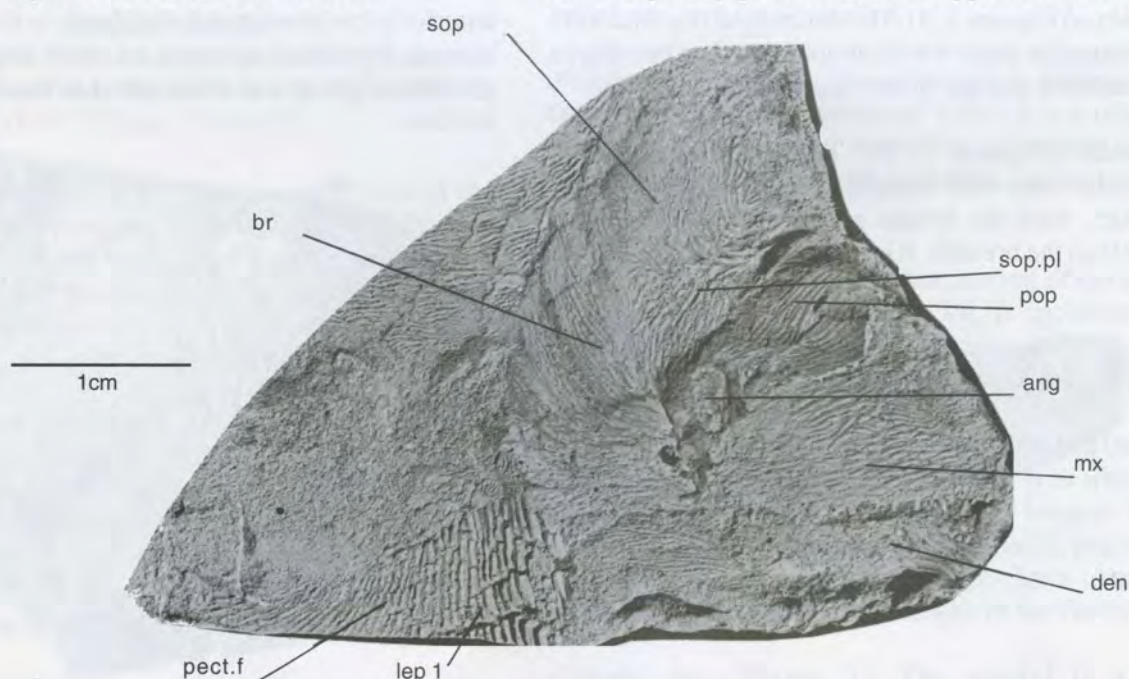


Figure 4. *Bethesdaichthys kitchingi* specimen V101 in lateral view showing pectoral fin, and dermal skull region detail. (See p.38 for abbreviations).

margin of large, pointed conical teeth, up to 2mm in height, arranged in one medial row consisting of more than 20 teeth, in both the maxilla and the mandible. These large teeth are flanked by numerous smaller outer teeth of less than 0.5mm in height; there are also pointed denticles present on the dermal bones of the palate.

Preopercular: (Figures 2, 3, 4). This is a relatively large bone, with a distinctive almost right-angled inflexion at the midline or posterodorsal corner of the postorbital blade of the maxilla. The preopercular consists of a narrow upright posterior limb which is located posterior to the postorbital blade of the maxilla, and a wedge-shaped anterodorsal blade situated above the maxilla. The preopercular canal is situated close to, and parallel to the dorsal margin of the preopercular. The preopercular dermal ornament consists of distinctive vertically inclined ridges ventral to the preopercular canal, and horizontally inclined ridges dorsal to the preopercular canal on the anterior blade, observed in specimens V101 (Figure 4) and PB/96/15.

Suborbitals: (Figures 2, 3). Four suborbital bones are present: one large wedge-shaped bone anterior to the maxilla, and three rounded bones in a row anterior to the preopercular, and inclined at an angle parallel to the ventral margin of the dermopterotic.

Operculo-Gular System

The opercular-gular system in *Bethesdaichthys kitchingi* comprises the dermohyal, opercular, and subopercular, the branchiostegal rays, and the gulars. The suspensorium is inclined at an angle of approximately 40-45 degrees to the horizontal in specimen BP/1/4373/3 (the horizontal is taken as the line of the upper jaw margin). The dermal ornament consists of well-developed straight and curved ganoine ridges (Figure 4).

Dermohyal (Figures 2, 3). The dermohyal is a relatively large triangular bone which abuts more than two thirds of the anterior margin of the opercular.

Opercular (Figures 2, 3). This is a large broad rectangular bone with straight margins, slightly longer than high, with the height approximately two thirds greater than the breadth. It is inclined at an angle of c45-

50 degrees to the horizontal, and is considerably higher than the adjacent subopercular.

Subopercular (Figures 2, 3, 4). The subopercular is not completely preserved, yet it appears to be slightly narrower than the opercular, and approximately 2/3 of its height. It tapers posteriorly, with the ventral margin terminating in a point at the anteroventral margin. A number of sensory pits and pit canals are visible close to the ventral bone margin (see Figure 3).

Branchiostegal rays (Figures 2, 3, 4, 5). The branchiostegal series was studied in specimens BP/1/4373/2 and BP/1/4373/134. There are nine rectangular branchiostegal rays present, with the most posterodorsal two elements immediately ventral to the subopercular slightly larger than the preceding rays; the posterior few rays are inclined at an angle similar to that of the ventral margin of the subopercular. The dermal ornament consists of ribs of ganoine running the length of the rays.

Gulars (Figures 2, 3). There are three gulars, two large narrow lateral gulars and one short ovate median gular visible in specimen BP/1/4373/134. This configuration is regarded as primitive among lower actinopterygians (Gardiner & Schaeffer 1989).

Lower Jaw

The lower jaw is well-preserved in specimens BP/1/4373/3 (Figure 5) and BP/1/4373/134. Fragments of the dermal ornamentation on the coronoids and prearticular are preserved in specimen BP/1/4373/3, and consist of small, fine denticles.

Dentary (Figures 2, 3, 4, 5). The dentary is a large, elongated bone which tapers anteriorly and has a depth/length ratio of approximately 1:4. The mandibular canal is visible; posteriorly it is close to the ventral border, anteriorly it is present about halfway up the dentary. The dermal ornament consists of well-developed short ganoine ridges and denticles close to the dorsal occlusal surface.

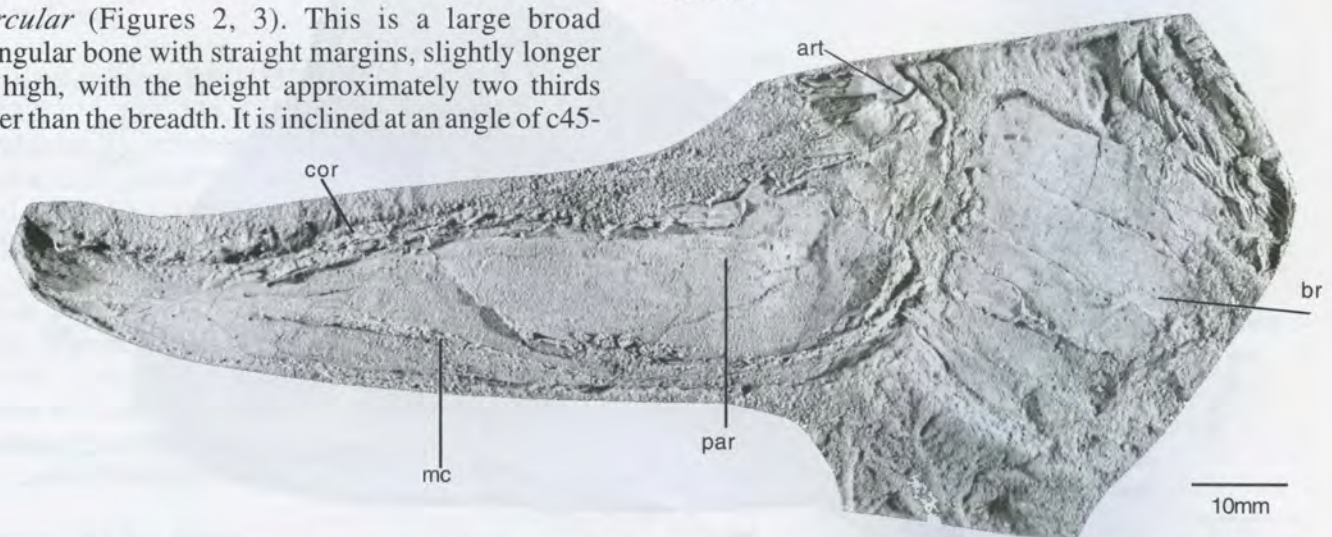


Figure 5. *Bethesdaichthys kitchingi* holotype BP/1/4373/3, medial view showing the lower jaw and posterior branchiostegal rays. (See p.38 for abbreviations.)

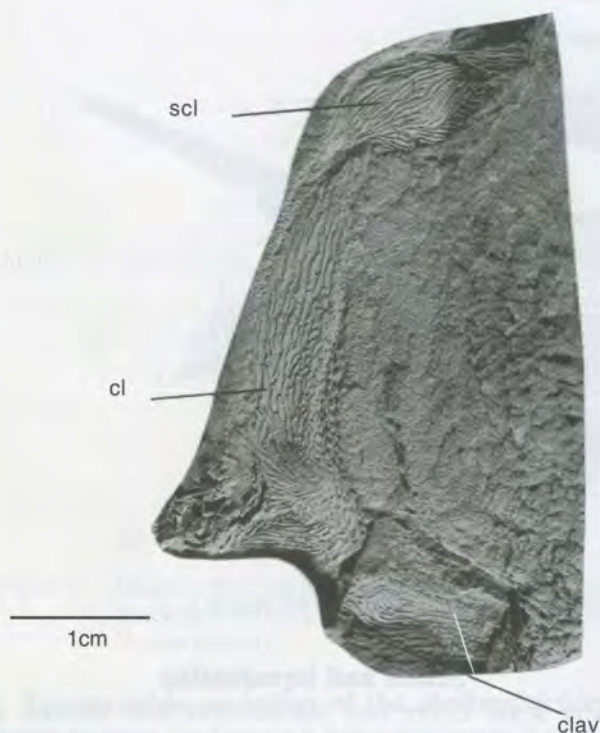


Figure 6. *Bethesdaichthys kitchingi* specimen PB/96/15 in lateral view, showing supracleithrum, cleithrum and clavicle dermal detail. (See p.38 for abbreviations.)

Angular: (Figures 2, 3, 4). The angular, although not completely preserved, seems to be, as in most early actinopterygians, a narrow, elongated crescentic bone which sutures with the posterior margin of the dentary, and abuts the preopercular. An incompletely preserved surangular was noted on specimen BP/1/4373/134.

Articular: (Figure 5). An inclined, angled articular is visible in BP/1/4373/2. A concave fossa is visible in profile, with the condyle of the quadrate also visible.

Pectoral Girdle

None of the bones of the pectoral girdle are completely preserved, but some are partly visible in specimens BP/1/4373/3 and PB/96/15.

Post-temporals: (Figures 2, 3). A dorsal section of the right post-temporal is visible in BP/1/4373/3. It is an elongate bone relative to the adjacent bones of the skull roof, in particular the extrascapular and parietal. The dermal ornament consists of well developed ganoine ridges aligned along the length of the bone.

Supracleithrum: (Figures 2, 3, 6). The supracleithrum is partially preserved in the two study specimens. Evidently it is about half as broad as the adjacent opercular, and longer than it. The distinctive dermal ornament consists of ridges running the length of the bone, and incorporating a dividing ridge which seems to extend the length of the bone.

Cleithrum: (Figures 2, 3, 6). The cleithrum consists of a relatively long, slender slightly curved vertical blade, and

a strongly convex ventral expanded region. The pectoral fin embayment on the posterior margin is partially preserved in PB/96/15 and appears to be fairly deep. It has a well developed dermal ornament with wavy ridges running the length of the posterior margin of the vertical blade, and shorter, broader, more horizontally inclined ridges on the anterior margin.

Clavicle: (Figures 3, 6). Most of the right clavicle is preserved in PB/96/15. It is an elongated triangular bone, which has a short posterior contact with the cleithrum. The dermal ornament consists of ridges and denticles horizontally inclined along the length of the bone.

Body and Fins

The complete body is not preserved in any specimens studied, but a composite image of the body shape and form was gained by studying specimens BP/1/4373/3, 37, 134, PB/95/6 and PB/96/15 (see Figure 7). These specimens indicate that *Bethesdaichthys* is a moderately sized, fusiform fish, with a total length of up to approximately 300mm, and a total body length in the region of 200mm. The head length of approximately 67mm in specimen BP/1/4373/3, is contained about four times in the total body length.

Distal fin preservation is not complete in the pectoral, pelvic and anal fins, but all the fins seem to be triangular, composed of numerous closely set fin-rays, with fringing fulcra on the leading edges of the fins. The fin-rays in the dorsal and caudal fins, although generally incomplete towards the distal margins, appear to branch once towards the distal ends of the fin-rays.

Pectoral fin: (Figures 4, 7). An anteroproximal portion of the fin is preserved in specimen V101. Clearly it is a broad based fin, with more than 30 fin-rays preserved. The anteroproximal fin-rays are short and relatively broad, and proximally jointed.

Pelvic fin: (Figure 7). The pelvic fin is preserved in a fragmentary state in specimen V101. It is a relatively large, moderately long based fin, consisting of +42 segmented fin-rays. The fin appears to start at scale row 11-12.

Anal fin: (Figure 7). The anterior portion of the anal fin is preserved in specimen PB/95/6. It apparently is a moderately long based fin which starts approximately at scale row 30-35.

Dorsal fin: (Figure 7). A proximal section of the fin is preserved in specimen BP/1/4373/37. It is triangular, consisting of +26 fin-rays, with the longest fin-ray situated at approximately fin-ray number 16, and starts at scale row c35. The fin-ray segments have distinctive striations running the dermal length of the fin-ray.

Caudal fin: (Figure 7). The caudal is a large heterocercal, elongated, triangular fin with a particularly

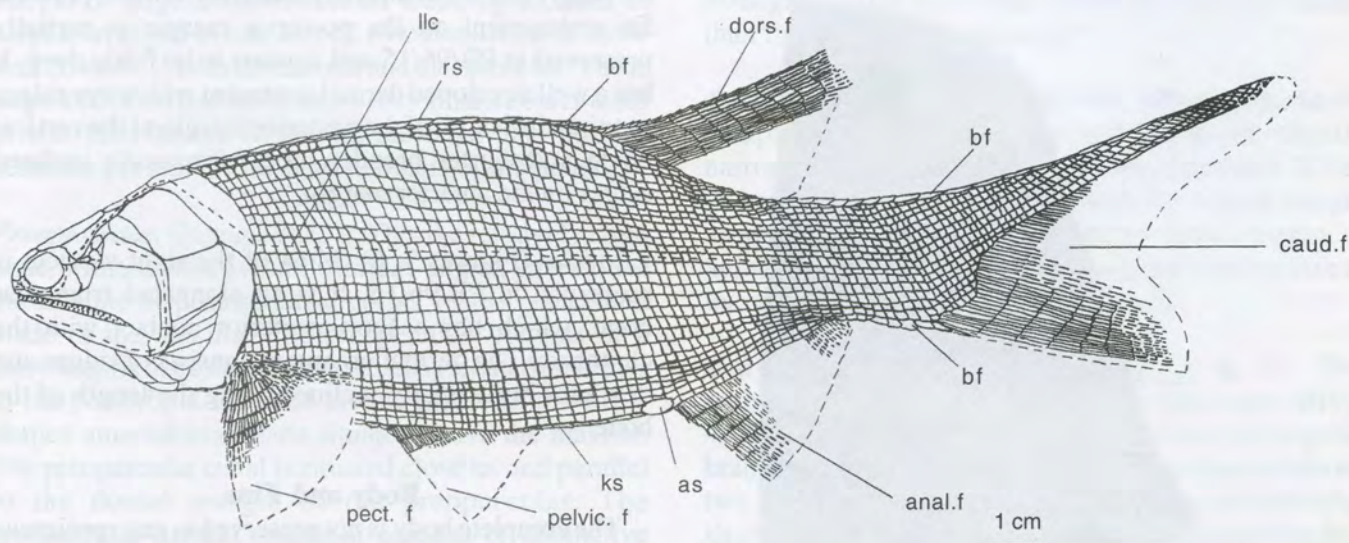


Figure 7. *Bethesdaichthys kitchingi*, restoration of fish in lateral view. (See p.38 for abbreviations.)

extended dorsal hypochordal lobe, which is preserved in somewhat fragmentary state only in specimen PB/95/6. The fin starts on average at scale row 50. The length of the caudal fin (cl) can be expressed as a ratio to total fish length (tfl), $cl/tfl = \text{approximately } 100:300 = 1:3$. The ventral aspect of the tail is not clearly preserved, but the anterior fin-rays on the ventral lobe appear to be relatively long.

Scales and Squamation

The scale cover and squamation was studied in specimens BP/1/4373/2, 3, 19, 37, 134; BP/1/116; PB/95/6; PB/96/15; V101, and TM 20. *Bethesdaichthys* exhibits rhombic scales (the largest, midflank scales are on average approximately 6x5mm in size), with strong peg and socket articulation between the dorsal and ventral margins of the scales, an anterodorsal angle or process to the scale, and each scale row overlapping the row posterior to it (Figure 8).

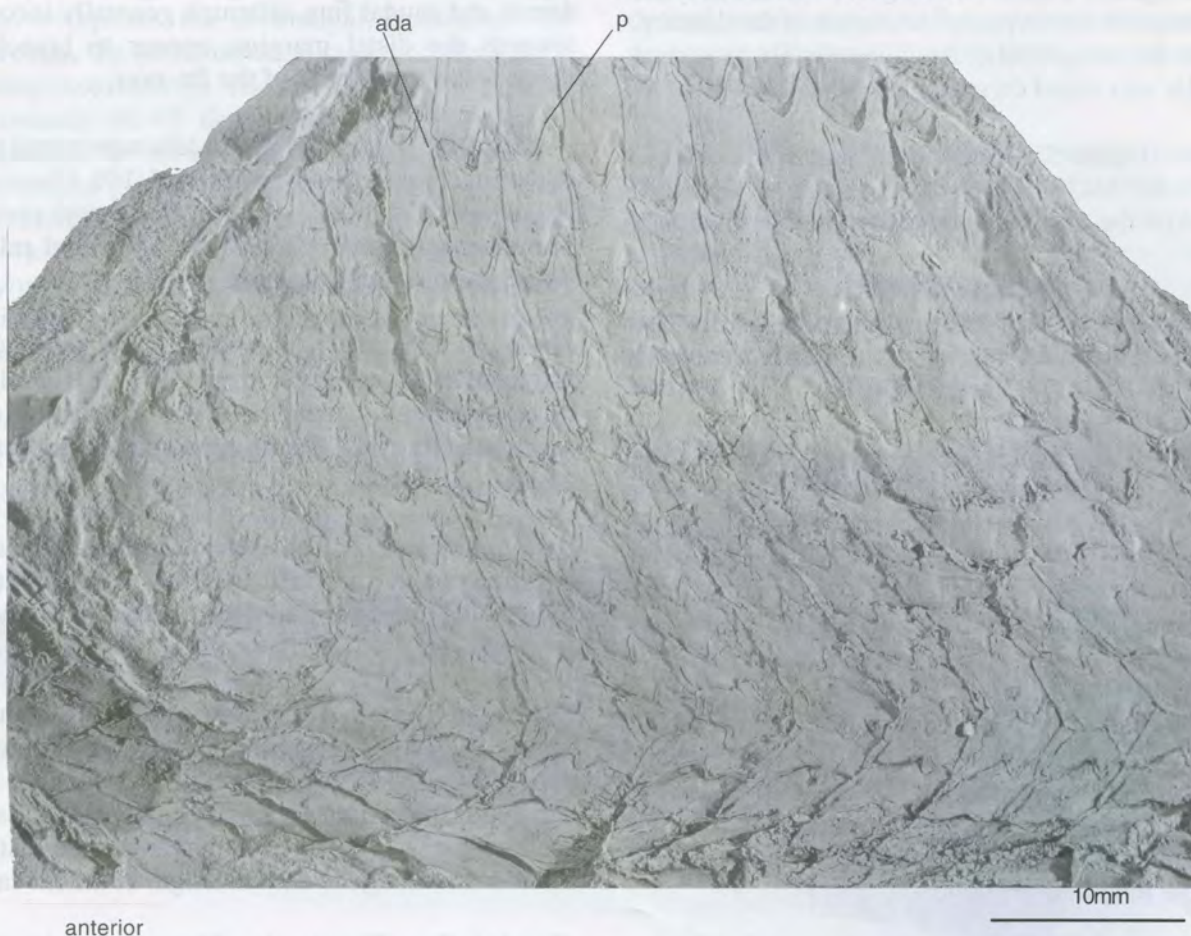


Figure 8. *Bethesdaichthys kitchingi* specimen BP/1/4373/2, medial view of midflank scales, showing peg and socket articulation, and anterodorsal angle.

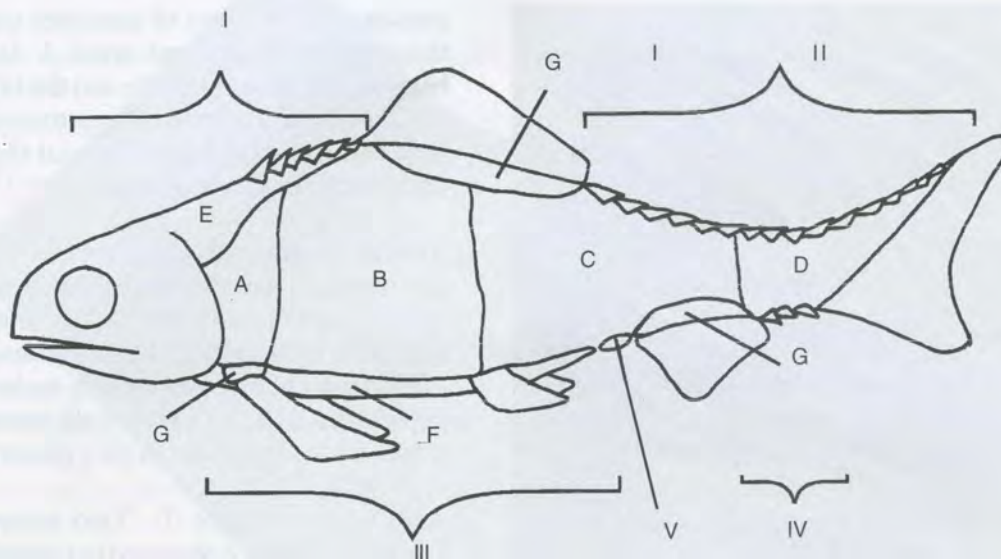


Figure 9. Diagram showing the various areas of scale cover in lower actinopterygian fishes (after Esin 1991). A, B, C, D, E, F, and G are areas of the scale cover on the lateral surfaces of the body; I - ridge scales; II - basal fulcra; III - keel scales; IV - basal fulcra; V - anal scale(s).

Topographic variation of the *Bethesdaichthys* scale cover (see Figure 9 for scale cover Areas and designations of scale types).

Area A: (Figures 10, 11). Scales in this area are situated anterior to the insertion of the pelvic fin. Well preserved scales are seen towards the posterior margin of Area A. The scales are almost rectangular, with a height (h) to length (l) ratio of approximately 2:1. They exhibit steeply inclined anterior and posterior margins, a well developed anterodorsal angle and a smooth anterior depressed field overlap surface anterior to the free field region. The dermal ornament is particularly prominent in this area and consists of elongated ridges, and shorter denticles of ganoine. The free field can basically be separated into two vertically adjacent and distinctive, but interlocking regions. The dorsal free field section consists of numerous (10-14) ridges, most of which are steeply inclined and are not continuous over the entire free field width. Of the posteriorly situated ridges, c5-7 terminate in posterior denticles. Some of the centrally situated dorsal free field ridges sometimes display a 'semi-circular layout' (this was also found to occur in area B). The ventral free field section, situated below the above-mentioned dorsal free field, consists of 8-10 horizontal ridges basically parallel to the ventral border, which terminate in c3-5 posterior denticles. There is a large smooth field anteriorly overlapped by the preceding scale on all the flank scale areas (A to C).

Area B: (Figure 11). The scales in area B are situated between the pelvic fin and the insertion of the dorsal fin. They are almost square, with a h/l ratio of approximately 3:2. The free field, as in area A, can be separated into two vertically adjacent but interlocking regions. In the dorsal free field section, 6-9 posteriorly situated ridges terminate in posterior denticles; in the ventral section of the scale 6-8 horizontally orientated ridges terminate in c3 posterior denticles. The ridges of the free field appear to be less prominent than in area A.

Area C (Figure 12). Scales in this area can be seen in PB/95/6 and PB/96/15. The scales in this area are longer than high, with a h/l ratio of approximately 2:3. The free field consists of 4-7 curved dorsal ridges, and 5-7 horizontally inclined ventral ridges. There are c3 prominent posterior denticles along the posterior scale margin.



Figure 10. *Bethesdaichthys kitchingi* specimen V101 in lateral view, showing dermal scale detail from Area A.

(i)



— 200µm

(ii)

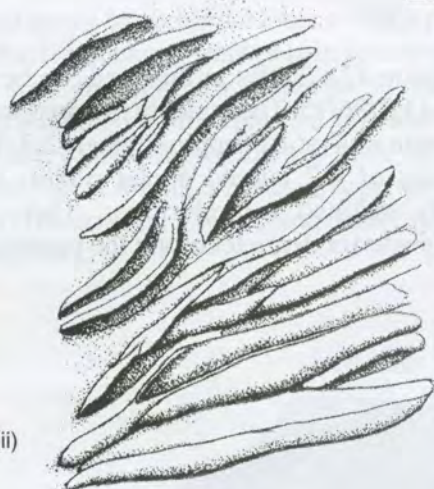


Figure 11 (i). SEM of *Bethesdaichthys kitchingi* specimen BP/1/4373/2b, showing dermal scale detail from Area A/B. (ii). Line drawing interpretation.

Area D: Scales in this area are not distinctive, but can be seen in BP/1/4373/37. Caudal scales are small and diamond-shaped, with a h/l ratio of approximately 1:2. The free field consists of approximately 2-3 faint curved dorsal ridges and 2-3 curved ventral ridges, separated by a faint diagonal ridge, and terminating in an entire margin.

Area E: Scales in this area are generally not well preserved and therefore have not been figured, they can be seen in specimens BP/1/4373/19, 37, 134. Scales of this area appear in *Bethesdaichthys* to occur along almost the entire dorsal margin, immediately ventral to the ridge scales. The scales are small and reduced compared to adjacent area A and B scales, with a h/l ratio of almost 1:1. They are triangular, consisting of c4 curved dorsal and c5 curved ventral ridges which taper posteriorly almost to a point.

Area F: Scales in this area are not completely preserved but can be seen in specimen BP/1/4373/134. This area

consists of c7-9 rows of narrower scales compared to those found in adjacent areas A and B, and occurs between the pectoral girdle and the insertion of the anal fin. They have a h/l ratio of approximately 1:2. The free field consists of c4-5 curved dorsal and c5 ventral ridges terminating in almost a point.

Area G: Scales in this area are incompletely preserved and therefore have not been figured, they can be seen in specimen BP/1/4373/134. Scales of this area are found in regions of the pelvic, dorsal and anal fins, and consist of c5-8 rows of tiny overlapping scales with a h/l ratio of approximately 1:3. The free field consists of c7 diagonal ridges which terminate in c3-4 posterior denticles.

Anal scales (Figure 7). Two enlarged, paired anal fulcral scales were observed in specimen PB/95/6, with a h/l ratio of approximately 1:2. The free field consists of c16 diagonally orientated ridges which terminate in a rounded apex and c3-4 posterior denticles.

Ridge Scales (Figures 7, 12). Ridge scales, although not entirely preserved, were observed in specimens BP/1/4373/37 and PB/96/15. They are enlarged and roughly triangular in shape, with a h/l ratio of approximately 2:3. Ridge scales appear to be present along the entire dorsal margin anterior to the dorsal fin, the free field consisting of c24 dermal ganoine ridges. Approximately 7-9 ridge scales are present posterior to the dorsal fin and anterior to the caudal fin, the free field consisting of a fainter ornament, and the scale more rounded than the anterior ridge scales.

Keel scales (Figure 7). Not well preserved, but fragmentary scales can be seen in specimens BP/1/4373/19 and 134. Keel scales occur between the pectoral girdle and the anal fin insertion. They appear to be paired, and are elongated, enlarged, triangular scales, with a h/l ratio of approximately 1:2. The free field consists of c4-5 ridges dorsally, separated by a diagonal ridge from c5 ventral ridges.

Basal fulcra

- Dorsal fin, basal fulcra (BP/1/4373/37)(Figure 7). Approximately 3-5 small triangular basal fulcra occur immediately anterior to the dorsal fin.
- Caudal fin, dorsal basal fulcra (PB/95/6)(Figure 7). A row at least 16 acutely triangular basal fulcra is situated above the caudal fin.
- Caudal fin, ventral basal fulcra (BP/1/4373/37)(Figure 7). A row of more than 4 triangular basal fulcra is situated immediately anterior to the insertion of the caudal fin.

Squamation

The scale rows are close to vertical on the flanks, tilted slightly anterodorsally at an angle of approximately 70 degrees to the horizontal (Figures 7, 8, 12). The caudal inversion is just posterior to the insertion of the caudal fin (Figure 7).

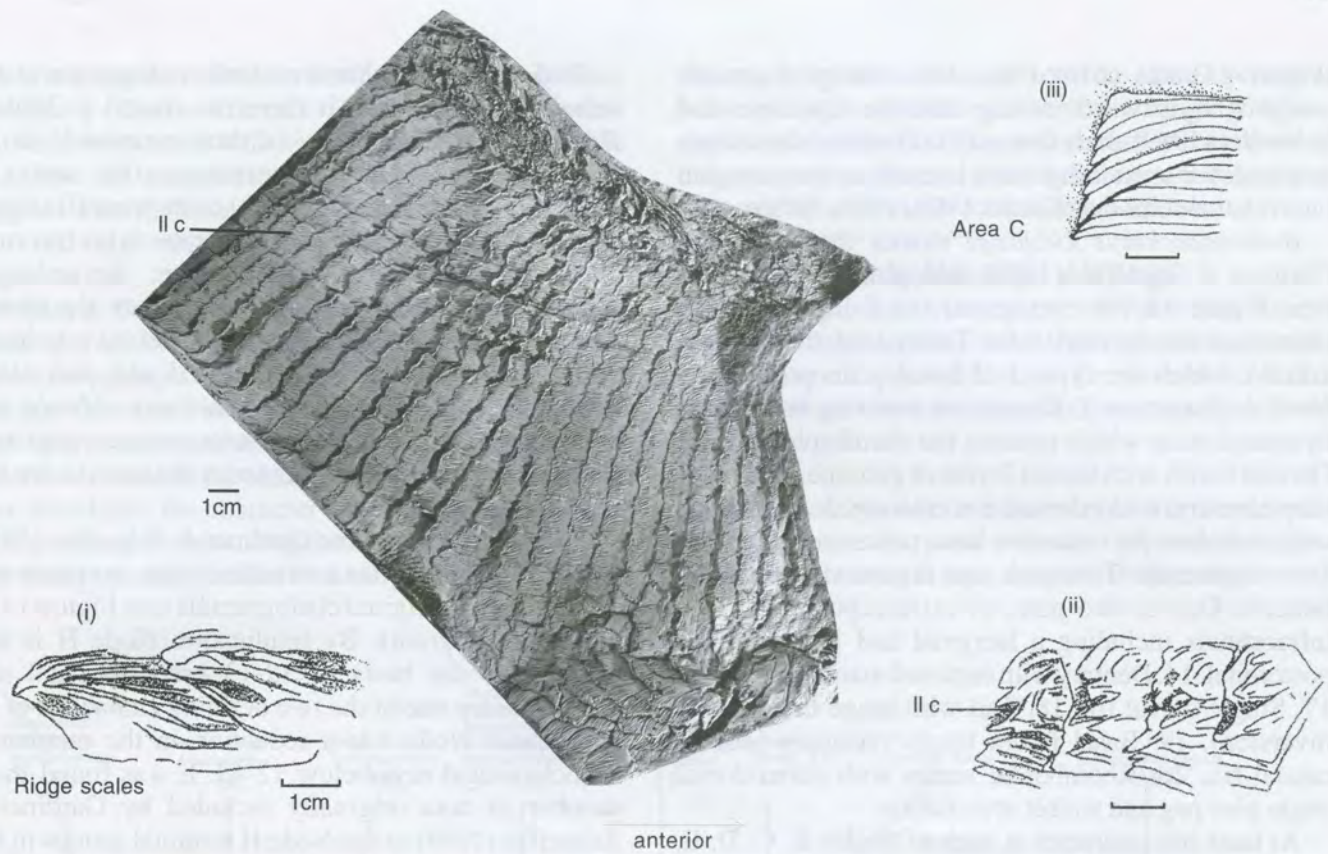


Figure 12. *Bethesdaichthys kitchingi* specimen PB/96/15 in lateral view showing dermal scale morphology. (i). Camera lucida interpretation showing ridge scales. (ii). Camera lucida interpretation showing lateral-line scales in Area B. (iii). Line drawing interpretation showing scale detail from Area C.

Scale counting data:

- Scale rows to pelvic fin (V101; BP/1/4373/19): 11, 11-12.
- Scale rows to dorsal fin (BP/1/4373/124): 35.
- Scale rows to anal fin (BP/1/4373/37): 30-35.
- Scale rows to caudal fin (BP/1/4373/124): 50.
- Scale rows to caudal inversion (BP/1/4373/124): 54.

Number of scales in a single scale column:

- In front of pelvic fin (BP/1/4373/134): 18-20.
- In front of anal fin (BP/1/4373/37): 22-25.
- In front of dorsal fin (BP/1/4373/37): 22-25.
- In front of caudal fin (BP/1/4373/37): 18-20.
- In front of the caudal inversion (BP/1/4373/37): c15.

Scale histology

The general histological structure of the scale can be seen in Figure 13. The scale consists of a basal layer of lamellar bone, overlain by a dentine layer containing an upright, branched plexus of dentine tubules. This layer is in turn overlain by a relatively thick (compared to the overall thickness of the scale), continuous multilayered 'ganoine' or enamel-like layer (see Richter & Smith, 1995, for discussion of the term ganoine). This type of scale histology, in particular the multilayered 'ganoine' is present in most lower actinopterygians, including *Polypterus* and *Lepisosteus* (Richter & Smith 1995).

Laterosensory System

The laterosensory canal system was studied in specimens BP/1/4373/19, 134 and PB/96/15 (Figure 12). It consists of a well developed canal system, which

is carried by a single row of flank scales over the entire length of the body (c7 scale rows ventral to the dorsal margin, in front of the pelvic fin region). The lateral line scale consists of an enlarged posterior aperture situated approximately midway on the posterior margin. A number of slit-like canal pores were observed in Area B.

PHYLOGENETICS AND INTERRELATIONSHIPS

The preservation of the specimens is of such a nature that essentially dermal characters only are preserved, and thus the comprehensive lower actinopterygian phylogenetic analysis of Gardiner & Schaeffer (1989)

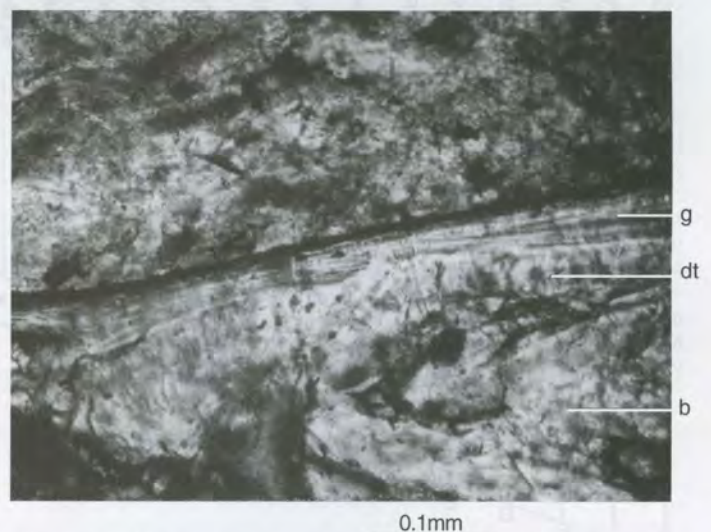


Figure 13. Thin-section photograph of *Bethesdaichthys kitchingi* specimen BP/1/4373/110, showing the structure of the scale layers. (See p.38 for abbreviations)

(Figure 14) was utilized as a basis for phylogenetic analysis. It is worth noting that the Gardiner and Schaeffer (1989) analysis is still utilized by researchers as a basis for examining lower or early actinopterygian interrelationships (see Coates 1993, 1998, 1999).

Bethesdaichthys kitchingi shares the following Gardiner & Schaeffer (1989) cladogram III characters (see Figure 14 for cladogram; the following nodal characters are derived from Table 1 of the original article), which are typical of basal actinopterygians: Node A characters: 2. Dermohyal covering head of the hyomandibular which notches the dermosphenotic. 3. Dermal bones with buried layers of ganoine. 4. Shield-shaped rostral with ethmoid commissure. 5. Nasal bone with notches for anterior and posterior nares. 6. Dermosphenotic T-shaped, and in contact with nasal bone. 8. One or two pairs of extrascapulars. 9. Two infraorbitals including a lacrymal and jugal, and no postorbital. 14. Dentary with enclosed mandibular canal. 17. Single dorsal fin. 18. Tail with hinge line (caudal inversion). 19. Basal fulcrum bordering upper lobe of caudal fin. 20. Rhomboidal scales with anterodorsal angle plus peg and socket articulation.

At least one character at each of Nodes B, C, D, E, H, and I is shared by the study taxon: Node B. 1. Acrodin crown on all teeth and separated from the collar enamel of the tooth shaft. Node C. 6. Fringing fulcrum on leading rays of all fins. Node D. 3. Supra-angular on mandible. Node E. 4. The presence of suborbital bones. Node H. 1. Dermopterotic present and overlaps or abuts dermosphenotic. Node I. Reduction in number of branchiostegal rays below primitive 12-13. Dermopterotic normally never overlaps more than one-third of dermosphenotic.

Bethesdaichthys shares no further characters at any subsequent nodes and is therefore rooted at Node I. *Bethesdaichthys kitchingi* is thus contained on the *Bobasatrania-Dorypterus* transformation series of the Gardiner & Schaeffer (1989) cladogram III (Figure 14), which is a side-branch separate from the main chondrosteian-neopterygian lineage. Accordingly, *Bethesdaichthys* and all taxa situated on the above-mentioned side branch are derived relative to stem-actinopterygians such as *Cheirolepis*, and stem-actinopterygians such as *Howqualepis*, *Mimia* and *Moythomasia*, but basal to stem-neopterygian taxa such as *Australosomus*, *Birgeria*, *Palaeoniscum* and *Perleidus*.

Re-examination of the Gardiner & Schaeffer (1989) Node H terminal taxa revealed that revision was required of the original cladogram III (see Figure 15 for revised cladogram). By implication Node H is also defined on the basis of 12-13 branchiostegal rays present, since one of the two defining characters of the subsequent Node I is a reduction in the number of branchiostegal rays below 12-13. It was found that a number of taxa originally included by Gardiner & Schaeffer (1989) in the Node H terminal groups in fact had less than 12-13 branchiostegal rays, and should be rooted at Node I, together with *Bethesdaichthys kitchingi*.

The following group of taxa comprising those analysed by Gardiner & Schaeffer (1989), and including *Bethesdaichthys*, are thus rooted at Node I: *Aetheretmon*, *Australichthys*, *Cycloptychius*, *Phanerosteon*, *Rhadinichthys canobiensis*, *Strepheoschema* and *Willomorichthys*.

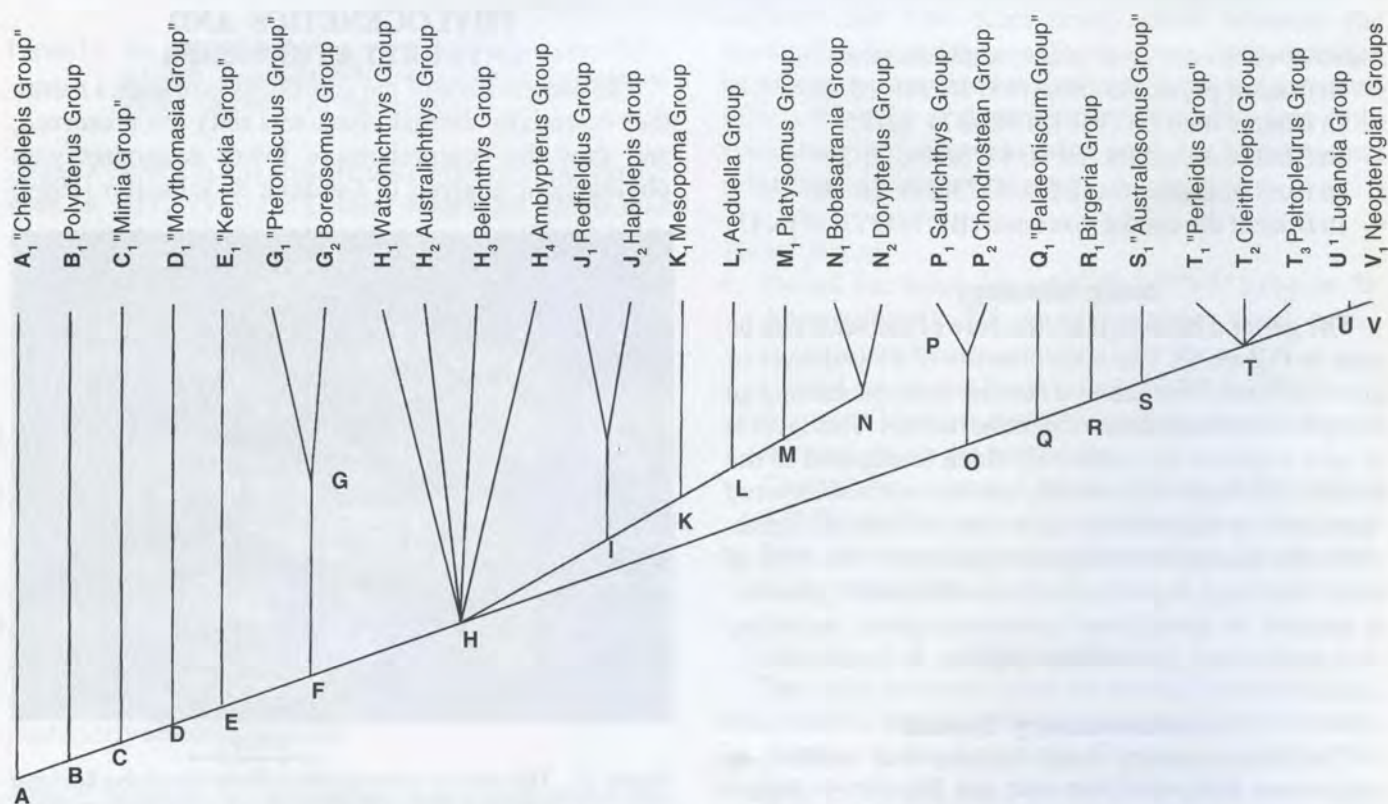


Figure 14. Cladogram for selected major groups of lower actinopterygians from Gardiner & Schaeffer (1989) cladogram III.

Rooted together with *Bethesdaichthys* at Node I are the Early Carboniferous South African forms *Australichthys* and *Willomorichthys*, with the other taxa also all essentially Carboniferous taxa. This suggests that *Bethesdaichthys* as a Late Permian form is relatively unspecialised or morphologically conservative.

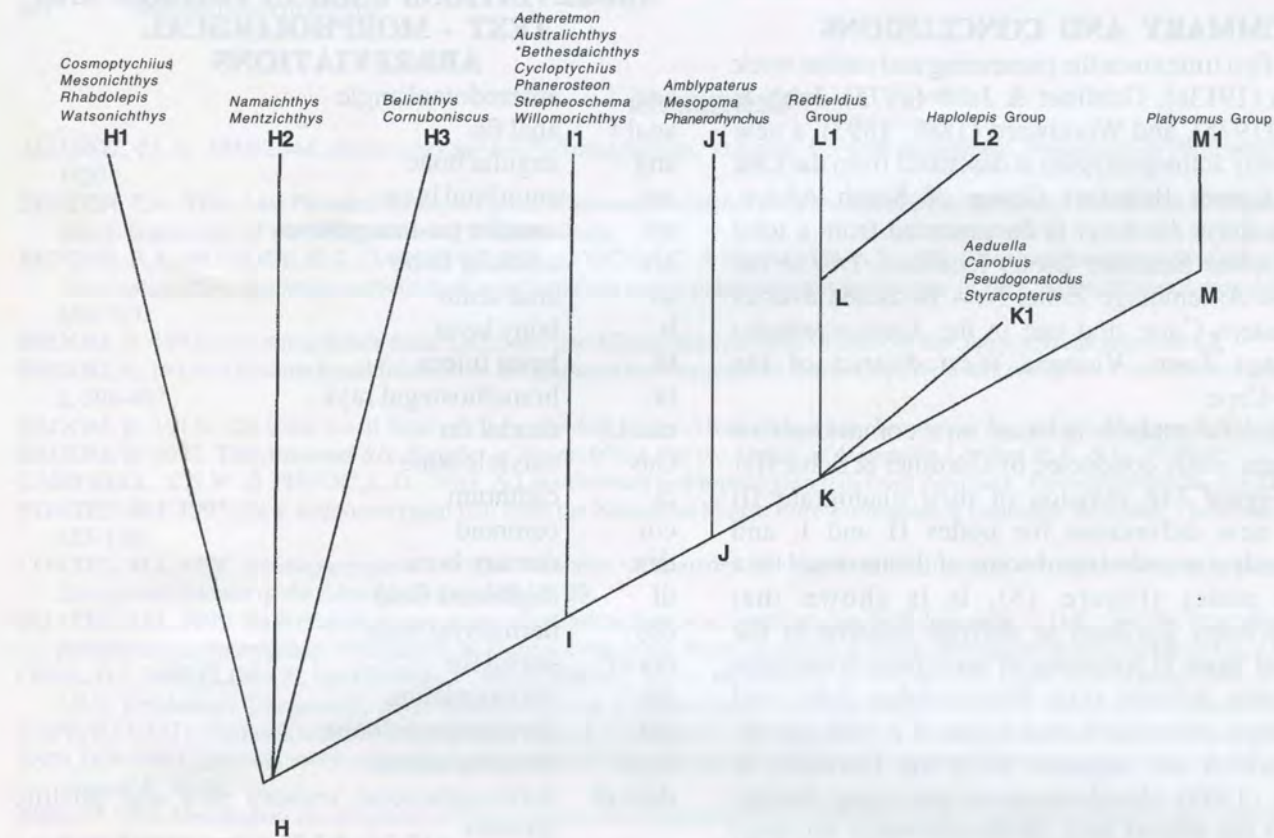
Poplin & Veran (1996) and Lund & Poplin (1997), in discussion of the interrelationships of various lower actinopterygian taxa, utilized a system of listing and ranking characters in terms of their basal, derived or more specialized nature, in order to clarify the primitive or derived nature of the characters which typify specific taxa. Similarly, the character states of the study taxon are documented below using this type of system to assist in defining the primitive/derived morphological nature of

the study species. The study taxon shares primitive actinopterygian characters such as fringing fulcra, rhomboidal scales with peg-and-socket articulation and anterodorsal angle, and shares the stem-neopterygian presence of a dermopterotic and suborbitals.

Bethesdaichthys kitchingi

Stem-actinopteran characters: subopercular shorter than opercular; unspecialized marginal dentition; maxilla with elongate postorbital blade; jaw articulation posterior to parieto-extrascapular suture; elongate body lobe of the tail.

Stem-neopterygian characters: dermopterotic present; premaxillary and antorbital separate; less than 12-13 branchiostegal rays; suborbitals present.



List of nodal characters for Figure 15

- NODE H. Dermopterotic present; at least 12-13 branchiostegal rays.
 H1. Dermopterotic with anterior narrowing, in contact with nasal.
 H2. Dermopterotic overlapping T-shaped dermosphenotic, not contacting nasal.
 H3. Dermopterotic widely separated from nasal; crescent- or sickle-shaped dermosphenotic.
 NODE I. Less than 12-13 branchiostegal rays present.
 I1. Dermosphenotic smaller than dermopterotic and/or T-, keystone-, or crescent-shaped; pelvic fin with short base.
 NODE J. Jaw articulation sited anterior to the parieto-extrascapular suture.
 J1. Maxilla postorbital blade less than length of infraorbital blade.

- NODE K. Jaw suspensorium vertical; terminal gape reduced; preopercular upright and triangular.
 NODE L. Single narial opening at junction of nasal, premaxillo-antorbital and rostral bones; in redfieldiids an additional adnasal enters narial margin; one branchiostegal ray; enlarged postcleithrum.
 NODE M. Marginal teeth peg-like or absent; crushing toothplates present; median fins two sets of radials; basal radials long and fewer in number than distal radials; body deep and laterally compressed, flank scales deepened.
 M1. Maxilla approaches right-angled triangle with curved corners; premaxillo-antorbital enlarged and elongated dorsally; andible deep posteriorly, tapering markedly towards premaxillo-antorbital.

* Indicates the study taxon

Figure 15. Revision of the Gardiner & Schaeffer (1989) cladogram III, including study taxon.

Specialized characters: very broad pectoral fin; high but relatively broad postorbital blade of the maxilla.

What these study taxon character sets show is that *Bethesdaichthys* has an almost equal mix of stem-actinopteran and stem-neopterygian characters, and thus a 'fairly equal' distribution of primitive and derived lower actinopterygian characters.

The earlier, more traditionally based lower actinopterygian studies of Gardiner (1967) and Schaeffer (1973), are perhaps useful in briefly encapsulating the interrelationships of the study species: *Bethesdaichthys kitchingi* appears to be related to members of the group of mostly Carboniferous forms which are close to 'the central stem group of palaeoniscid evolution' (Gardiner 1967), and Schaeffer's (1973) unspecialized 'core' of Devonian-Permian lower actinopterygians.

SUMMARY AND CONCLUSIONS

For the first time since the pioneering and earlier work of Broom (1913a), Gardiner & Jubb (1975), Jubb & Gardiner (1975), and Woodward (1889, 1893), a new taxon of early actinopterygian is described from the Late Permian Lower Beaufort Group of South Africa. *Bethesdaichthys kitchingi* is documented from a total of three Lower Beaufort Group localities, two in the *Dicynodon* Assemblage Zone, New Bethesda district of the Eastern Cape, and one in the *Tapinocephalus* Assemblage Zone, Victoria West district of the Northern Cape.

Phylogenetic analysis is based on a comprehensive phylogenetic study conducted by Gardiner & Schaeffer (1989) (Figure 14); revision of their cladogram III revealed new definitions for nodes H and I, and consequently a re-ordering of some of the terminal taxa at these nodes (Figure 15). It is shown that *Bethesdaichthys kitchingi* is derived relative to the unresolved 'node H polytomy of taxa' (which includes the southern African taxa *Mentzichthys jubbi* and *Namaichthys schroederi*), and is part of a 'side-group' of taxa which are separate from the Gardiner & Schaeffer (1989) chondrosteian-neopterygian lineage leading to the teleost taxa. *Bethesdaichthys kitchingi* exhibits a similarly conservative unspecialised basic skull morphology comparable to that found in various Carboniferous taxa such as *Australichthys*, *Cycloptychius* and *Willomorichthys*. It thus appears to be a relatively primitive Late Permian taxon comparable to taxa which have their origins in the Early Carboniferous. Phylogenetic analysis indicates that *Bethesdaichthys kitchingi* is part of a group of taxa which are found in Britain, Europe and South Africa and thus are not confined to one region. *Bethesdaichthys kitchingi* is morphologically conservative when compared with Late Permian actinopterygian taxa such as *Ebenaqua richiei* from the Late Permian Rangal Coal Measures, Blackwater, central Queensland, Australia, or *Aeduella* and *Dorypterus* from the Permian of Europe and England respectively.

Bethesdaichthys kitchingi is part of a Lower Beaufort Group, Late Permian (Tatarian) high latitude freshwater ichthyofauna which consists essentially of extinct lower actinopterygian taxa (Bender 2000). This ichthyofauna is made up of the following taxa: *Atherstonia scutata*, *Atherstonia minor*, *Atherstonia seeleyi*, *Bethesdaichthys kitchingi*, *Caruichthys ornatus*, *Elonichthys whaitsi*, *Namaichthys digitata*, and *Pteroniscus meiringi*.

In terms of its biostratigraphic implications, *Bethesdaichthys kitchingi* has been documented from the *Tapinocephalus* Assemblage Zone and the *Dicynodon* Assemblage Zone, thus indicating a biostratigraphic range spanning five Assemblage Zones and all of the Late Permian Lower Beaufort Group apart from the basal *Eodicynodon* Assemblage Zone.

ABBREVIATIONS USED IN FIGURES AND TEXT - MORPHOLOGICAL ABBREVIATIONS

ada	anterodorsal angle
anal f	anal fin
ang	angular bone
ant	antorbital bone
apl	anterior pit-line groove
art	articular bone
as	anal scale
b	bony layer
bf	basal fulcra
br	branchiostegal rays
caud.f	caudal fin
clav	clavicle bone
cl	cleithrum
cor	coronoid
den	dentary bone
df	depressed field
dhy	dermohyal bone
dors.f	dorsal fin
dpl	dermopalatine
dpt	dermopterotic bone
dsph	dermosphenotic
dsph.pl	dermosphenotic sensory pits and pit-line grooves
dt	dentine layer
ent	entopterygoid
exsc	extrascapular bone
fr	frontal bone
frf	fringing fulcra
g	ganoine layer
ioc	infraorbital sensory-line canal
ju	jugal bone
ks	keel scale
la	lachrymal
l.gu	lateral gular bone
llc	lateral-line canal
ll.p	pit-line for main lateral-line
mc	mandibular sensory-line canal
mx	maxilla bone
na	nasal bone

n.exc	excurrent or posterior naris
n.inc	incurrent or anterior naris
op	opercular bone
op.pl	opercular sensory pits and pit-line grooves
p	peg
pa	parietal bone
par	prearticular
pcl	postcleithrum
pect.f	pectoral fin
pelvic.f	pelvic fin
pmx	premaxilla bone
pop	preopercular bone
popc	preopercular sensory canal
pop.pl	preopercular sensory pits and pit-line grooves
pt	post-temporal bone
ro	rostral bone
rs	ridge scale
scl	supracleithrum bone

sob	suborbital bones
soc	supraorbital sensory-line canal
sop	subopercular bone
sop.pl	subopercular sensory pits and pit-line grooves

ACKNOWLEDGEMENTS

As this article was part of a PhD study, I would like to thank project supervisors Professor Bruce Rubidge and Dr John Long, also Professor James Kitching, for their invaluable support and advice over a number of years. I would also like to thank Dr Michael Coates for his invaluable comment and advice. Thanks to my employers, the Council for Geoscience, and a number of its members, including the directors for their support; appreciation is also expressed to colleagues at the BPI Palaeontology, Wits University for their support and assistance. Thanks also to: Mr and Mrs Esterhuizen and Clive Kingwell of the farm Blourug and Lionel de la Harpe at Wilgerbosch, for their hospitality, help and enthusiasm; Rochelle Vlok curator at the Victoria West Museum; Geoscience Museum Artist Anke Raath for assistance with the diagrams; and Bernice McLean for field assistance and close friendship.

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CRANIAL ANATOMY OF THE GIANT MIDDLE TRIASSIC TEMNOSPONDYL *CHERNINIA MEGARHINA* AND A REVIEW OF FEEDING IN MASTODONSAURIDS

by

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ABSTRACT

The skull of *Cherninia* ('*Parotosuchus*') *megarhina*, a giant but poorly known mastodonsaurid temnospondyl from the Upper Horizon of the Middle Triassic N'tawere Formation of the Upper Luangwa Valley, Zambia, is redescribed and refigured in detail for the first time. *Cherninia megarhina* is highly derived in most aspects of its cranial morphology and is characterised by the presence of a massively broad and elongated snout, relatively tiny orbits that are set well back on the skull roof, small, near-laterally directed tabular horns, an occipital sensory sulcus, and prominent, forked ridges on the skull roof. The palate is characterised by the presence of a ventral exoccipital-pterygoid contact, a short basicranial suture, a narrow parasphenoid body, a broad pterygoid body, and choanae that are placed far forward of the interpterygoid vacuities. The presence in *Cherninia megarhina* of numerous cranial autapomorphies justifies its separation from *Parotosuchus*. These autapomorphies are shared with *Cherninia* ('*Parotosuchus*') *denwai* from the Middle Triassic Denwa Formation of India. The lateral orientation of the tabular horns and morphology of the otic region suggests that *Cherninia megarhina* is slightly more derived than the Indian species. Mastodonsaurids have traditionally been perceived as passive, benthic suction-feeders. However, recent work on the anatomy and functional morphology of the skeleton of mastodonsaurids suggests that they were designed for active swimming and predation. As such, it is hypothesised that prey capture was achieved using sideways sweeps of the head rather than suction-feeding.

KEYWORDS: Temnospondyl, Triassic, *Cherninia megarhina*, Mastodonsauridae, feeding

INTRODUCTION

The Mastodonsauridae, the senior synonym of the more widely known taxon Capitosauridae (Damiani in press a), is a monophyletic clade of Mesozoic stereospondyls that were widely distributed throughout Triassic Pangaea. Mastodonsaurids were morphologically diverse and were the most abundant and widely distributed of any temnospondyl group, and their ubiquity in non-marine Triassic strata has led to their being amongst the principal vertebrate groups used in biostratigraphy and correlation of Triassic tetrapod faunas (Hancox *et al.* 1995; Ochev & Shishkin 1989; Lucas 1998).

Despite a long history of study dating back to the first half of the 19th century, the taxonomy of the Mastodonsauridae has long been problematic and there remains little consensus as to the taxonomic composition of the group or the relationships within it (Schoch 2000; Damiani in press a). This is due, in part, to the sheer abundance of fossil material attributable to the Mastodonsauridae and to the effects of excessive taxonomic 'splitting', both of which resulted in a large number of names erected on undiagnostic material (Ochev 1966; Welles & Cosgriff 1965; Damiani in press a). The first serious attempt at rationalizing mastodonsaurid taxonomy was the landmark review of Welles & Cosgriff (1965), who surveyed all then known

species and reduced the number of valid genera to four (*Parotosuchus*, *Paracyclotosaurus*, '*Kestrosaurus*', *Cyclotosaurus*) by synonymising most species or referring to them as *nomina vana*. Welles and Cosgriff's paper proved highly influential and most subsequent descriptions of mastodonsaurids were referred to one of these four genera, usually *Parotosuchus*. Although this taxonomy has proved largely stable, recent work on mastodonsaurid systematics (Schoch & Milner 2000; Damiani in press a) has shown that this taxonomy is largely artificial and, perhaps ironically, both authors recognised a greater number of genera within the Mastodonsauridae than the four recognised by Welles & Cosgriff (1965).

The subject of this paper, the mastodonsaurid *Cherninia* ('*Parotosuchus*') *megarhina*, was first described in a brief note by Chernin & Cruickshank (1970) based on a poorly preserved partial skull (BP/1/4223) from the Upper Horizon of the Middle Triassic N'tawere Formation of Zambia (Drysdaal & Kitching 1963). Chernin and Cruickshank provided only an outline drawing of the skull roof of the specimen which they referred to '*Parotosuchus*' *pronus* (Howie 1970) from the Middle Triassic Manda Formation of Tanzania, primarily on the basis of the shape of the tabular horns but despite the marked difference in the size and shape of the snout. Chernin (1974) provided a more detailed

description and drawing of the skull roof which included the supposed course of the lateral line sulci and, apparently, an interpremaxillary foramen, although most of the sutures could not be determined. The fragmentary palate was only briefly described but not illustrated. Chernin (1974) tentatively retained the specimen in '*P. pronus*' and argued that the great difference in the size of the snout between BP/1/4223 and the smaller '*P. pronus*' was due to "genetic variability". Chernin also tentatively referred a second skull (BP/1/4221) from the same locality as BP/1/4223 to '*P. pronus*'. Chernin & Cosgriff (1975) provided a revised outline drawing of the skull roof of BP/1/4223 which differed from that of Chernin (1974) in the broader snout proportions and in the size and shape of the nostrils and tabular horns. On this basis, Chernin and Cosgriff referred BP/1/4223 to a new species, '*P. megarhinus*'. The second skull described by Chernin (1974), BP/1/4221, was also tentatively referred by Chernin and Cosgriff to '*P. megarhinus*' but is significantly smaller than BP/1/4223.

In their recent review of the Stereospondyli, Schoch & Milner (2000) recognised, but did not discuss, the distinctive cranial proportions of '*Parotosuchus megarhinus*' and suggested that it may warrant a new genus within the 'Capitosauroidae'. In the most recent review of mastodonsaurid taxonomy which included an examination of the holotype (BP/1/4223) and referred specimen (BP/1/4221) of '*P. megarhinus*', Damiani (in press a) listed several cranial autapomorphies of the holotype specimen (see Emended diagnosis below) and erected for it a new genus, *Cherninia*. Principal amongst these autapomorphies are the massively developed snout, the presence of an occipital sensory sulcus and the presence of paired, forked ridges on the skull roof. However, Chernin & Cosgriff's (1975) referred specimen of '*P. megarhinus*', BP/1/4221, was transferred by Damiani (in press a) to '*P. pronus*', for reasons discussed in that paper. On the basis of the listed autapomorphies of *Cherninia*, Damiani (in press a) also referred to *Cherninia* the recently described mastodonsaurid '*Parotosuchus denwai*' (Mukherjee & Sengupta 1998), from the Middle Triassic Denwa Formation of central India. The similarity of that taxon with *C. megarhina* was earlier noted by Bandyopadhyay & Sengupta (1999), but not discussed. As the focus of Damiani's paper was a taxonomic revision of the Mastodonsauridae and not anatomical descriptions, he did not redescribe the holotype skull of *C. megarhina*.

Accordingly, this paper provides a full redescription and a new, revised reconstruction of the skull of *Cherninia megarhina* which differs significantly from previous reconstructions. Airbrasive and mechanical preparation of the skull has revealed hitherto unknown details of the skull roof including the sutural pattern, and permits the first drawing and detailed description of the palate. In view of the ongoing debate (Milner 1990; Maryanska & Shishkin 1996; Schoch 2000; Damiani in press a) concerning the intrarelationships of 'capitosauroid' temnospondyls, detailed osteological descriptions especially of the more poorly known taxa

such as *C. megarhina* are crucial for resolving phylogenetic relationships.

Finally, the feeding strategy of mastodonsaurids has attracted considerable attention from temnospondyl workers. The traditional view held that mastodonsaurids were passive, benthic suction-feeders, while other workers favoured a more active, predatory feeding strategy. In this paper I review aspects of the anatomy and functional morphology of mastodonsaurids in relation to feeding and suggest a likely strategy for prey capture.

SYSTEMATIC PALAEONTOLOGY

TEMNOSPONDYLI Zittel 1887-1890

STEREOSPONDYLI Zittel 1887-1890 *sensu*

Yates & Warren 2000

MASTODONSAUROIDEA Lydekker 1885 *sensu*

Damiani in press a

MASTODONSAURIDAE Lydekker 1885 *sensu*

Damiani in press a

CHERNINIA Damiani in press a

Type species. Cherninia ('*Parotosuchus*') *megarhina* (Chernin & Cosgriff 1975).

Referred species. Cherninia ('*Parotosuchus*') *denwai* (Mukherjee & Sengupta 1998).

Emended diagnosis. Distinguished from all other mastodonsaurids by the following autapomorphic characters: Snout hyper-elongated; skull table (i.e. postorbital portion of skull roof) exceptionally short; nostrils large, confluent with skull margin anteriorly; skull roof with paired, forked ridges anterior to orbits; loose patch of pustular ornament on jugals and prefrontals; occipital sensory canal present; temporal sensory canal extending to tips of tabular horns; postparietals antero-posteriorly short but exceptionally broad; choanae located far forward of the interpterygoid vacuities.

CHERNINIA MEGARHINA (Chernin and Cosgriff)
Damiani in press a

Parotosaurus pronus (Howie) Chernin &
Cruickshank 1970

Parotosaurus pronus (Howie) Chernin 1974, in part
Parotosaurus megarhinus Chernin & Cosgriff 1975

Parotosuchus megarhinus Chernin 1978

Holotype. BP/1/4223, a partial skull with associated cranial fragments, repositied in the Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa.

Type locality and Horizon. Locality 15, south of the Sangu River 3.5 miles west of Sitwe, in the Upper Luangwa Valley, Zambia (Drysdall & Kitching 1963); Upper Horizon of the N'tawere Formation, Anisian (e.g. Battail 1993; Hancox 2000). This horizon has also yielded the brachyopid temnospondyl *Batrachosuchus*

concordi (Chernin 1977), the dicynodonts *Zambiasaurus* and *Sangusaurus* (Cox 1969), and the cynodont *Luangwa* (Brink 1963).

Diagnosis. As for the genus. The referred species, *Cherninia denwai*, differs from *C. megarhina* in having more posteriorly directed tabular horns, a broader otic notch, a more deeply concave occipital skull margin, well expressed sensory canals, a bony protuberance on the occipital face of the tabular, and, possibly, in possessing a septomaxilla and lacking a circum-narial sulcus.

DESCRIPTION

Preservation

The holotype and only known skull of *Cherninia megarhina* was found fragmented and encased in a soft matrix, the "N'tawere green and purple marls" (Dixey 1937), associated with clumps of extremely hard, black manganese. Until now much of this matrix still covered the skull, and it was decided to undertake additional preparation using an airbrasive unit and pneumatic drill, revealing the skull roof and palate in detail for the first time. The bone is generally poorly preserved with numerous cracks, ranging from broad to hairline in width, present throughout. The skull has clearly suffered from post-mortem distortion which is especially evident on the snout which appears flat but somewhat undulating. Consequently it is difficult to determine such characteristics as the overall depth of the skull and snout, and the presence or absence of a preorbital step. Ornament and sutural patterns on the more posterior parts of the skull roof are well exposed. Anteriorly a thin, resistant layer of matrix clings to the skull roof and could not be removed without serious damage. The ventral surface of the skull roof remains largely covered by manganese-rich matrix which again proved resistant to mechanical removal. Matrix has been cleared from most of the palate except anteriorly, where considerable damage to the bone has occurred.

Skull roof (Figures 1A-3A)

The most prominent aspect of the skull of *Cherninia megarhina* is the extraordinarily massive snout that is expanded both antero-posteriorly and transversely so that the lateral margins are near parallel-sided and the anterior rim is broadly parabolic. The length of the skull, from the tip of the snout to the posterior border of the skull deck, is approximately 800 mm. Posteriorly the cheek region of the skull appears to have been slightly 'flared'. The shape of the skull in the new reconstruction (Figure 3) resembles Chernin's (1974) initial restoration but differs markedly from that of Chernin & Cosgriff (1975) in that the snout as restored by the latter authors is overly broad. A similarly broad but much less elongated snout occurs in *Tatrasuchus kulczyckii* (Maryanska & Shishkin 1996), '*Kupferzellia*' *wildi* (Schoch 1997) and *Cyclotosaurus* (Fraas 1889, 1913; Schoch & Milner 2000), and contrasts with the more

slender, triangular snouts of all other mastodonsaurids. However, the shape and relative proportions of the skull of *C. megarhina* are nearly identical to that of the smaller (570 mm skull length) *Cherninia denwai* (Mukherjee & Sengupta 1998). In *C. denwai* and *C. megarhina*, the snout (i.e. the skull roof anterior to the orbits) accounts for 75 and 80 percent of the total length of the skull, respectively, whereas in most other adult mastodonsaurids the snout accounts for between 65-70 percent of the total skull length. *Cherninia* is thus clearly peramorphic (*sensu* McNamara 1986) with respect to other mastodonsaurids, having undergone increased development of the snout as compared to closely related taxa.

Relative to the size of the skull as a whole the orbits are tiny, set very close together and positioned well back on the skull roof, with their long axes pointing toward the midline. This is identical to the situation in *Cherninia denwai* (Mukherjee & Sengupta 1998). The preserved left orbit is elevated above the surrounding plane of the skull roof so that an interorbital trough is present, as is typical for mastodonsaurids except *Mastodonsaurus* (Schoch 1999). Only a small portion of the right orbit was preserved. The preserved portion of the rim of the parietal foramen indicates that its outline was circular or sub-circular (cf. Chernin 1974), unlike the transversely widened foramen figured by Chernin & Cosgriff (1975). In *C. denwai* the parietal foramen is somewhat irregular in shape but the surrounding area appears to have been damaged. In contrast to Chernin (1974), there is no evidence of an interpremaxillary foramen.

Most of the left and a small margin of the right external naris is preserved. The more complete left nostril indicates that they were exceptionally large in size, oval, and had their long axes parallel to the midline. The anterior portion of the nares appear to have been confluent with the skull margins, as in *Cherninia denwai*. Previous reconstructions of the nostrils (Chernin 1974; Chernin & Cosgriff 1975) are incorrect in being too small and separated from the skull margin in the conventional manner. This condition is clearly an autapomorphy of *Cherninia*, and, as far as can be determined, is unique within the Stereospondyli. In addition, a clearly defined sulcus is present around the margin of the left naris; this sulcus is not apparent on the right naris because of poor preservation. A sulcus in this position was not described in *C. denwai*, and may thus represent an autapomorphy of *Cherninia megarhina*. In *C. denwai* an undifferentiated, ornamented 'lump' of bone within the narial cavity was identified as a septomaxilla (Mukherjee & Sengupta 1998). No trace of such an element is present in *C. megarhina*, although it may easily have been dislodged and hence not preserved. Within the left narial cavity of *C. megarhina* the anterior portion of the choana can clearly be seen, as in *C. denwai* (Mukherjee & Sengupta 1998). This indicates that, as in *C. denwai*, the choanae in *C. megarhina* were positioned extremely far forward on the palate.

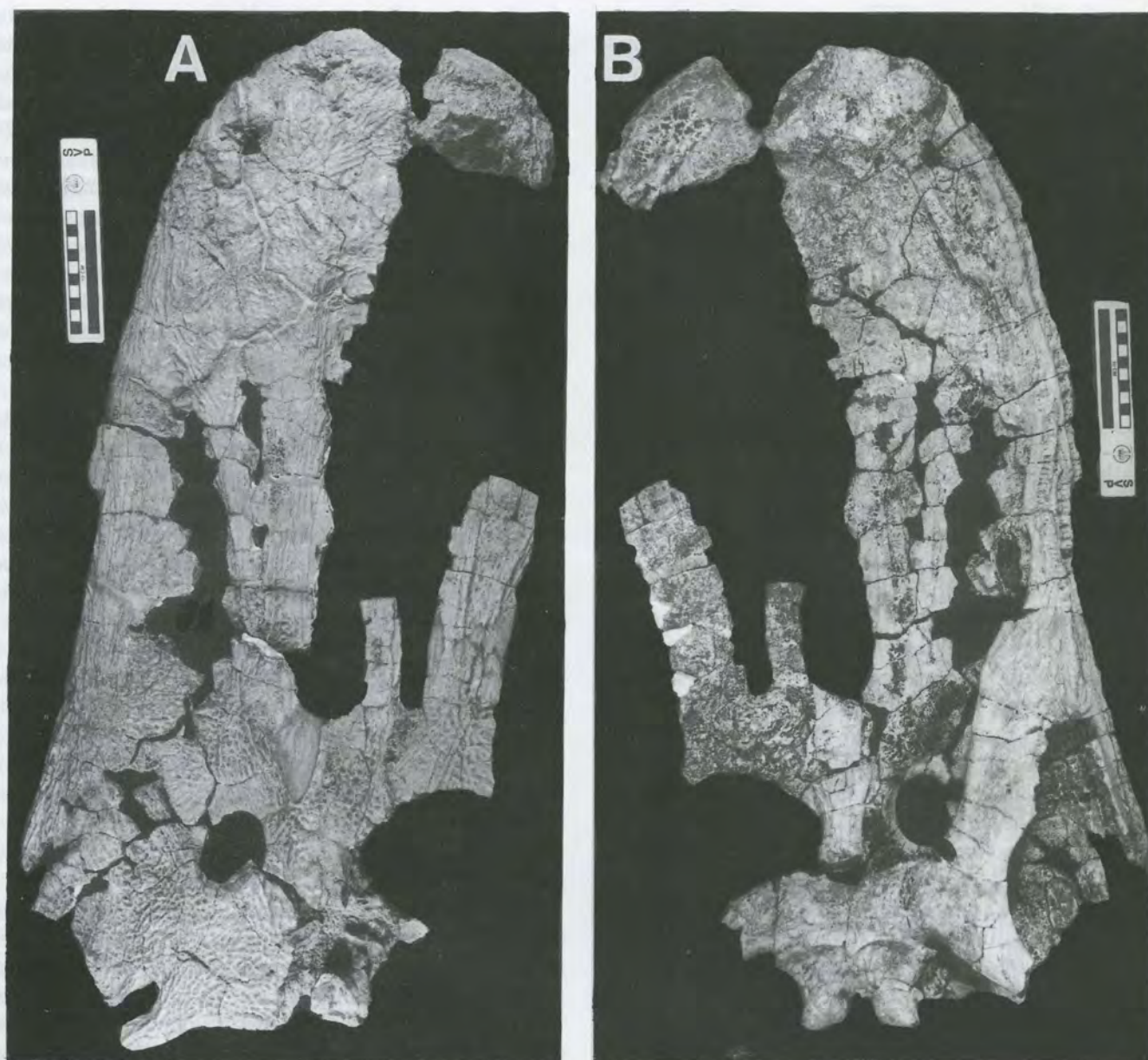


Figure 1. Photographs of the skull of *Cherninia megarhina* (Chernin and Cosgriff), BP/1/4223, from the Upper Horizon of the Middle Triassic N'tawere Formation of the Upper Luangwa Valley, Zambia, in A, dorsal and B, ventral views.

Ornament on the more posterior parts of the skull roof consists mainly of small, shallow, circular to sub-circular pits up to 2 mm in depth. These are separated by low but broad walls which are generally more conspicuous than the pits themselves. Ridge-groove type ornament is present on the jugal, frontal, prefrontal, and to a lesser extent on the squamosal. Further anteriorly the ornament is not well exposed but ridge-groove type ornamentation appears to have been the predominant sculpture pattern up to the tip of the snout. An unusual aspect of the dermal sculpturing of *C. megarhina* is the presence of a loose patch of pustular-type ornamentation on the left (and presumably right) jugal and prefrontal. An identical patch is present in the same position in *Cherninia denwai* (Sengupta pers. com.), and thus represents an autapomorphy of *Cherninia*. Elsewhere pustular ornament is present in most members of the Plagiosauridae (Huene 1922; Nilsson 1937), the lapillopsid *Lapillopsis* (Yates 1999), the

basal stereospondyl *Peltobatrachus* (Panchen 1959), the dissorophoid *Micropholis* (Boy 1985), the rhytidosteid *Pneumatostega* (Cosgriff & Zawiskie 1979), and the laidleriid *Laidleria* (Warren 1998), but the significance of such ornamentation is as yet unknown.

The sensory canal system on the skull roof is very poorly preserved, in contrast to Chernin's (1974: 43) statement that the "course of the canals is distinctly marked by a series of enlarged pits and grooves". The lack of visible canals appears to be due, at least in part, to the poor preservation of the bone in general. Anteriorly the sensory canals, if present, are obscured by the thin layer of mudstone adhering to the bone surface. Posteriorly sections of two sensory canals are partially preserved. The temporal canal cannot be traced anteriorly but posteriorly it skirts the otic rim of the tabular and reaches the tip of the tabular horn, as in *Cherninia denwai*. This contrasts strongly with all

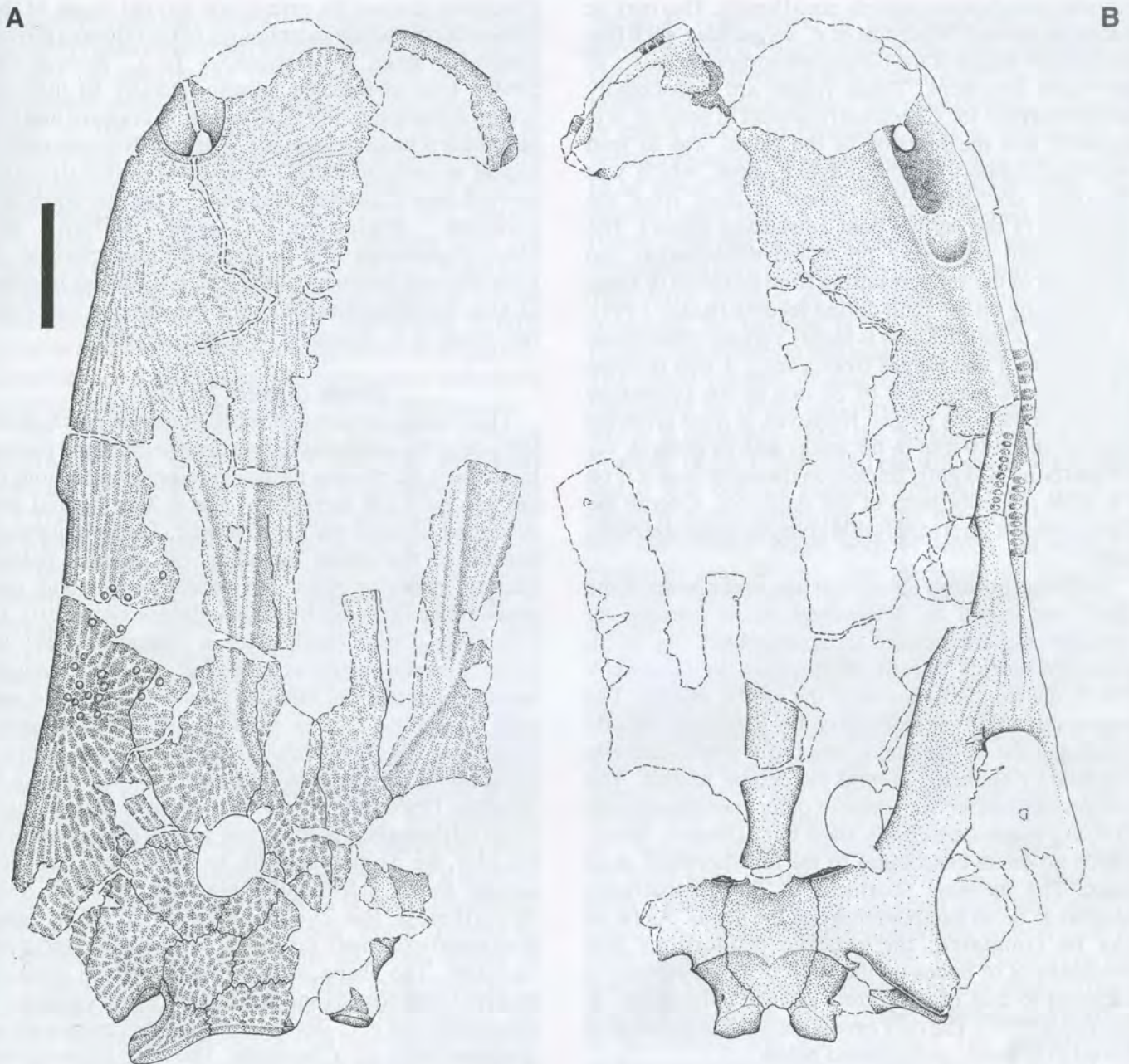


Figure 2. Interpretive drawings of the skull of *Cherninia megarhina* (Chernin and Cosgriff), BP/1/4223, from the Upper Horizon of the Middle Triassic N'taware Formation of the Upper Luangwa Valley, Zambia, in A, dorsal and B, ventral views. Unshaded areas represent either matrix, plaster or broken bone. Scale bar equals 10 cm.

other mastodonsaurids in which the temporal canal terminates on the supratemporal. An occipital sulcus is also present. This sulcus is smooth and continuous and runs along the posterior margin of the skull deck. In *C. denwai* (Mukherjee & Sengupta 1998) an occipital sulcus was not figured, although examination of Figure 2 in that paper, as well as photographs of the specimen, indicates that this sulcus is present. Within the Mastodonsauroidea (*sensu* Damiani in press a: *Benthosuchus*, Mastodonsauridae, Heylerosauridae) an occipital sulcus is present only in *Benthosuchus* (Bystrow & Efremov 1940; Getmanov 1989) and *Cherninia*.

One of the most extraordinary features of the skull roof of *Cherninia megarhina* is the presence of a pair

of forked, longitudinally oriented ridges, each of which originates on the prefrontals just anterior to the orbits before bifurcating and diverging anteriorly, terminating within the anterior half of the snout. The posterior portion and lateral fork of each ridge is a single, raised, thickened ridge of dermal bone, but the medial fork divides into a pair of ridges separated by a shallow trough. These remarkable structures were first reported but not described in *Cherninia denwai* (Mukherjee & Sengupta 1998), although in that species they appear to originate on the frontals between the orbits, rather than on the prefrontals. Interestingly, in *C. megarhina* the length of the bifurcated portion of each ridge is much greater than the length of the single, posterior portion, whereas in *C. denwai* the bifurcated and un-bifurcated

portions are of approximately equal length. This may be due to the overall larger size of *C. megarhina*, such that the relative length of the bifurcated portion increases as the snout lengthens. These ridges are undoubtedly autapomorphic for *Cherninia* (Damiani in press a). It is apparent that the function of the ridges was to lend structural support for the massive snout, which was otherwise not particularly robust judging from the thickness of the dermal bone (discussed below). The ridges could thus have prevented deformation and fracturing of the snout resulting from torsional or shear forces acting on the skull during feeding (Kathe 1999).

Dermal bone thickness is highly variable throughout the skull roof and ranges from a mere 4 mm in some areas up to a maximum of 20 mm in the immediate vicinity of the bony ridges. However, in most areas the bone is under 10 mm in thickness and, in general, the dermal bone is slightly thicker on the snout than it is on the more posterior parts of the skull roof. Overall the dermal bone is surprisingly thin given the giant size of the skull.

Although not all of the sutures and hence bones of the skull roof could be determined, those present are typically mastodonsaurid in arrangement. As in all mastodonsaurids except *Wetlugasaurus* (Sennikov 1981), the frontal bones enter the orbital margin. The supratemporal is excluded from the margin of the otic notch and the postorbital is markedly antero-laterally expanded ('hooked') around the orbital margin. The postparietals differ from those of other mastodonsaurids in being antero-posteriorly short but extremely broad, which no doubt contributes to the foreshortened skull deck. The extreme shortness of the postparietals appears to be an autapomorphy of the genus. As far as can be compared, the relative proportions and arrangement of bones on the skull of *C. megarhina* is identical to that of *Cherninia denwai* (Mukherjee & Sengupta 1998). The only exception is the orientation of the tabular horns, as discussed below.

The tabular horns of *Cherninia megarhina* are directed almost exclusively laterally, rather than postero-laterally as in most derived Middle Triassic mastodonsaurids (Damiani in press a). Consequently the occipital margin of the skull deck is straight to slightly concave, in contrast to most other mastodonsaurids in which this margin is strongly concave. Distally the tabular horns are unexpanded and of uniform width throughout their length, as in *Wellesaurus peabodyi* (Welles & Cosgriff 1965), *Mastodonsaurus giganteus* (Schoch 1999) and '*Parotosuchus*' *africanus* (Chernin 1978). Thus they lack the antero-distal 'lappet' present in '*Parotosuchus*' *pronus* (Howie 1970), *Eryosuchus* (Ochev 1972) and *Paracyclotosaurus* (Watson 1958; Hancox *et al.* 2000). The orientation of the tabular horns in *C. megarhina* narrows the otic notch distally, so that the channel between the tabular and squamosal broadens anteriorly. Chernin's (1974: Figure 8) diagram of the otic area is inaccurate in this respect because the anterior rim of the otic notch is shown as being angular rather than rounded. In

Cherninia denwai the orientation but not shape of the tabular horns and the morphology of the otic area differs somewhat from *C. megarhina*. In *C. denwai* the tabular horn is directed postero-laterally so that the occipital margin of the skull is deeply concave and the otic notch is broad posteriorly. These differences would appear to indicate that *C. megarhina* is slightly more derived than *C. denwai*, as closure of the otic notch is a common evolutionary trend within the Mastodonsauridae and is generally characteristic of more derived members of the group (Damiani in press a). One further difference is that the anterior rim of the otic notch in *C. denwai* is curiously angular.

Palate (Figures 1B-3B)

The ventral surface of the skull preserves much of the left side of the palate including the marginal and palatal tooth rows, the choana, the basicranium, and portions of the left and right pterygoids, and is here figured and described in detail for the first time. The anteriormost portion of the palate including the anterior palatal vacuity, vomerine tusks, and transvomerine tooth row are completely hidden by the manganese-rich matrix. In *Cherninia denwai* (Mukherjee & Sengupta 1998) the anterior palatal vacuity is paired but set within a single, common depression. The left choana is elongated and oval in outline, not as broad as in *Wetlugasaurus* (Sennikov 1981) or *Watsonisuchus* (Damiani in press a) yet not as narrow as in *Parotosuchus* (Maryanska & Shishkin 1996; Damiani 1999, in press a). The margins of the left interpterygoid vacuity are not clear anteriorly because the vomer appears to have been crushed against and is indistinguishable from the skull roof. Nevertheless the choana appears to have been positioned extremely far forward of the interpterygoid vacuities. The shape of the choana and its position relative to the nostrils and the interpterygoid vacuities is identical to that in *C. denwai*, and probably represents an autapomorphy of *Cherninia*. The left subtemporal vacuity is only partially preserved but it appears to have been transversely narrow, as in *C. denwai*. This narrowing appears to be a result of the marked widening of the body of the pterygoid, as discussed below.

The body of the parasphenoid, forming most of the basicranium, has a very short suture with the pterygoid. This primitive state contrasts with the generally highly derived nature of the skull and its overall size. Other highly derived mastodonsaurids such as *Mastodonsaurus* (Schoch 1999), *Cyclotosaurus* (Fraas 1889, 1913) and *Paracyclotosaurus* (Watson 1958; Hancox *et al.* 2000) all possess elongated basicrania. In addition, the body of the parasphenoid is remarkably narrow and posteriorly forms a free margin between the exoccipitals. A similarly narrow parasphenoid with a short pterygoid suture is present in *Cherninia denwai* (Mukherjee & Sengupta 1998). A well developed *crista muscularis* crosses the body of the parasphenoid level with the posterior border of the body of the pterygoid, merging in the midline as a posteriorly directed point. Remarkably, the *crista*

muscularis continues laterally where it directly overlies the suture between the pterygoid and exoccipital. As far as can be determined this situation is unique to *Cherninia megarhina*. The area directly below each 'half' of the *crista muscularis* forms a trough or 'pocket' that is traditionally thought of as the area for insertion of the *rectus capitis* vertebro-cranial musculature (Watson 1962; Dutuit 1976). In *C. denwai* the *crista muscularis* of the parasphenoid does not appear to merge in the midline but the area is not well preserved. None of the cultriform process of the parasphenoid is preserved. An ossification a little anterior to the body of the parasphenoid is tentatively identified as a sphenethmoid and/or part cultriform process, and is discussed below (see Endocranium).

The exoccipitals bear a long, anteriorly directed subotic process which sutures with the pterygoids ventrally. At the junction of these bones laterally there is a triangular 'swelling' or 'bulge' as is seen in many derived mastodonsaurids including *Mastodonsaurus* (Schoch 1999), *Paracyclotosaurus* (Watson 1958; Hancox *et al.* 2000) and *Cyclotosaurus* (Ingavat & Janvier 1981). On the left-hand side of the skull this 'swelling' is damaged, giving a false impression of a ventral exoccipital-ptyerygoid groove, as in some primitive mastodonsaurids such as '*Parotosuchus gunganj*' (Warren 1980) and *Parotosuchus haughtoni* (Damiani in press b). The exoccipital-ptyerygoid suture also directly coincides with the lateral portions of the *crista muscularis* of the parasphenoid. In *Cherninia denwai* (Mukherjee & Sengupta 1998) the exoccipitals appear to have been dislodged from their natural position so that the presence or absence of a ventral exoccipital-ptyerygoid contact and of a lateral 'bulge' cannot be determined, although the subotic processes appear to have been similarly elongated. Each exoccipital in *C. megarhina* bears three foramina. The largest, the jugular foramen, lies at the junction between the body of the exoccipital and its paroccipital process (of which only a short stump is preserved), and transmitted cranial nerves IX (glossopharyngeal) and X (vagus). The foramen for cranial nerve XII (hypoglossal) lies on the lateral edge of the condyle a little posterior to the base of the paroccipital process, but is not visible in ventral view. A third foramen, visible in ventral view, lies anterior and ventral to the glossopharyngeal foramen and probably transmitted a nutritive vessel (cf. Bystrow & Efremov 1940). The exoccipital condyles are positioned close to the posterior border of the body of the parasphenoid, so that the condyles are 'unstaked'.

The better preserved left pterygoid of *Cherninia megarhina* is the basis for the description of this complex element. The right pterygoid is represented by the articulated basicranial portion and a near-complete but isolated palatal ramus. The basicranial process of the pterygoid (i.e. that portion of the body of the pterygoid which contacts the parasphenoid) is elongated medially, so that the body of the pterygoid is exceptionally broad. This produces a narrowing (noted earlier) of both the body of the parasphenoid and of the subtemporal

vacuities. The latter, in particular, are noticeably narrower than is usual in mastodonsaurids. The body of the pterygoid gives rise to two main branches: the palatal ramus and quadrate ramus. The palatal ramus is unusual in that it lacks ornamentation. This is uncommon in mastodonsaurids but ornament in this area also appears to be absent in *Mastodonsaurus* (Schoch 1999). The palatal ramus bears a very well developed transverse flange of the pterygoid (broken on the left pterygoid but complete on the right) which is oriented ventro-laterally. The distal portion of the palatal ramus probably contacted the palatine in the usual mastodonsaurid fashion, but sutures in this area could not be determined. The distal portion of this ramus is also markedly roughened by ridges and furrows, the significance of which is uncertain. Only the proximal portion of the quadrate ramus is preserved but its curvature suggests that it was convex ventrally. Dorsally the quadrate ramus gives rise to two processes, the ascending ramus and the oblique ridge, both of which are partially preserved (see below). The pterygoid of *Cherninia denwai* (Mukherjee & Sengupta 1998) closely resembles that of *C. megarhina* in possessing a broad body that constricts both the parasphenoid and the subtemporal vacuities, the convex quadrate ramus, and the lack of ornament on the palatal ramus.

The dentition consists of a marginal tooth row on the premaxilla and maxilla, and an inner tooth row on the vomer, palatine and ectopterygoid. Except where obscured by matrix, the inner tooth row is complete, as in *Cherninia denwai* (Mukherjee & Sengupta 1998). No teeth were preserved on either dental arcade but tooth sockets indicate that the teeth were very closely spaced and strongly antero-posteriorly compressed, in the usual mastodonsaurid fashion. Tooth sockets on the marginal row appear to increase in size slightly from posterior to anterior, although the posterior-most portion of the maxilla was not preserved. The palatal tooth sockets appear to have been of uniform size throughout and of approximately half the size as the maxillary tooth sockets. A large pit for the palatine tusk is present immediately posterior to the choana. The ectopterygoid does not bear a tusk.

Occiput

The poorly preserved occiput was adequately figured by Chernin (1974), to which the reader is referred, and, as no further aspects of the occiput were exposed during preparation of the skull, a drawing is unnecessary. The occiput is preserved mainly on the left side in two sections: an upper section which includes the tabular, postparietal, squamosal and part exoccipital, and a lower section which includes part exoccipital, parasphenoid and pterygoid. These sections do not join perfectly as large areas of bone are missing, particularly on the more lateral parts of the occiput. Nevertheless, a detailed description and comparison of the occiput is presented in light of the well preserved occiput of *Cherninia denwai* (Mukherjee & Sengupta 1998). However, the occiput of that species has clearly undergone considerable

compaction. It is worth noting that figure six in Mukherjee & Sengupta (1998) shows the occiput of *C. denwai* and not '*P. crookshanki*, the figures having been inadvertently transposed (Sengupta pers. com.).

The occiput of *Cherninia megarhina* appears to have been moderately vaulted judging from the down-turning of the medial portions of the quadrate rami of the pterygoids. Thus the quadrate condyles would have been positioned ventral to the occipital condyles. The same degree of down-turning is present in *Cherninia denwai* (Mukherjee & Sengupta 1998) and most mastodontosaurids except *Cyclotosaurus* (Ingavat & Janvier 1981; Schoch & Milner 2000) and *Mastodontosaurus* (Schoch 1999). The quadrate rami give rise to two processes, the ascending ramus (*lamina ascendens* of Bystrow & Efremov 1940) and the oblique ridge, only small sections of the proximal portions of which are preserved on both sides of the skull. The arrangement of these bony processes appear to have been typically mastodontosaurid. The ascending ramus is a tall, thin lamina of bone which arises from the occipital margin of the quadrate ramus. The proximal portions clearly curve medially and appear to terminate near the edge of the basicranial process of the pterygoid, thereby forming the anterior wall of the middle ear cavity in the usual mastodontosaurid fashion. The presence or absence of a *crista praeotica* (Shishkin 1960; 'dorsal column' of Warren 1980; '*crista praeotica lamina ascendens*' of Getmanov 1989) on the medial margin of the ascending ramus cannot be determined because of incomplete preservation. This structure, a vertical thickening of the medial margin of the ascending ramus, is apparently present in all stereospondyls in which the area is known except brachyopids (Damiani & Warren 1996). The oblique ridge arises from the occipital margin of the quadrate ramus medial to the ascending ramus, and is just visible in occipital view. Its dorsal margin is incomplete.

The occipital portion of the squamosal is only partially preserved and consists of a descending flange (largely incomplete) and the *crista falciformis*. Unlike in most mastodontosaurids, especially those of comparably large size, the *crista falciformis* is very poorly developed, only projecting some five millimetres from the descending flange of the squamosal. A similarly poorly developed *crista falciformis* was reported for *Cherninia denwai*.

The posttemporal fenestrae, supraoccipital foramen and foramen magnum have clearly been affected by compaction so that their size and shape cannot be accurately described. The body of the exoccipitals are massive in being dorso-ventrally short but exceptionally broad, as in *Cherninia denwai*. In contrast, the body of the exoccipitals in most other mastodontosaurids is considerably less robust. The long paroccipital process bears a sharp crested bony ridge, or *crista muscularis*, which runs the length of the paroccipital process ventrally. This ridge continues onto the ventral surface of the tabular horn as the prominent *crista tabularis*

externa (Bystrow & Efremov 1940), terminating near the tip of the horn. The presence or absence of a *crista terminalis* cannot be determined because manganese-rich matrix covers much of the ventral surface of the tabular proximally. There is no trace of any bony protuberance on the occipital face of the tabular dorsally, unlike in *C. denwai*.

Endocranium

The endocranium is generally poorly preserved, particularly the dorsal surface of the parasphenoid and middle ear areas which are obscured by recalcitrant matrix. Of the former, a near-laterally directed ridge of bone on the right-hand side, likely the *crista parapterygoidea* (Bystrow & Efremov 1940), is visible jutting out from the underlying matrix. No other structures are visible in this area.

Anterior to the body of the parasphenoid a large but poorly preserved ossification, which may or may not represent two separate bones, is present (Figure 2B). Little structural details are apparent except as follows. The larger, posterior section markedly broadens anteriorly and, except where broken or obscured by matrix, the lateral margins curve smoothly downward and inward and are apparently contiguous with a deep but narrow ossification. The bony texture of this ossification is spongy. The ventral surface of the element is generally smooth and there are no visible foramina or canals. This element is tentatively identified as a sphenethmoid as it is clearly too broad, deep and irregular in shape to represent the cultriform process of the parasphenoid, but nevertheless does not resemble the typical stereospondyl sphenethmoid structure as described by Bystrow & Efremov (1940). The smaller, anterior element is uniformly wide, has a smooth ventral surface, but appears to be only a few millimetres thick. It may represent part of the cultriform process of the parasphenoid but if so is extraordinarily wide to a degree unparalleled among mastodontosaurids.

The dorsal surface of the left pterygoid bears a wide *sulcus marginalis* (Bystrow & Efremov 1940) on its lateral edge bordering the subtemporal vacuity, and a prominent *torus marginalis* (Bystrow & Efremov 1940) on its medial edge bordering the interpterygoid vacuity. These structures apparently bordered the embryonic palatoquadrate cartilage (Bystrow & Efremov 1940; Romer 1947). Anterior and slightly medial to the inner margin of the right ascending ramus of the pterygoid is an ossification which is tentatively identified as an epipterygoid. The element is poorly preserved and apparently incomplete, but appears to have possessed a large base abutting against the basicranial process of the pterygoid and a robust ascending process. Its identification as an epipterygoid is consistent with the position of the element and its robust nature, judging from well known mastodontosaurid material (e.g. Howie 1970; Schoch 1999; Damiani in press b).

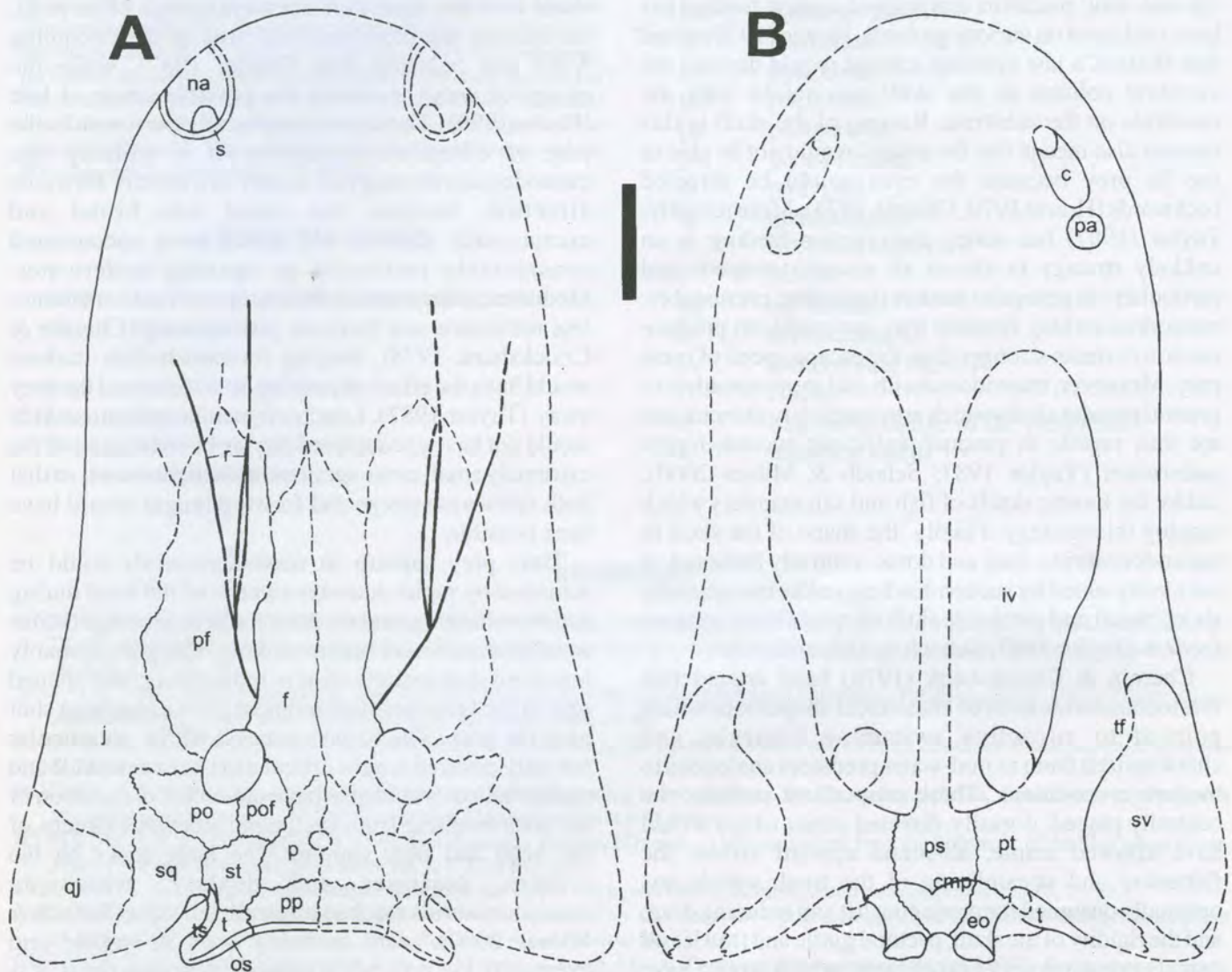


Figure 3. Reconstructions of the skull of *Cherninia megarhina* (Chernin and Cosgriff), BP/1/4223, from the Upper Horizon of the Middle Triassic N'tawere Formation of the Upper Luangwa Valley, Zambia, in A, dorsal and B, ventral views. Scale bar equals 10 cm.

FEEDING IN MASTODONSAURIDS

The lifestyle of mastodonsaurid temnospondyls has long presented a puzzle to temnospondyl workers particularly in relation to their method of feeding. Adult mastodonsaurids were large, carnivorous, dorso-ventrally flattened and superficially crocodile-like in appearance. As with most stereospondyls (Warren & Snell 1991; Schoch & Milner 2000), mastodonsaurids probably spent most of their time in water, with limited potential for terrestrial excursions. Evidence for this comes from a number of sources: the skull and trunk was dorso-ventrally flattened and streamlined; the postcranial skeleton, in particular the limbs, were generally weak and poorly ossified in most genera, while the carpals, tarsals and digits were usually unossified; lateral line sensory sulci were well developed; long bone histology points to aquatic adaptations; limb-trunk ratios may not have accommodated effective movement on land; an increased number of presacral vertebrae relative to terrestrial taxa; the disproportionately large skull which would have hindered effective terrestrial locomotion; and depositional environments which

include fluvial, lacustrine, nearshore marine and marine facies (Watson 1958; Howie 1970; Chernin & Cruickshank 1978; DeFauw 1989; Schoch 1999; Damiani 2000; Schoch & Milner 2000).

Watson (1958, 1962) considered mastodonsaurids to have been essentially bottom-dwelling (i.e. benthic) animals. Opening of the mouth was thought to occur by the action of a *depressor mandibulae* muscle which originated on the highest point of the occiput and inserted onto the post-glenoid area of the mandible, contraction of which would raise the skull if the jaw rested on the substrate. Watson thus envisaged a lie-and-wait strategy in which approaching prey would be engulfed by suction-feeding in a manner similar to various extant fish and salamanders. The hypothesis that mastodonsaurids were passive, benthic animals has been adopted by other workers (Ochev 1966; Sennikov 1996; Shishkin 2000), the implication being that suction-feeding or at least a 'snap-and-grab' feeding strategy was employed. DeFauw (1989), while favouring more active swimming, also employed a suction-feeding strategy in mastodonsaurids.

The hypothesis that mastodonsaurids were benthic, 'sit-and-wait' predators that utilized suction-feeding has been criticized on various grounds. Howie (1970) noted that Watson's jaw opening scheme would depress the vertebral column as the skull was raised with the mandible on the substrate. Raising of the skull in this manner also means that the animal would not be able to see its prey because the eyes would be directed backwards (Howie 1970; Chernin 1974). More recently, Taylor (1987) has stated that suction-feeding is an unlikely strategy in almost all aquatic tetrapods and particularly in generalist feeders (including, presumably, mastodonsaurids), because they are unable to produce suction currents stronger than the escape speed of most prey. Moreover, mastodonsaurids and stereospondyls in general possess skulls which are completely akinetic and are thus unable to produce sufficient suction forces underwater (Taylor 1987; Schoch & Milner 2000), unlike the kinetic skulls of fish and salamanders which employ this strategy. Finally, the shape of the skull in mastodonsaurids, long and dorso-ventrally flattened, is not ideally suited for suction-feeding, unlike the optimally short, broad and parabolic skull of specialized suction-feeders (Taylor 1987; Schoch & Milner 2000).

Chernin & Cruickshank (1978) have argued that mastodonsaurids showed anatomical adaptations which pointed to an active swimming lifestyle, and characterised them as mid-water predators analogous to modern crocodilians. These adaptations include: the centrally placed, dorsally-directed orbits which would have allowed ample, all-round upward vision; the flattening and streamlining of the trunk which was optimally designed for producing lift and reducing drag; and the rigidity of the skull, pectoral girdle and (to a lesser extent) presacral vertebral column, which would have acted as a strut to transmit the propulsive force produced by the tail which was generally weakly ossified and perhaps highly flexible (Howie 1970; Chernin 1974; Chernin & Cruickshank 1978). Mechanisms for opening the mouth that do not require the mandible to rest on the substrate were proposed by Howie (1970) and Chernin (1974), both requiring the action of a *depressor mandibulae* that lowers the jaw (and a *cleidomastoideus* to raise the skull in the case of Howie) if it was not grounded. It is also interesting to note that virtually all amphibious tetrapods with dorsally-directed orbits, such as hippopotami, crocodilians, and various anurans and salamanders, usually lurk close to the water surface with only the eyes protruding. The hypothesis that mastodonsaurids were active rather than passive predators has been supported by Cosgriff & Hammer (1983), DeFauw (1989) and Schoch & Milner (2000).

If mastodonsaurids were not passive, benthic suction-feeders but active, surface or sub-surface predators, how did they feed? As with crocodilians, mastodonsaurids possess a simple, orthally-hinged, open-and-shut 'pincers' jaw (Taylor 1987) that would snap shut onto prey. The mastodonsaurid skull is long, moderately narrow (in most taxa), and highly dorso-

ventrally flattened, especially anterior to the orbits. This shape is well designed for sideways sweeps of the head, minimizing the cross-sectional area to the oncoming water and reducing drag (Taylor 1987), while the elongated snout increased the possible range of bite (Kathe 1999). The latter is especially pertinent in the case of *Cherninia megarhina*. It is unlikely that mastodonsaurids snapped at prey in a strictly forwards direction, because the snout was broad and exceptionally shallow and would have encountered considerable resistance to opening underwater. Moreover, if the jaw was slightly open so as to encounter less resistance and facilitate jaw opening (Chernin & Cruickshank 1978), lunging forward in this manner would have the effect of pushing both water and the prey away (Taylor 1987). Lonchorhynchine trematosaurids would not have encountered this problem because of the extremely small cross-sectional area of the snout, so that both sideways sweeps and forward lunges would have been possible.

Thus prey capture in mastodonsaurids could be achieved by rapid sideways sweeps of the head during active swimming, and the prey could be kept sight of for as long as necessary before striking. The jaws probably remained shut initially so as to reduce drag, and opened only at the latest possible moment before snapping shut onto the prey. The hamate process of the prearticular not only ensured a tight articulation between skull and mandible, but would also have prevented dislocation of the jaws resulting from such rapid sideways sweeps of the head and prey capture. The large tusks on the vomers, palatines and dentary, which in mastodonsaurids reached unparalleled sizes (Schoch & Milner 2000), were probably used to impale and eventually kill prey when snapped shut onto them. It is also likely that the tusks were used to hold and drown prey, perhaps underwater if taken at the surface as in crocodilians. This is suggested by the deep and massive adductor musculature and the posterior deepening of the mandible, both of which are adaptations for holding (Busbey 1995; Schoch & Milner 2000). Mastodonsaurids were probably generalist aquatic top-predators (Sennikov 1996), with a putative diet of fish, amphibians and small reptiles. However, the deep mandibles, massive tusks and jaw musculature would have allowed for larger prey to be taken (Schoch & Milner 2000). It is doubtful that the marginal dentition, which consists of an exceptionally large number of uniform, tightly packed, transversely compressed, slightly recurved teeth, played an important role in prey capture, but may have aided in holding prey in the mouth (Schoch & Milner 2000).

ACKNOWLEDGEMENTS

The holotype of *Cherninia megarhina* was collected in 1961 by Prof. J. W. Kitching of the Bernard Price Institute for Palaeontological Research (BPI), Johannesburg. I am grateful to Dr D. P. Sengupta (Indian Statistical Institute, Calcutta) for providing valuable information on the skull of *Cherninia denwai* and for confirming my suspicions about the transposed figure captions in Mukherjee & Sengupta (1998). I also thank Prof. B. S. Rubidge (BPI, Johannesburg)

for comments on an earlier version of the manuscript, and Drs A. A. Warren (La Trobe University, Melbourne) and P. J. Hancox (University of the Witwatersrand, Johannesburg) for information and discussions. Mr Richard Lewis (formerly BPI, Johannesburg) performed the initial airbrasive preparation of the skull. Reviews of the manuscript by Drs Andrew Milner (Birkbeck College, London) and Rainer Schoch (Humboldt Universität, Berlin) improved the quality of this work. The author is supported by a University of the Witwatersrand postdoctoral fellowship.

ABBREVIATIONS

c	choana
cmp	<i>crista muscularis</i> of the parasphenoid
eo	exoccipital
f	frontal
iv	interpterygoid vacuity
j	jugal
na	naris
os	occipital sulcus

p	parietal
pa	palatine tusk pit
pf	prefrontal
po	postorbital
pof	postfrontal
pp	postparietal
ps	parasphenoid
pt	pterygoid
qj	quadratojugal
r	ridges on skull roof
s	sulcus
sq	squamosal
st	supratemporal
sv	subtemporal vacuity
t	tabular
tf	transverse flange of the pterygoid
ts	temporal sulcus

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PRELIMINARY PHYLOGENETIC ANALYSIS AND STRATIGRAPHIC CONGRUENCE OF THE DICYNODONT ANOMODONTS (SYNAPSIDA: THERAPSIDA)

by

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ABSTRACT

A preliminary phylogenetic analysis of 20 well-known dicynodont taxa was conducted using modern cladistic methods. Many past phylogenetic hypotheses were corroborated, but others conflict with the results of this analysis. Most notably, *Diictodon*, *Robertia*, and *Pristerodon* are reconstructed in more basal positions than previously suggested, whereas *Endothiodon* and *Chelydontops* occupy a more crownward position. These findings are consistent with novel evolutionary scenarios for characters such as the presence of postcanine teeth and anterior palatal ridges.

The Relative Completeness Index and Gap Excess Ratio were used to examine the degree of fit between the most parsimonious cladograms of this study and the stratigraphic record of the dicynodonts. Although the results of this analysis suggest that the preferred cladogram is relatively consistent with stratigraphy, the presence of some ghost ranges and ghost lineages imply that the fossil record of dicynodonts is not as complete as is sometimes stated. These findings are important because there is a long tradition of intensive collecting in regions where dicynodont fossils are common; sections of several dicynodont lineages may not be preserved in these areas.

KEYWORDS: Dicynodontia, Phylogeny, Stratigraphy, Anomodontia, Synapsida, Karoo Basin

INTRODUCTION

The dicynodont therapsids (*sensu* Hopson & Barghusen 1986; Modesto *et al.* 1999; Rybczynski 2000) represent a diverse radiation of specialized herbivorous non-mammalian synapsids that range in age from the Late Permian to Late Triassic and are known from every continent. The dicynodont fossil record from the Beaufort Group of South Africa is especially rich and well documented since the first description of therapsid fossils by Owen (1845). Together with a handful of more basal forms (e.g., *Patranomodon*, *Venyukovia*, *Otsheria*, *Ulemica*, *Suminia*), dicynodonts form the Anomodontia (*sensu* Hopson & Barghusen 1986; Modesto *et al.* 1999; Rybczynski 2000), a clade of basal eutherapsids (Sidor & Hopson 1998). The exact placement of Anomodontia within Therapsida is still unclear (compare e.g., Gauthier *et al.* 1988; Hopson & Barghusen 1986; Sidor & Hopson 1998), but this issue is not the focus of this paper.

Despite the large number of specimens and the long history of work surrounding the group, the phylogenetic relationships of dicynodonts are still problematic. Many early workers, such as Robert Broom, concentrated on simply collecting and describing isolated, often poorly preserved or prepared skulls, and paid less attention to issues such as functional morphology, systematics, or even descriptions of postcranial skeletal elements. As a result, the group was extremely over-split (see Haughton & Brink's 1954 bibliographic database for the results of

this tendency). Recent workers (e.g., Cluver & Hotton 1981; Cluver & King 1983; Keyser 1975, 1993; Keyser & Cruickshank 1979; King 1988, 1993; King & Rubidge 1993) have reduced the number of recognized taxa to a more manageable number, but the lineage status of most of these taxa has not been rigorously tested. Cluver & King (1983), King (1988; 1990), Cox (1998), and Surkov (2000) published cladistic analyses of the group, but the absence of a list of characters examined or character codings for the taxa included in these works makes it difficult to independently test their hypotheses. The analyses of Modesto *et al.* (1999), Modesto & Rybczynski (2000), and Rybczynski (2000) are methodologically stronger, but the focus of these works has been on the relationships of non-dicynodont anomodonts and they include relatively few dicynodont taxa. Nevertheless, all of these analyses represent important first steps toward an understanding of dicynodont phylogeny.

In the following study, I present a new, preliminary phylogenetic analysis of the dicynodonts. My primary goal is to examine the interrelationships of the better known Permian dicynodont taxa using up-to-date methods and technologies, such as the computer parsimony algorithm PAUP. Because considerable work remains to be conducted on most dicynodont taxa, the present analysis is not intended to be an exhaustive treatment of dicynodont phylogeny. Instead, it represents a rigorous test of the hypotheses of relationship and homology made by previous authors. Furthermore, I examine the results of this phylogenetic

analysis in the context of stratigraphy to determine how well the morphologically parsimonious cladograms fit the known fossil record.

INSTITUTIONAL ABBREVIATIONS

AM:	Albany Museum, Grahamstown, South Africa
AMNH:	American Museum of Natural History, New York, USA
BMNH:	Natural History Museum, London, England
BP:	Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa
GSP:	Geological Survey of South Africa, Pretoria, South Africa
NM:	National Museum, Bloemfontein, South Africa
PIN:	Paleontological Institute, Moscow, Russian Federation
ROZ:	Roy Oosthuizen Collection, South African Museum, Cape Town, South Africa
SAM:	South African Museum, Cape Town, South Africa
TM:	Transvaal Museum, Pretoria, South Africa
UCMP:	University of California Museum of Paleontology, Berkeley, USA

METHODS

Phylogenetic Analysis

A matrix consisting of 20 anomodont taxa and 40 morphological characters was constructed and subjected to a maximum parsimony analysis using PAUP 4.0b4a (Swofford 2000). The characters used are listed and discussed in detail in Appendix 1, the matrix is shown in Appendix 2, and the sources of character codings are given in Appendix 3. Multistate characters were treated as unordered and all characters were equally weighted. Unknown and inapplicable characters were coded “?” (Strong & Lipscomb 2000). The heuristic search algorithm was used and 1000 random addition sequence replicates were run to prevent the searches from becoming trapped in a local tree-length minimum (Maddison 1991). Support for the recovered clades was measured by decay analysis (Bremer 1988).

Many of the characters in this analysis are based on proposed synapomorphies that have been used by King (1988, 1990), Cox (1998), and Surkov (1998, 2000) to diagnose dicynodont clades or grades of organization they have proposed or characters used in Modesto *et al.* (1999) and Rybczynski (2000). As noted above, although all of these authors used cladistic principles to construct their phylogenetic hypotheses, only the analyses of Modesto *et al.* (1999) and Rybczynski (2000) were based on discrete-state characters and constructed using a computer parsimony algorithm (e.g., PAUP). Accordingly, I have reinterpreted many of the characters so that they have discrete states that can be coded in a matrix. The character states and codings that I have used are based mainly on my observations of dicynodont specimens in various institutions in the United States, South Africa, and Russia. A detailed discussion of the character states and my reasons for coding different taxa as I have are provided in Appendix 1. Because this

analysis includes many characters from past phylogenetic analyses of dicynodonts and newer methods than most, it represents a rigorous test of previous phylogenetic hypotheses.

The skull has long been the primary focus of studies of dicynodonts, and this bias is reflected in collections of dicynodont material as well as studies of their morphology and systematics. Early dicynodont taxonomists placed much emphasis on skull proportions, patterns of facial and skull roof sutures, and the presence or absence of bones such as the postfrontal or septomaxilla (e.g., Broom 1932). I have avoided many of these characters because more recent authors (e.g., Cluver & Hotton, 1981; Cluver & King, 1983; Keyser 1975; King 1993; Rubidge 1984; Toerien 1953; Tollman *et al.* 1980) have shown that they are highly variable within dicynodont genera, species, and presumed age classes. They are also susceptible to alteration by taphonomic processes such as weathering or plastic deformation. Since the seminal work of Toerien (1953), much greater attention has been paid to the structure and functional relationships of the palate and mandible of dicynodonts because these regions are rich sources of potentially informative characters that show less individual variation. Other potentially informative regions of the skull, such as the braincase, have not been thoroughly examined to determine if they preserve a useful phylogenetic signal. The majority of the cranial characters I have used in this analysis are features of the palate and mandible, although some deal with other regions of the skull.

So much attention has been paid to the dicynodont skull, including the recent focus on the feeding system, that other sources of phylogenetic characters have remained almost completely unexplored in the dicynodont literature. Despite well over a century of collection and description, the postcranial skeleton of dicynodonts remains poorly known; only scattered descriptions of its osteology or functional morphology are available (e.g., Boonstra 1966; Broom 1905; Camp & Welles 1956; Cluver 1978; Cox 1959, 1972; DeFauw 1986; King 1981a, 1981b, 1985; Olson & Byrne 1938; Pearson 1924; Rubidge *et al.* 1994; Walter 1986; Watson 1960). This lack of published information is unfortunate because these works and others that have attempted to include postcranial characters in systematic studies (Camp 1956; King 1988; Surkov 1998) strongly suggest that dicynodont postcrania preserve a valuable and informative phylogenetic signal. The consideration of postcranial characters has enabled more parsimonious explanations of patterns of evolution to be discovered in broader studies of synapsids (Hopson 1995; Rowe & van den Heever 1986). The five postcranial characters that I have included appear to be phylogenetically informative and are easily coded even for poorly preserved or prepared specimens.

Eighteen dicynodont genera form the ingroup and two non-dicynodont anomodonts (*Patranomodon* and *Otsheria*) are used as outgroups. Because the monophyly of the Anomodontia is accepted (Hopson, 1991; Hopson & Barghusen 1986; Modesto *et al.* 1999; Rybczynski

2000; Sidor & Hopson 1998) and I am concerned only with relationships among dicynodonts, I did not include any non-anomodont outgroups in this analysis. *Patranomodon* is a useful outgroup because it is a basal anomodont (Modesto *et al.* 1999; Rubidge & Hopson 1990, 1996; Rybczynski 2000) represented by a very well-preserved skull and associated postcranial elements that retain many primitive anomodont characters. *Otsheria* is a venyukovoid anomodont (*sensu* Modesto *et al.* 1999; Rybczynski 2000), and represents a slightly more advanced grade of anomodont evolution. *Anomocephalus*, the most basal known anomodont (Modesto & Rubidge 2000; Modesto *et al.* 1999), was not used as an outgroup because the only known specimen (BP/1/5582) does not preserve many of the characters I have used.

The ingroup taxa in this analysis are known primarily from the Late Permian of Africa, with the exceptions of *Lystrosaurus*, *Myosaurus*, and *Kannemeyeria*, which appear in the Triassic. The focus of this analysis is the pattern of relationships among the Permian dicynodont taxa, and I have tried to include as many of the well-known genera as possible. The Triassic genera are mainly intended to serve as place-holders, and the results of this and other studies (Cluver & King 1983; Cox 1965, 1998; Cox & Li 1983; Keyser & Cruickshank 1979; King 1988, 1990) suggest that most Triassic dicynodonts are members of the monophyletic clade including *Dicynodon*, *Lystrosaurus*, and *Kannemeyeria*. Future analyses that include additional Triassic taxa can be used to test this assumption. All included genera have been recently described, redescribed, or revised in the literature, and I have had the opportunity to personally examine specimens that can be referred confidently to these taxa (Appendix 3). Although the taxonomy of the included genera is not the focus of this paper, my treatment of *Eodicynodon*, *Chelydontops*, and *Tropidostoma* necessitates some explanation.

Two described species currently are assigned to the genus *Eodicynodon*, *Eodicynodon oosthuizeni* (Barry 1974a) and *Eodicynodon oelofseni* (Rubidge 1990b). Although the taxa share several diagnostic features, a number of notable differences also exist, including the presence or absence of a canine tusk, the size and arrangement of the postcanine teeth, and the morphology of the lower jaw (Rubidge 1990b). Also, many more specimens of *E. oosthuizeni* have been collected (over 20 well-preserved skulls versus the holotype and a second specimen (NM QR3003) that is probably referable to *E. oelofseni*, both of which are poorly preserved; Rubidge, 1990a; personal observation) and its cranial and postcranial osteology have been much more thoroughly described (Barry 1974b; Cluver & King 1983; Rubidge 1984, 1985, 1990a; Rubidge *et al.* 1994). Because of these discrepancies, I have considered only *E. oosthuizeni*, and my character state codings for *Eodicynodon* should be considered valid only for this species.

Cluver (1975) described the taxon *Chelydontops altidentalis* based on two specimens (SAM 11558 and

SAM 12259) discovered in the *Tapinocephalus* Assemblage Zone. Recently, Cox (1998) has proposed synonymizing *C. altidentalis* with the genus *Prodicynodon*, creating the new combination *Prodicynodon altidentalis*. Although the holotype (SAM 11558) and referred (SAM 12259) specimens of *Chelydontops* are not completely preserved, they do show a distinct, diagnostic suite of features, including a relatively wide intertemporal bar, a dome-like pineal boss, a shelf-like area lateral to the upper postcanine teeth, a large, leaf-shaped palatal exposure of the palatine, a distinctly developed coronoid eminence, and a median palatal ridge that has a flattened, expanded, diamond-shaped area anteriorly. The holotypes of both *Prodicynodon pearstonensis* (AM 2551) and *P. beaufortensis* (AMNH 5509) are very fragmentary and preserve only the snout and anterior portion of the lower jaw. The palate is not fully exposed in either specimen, and the details of the intertemporal region are also unknown. Because both specimens preserve almost no information regarding their possible affinities with *Chelydontops altidentalis*, I believe it is premature to refer this taxon to the genus *Prodicynodon*. I agree with Keyser (1993) that both *P. pearstonensis* and *P. beaufortensis* should be regarded as *nomina dubia* until more informative material is discovered. The codings for *Chelydontops* in this analysis are based on my observations of the two SAM specimens.

The genus *Tropidostoma* is problematic because although there is considerable variation in the width of the intertemporal region in the taxon, most of the specimens referred to it are otherwise very similar. Keyser (1973) largely ignored this variation in his revision of *Tropidostoma*, but Cluver & King (1983) favored placing specimens with narrow intertemporal regions in *Tropidostoma* while retaining the genus *Cteniosaurus* for specimens with wider intertemporal regions. The holotype specimen for *Tropidostoma* (BMNH R868) has a relatively narrow intertemporal region, with the parietals exposed in a median depression between the postorbitals, which partially overlap them. In my observations, I have found that this pattern is relatively constant, although the depth of the depression, degree of overlap, and overall width of the intertemporal bar can be quite variable. These features also are highly susceptible to alteration by plastic deformation (for example, the holotype of *T. dunni* (BMNH R866) has a narrower intertemporal region than the holotype of *T. microtrema* (BMNH R868), but the former specimen has clearly been laterally compressed). For these reasons, as well as the fact that there is almost no other morphological difference between *Cteniosaurus* and *Tropidostoma*, I have followed Keyser (1973) and treat them as synonyms.

Stratigraphic Analysis

The biostratigraphic relationships of dicynodonts, especially those of the Karoo Basin of South Africa, have a long history of study (e.g., Broom 1906; Keyser

& Smith 1977-1978; Kitching 1977; Lucas 1996, 1998; Rubidge 1995a; Seeley 1892; Watson 1914) and frequently have been used to add a temporal dimension to phylogenetic and adaptational hypotheses about the group. Because of this tradition, and the fact that the Beaufort Group and its eight assemblage zones have been the subject of recent scrutiny (Rubidge 1995a), dicynodonts are an ideal group with which to examine the fit between stratigraphy and phylogeny.

A number of methods have been proposed recently to measure the fit between stratigraphic data and cladograms (e.g., Benton & Storr, 1994; Gauthier *et al.* 1988; Huelsenbeck 1994; Norell & Novacek 1992a, 1992b; Wills, 1999). There has also been debate over whether and how one should include stratigraphic data in phylogenetic analyses (e.g., Clyde & Fisher 1997; Fisher 1992, 1994, 1997; Fox *et al.* 1997, 1999; Norell & Novacek 1997; Rieppel 1997; Smith 2000; Thewissen 1992). In this analysis the Relative Completeness Index (RCI) metric of Benton & Storrs (1994) and the Gap Excess Ratio (GER, Wills, 1999) were used to examine the nature of the gaps in the fossil record required by the morphologically parsimonious cladograms. A cladogram that implies fewer or shorter gaps in the fossil record is a more highly corroborated hypothesis than an equally parsimonious cladogram that requires longer or more numerous gaps.

I calculated the RCI and GER for all of the most parsimonious cladograms of this analysis. In addition, these metrics were calculated for cladograms up to four steps longer and a cladogram based on the topology of King (1988, 1990), but only including the taxa I examined (Figure 1c), to determine if any of these hypotheses fit the known fossil record better than the morphologically most parsimonious cladograms. The Basic program "Ghosts" (version 2.4, 1000 random replicates, polytomies resolved as the worst case; Wills 1999) also was used to determine whether the most parsimonious cladograms of this analysis and the cladogram of King (1988, 1990) fit the fossil record significantly better than random. Stratigraphic data were taken from Rubidge (1995a) and King (1988). Because all taxa in the analysis except *Otsheria* are known from southern Africa, potential biases caused by different preservation rates or biostratigraphic correlation difficulties should be minimal. Taxa known to occur in only part of an assemblage zone were not treated differently than taxa found throughout an assemblage zone. This assumption simplifies data analysis, but reduces resolution.

To calculate the RCI (Benton & Storrs 1994; see also Benton & Hitchin 1996; Benton & Simms 1995; Benton & Storrs 1996; Hitchin & Benton 1997a) Minimum Implied Gaps (MIGs; see Benton 1994; Norell 1993; Norell & Novacek 1992a, 1992b; Smith & Littlewood 1994; Storrs 1993; Weishampel & Heinrich 1992) were assessed for the most parsimonious cladograms as well as the cladogram based on King's (1988, 1990) topology. This is easily done by coding a stratigraphic character (Appendices 1, 2) in MacClade 3.08 (Maddison &

Maddison 1999; see also Fisher 1992) and noting the number of steps added. The Simple Range Length (SRL; Storrs, 1993) for each taxon was measured by counting the number of assemblage zones in which that taxon appears. These values were then substituted into the equation given in Benton & Storrs (1996) and the equation was solved for RCI. Because the RCI takes into account time duration and missing time, not just the relative ranks of clades, it has been suggested as an estimate of the completeness of the fossil record of the group in question implied by a phylogenetic hypothesis (Hitchin & Benton 1997a; although see Wagner 2000).

The RCI is known to be sensitive to the choice of taxa and magnitude of time examined (Benton & Storrs 1994; Hitchin & Benton 1997a). It may also be affected by number of taxa and clade asymmetry (Siddall 1996; 1997; but see Benton *et al.* 1999; Hitchin & Benton 1997a, 1997b). However, these biases should not be a problem in this analysis because the identities and number of included taxa, as well as the magnitude of time in consideration, are the same for all of the cladograms in question. Although there are slight differences in asymmetry among the cladograms, they are unlikely to be large enough to affect the results seriously. The randomization procedure implemented in "Ghosts" also helps to control for cladogram size and balance biases when estimating the significance of the RCI (Wills 1999).

The Gap Excess Ratio (GER) has been proposed by Wills (1999) as a means to examine the fit of a cladogram to stratigraphy by examining the amount of ghost ranges required. The GER represents the excess ghost range above and beyond the minimum possible value for a set of stratigraphic data, expressed as a fraction of the total range of ghost values possible for that data (Wills 1999). To calculate the GER, the minimum and maximum number of implied gaps possible for the stratigraphic data set used here were calculated. These values were then substituted into equation 3 of Wills (1999) with the MIG (see above) for each of the most parsimonious cladograms of this analysis, the cladograms several steps longer, and the cladogram of King (1988, 1990). The GER appears not to be biased by the number of taxa included in the cladograms being compared (Benton *et al.* 1999; Wills 1999), but this potential source of error is not a concern because all of the cladograms included in this analysis have the same number of taxa. It can be affected by symmetry differences among examined cladograms (Benton *et al.* 1999), but variation in symmetry among the cladograms in this analysis is minimal and should not cause undue bias. As with the RCI, the randomization procedure of "Ghosts" helps to control for cladogram size and shape biases when calculating the significance of the GER (Wills 1999).

RESULTS

Phylogenetic analysis

The parsimony analysis recovered a single most parsimonious cladogram with a length of 125 steps, a consistency index of 0.57, and a retention index of 0.67

(Figure 1a). The topological results of the analysis are presented in Figure 1. For comparison, a cladogram based on the topology of King (1988, 1990), but including only the taxa and characters examined here (Figure 1c), has a length of 136 steps, a consistency index of 0.53, and a retention index of 0.59.

Tree decay analysis shows that most of the hypothesized clades in this phylogeny are relatively weakly supported. At 126 to 127 steps, the major clades of dicynodonts are resolved, but most resolution within these clades is lost (Figure 1b). The observed loss of resolution is likely due to the generally short branch lengths within the major clades. At 128 steps, the ingroup is resolved from the outgroup, but no branches within the ingroup are resolved. All resolution is lost at 133 steps. A large number of character state changes take place on the branch separating the ingroup from the outgroup, resulting in the strong decay support for that node.

The topological results of this analysis are generally compatible with those of King (1988, 1990), although some differences do exist. Most notably, *Robertia* and *Diictodon*, and *Pristerodon* are reconstructed in a more basal position, whereas *Endothiodon* and *Chelydontops* appear in a more crownward position. Although clades including the same taxa as the Cryptodontinae and Emydopidae of King (1988, 1990) are present in the most parsimonious cladogram of this analysis, the relationships within these clades are slightly different (Figure 1a, Nodes I, L; Figure 1c, Nodes C, E). The results are also compatible with those of Modesto *et al.* (1999), Modesto & Rybczynski (2000), Rybczynski (2000) and Surkov (2000), although there are notable differences in taxon sampling.

Character state transformations were optimized on the most parsimonious cladogram using the Delayed Transformation (DELTRAN) algorithm of MacClade 3.08a (Maddison & Maddison, 1999) to arrive at the following diagnoses of the recovered clades.

The clade including *Eodicynodon*, *Kannemeyeria*, and all descendants of their most recent common ancestor (= Dicynodontia *sensu* Modesto *et al.* 1999; Rybczynski 2000; Figure 1a, Node A) is diagnosed by the absence of premaxillary teeth (Character 2, State 1), the presence of a caniniform process (6, 1), a posterior median ridge with an expanded, flattened anterior area on the palatal surface of the premaxilla (8, 1), a lateral squamosal fossa for the origination of the lateral branch of the M. Adductor Mandibulae Externus (21, 1), a rounded, bulbous surface of the palatal exposure of the palatine suggesting a keratinized covering (22, 1), a single, median nasal boss (23, 1), a dorsolateral notch in the squamosal (32, 1), a relatively long interpterygoid vacuity that does not reach the level of the palatal exposure of the palatines (33, 1), and a lateral palatal fenestra located at the level of the anterior portion of the palatal exposure of the palatines (35, 1). It is important to note that some of these characters (e.g., 21, 1) would likely diagnose more inclusive clades if more non-dicynodont anomodonts were included in the analysis.

The clade including *Robertia*, *Kannemeyeria*, and all descendants of their most recent common ancestor (Figure 1a, Node B) is diagnosed by the presence of fused premaxillae (3, 1), upper postcanine teeth located medially, with the more posterior teeth approaching the lateral margin of the maxillae (4, 1), lower postcanine teeth located on a medial shelf or swelling (10, 1), and a reduced transverse flange of the pterygoid (37, 1). In addition, this clade is ambiguously diagnosed by the presence of a symphyseal region of the lower jaw with an upturned margin and a scooped-out depression on its posterior surface (18, 1).

The clade including *Diictodon*, *Robertia*, and all descendants of their most recent common ancestor (= Robertiidae *sensu* King 1988, 1990; Figure 1a, Node C; Figure 1c, Node A) is diagnosed by the presence of a caniniform process with a notch anterior to it (6, 2), paired anterior ridges that converge posteriorly on the palatal surface of the premaxilla (7, 1), contact between the anterior portion of the squamosal and the maxilla (34, 1), the presence of an ectepicondylar foramen (38, 1), and the presence of a cleithrum (39, 1). In addition, this clade is ambiguously diagnosed by the presence of an elongate dentary table bounded medially by a tall, thin, dorsally-convex blade (15, 2), and a relatively small lateral dentary shelf (17, 1). The presence of paired, anterior palatal ridges that converge posteriorly may diagnose a more inclusive clade, but the testing of this hypothesis must wait until future analyses that include currently undescribed specimens collected in the lower *Tapinocephalus* Assemblage Zone of South Africa (Rubidge, personal communication, 2000; also see Appendix 1).

The clade including *Endothiodon*, *Kannemeyeria*, and all descendants of their most recent common ancestor (Figure 1a, Node D) is diagnosed by the presence of a relatively flat surface of the premaxillary secondary palate lateral to the posterior median palatal ridge (9, 2), the presence of a posterior dentary sulcus (16, 1), and a relatively smooth palatal surface of the palatine with fine pitting suggestive of a keratinized covering (22, 2).

The clade including *Endothiodon*, *Chelydontops*, and all descendants of their most recent common ancestor (= Endothiodontoidea *sensu* King 1988, 1990; Figure 1a, Node E; Figure 1c, Node B) is diagnosed by the presence of a shelf-like area lateral to the upper postcanine teeth (5, 1), paired nasal bosses located near the dorsal margin of the external nares (23, 2), and a strongly developed bony boss around the pineal foramen (26, 1).

The clade including *Pristerodon*, *Kannemeyeria*, and all descendants of their most recent common ancestor (Figure 1a, Node F) is diagnosed by contact between the palatine and premaxilla (27, 1), and contact between the anterior portion of the squamosal and the maxilla (34, 1).

The clade including *Kingoria*, *Kannemeyeria*, and all descendants of their most recent common ancestor (Figure 1a, Node G) is diagnosed by the absence of upper postcanine teeth (4, 3), a posterior median palatal

ridge that lacks an expanded, flattened anterior area (8, 2), the absence of lower postcanine teeth (10, 2), a mid-ventral vomerine plate that is of constant width (12, 1), and an expanded femoral head that encroaches on the anterior surface of the bone (31, 1).

The clade including *Kingoria*, *Myosaurus*, and all descendants of their most recent common ancestor (Figure 1a, Node H) is diagnosed by the presence of a postcaniniform keel (1,1), an embayment of the palatal rim anterior to the caniniform process (14, 1), the absence of a dentary table (15, 0), and a shovel-shaped symphyseal region of the lower jaw (18, 3). This clade is also ambiguously diagnosed by the presence of a well-developed lateral dentary shelf (17,3), although this feature may characterize a more inclusive clade.

The clade including *Emydops*, *Myosaurus*, and all

descendants of their most recent common ancestor (= Emydopidae *sensu* King, 1988, 1990, although see above; Figure 1a, Node I; Figure 1c, Node C) is diagnosed by the presence of groove-like depressions lateral to the posterior median palatal ridge (9, 1), a narrow, blade-like mid-ventral vomerine plate (13, 1), a squamosal with a relatively straight contour in occipital view (32, 0), and the presence of an ectepicondylar foramen on the humerus (38, 1).

The clade including *Myosaurus*, *Cistecephalus*, and all descendants of their most recent common ancestor (Figure 1a, Node J; also see Cluver, 1974b) is diagnosed by the presence of a foramen on the palatal surface of the palatine (24, 1) and a partial closing-off of the snout by the anterior margins of the orbits (25, 1).

The clade including *Tropidostoma*, *Kannemeyeria*,

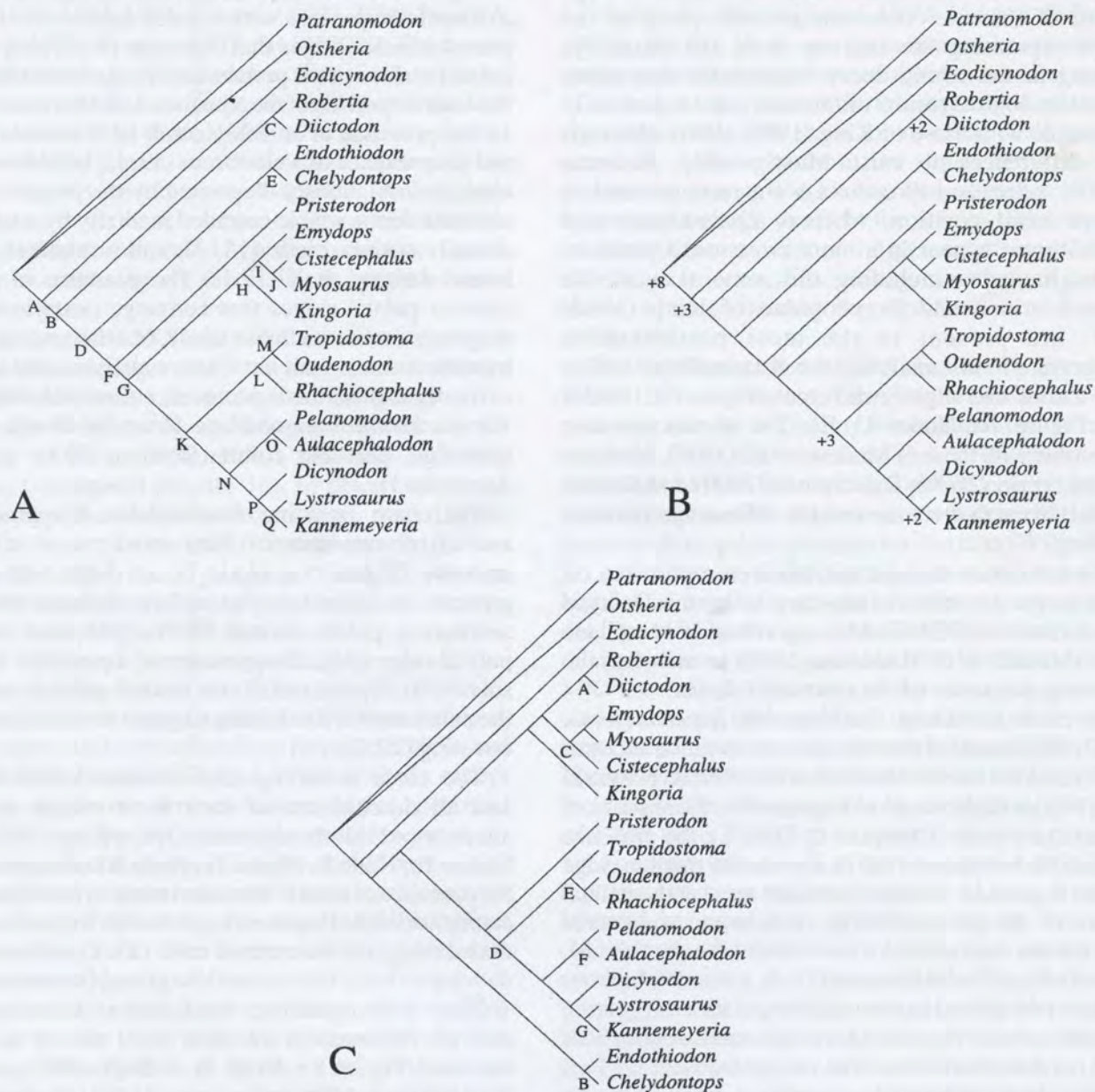


Figure 1: A: Single most parsimonious cladogram of this analysis (length 125 steps, CI = 0.57, RI = 0.67). The lettered nodes are discussed in the text. B: Cladogram showing the results of the decay analysis. Numbers indicate the number of steps beyond the most parsimonious cladogram required for a given node to collapse. Unnumbered nodes collapse at one step beyond the most parsimonious cladogram. C: Cladogram based on the topology of King (1988, 1990), but including only the taxa examined in this analysis. Lettered nodes are higher taxa given in King (A = Robertiidae, B = Endothiodontoidea, C = Emydopidae, D = Dicynodontidae, E = Cryptodontinae, F = Aulacephalodontinae, G = Kannemeyeriinae).

TABLE 1

Results of the stratigraphic analysis. SMIG is the sum of Minimum Implied Gaps for each cladogram examined (= the number of steps added by the stratigraphic character in MacClade). RCI is the Relative Completeness Index for each cladogram examined. GER is the Gap Excess Ratio for each cladogram examined. The cladograms from the decay analysis have been broken down by their length, given in parentheses. Because more than one cladogram exists at each of the lengths in the decay analysis, the range of SMIG, RCI, and GER values is given.

Cladogram	SMIG	RCI	GER
Preferred Cladogram	14	0.632	0.863
King (1988, 1990)	18	0.526	0.784
Decay Results (126)	13 - 18	0.658 - 0.526	0.882 - 0.784
Decay Results (127)	12 - 28	0.684 - 0.263	0.902 - 0.588
Decay Results (128)	11 - 30	0.711 - 0.211	0.922 - 0.549
Decay Results (129)	11 - 31	0.711 - 0.184	0.922 - 0.529

and all descendants of their most recent common ancestor (= *Dicynodontidae sensu* King, 1988, 1990; Figure 1a, Node K; Figure 1c, Node D) is diagnosed by the presence of paired anterior ridges that do not converge posteriorly (7, 2), a narrow, blade-like mid-ventral vomerine plate (13, 1), a palatal surface of the palatine that is highly rugose and pitted, suggesting a keratinized covering (22, 3), paired nasal bosses near the dorsal or posterodorsal margin of the external nares (23, 2), an expanded humeral head that encroaches on the dorsal surface of the bone (30, 1), and the presence of five sacral vertebrae (36, 2). In addition, this clade is ambiguously diagnosed by an elongate dentary table that is bounded by low ridges (15, 3) and a relatively small lateral dentary shelf (17, 1), although both of these features may characterize a more inclusive clade.

The clade including *Tropidostoma*, *Rhachiocephalus*, and all descendants of their most recent common ancestor (= *Cryptodontinae sensu* King, 1988, 1990, although see above; Figure 1a, Node L; Figure 1c, Node E) is diagnosed by the presence of a postcaniniform crest (28, 1).

The clade including *Tropidostoma*, *Oudenodon*, and all descendants of their most recent common ancestor (Figure 1a, Node M) is diagnosed by parietals that are exposed in a groove or depression between the postorbitals, which partially overlap them (20, 1) and a relatively long interpterygoid vacuity that reaches the level of the palatal exposure of the palatines (33, 2).

The clade including *Pelanomodon*, *Kannemeyeria*, and all descendants of their most recent common ancestor (Figure 1a, Node N) is diagnosed by the presence of a labial fossa (19, 1).

The clade including *Pelanomodon*, *Aulacephalodon*, and all descendants of their most recent common ancestor (= *Aulacephalodontinae sensu* King, 1988, 1990; Figure 1a, Node O; Figure 1c, Node F) is diagnosed by a relatively wide intertemporal region in which the postorbitals are steeply placed on the lateral sides of the skull and concave laterally (20, 2) and the presence of a transverse ridge across the snout at the level of the prefrontals (40, 1).

The clade including *Dicynodon*, *Kannemeyeria*, and all descendants of their most recent common ancestor (Figure 1a, Node P) is diagnosed by a moderately rugose

and pitted palatal surface of the palatine that is suggestive of the presence of a keratinized covering (22, 4) and a relatively short interpterygoid vacuity that does not reach the level of the palatal surface of the palatines (33, 0).

The clade including *Lystrosaurus*, *Kannemeyeria*, and all descendants of their most recent common ancestor (*Kannemeyeriinae sensu* King, 1988, 1990; Figure 1a, Node Q; Figure 1c, Node G) is diagnosed by a wedge-shaped symphyseal region of the lower jaw (18, 4) and six sacral vertebrae (36, 3).

Stratigraphic Analysis

The results of the stratigraphic analysis are summarized in Table 1. The most parsimonious cladogram has a MIG value of 14, an RCI value of 0.632 and a GER value of 0.863. The RCI value is above the mean value of 0.498 found by Hitchin & Benton (1997) for continental tetrapods, and comparable to the mean of 0.601 reported by Benton *et al.* (1999) for five non-mammalian synapsid cladograms. The GER values are notably higher than the average of 0.654 for the same five non-mammalian synapsid cladograms and the average of 0.765 for continental tetrapods (Benton *et al.* 1999). The cladogram of King (1988, 1990) has a MIG value of 18, an RCI value of 0.526, and GER value of 0.784. Both the most parsimonious cladogram of this analysis and the cladogram of King were found to fit the fossil record significantly better than random ($p < 0.001$).

As noted above, MIG, RCI, and GER values were also calculated for cladograms up to four steps longer than the most parsimonious cladogram (i.e., up to 129 steps) to determine if any of these topologies fit the fossil record better than the most parsimonious cladogram. MIG values for these cladograms range from 11 to 31, RCI values range from 0.711 to 0.184, and GER values range from 0.922 to 0.529. Thus, although some of these topologies fit the known stratigraphic record of dicynodonts better than the morphologically most parsimonious cladogram, most require more and/or longer gaps. Also, the cladograms that are closest in length to the most parsimonious cladogram have metric scores that are less variable and closer to those of the most parsimonious cladogram than those that are longer (i.e., the 126 step cladograms have MIG values of 13-18, while the 129 step cladograms have MIG values of

11-31). The cladograms that do have a closer fit to the fossil record have topologies that are generally congruent with that of the most parsimonious cladogram. Many of the major clades of dicynodonts are resolved in these cladograms (e.g., Figure 1a, nodes C, H, K, P, and Q), but the relationships among the taxa in these clades varies. Also, the positions of *Endothiodon*, *Chelydontops* and *Pristerodon* tend to be variable in these cladograms.

DISCUSSION

The topologies of the cladograms recovered in this analysis differ in some respects from those published by past authors, but are similar in others. Because this analysis represents a test of these previous hypotheses of homology and relationship, cases of congruence can be interpreted as corroboration, whereas cases of incongruence represent falsification. However, similarities between the results presented here and those of past workers also may reflect the fact that many of the characters examined are based on features that they used to construct their trees. In addition, the large number of palatal and jaw characters included could be misleading if these areas are prone to homoplasy related to feeding methods and dietary preferences. Future analyses that include a greater diversity of characters should be able to test this phylogenetic signal. In the following discussion, I have limited my comparisons mainly to the cladogram of King (1988, 1990) because only that cladogram and the cladogram of Cluver & King (1983), which has a nearly identical topology, include taxon sampling comparable to that undertaken in this analysis. Although the topological differences are discussed in some detail, it is important to note that the results of this analysis are largely compatible with those of Cluver & King (1983) and King (1988, 1990), corroborating many of their results.

The preferred cladogram of this analysis reconstructs the clade including *Robertia*, *Diictodon*, and their most recent common ancestor (= Robertiidae of King 1988, 1990) in a relatively basal position, just one node above *Eodicynodon* (Figure 1a, Node B). King (1988, 1990) favored a more crownward position for this clade, nesting it within the clade including *Kingoria*, *Myosaurus*, and all descendants of their most recent common ancestor (Figure 1c). Much of the available evidence is equivocal when comparing these two alternatives. For example, the postcranial skeleton of *Robertia* and *Diictodon* retain several plesiomorphic character states, such as relatively weakly developed humeral and femoral heads (DeFauw 1986; King 1981; Surkov 1998). The postcrania that have been described for *Kingoria* and *Cistecephalus* (Cluver 1978, DeFauw 1986, King 1985) suggest that at least some members of that clade possess more derived postcranial skeletons (although my observations of two undescribed *Emydops* humeri, SAM K5974, SAM K10009, suggest that taxon retained a more primitive humeral morphology). However, members of both clades possess an ectepicondylar foramen and an ossified cleithrum, features that are

otherwise rare in dicynodonts and suggestive of close relationship.

Differing interpretations of morphological features are also an issue. King (1988, 1990) considered the notch anterior to the caniniform process of *Diictodon* and *Robertia* to be homologous with the embayment of the palatal rim found in taxa such as *Emydops* and *Myosaurus*. I have treated these features as separate characters; a notched caniniform process is considered to be a type of caniniform process (Character 6, State 2), whereas the embayment is an unrelated feature (Character 14). My justification for this decision is based on the fact that in my observations of specimens of *Diictodon* and *Robertia*, I found little evidence of the pronounced lateral bowing of the palatal rim that forms the embayment in taxa such as *Emydops* or *Myosaurus*. Also, there is not a depression on the medial surface of the palatal rim near the caniniform process as in *Kingoria*. Instead, the notch seems to be formed by a modification of the anterior edge of the caniniform process, such that the edge originates medial to the palatal rim, as opposed to being contiguous with it. Thus the notch likely represents a transformation of the caniniform process, and therefore a notched caniniform process must be considered a type of (i.e., homologous with) caniniform process. This interpretation of these characters is more consistent with the hypothesis that *Diictodon* and *Robertia* are not closely related to taxa such as *Kingoria* or *Emydops*. The more basal placement of *Diictodon* and *Robertia* also better fits the known fossil record of dicynodonts (Figure 2) and more parsimoniously explains the evolution of characters such as the posterior dentary sulcus, postcaniniform keel, and the morphology of the dentary symphysis.

King (1988, 1990) also favored a more basal position for *Endothiodon* and *Chelydontops* than I have presented here (Figure 1a, Node D; Figure 1c, Node B). In some ways (e.g., presence of premaxillary teeth, relatively short premaxillary secondary palate, long, narrow maxillae that lack a caniniform process, midventral plate of vomers with an expanded area posterior to the junction with the premaxilla) the cranial morphology of *Endothiodon* is highly suggestive of this taxon being part of a very basal dicynodont lineage, perhaps even more basal than *Eodicynodon*. However, several other features (e.g., relatively narrow intertemporal region, jugal modified for the possible origination of a masseter-like muscle; Cox 1964; Ray 2000), reduced transverse flange of the anterior pterygoid process, quadrate that allows propalinal sliding of the jaw, presence of a posterior dentary sulcus) as well as its stratigraphic occurrence in the *Pristerognathus* to *Cistecephalus* Assemblage Zones of South Africa (Rubidge 1995a) suggest that *Endothiodon* is actually a more advanced, highly autapomorphic dicynodont. If the hypothesis that *Chelydontops* is the sister taxon of *Endothiodon* is correct (supported in this analysis by two synapomorphies; see Results and below), then the more crownward position of these taxa becomes more logical.

Chelydontops is known from the *Tapinocephalus* Assemblage Zone of South Africa and possesses two synapomorphies (a shelf lateral to the maxillary teeth and a dome-like pineal boss) that unite it with *Endothiodon* in this analysis (I do not consider *Chelydontops* to possess premaxillary teeth; see Appendix 1, Character 2). In most other respects, *Chelydontops* is much more similar to "typical" dicynodonts than to *Endothiodon*. In particular, the relatively wide intertemporal region, possible evidence for the secondary loss of the anterior palatal ridges (Appendix 1, Character 7), and the morphology of the palatines, posterior median palatal ridge, and lower jaw give the two known specimens of *Chelydontops* a very *Pristerodon*-like appearance. This superficial similarity may indicate that the lineages including *Endothiodon* and *Chelydontops* (Figure 1a, Node E) and *Pristerodon* and *Kannemeyeria* (Figure 1a, Node F) evolved from a *Pristerodon*-like common ancestor, supporting the more crownward placement of *Endothiodon* and *Chelydontops* proposed here. In addition, this hypothesis suggests that some apparently plesiomorphic features of *Endothiodon*, such as premaxillary teeth and the unusual morphology of the premaxilla and maxilla, are actually reversals, and that *Chelydontops* may be a useful model for many features of a hypothetical ancestor of *Endothiodon* (also see Cox 1998).

The more basal position of *Pristerodon* suggested in this analysis (Figure 1a, node F) is supported by the retention of several plesiomorphic character states in that taxon, including weakly developed anterior palatal ridges that converge with an expanded area of the posterior median ridge, a relatively wide intertemporal region, a relatively small dentary table, a relatively large lateral dentary shelf, the presence of maxillary and dentary teeth, and the relatively smooth but finely pitted palatal surface of the palatines. King (1988, 1990) favored a more crownward placement (Figure 1c) based on the modification of the posterior dentary sulcus into a "deep, thin-walled sulcus" (King 1988, p. 71). Although I have included only the presence or absence of a dentary sulcus in the data matrix presented here, in my personal observations I have found the dentary sulcus of *Pristerodon* to more closely resemble that of *Chelydontops* or *Endothiodon* than that of taxa such as *Tropidostoma*. I consider these observations to be consistent with the more basal position suggested by the preferred cladogram, and future analyses that take into account the detailed morphology of the dentary sulcus (not just its presence or absence) can further test this hypothesis.

The placement of *Pristerodon* suggested by this analysis also has important implications for one other character, the presence of paired anterior ridges that converge posteriorly. When this character is optimized on the preferred cladogram of this analysis, it appears to have evolved independently in *Pristerodon* and the common ancestor of *Robertia* and *Diictodon*. However, this reconstruction is likely to be an artifact of the taxa included in the analysis. In addition to *Diictodon*,

Robertia, and *Pristerodon*, several specimens collected in the lower *Tapinocephalus* Assemblage Zone (e.g., BP/1/5580, BP/1/5589, NM QR3145, NM QR3505; Rubidge, personal communication, 2000) also possess this arrangement of the palatal ridges. In all cases the ridges converge with an expanded, flattened area of the posterior median ridge. In some specimens (e.g., NM QR3145, NM QR 3505) the expanded area of the posterior median ridge is Y-shaped, while in others (e.g., BP/1/5589, *Diictodon*, *Pristerodon*) the expanded area is narrower and V-shaped. Although not included in this analysis, the morphology and stratigraphic occurrence of these specimens suggest that they likely would fall on the branch between *Eodicynodon* and the clade including *Robertia* and *Diictodon* in the cladogram presented here (Modesto & Rubidge pers. comm.). If this hypothesis is correct, then it is possible that convergent anterior ridges evolved only once, and were later lost in the clades including *Chelydontops* and *Endothiodon* (Figure 1a, Node E) and *Kingoria* and *Myosaurus* (Figure 1a, Node H). These hypothesized losses are corroborated by the fact that both *Chelydontops* and *Emydops* possess posterior palatal ridges with an expanded anterior area and an anterior palatal morphology suggestive of being derived from an ancestor that possessed ridges (Appendix 1, Character 7). The parallel anterior ridges in taxa such as *Tropidostoma* or *Dicynodon* likely represent a modification of the convergent ridge morphology.

The taxa *Emydops*, *Myosaurus*, and *Cistecephalus* are reconstructed as forming a clade (Figure 1a, Node I) that has the same membership as the Emydopidae of King (1988, 1990; Figure 1c, Node C). However, the relationships among the taxa in the clade presented here are different than those of King; instead of *Emydops*, *Cistecephalus* is reconstructed as the sister taxon of *Myosaurus*. This pattern of relationship is supported by two synapomorphies in this analysis (the presence of a foramen on the palatal surface of the palatine, and posteromedially extended anterior orbital margins that partially close off the back of the snout). Both of the proposed synapomorphies are quite distinctive, and I have only observed these features in *Cistecephalus*, *Myosaurus*, and *Cistecephaloides* (which Cluver (1974a) proposed was closely related to *Cistecephalus*; a palatal foramen has also been reported in *Kawingasaurus*, another potential relative of *Cistecephalus* (Cox, 1972); also see Appendix 1, Characters 24, 25). In addition, the synapomorphies King (1988, 1990) proposed to support a close relationship between *Myosaurus* and *Emydops* to the exclusion of *Cistecephalus* (reduced upper teeth, long, straight anterior pterygoid rami, and a shortened basicranial region) also can be found in *Cistecephalus*, and are thus diagnostic of a more inclusive clade. Cluver (1974b) also noted the possibility of a close relationship between *Cistecephalus* and *Myosaurus*, and suggested that both taxa could be derived from a *Myosauroides*-like ancestor.

Tropidostoma, *Oudenodon*, and *Rhachiocephalus* form a clade (Figure 1a, Node L) that has the same membership as the Cryptodontinae of King (1988, 1990; Figure 1a, Node E), but here again the relationships of the taxa within the clade are different. In this case, *Oudenodon* and *Tropidostoma* are reconstructed as being more closely related to each other than either is to *Rhachiocephalus*, whereas King favored a sister group relationship between *Oudenodon* and *Rhachiocephalus*. King (1988, 1990), used the loss of teeth as a synapomorphy to unite *Rhachiocephalus* and *Oudenodon* and exclude *Tropidostoma*. Although *Tropidostoma* does possess upper and lower postcanine teeth (some specimens also possess tusks), there are several other features that strongly suggest a close relationship between *Tropidostoma* and *Oudenodon*.

In this analysis, two synapomorphies unite *Oudenodon* and *Tropidostoma*, the presence of a relatively long interpterygoid vacuity that reaches the level of the anterior portion of the palatines and a temporal region in which the postorbitals partially overlap the parietals, with the parietals exposed in a median groove or depression. King (1988, 1990) used the latter feature to diagnose her Tropidostomini, but in my observations this character state also characterizes nearly all *Oudenodon* specimens, suggesting it is diagnostic for a more inclusive clade. The intertemporal region of *Rhachiocephalus* is distinctly different because it is narrower and the postorbitals nearly completely overlap the parietals. In addition, the detailed morphology of the nasal bosses also supports the topology presented here. All three taxa possess paired nasal bosses, but the bosses of *Tropidostoma* and *Oudenodon* are less elongate and usually centered approximately over the center of the external narial openings. The bosses of *Rhachiocephalus* tend to be more elongate and ridge-like, and usually are located posterodorsal to the narial opening. *Rhachiocephalus* also tends to be larger than either *Oudenodon* or *Tropidostoma*, and it possesses a distinct pineal boss, which the other taxa lack. However, it is important to note that the results of the decay analysis show that only one additional morphological step is required to make *Rhachiocephalus* the sister taxon of *Oudenodon*.

The evolutionary history of the dentition of dicynodonts implied by the preferred cladogram of this analysis also deserves mention because it requires gains and losses of teeth that initially seem somewhat counter-intuitive. Basal anomodonts possess laterally placed teeth on the premaxilla, maxilla, and dentary, whereas many advanced dicynodonts have completely replaced their teeth with a keratinized beak. Several other dicynodonts possess a keratinized beak but also retain some teeth. Some of these taxa (e.g., *Robertia*, *Emydops*, *Pristerodon*, *Tropidostoma*) have been considered basal members of toothless clades that document the process of tooth loss (Cox 1998; Watson 1948). However, the preferred cladogram of this analysis implies that the presence of teeth in some of these taxa represent reversals to a toothed state from a toothless ancestor.

The cladogram presented here suggests that premaxillary teeth were lost in the common ancestor of *Eodicynodon* and *Kannemeyeria* (Figure 1a, Node A), but a reversal later occurred in *Endothiodon*. This reversal may characterize the lineage including both *Endothiodon* and *Chelydontops* (Figure 1a, Node D), depending on how the palate of *Chelydontops* is interpreted (Appendix 1, Character 2). I do not consider *Chelydontops* to possess premaxillary teeth, but the presence of teeth very close to the maxilla/premaxilla suture in that taxon supports the hypothesis that a secondary anterior lengthening of the upper tooth row occurred in this clade.

Maxillary teeth were independently lost in *Diictodon* and the common ancestor of *Kingoria* and *Kannemeyeria* (Figure 1a, Node G). The loss in *Diictodon* is corroborated by an undescribed, toothed *Diictodon*-like specimen from the lower *Tapinocephalus* Assemblage Zone (Rubidge pers. comm., 2000). The loss in the ancestor of *Kannemeyeria* and *Kingoria* is more interesting because it implies reversals to a toothed state in *Emydops* and *Tropidostoma*. However, these reversals are also required in some optimizations of this character on the cladogram of King (1988, 1990), as is an additional reversal to a toothed state in *Robertia*. The implied reversal in *Robertia* is not well supported because the undescribed, toothed *Diictodon*-like specimen strongly suggests that the common ancestor of *Diictodon* and *Robertia* was also toothed.

A similar pattern is observed for the dentary teeth. The presence of dentary teeth is the basal character state for Anomodontia, and medially-placed dentary teeth characterize the clade including *Robertia*, *Kannemeyeria*, and all descendants of their most recent common ancestor (Figure 1a, Node B). The complete loss of teeth took place independently in *Diictodon* and the common ancestor of *Kingoria* and *Kannemeyeria* (Figure 1a, Node G), and reversals to a toothed state occurred in *Emydops* and *Tropidostoma*. Some optimizations of this character on the cladogram of King (1988, 1990) also require a similar pattern of loss and reversal, as well as an additional reversal to a toothed state in *Robertia*. However, this reversal appears less likely because the undescribed, toothed *Diictodon*-like specimen strongly suggests that the common ancestor of *Diictodon* and *Robertia* possessed a toothed dentary.

The patterns of tooth loss and gain in the skull and jaw implied by the preferred cladogram of this analysis suggest that some degree of plasticity existed in the developmental processes responsible for the formation of the dentition in dicynodonts. This perhaps is not surprising given that much of tooth development is the result of epithelium-mesenchyme interactions that can be altered easily by slight modifications in developmental sequences or the behavior of cell populations. In addition, it has been shown that chick epithelium retains the ability to participate in tooth formation (Kollar 1972; Kollar & Fisher 1980), despite coming from a lineage that has been toothless since at least the Early Tertiary. The

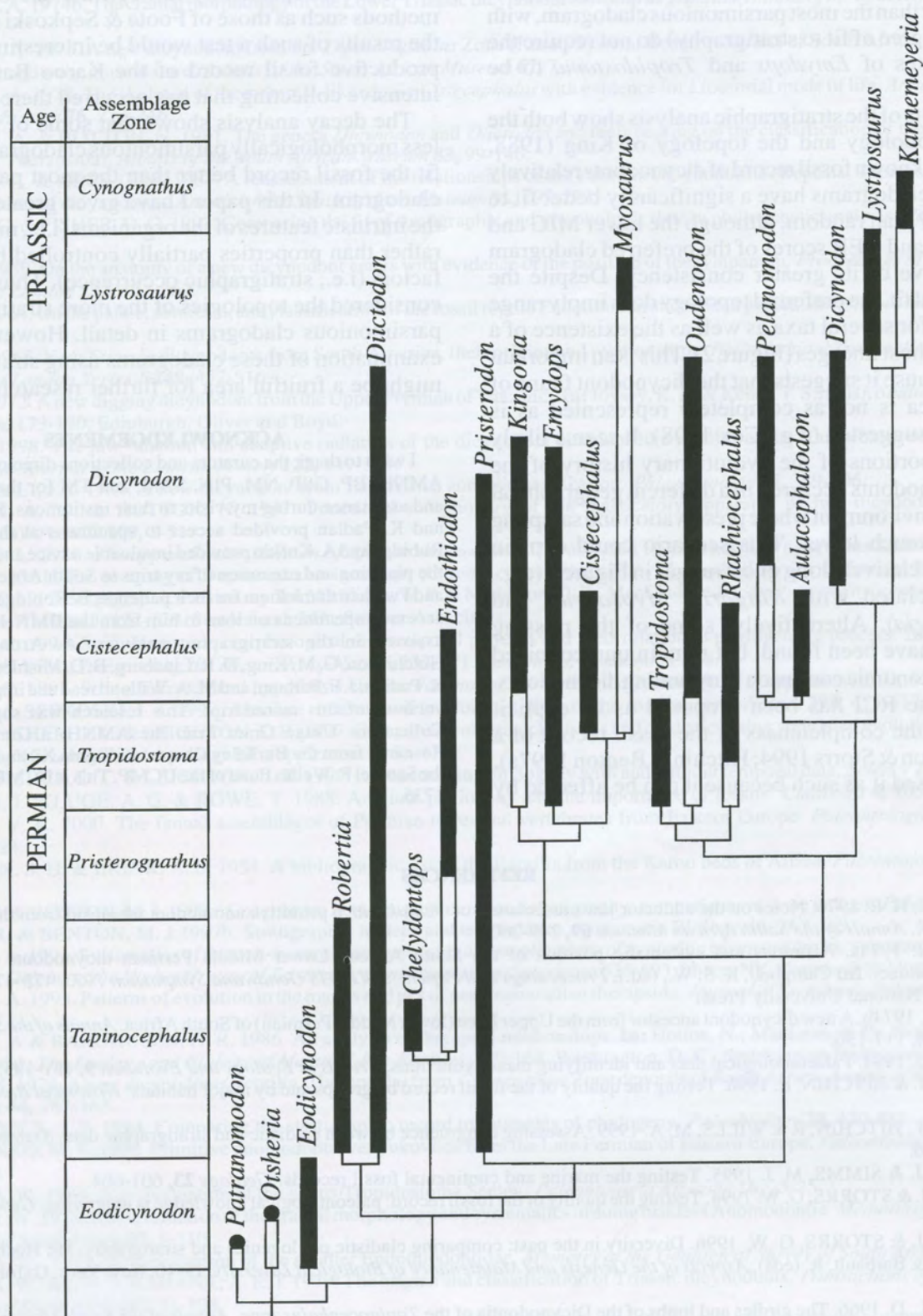


Figure 2: Cladogram based on that of Figure 1a showing the stratigraphic ranges of the included taxa. Solid bars indicate known ranges and open bars indicate ghost ranges implied by the cladogram. Thin lines indicate ghost lineages implied by the cladogram. Stratigraphic ranges and assemblage zones are based on Rubidge (1995a). Because *Patranomodon* and *Otsheria* are each known from a single specimen their stratigraphic ranges are approximate. The stratigraphic range of *Chelydontops* also is not well constrained and therefore approximate. The range of *Kingoria* is an approximation based on data presented in King (1988).

losses and reversals required by this cladogram likely occurred over a much shorter period of time, possibly ten million years or less. It is important to note that slightly less parsimonious cladograms (two morphological steps longer than the most parsimonious cladogram, with the same degree of fit to stratigraphy) do not require the toothed states of *Emydops* and *Tropidostoma* to be reversals.

The results of the stratigraphic analysis show both the preferred topology and the topology of King (1988, 1990) fit the known fossil record of dicynodonts relatively well. Both cladograms have a significantly better fit to stratigraphy than random, although the lower MIG and higher RCI and GER scores of the preferred cladogram are indicative of its greater consistency. Despite the good general fit, the preferred topology does imply range extensions for several taxa as well as the existence of a number of ghost lineages (Figure 2). This is an important finding because it suggests that the dicynodont fauna of South Africa is not as completely represented as is sometimes suggested (e.g., Cox 1998). It seems likely that some portions of the evolutionary history of the Karoo dicynodonts occurred in a different geographical location or environment where preservation and sampling rates were much lower. This scenario could explain some of the relatively long ghost ranges in Figure 2 (e.g., those associated with *Kingoria*, *Myosaurus*, and *Kannemeyeria*). Alternatively, some of the missing taxa could have been found, but remain unrecognized due to the taxonomic confusion surrounding dicynodonts. Although the RCI has been proposed as an explicit measure of the completeness of the fossil record of a group (Benton & Storrs 1994; Hitchin & Benton 1997a), I have not used it as such because it can be affected by

factors such as the accuracy of the cladogram examined, sampling rates, and extinction (Paul 1998; Wagner 1998, 2000). The gaps implied by the preferred cladogram can be tested independently through the use of statistical methods such as those of Foote & Sepkoski (1996), and the results of such a test would be interesting given the productive fossil record of the Karoo Basin and the intensive collecting that has occurred there.

The decay analysis shows that some of the slightly less morphologically parsimonious cladograms actually fit the fossil record better than the most parsimonious cladogram. In this paper I have given greater weight to the intrinsic features of the organisms (i.e., morphology) rather than properties partially controlled by extrinsic factors (i.e., stratigraphic occurrence). Thus I have not considered the topologies of the more stratigraphically parsimonious cladograms in detail. However, further examination of these cladograms using stratocladistics might be a fruitful area for further research.

ACKNOWLEDGEMENTS

I wish to thank the curators and collections directors of the AM, AMNH, BP, GSP, NM, PIN, SAM, and TM for their hospitality and assistance during my visits to their institutions. P. A. Holroyd and K. Padian provided access to specimens at the UCMP. B. Rubidge and A. Kurkin provided invaluable advice and assistance in the planning and execution of my trips to South Africa and Russia, and I wish to thank them for their patience. B. Rubidge also allowed access to specimens on loan to him from the BMNH. M. A. Wills assisted in the stratigraphic analysis. A. Aronowsky, J.R. Hutchinson, G. M. King, D. R. Lindberg, B. D. Mishler, S. Modesto, K. Padian, J. F. Parham, and M. A. Wills all read and improved earlier versions of this manuscript. This research was supported by a Collections Usage Grant from the AMNH, a Grant-in-Aid-of-Research from the Berkeley Chapter of Sigma Xi, and a grant from the Samuel P. Welles Fund of the UCMP. This is UCMP contribution 1736.

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APPENDIX 1

Description and discussion of characters used in phylogenetic analysis

Morphologic Characters

- 1) Keel-like extension of the palatal rim posterior to the caniniform process present (1) or absent (0).
A postcaniniform keel is found in *Emydops*, *Kingoria*, *Cistecephalus*, and *Myosaurus*. The holotypes of *Kombuisia* (BP/1/5344) and *Cistecephaloides* (SAM 6243) also possess this feature, although these taxa have not been included in this analysis. The keel has a rounded ventral edge, a steep-sided, wall-like lateral side, bears teeth in some *Emydops* specimens, and is formed by a continuation of the lateral palatal rim posterior to the caniniform process. Its height is variable; *Kingoria* and *Emydops* tend to have taller keels whereas *Cistecephalus* and *Myosaurus* have lower, less distinct keels. The postcaniniform keel is distinct from the postcaniniform crest (Character 28) because the crest has a sharp ventral edge, a smoothly sloping lateral side, and, in well-preserved specimens (e.g., SAM K5227, *Oudenodon*), can be seen to arise from the posteromedial side of the caniniform process. The character has been coded as "?" for taxa that lack caniniform processes because it is not directly applicable to them.
- 2) Premaxillary teeth present and located laterally (0), medially (1), or absent (2).
Most non-dicynodont anomodonts (*sensu* Modesto *et al.*, 1999; Rybczynski 2000) resemble the majority of synapsids by possessing premaxillary teeth that are located near the anterior or lateral margins of the palatal surface of the bone. *Galeops* may be an exception to this trend (Brinkman 1981), although undescribed specimens tentatively identified as *Galeops* in the collections of the South African Museum (SAM 4005, SAM 12261) have clear evidence of premaxillary teeth located near the margins of the palate. *Endothiodon* possesses 2 premaxillary teeth, but these are located posteromedially on the premaxillary secondary palate, well away from the margins of the premaxilla. *Chelydontops* also has been reported as having at least one tooth very near the premaxilla/maxilla suture (Cluver 1975), but my examination of the holotype (SAM 11558) and referred specimen (SAM 12259) has shown the suture to be poorly preserved in both cases. The most anterior tooth may touch the premaxilla/maxilla suture in the holotype, but it is not completely or nearly completely surrounded by the premaxilla as the premaxillary teeth are in *Endothiodon*, and as a result I have coded *Chelydontops* as lacking premaxillary teeth. All other dicynodont taxa included in this analysis clearly lack premaxillary teeth.
- 3) Premaxillae fused (1) or unfused (0).
The premaxillae are unfused and sutured together in the majority of synapsid taxa. A suture between the premaxillae is also visible in non-dicynodont anomodonts and in well-preserved specimens of *Eodicynodon* (e.g., ROZ 1, NM QR 2905, NM QR2989, NM QR2990). The premaxillae are indistinguishably fused in all other described dicynodont taxa.
- 4) Upper postcanine teeth located near lateral margins of maxilla (0), located more medially, but with more posterior teeth often approaching the lateral margin of maxilla (1), located medially and with teeth a constant distance from the margin of the maxilla (2), or absent (3).
The upper postcanine teeth are located near the lateral margin of the maxillae in non-dicynodont anomodonts, an arrangement similar to that of the majority of synapsid taxa. *Eodicynodon* is unique among dicynodonts in having postcanine teeth placed far laterally. In *E. oosthuizeni* the teeth are in line with the midline of the canine tusk on the posterior surface of the caniniform process, while in *E. oelofsoni* a tusk is absent and a row of teeth is present near the lateral margin of the palate (Rubidge, 1990b). A few specimens of *E. oosthuizeni* also have one or two medially placed postcanine teeth (e.g., ROZ 9, ROZ 11, NM QR2905, NM QR2989), but the nature of this variation has not yet been examined in detail. Because of the relative rarity of these specimens and the distinct lateral placement of at least some of the postcanine teeth visible in most *E. oosthuizeni* and *E. oelofsoni* specimens, I have chosen to code *Eodicynodon* as having laterally placed teeth.
In *Pristerodon*, *Robertia*, and *Chelydontops* the postcanine teeth are found in rows that are located on the medial part of the maxilla anteriorly, but approach the lateral margin of the palate more posteriorly. There are minor variations in this pattern (e.g., the "rows" are sometimes poorly formed in *Robertia*, the exact placement of the teeth is variable in *Pristerodon*; Keyser, 1993), but this variation does not appear to be of phylogenetic importance. I have given this coding to *Emydops* and *Tropidostoma* as well, although these taxa tend not to show the pattern as clearly. Their tooth rows are usually short (i.e., have few teeth) and located towards the posterior and lateral portion of the maxilla, although not as far laterally as in *Eodicynodon*. They often show a weak medial to lateral trend, and these teeth may be homologous with the more posterior teeth in the other taxa. If this hypothesis is accurate, then the coding used here should not be misleading.
The postcanine teeth of *Endothiodon* are located in medially placed, laterally concave rows. Although curved, these tooth rows remain a constant distance from the lateral margins of the palate because they also are laterally concave. This morphology is unlike the condition in e.g. *Pristerodon* because there the tooth rows approach the lateral margin of the palate posteriorly. All other taxa included in this analysis lack postcanine teeth.
- 5) Shelf-like area lateral to the upper postcanine teeth present (1) or absent (0).
Endothiodon and *Chelydontops* possess a flattened or slightly concave, shelf-like area lateral to the upper postcanine teeth (Cluver 1975; Cox 1964). When well preserved, these areas have a somewhat rugose texture suggesting a keratinous covering (e.g., BP/1/1659, *Endothiodon*, SAM 12259, *Chelydontops*). In *Chelydontops* the shelf is raised slightly above the level of the more anterior portion of the secondary palate, whereas in *Endothiodon* it is closer to the level of the anterior portion of the palate. The shelf is relatively longer in *Endothiodon*, but this may be related to the relatively longer tooth rows present

in that taxon. The non-dicynodont anomodonts and other toothed dicynodonts included in this analysis do not possess a shelf lateral to the upper tooth rows. The toothless dicynodonts have been coded as “?” because the character is not directly applicable to them.

- 6) Caniniform process absent (0), present (1), present with notch anterior to it (2).

In non-dicynodont anomodonts and *Endothiodon* the maxillary rim of the palate is not extended ventrally into a caniniform process. In his description of *Chelydontops*, Cluver (1975) reported that a caniniform process was absent. However, a caniniform process is present in SAM 12259, albeit weakly developed. The majority of dicynodonts (including *Chelydontops*) possess a caniniform process that is a smooth continuation of the palatal rim. The detailed morphology of the process in varies among taxa (compare e.g., *Placerias*, *Kannemeyeria*, *Emydops*, *Oudenodon*, and *Cistecephalus*). This variation is likely related to factors such as function and presence or absence of a canine tusk, and I have not distinguished the variants in my codings. In *Diictodon* and *Robertia* a distinctive notch in the palatal rim is present so that the anterior edge of the caniniform process is set off from the palatal rim and meets the palatal surface of the maxilla medial to the rim. Well-preserved specimens of *Eodicynodon* possess a notch in the palatal rim anterior to the canine tusk, but this is not homologous with the condition in *Diictodon* or *Robertia* because the notch is within the caniniform process and the anterior edge of the process is not set off from the palatal rim.

- 7) Paired anterior ridges on premaxilla absent (0), present but converge posteriorly (1), or present and do not converge (2).

Non-dicynodont anomodonts and *Eodicynodon* do not possess paired anterior ridges on the palatal surface of the premaxilla. Several undescribed dicynodont specimens collected in the lower *Tapinocephalus* Assemblage Zone (e.g., NM QR3145, NM QR3505; Rubidge, personal communication, 2000) possess weakly-developed, paired anterior ridges that converge with a Y-shaped, expanded, flattened anterior portion of the median palatal ridge. A similar condition is found in *Robertia*, *Diictodon*, and *Pristerodon*, except that the ridges are more weakly convergent and the expanded, flattened portion of the posterior median ridge is narrower and V-shaped. I did not distinguish between these morphologies in my coding of this character because the undescribed specimens were not included in this analysis.

Tropidostoma, *Oudenodon*, *Rhachiocephalus*, *Aulacephalodon*, *Dicynodon*, *Lystrosaurus*, and *Kannemeyeria* all possess well-developed anterior ridges that are roughly parallel, although some individual specimens of these taxa (e.g., SAM K1496, *Lystrosaurus*) show slight convergence of the ridges. A variably developed depression is often present between the ridges in these taxa.

Chelydontops, *Endothiodon*, *Emydops*, *Kingoria*, *Cistecephalus*, *Myosaurus*, and *Pelanomodon* lack distinct anterior palatal ridges. Some specimens of these taxa (e.g., BP/1/3858 and BP/1/1562, *Kingoria*; SAM 11060 and SAM K6623, *Emydops*; SAM 11558, *Chelydontops*) bear a depression at the front of the mouth that has slightly raised lateral edges that are suggestive of highly reduced ridges, indicating that the ridgeless condition in these and closely related taxa may represent a secondary loss. *Pelanomodon* also lacks anterior ridges (Cluver and King, 1983) and the anterior area of the premaxillary secondary palate of specimen GSP AF9183 is smooth and flat. Anterior palatal ridges are absent in *Endothiodon*, and the premaxillary secondary palate is unique in being highly vaulted (Cox, 1964; Latimer *et al.*, 1995; Ray, 2000).

- 8) Posterior median ridge on premaxilla absent (0), present with a flattened, expanded anterior area (1), or present without a flattened, expanded anterior area (2).

Non-dicynodont anomodonts do not possess a posterior median ridge on the palatal surface of the premaxilla. A wide, thick median ridge that flattens and fans out anteriorly is present in *Eodicynodon*. The ridge is thinner and more blade-like in most other dicynodont taxa. *Robertia*, *Diictodon*, *Pristerodon*, *Emydops*, and several undescribed specimens collected in the lower *Tapinocephalus* Assemblage Zone (e.g., NM QR3145, NM QR3505; Rubidge, personal communication, 2000) possess a thinner median ridge that flattens and expands into a slightly raised, Y-shaped or V-shaped area that converges with the anterior ridges in some cases (see Character 7). The median ridge of *Chelydontops* also flattens and expands anteriorly, but the expanded area is diamond-shaped. Most of the other taxa included in this analysis possess a thin median ridge that becomes lower anteriorly but lacks a distinct expanded area. The median ridge is relatively weakly developed in *Kingoria*, and unusually modified so that it is T-shaped in cross-section in *Myosaurus* (Cluver, 1974b). For simplicity, I have distinguished only between taxa that possess an expanded anterior portion of the median ridge and those that do not when the ridge is present. This distinction should be appropriate for the level of taxon sampling attempted in this analysis, although further subdivision of this character may be desirable in future analyses that include a greater number of taxa.

- 9) Palatal surface of premaxilla with well-defined depressions with curved sides lateral to median ridge (0), with groove-like depressions that have straight sides and a rounded anterior end (1), or relatively flat with poorly defined or no depressions present (2).

Non-dicynodont anomodonts do not possess a median palatal ridge, and those included in this analysis (*Patranomodon* and *Otsheria*) have been coded as “?” because this character is not directly applicable to them. *Eodicynodon* possesses a distinct depression in the premaxillary secondary palate on each side of the posterior median ridge. The depressions are roughly oval-shaped with the long axis of the oval trending antero-posteriorly. The sides of the depressions are curved and the anterior and posterior ends are slightly pointed. Similar depressions are found in *Diictodon* and *Robertia*, although the depressions are slightly shallower in *Robertia* than in the other two taxa.

Emydops, *Cistecephalus*, and *Myosaurus* possess more groove-like depressions lateral to the median ridge that have straight

edges, a rounded anterior end, and an open posterior end. *Myosaurus* is unique in having thin, channel-like depressions that are partially enclosed by the crossbar of the T-shaped median ridge located between the median ridge and the depressions in the palatal surface. Cluver (1974b) compared these channels to features found on the dorsal surface of the premaxilla in *Lystrosaurus* that may have been associated with a vomeronasal organ. I have given *Myosaurus* the same coding as *Emydops* and *Cistecephalus* because all three taxa possess groove-like palatal depressions, and the channels medial to them in *Myosaurus* seem to be unrelated, autapomorphic features.

The rest of the taxa in this analysis have do not possess depressions set off from the rest of the palatal surface by distinct margins. Instead, the palatal surface lateral to the median ridge is flat or slightly concave and smoothly merges with the palatal rim. The exact morphology of the area seems to be variable both among and within these taxa and is susceptible to alteration by plastic deformation of the skull. I have included this series of morphologies under a single character state because they all can be distinguished easily from the other two states and the variability among them appears to be random.

- 10) Lower teeth present on dorsal surface of dentaries (0), present on a medial swelling or shelf (1), or absent (2).

The lower teeth of all non-dicynodont anomodonts for which jaws are known are located on the dorsal surface of the dentaries. In *Patranomodon* and *Suminia* the teeth are located slightly medially on the dorsal surface, and the dentary forms a narrow rim just lateral to base of the tooth crowns. The dorsal surface of the jaw has been expanded laterally to form a wide, flat surface in *Ulemica*, especially in large specimens (Ivakhnenko, 1996). The teeth are located on the medial side of this surface, but still clearly on the dorsal surface of the jaw. I have not distinguished between these variants in coding this character because only *Patranomodon* is included in this analysis. A lower jaw is not known for *Otsheria*, although Ivakhnenko (1996) noted that it may have been very similar to the jaw specimens assigned to *Venyukovia*. *Eodicynodon* also has teeth located towards the medial side of the dorsal dentary surface (Rubidge, 1984, 1990a, 1990b).

The other toothed dicynodonts included in this analysis all have dentary teeth located on some type of medial shelf or swelling. *Robertia* and an undescribed, toothed, *Diictodon*-like specimen collected in the lower *Tapinocephalus* Assemblage Zone (BP/1/5589; Rubidge, personal communication, 2000) possess a row of teeth on the blade-like ridge that forms the medial boundary of dentary table. *Endothiodon* and *Chelydontops* have teeth located on a swelling of the dentary ramus that is medial and slightly below the level of the posterior dentary sulcus, although the condition is more strongly developed in *Endothiodon*. *Emydops* and *Pristerodon* possess teeth on a raised swelling or shelf that is medial to the posterior dentary sulcus. In *Tropidostoma* the dentary teeth are located on a raised swelling that is medial to the junction of the dentary table and posterior dentary sulcus. I have not distinguished between these variations in coding this character because the differences between the variants are relatively minor. All other taxa in this analysis lack dentary teeth. I have coded *Pelanomodon* as “?” because no jaw that is definitely referable to this taxon is currently known (Cluver and King, 1983).

- 11) Vomers fused (1) or unfused (0).

Most non-dicynodont anomodonts and *Eodicynodon* resemble many other basal synapsids in possessing a clear midline suture between the vomers. Although the mid-ventral plate of the vomers is poorly preserved in the only known specimen of *Otsheria* (PIN 1758/5), careful scrutiny has uncovered no indication of a midline suture. The vomers may also be fused for at least part of their length in *Suminia* (Rybczynski 2000). All other dicynodont taxa included in this analysis possess vomers that are indistinguishably fused.

- 12) Mid-ventral plate of vomers with an expanded area posterior to junction with premaxilla (0) or with out a notably expanded area posterior to junction with premaxilla (1).

The palatal exposure of the mid-ventral plate of the vomers of *Patranomodon*, *Eodicynodon*, *Robertia*, an undescribed *Diictodon*-like specimen collected in the lower *Tapinocephalus* Assemblage Zone (BP/1/5589, Rubidge, personal communication, 2000), and well-preserved specimens of *Endothiodon* (e.g., BP/1/1659) possess a small, oval-shaped expansion just posterior to the premaxilla/vomer suture. The expanded area is slightly larger in *Patranomodon* than in the other taxa. All of the other dicynodont taxa included in this analysis and *Otsheria* possess mid-ventral vomerine plates that are of constant width in palatal view.

- 13) Mid-ventral plate of vomers relatively wide in ventral view (0) or more narrow and blade-like in ventral view (1).

The mid-ventral vomerine plates of most non-dicynodont anomodonts, *Eodicynodon*, *Robertia*, *Pristerodon*, *Tropidostoma*, *Endothiodon*, *Chelydontops*, *Kingoria*, and *Aulacephalodon* all have relatively wide ventral surfaces. In some of these taxa (e.g., *Tropidostoma*, *Pristerodon*) the lateral edges of the plate have the form of slightly raised ridges in palatal view, giving the ventral surface of the plate a trough-like appearance. In coding this character I have not distinguished between taxa that have vomerine troughs and those that do not because distortion or damage can easily remove the thin edges of the trough. Although not preserved well in the only known specimen, the mid-ventral plate of the vomers of *Otsheria* appears to have had a relatively narrow palatal surface, a condition unique among non-dicynodont anomodonts (although the plate may have widened dorsally). The rest of the taxa included in this analysis have vomerine plates that are quite thin and blade-like in palatal view.

- 14) Embayment of palatal rim anterior to caniniform process or tusk absent (0) or present (1).

The palatal rims of *Emydops*, *Cistecephalus*, and *Myosaurus* all bow laterally anterior to the level of the caniniform process, forming an embayment on the surface of the secondary palate. The palatal rim of *Kingoria* does not have a strong embayment,

although a small, shallow depression on the medial surface of the rim just anterior to the caniniform process is present. I have coded this feature as an embayment because its morphology and position strongly suggest that is likely to be either a reduced or incipiently-developed embayment. Nearly all other taxa included in this analysis possess palatal rims that do not bow laterally to form an embayment. I have coded *Patranomodon*, *Otsheria*, and *Endothiodon* as “?” because they lack a distinct caniniform process, and thus this character is not directly applicable to them.

- 15) Dentary table absent (0), present as a small, rounded expansion of the dorsal surface of the dentary located near the symphysis (1), present as an elongate grooved surface on the dorsal surface of the dentary bounded laterally by a low ridge and medially by a tall, thin, dorsally convex blade (2), or present as an elongate grooved surface on the dorsal surface of the dentary bounded by low ridges (3).

The anterior dorsal surface of the dentary rami of non-dicynodont anomodonts are not expanded laterally to form a distinct dentary table. Although not included in this analysis, I do not consider the expanded dorsal surface of the dentary found in some large specimens of *Ulemica* (e.g., PIN 157/5, PIN 157/1113) to be homologous with the dentary table because it is located relatively posteriorly on the jaw ramus and is not dorsally-concave.

Eodicynodon possess a dentary table that has the form of a small, dorsally-concave, oval-shaped expansion of the dorsal surface of the dentary ramus just posterior to the dentary symphysis. A similar condition is also found in *Chelydontops* (SAM 12259) and *Pristerodon* (e.g., SAM K1658, SAM 10161, although this feature is more weakly developed in some *Pristerodon* specimens).

In *Robertia* and *Diictodon* the dentary table is more elongate and has a groove-like morphology. The lateral margin of the groove is formed by a low ridge and the medial margin is formed by a tall, thin, dorsally-convex blade. The blade bears teeth in *Robertia* and an undescribed *Diictodon*-like specimen collected in the lower *Tapinocephalus* Assemblage Zone (BP/1/5589, Rubidge, personal communication, 2000), but is toothless in *Diictodon*. *Tropidostoma*, *Oudenodon*, *Rhachiocephalus*, *Aulacephalodon*, *Dicynodon*, *Lystrorhynchus*, and *Kannemeyeria* also possess elongate, groove-like dentary tables, but in these taxa both the lateral and medial margins are formed by low ridges.

Kingoria, *Emydops*, *Myosaurus*, *Cistecephalus*, and *Endothiodon* all lack a distinct dentary table. However, some *Kingoria* specimens (e.g., SAM K8069, SAM K1260a) possess a small dentary table-like expansion of the dorsal dentary surface that is reminiscent of the condition in *Eodicynodon*, suggesting that the absence of a table in this taxon may be a secondary loss. I have coded *Pelanomodon* and *Otsheria* as “?” because no jaw material that is definitely referable to these taxa is currently known (Cluver and King 1983; Ivakhnenko 1996).

- 16) Posterior dentary sulcus present (1) or absent (0).

Many dicynodont taxa possess a longitudinal sulcus on the dorsal surface of the dentary rami posterior to the jaw symphysis. The sulcus is usually relatively deep, has a concave floor, and is located posterior to the dentary tables and lateral to the dentary teeth when they are present. However, the exact morphology of the sulcus varies among the taxa included in this analysis. In *Oudenodon*, *Tropidostoma*, *Rhachiocephalus*, *Aulacephalodon*, *Dicynodon*, *Lystrorhynchus*, and *Kannemeyeria* the sulcus is relatively narrow with tall, thin walls, and it merges with the dentary tables anteriorly. The sulcus is wider with lower walls in *Chelydontops*, *Endothiodon*, and *Pristerodon*, and it also extends farther forward in these taxa than in taxa such as *Oudenodon*. In *Emydops* the sulcus is relatively shallow and not as distinctly developed as in some taxa, but is still relatively long. Some specimens of *Cistecephalus* (e.g., SAM 10665) possess a small, shallow groove, bounded laterally by a raised ridge and a groove-like depression, in the same position as the sulcus in other taxa. For simplicity, I have chosen not to code these variants with different states in this analysis because they all share some morphological features and a similar position. However, subdivision of this state into one or more additional states may be desirable for more detailed future analyses that include additional taxa.

A dentary sulcus is absent in non-dicynodont anomodonts, *Eodicynodon*, *Diictodon*, *Robertia*, *Kingoria*, and *Myosaurus*. I do not consider the expanded dorsal surface of the dentary found in large specimens of *Ulemica* to be homologous with the dentary sulcus because the surface is not concave and lacks distinct lateral and medial walls. Although the occlusal pits developed on this surface are suggestive of being an incipient sulcus, the phylogenies of Modesto *et al.* (1999) and Rybczynski (2000) strongly suggest they are an autapomorphy of *Ulemica*. I have coded *Pelanomodon* and *Otsheria* as “?” because no jaw material that is definitely referable to these taxa is currently known (Cluver and King 1983; Ivakhnenko 1996).

- 17) Lateral dentary shelf present but relatively small (1), present as a boss-like swelling that is located near ventral margin of jaw ramus (2), present and well-developed (3), or absent (0).

The lateral dentary shelf of dicynodonts represents the insertion point for the lateral branch of the M. Adductor Mandibulae Externus (Barghusen 1976; Cluver 1971, 1975; Crompton and Hotton 1967; King 1981a, 1994; King *et al.*, 1989). This feature is absent in *Patranomodon* and not strongly developed in *Galeops* (Brinkman 1981; King 1994). A depression on the coronoid eminence with a relatively short shelf leading anteriorly from it likely represents the insertion in *Ulemica* and *Suminia* (Barghusen 1976; King 1994, King *et al.*, 1989; Rybczynski 2000). The shelf tends to have a wider, more rounded lateral surface in *Ulemica*, while in *Suminia* the lateral surface is thinner and narrower.

In *Eodicynodon*, *Emydops*, *Cistecephalus*, *Myosaurus*, and *Pristerodon* the shelf is relatively large and tends to project prominently from the lateral surface of the jaw, although there is minor variation in its exact morphology and position. Almost all of the other dicynodont taxa included in this analysis possess much more weakly developed lateral shelves. Although there is also some variation among these taxa, the shelves generally tend to have a low, rounded, somewhat rugose, lump-

like or ridge-like morphology anteriorly that grades into a thinner, more shelf-like area posteriorly. In *Endothiodon* the insertion of the lateral external adductor is uniquely modified into a prominent, bulbous, oval-shaped swelling on the lateral surface of the jaw, just anterior to the mandibular fenestra and extending to the ventral margin of the ramus (Ray 2000). I have coded *Pelanomodon* and *Otsheria* as “?” because no jaw material that is definitely referable to these taxa is currently known (Cluver and King 1983; Ivakhnenko 1996).

- 18) Symphyseal region of lower jaw with an upturned margin that is raised above the level of the dorsal surface of the jaw rami and has a scooped-out depression on its posterior surface (1), drawn into a sharp, spiky beak (2), shovel-shaped with a rounded or squared-off edge and a weak depression on its posterior surface (3), with a wedge-shaped margin that does not extend much above the dorsal surface of the jaw rami and has a groove-like depression on its posterior surface (4), or smoothly rounded and bearing teeth (0).

The jaw symphysis of non-dicynodont anomodonts resembles that found in most synapsid taxa. The anterior surface of the symphysis is smoothly rounded and the dorsal surface bears teeth. In *Eodicynodon*, the symphysis is shovel-shaped, toothless, projects anterodorsally, and bears a weak depression on its posterior surface. A similar condition is found in *Kingoria*, *Emydops*, *Cistecephalus*, and *Myosaurus*. The detailed morphology of the region varies slightly among these taxa (i.e., the symphysis is relatively wider in *Cistecephalus* than in *Kingoria* or *Emydops* and the dorsal edge is rounded in *Kingoria* and *Emydops* and squared-off in *Myosaurus* and *Cistecephalus*), but the overall appearance is similar enough in all of these taxa to be accurately represented by a single character state.

Most of the other taxa included in this analysis possess a curved, upturned, toothless jaw symphysis that projects nearly vertically above the level of the dorsal surface of the dentary rami. A depressed area is present on the posterior surface of the symphysis, but it is deeper and more elongate than in taxa such as *Kingoria*, giving it a more groove-like appearance. The jaw symphyses of *Lystrosaurus* and *Kannemeyeria* are relatively straight and wedge-shaped, and the anterodorsal end does not project far above the dorsal surface of the dentary rami. The depressed area on the posterior surface is deeper and more elongate and distinctly groove-like in these taxa than in others included in this analysis. *Endothiodon* is unique among the taxa examined here in possessing a jaw symphysis that is drawn into a conical spike that projects nearly vertically above the dentary rami. I have coded *Pelanomodon* and *Otsheria* as “?” because no jaw material that is definitely referable to these taxa is currently known (Cluver and King 1983; Ivakhnenko 1996).

- 19) Labial fossa present (1) or absent (0).

The labial fossa is a distinctive foramen bounded by the palatine, jugal, and maxilla located on the posterior surface of the caniniform process, and likely served as a passage for a blood vessel (Cluver 1971; King 1981a). *Pelanomodon*, *Aulacephalodon*, *Dicynodon*, *Lystrosaurus*, and *Kannemeyeria* all possess labial fossae, while all other taxa in the analysis do not.

The holotype of *Patranomodon* (NM QR3000) is interesting because it possesses a single foramen on the right side and two foramina that are divided by a thin bar on the left side that are bounded by the jugal, palatine, and maxilla. Although these features are potential positional homologues of the labial fossa, I have not coded them as such for two reasons. First, despite the similarity in position, the overall morphology of the foramina as well as the area surrounding them are very different than what is typical of the labial fossa. Second, because the holotype is the only known specimen of *Patranomodon*, it is difficult to be certain that the foramina are real features, and not the result of postmortem damage, pathology, or individual variation. If additional specimens of *Patranomodon* that also possess these foramina are discovered, a reassessment of the homologies of the labial fossa may be necessary.

- 20) Parietals widely exposed on the skull roof (0), postorbitals partially overlap parietals on skull roof, but parietals are exposed in a central groove or depression (1), parietals exposed on skull roof and postorbitals steeply placed on the lateral sides of the skull and concave laterally (2), postorbitals overlap parietals nearly completely but intertemporal region not crest-like (3), or postorbitals form a narrow, crest-like intertemporal region with minor exposure of parietals along the dorsal surface (4).

In non-dicynodont anomodonts and *Eodicynodon* the intertemporal skull roof is relatively wide and the parietals have a broad exposure between the postorbitals. A similar condition is found in *Emydops*, *Chelydontops* (although both the holotype and referred specimen of this taxon have been laterally compressed, making the intertemporal region appear narrower), *Robertia*, *Pristerodon*, and *Myosaurus*. However, in these taxa the intertemporal region is slightly longer relative to the total length of the skull than in *Eodicynodon* or the non-dicynodont anomodonts. *Cistecephalus* also possesses a wide intertemporal region, but in that taxon (as well as *Cistecephaloides* and *Kawingasaurus*; Cluver 1974a; Cox 1972) it has been modified so that it is rounded, dorsally convex, and partially roofs over the temporal openings. I have also coded *Lystrosaurus* with this state, although in that genus the postorbitals slope slightly more ventrolaterally than in the other taxa. Even though the intertemporal regions of *Aulacephalodon* and *Pelanomodon* are also wide, they have been given a separate character state because the postorbitals are nearly perpendicular to the parietal portion of the intertemporal skull roof and are concave laterally (the postorbitals of all other examined taxa are flat to slightly convex).

Diictodon, *Tropidostoma*, *Oudenodon*, and *Kingoria* all possess narrower intertemporal regions in which the postorbitals overlap the parietals fairly extensively, but some exposure of the parietals on the skull roof is still present. In *Oudenodon* and *Tropidostoma* (also see Methods) the parietals are exposed between the postorbitals in a groove-like depression, whereas in *Diictodon* and *Kingoria* the parietal exposure is flatter and less groove-like. The postorbitals make contact along the midline of the skull in some specimens of *Kingoria* and *Diictodon*, although this morphology can be exaggerated by

postmortem lateral compression of the skull (Keyser 1975). Although there are slight differences between the morphologies seen in *Diictodon* and *Kingoria* versus those of *Oudenodon* and *Tropidostoma*, I have coded all four taxa with the same state for simplicity. Subdividing this state into two separate states does not alter the topological results of this analysis. *Dicynodon* and *Rhachiocephalus* possess relatively narrow intertemporal regions characterized by complete or nearly complete overlap of the postorbitals over the parietals for most of the intertemporal length of the skull. The postorbitals in these taxa slope ventrolaterally at a sub-vertical angle. *Kannemeyeria* and *Endothiodon* are also characterized by narrow intertemporal regions, but in these taxa the postorbitals are nearly vertical, giving the region a more distinctly crest-like appearance. There is minor exposure of the parietals in the dorsal surface of the crest in both taxa, although the exposure is somewhat wider and more groove-like in *Endothiodon*.

- 21) Squamosal with lateral fossa for the origin of the lateral branch of the M. Adductor Mandibulae Externus (1) or without lateral fossa (0).

All of the dicynodonts included in this analysis possess an expanded, shallow fossa on the posterolateral surface of the squamosal from which the lateral branch of the external adductor muscle arose (Barghusen 1976; Crompton and Hotton 1967; King 1994; King *et al.*, 1989). A similar, although somewhat more weakly developed condition is found in *Ulemica* and *Suminia*, indicating that some non-dicynodont anomodonts possessed a musculature arrangement similar to dicynodonts (Barghusen 1976; King 1994; King *et al.*, 1989; Rybczynski 2000). However, the posterolateral surface of the squamosal in *Patranomodon* is relatively narrow and thin, and lacks a distinct fossa; which King (1994) interpreted as evidence for the absence of an external lateral adductor in this taxon. Although the squamosals of the only known specimen of *Otsheria* (PIN 1758/5) are not fully prepared, in my examination of the specimen I found the exposed area resembles the squamosals of *Patranomodon* much more closely than those of *Suminia* or *Ulemica*. I have interpreted this as indicative of the absence of lateral fossa, and thus the absence of an external lateral adductor. Further preparation of the holotype and/or discovery of additional specimens of *Otsheria* will be necessary to test this hypothesis.

- 22) Palatal surface of the palatine without evidence of a keratinized covering (0), with a rounded, bulbous surface texture that may have had a keratinized covering (1), relatively smooth, but with fine pitting and texturing suggestive of a keratinized covering (2), highly rugose and textured with pitting suggestive of a keratinized covering (3), moderately rugose with pitting suggestive of a keratinized covering (4).

The palatines of *Patranomodon* possess an anterior process that extends for a short distance along the medial surface of the maxilla. This palatal exposure of the palatines is relatively smooth and does not show evidence of the many small nutritive foramina necessary for a keratinized covering. There is some evidence that small palatal teeth or denticles were present on the posterior portion of the palatines near their junction with the pterygoids in *Patranomodon* (Rubidge and Hopson 1996). The palatines of *Otsheria* also possess a short anterior process that meets the maxilla, and the palatal surface of the bone is very smooth along its entire length, showing no signs of the presence of denticles or a keratinized covering.

Recently, Rybczynski (2000) hypothesized that the rugose surface texture of the palatines of *Suminia* was indicative of the presence of palatine denticles in that taxon as well. She also coded the dicynodonts included in her data matrix (*Dicynodon*, *Pristerodon*, and *Eodicynodon*) as possessing an "area of the palatines [that is] rugose and pitted as if to hold denticles" (Rybczynski 2000, p.356). In my examination of *Suminia* specimens that have the palatines exposed (PIN 2212/33, PIN 2212/62), I found that the more anterior portion of the palatal exposure of the palatines possessed many small pits that intersect with the surface of the bone at a low angle, whereas the more posterior portion included a few large pits that were nearly perpendicular with the surface of the bone. Although the larger, posterior pits may indeed be alveoli for denticles, the morphology of the smaller, anterior pits strongly resembles the nutritive foramina found on horn-covered areas of the secondary palate of dicynodonts and turtles. I interpret these observations as indicating that at least the anterior portion of the palatal exposure of the palatine possessed a keratinized covering, although denticles were likely present more posteriorly. The pits on the palatal exposure of the palatines of well-preserved dicynodont specimens also tend to be very small and meet the surface of the bone at a low angle, which is more consistent with nutritive foramina for a keratinized covering than alveoli for teeth or denticles.

Each of the palatines of *Eodicynodon* possess a raised, oval-shaped area that meets the maxillary contribution of the secondary palate. This area has a rounded, bulbous surface and it has been suggested that it played a role in mastication (Cox 1998, King 1990). The fine details of the surface texture of the bone are not well preserved in most specimens, but three acid prepared specimens in the Roy Oosthuizen Collection (ROZ 1, ROZ 9, and ROZ 11) possess a slightly rugose, pitted texture that is suggestive of the presence of a keratinized covering in life.

Diictodon, *Robertia*, *Pristerodon*, *Chelydontops*, *Emydops* and *Cistecephalus* possess palatines that have a medially expanded anterior area at the level of the secondary palate. The shape of this expanded area varies from roughly square in *Emydops* and *Robertia* to leaf-shaped in *Pristerodon* and *Chelydontops*. The bone surface of the palatal exposure of the palatines in these taxa is relatively smooth but contains numerous small nutritive foramina that provide strong evidence for the presence of a keratinized covering. The surface of palatal exposure of the palatines in *Endothiodon* has a different shape and a slightly rougher texture, but is otherwise very similar to the condition in these taxa.

The palatal exposure of the palatines of *Oudenodon*, *Tropidostoma*, *Aulacephalodon*, and *Rhachiocephalus* all possess a highly rugose posterior area that is raised slightly above the level of the secondary palate and a less rugose anterior area that is flush with the secondary palate. Both areas are covered with numerous small nutritive foramina that indicate the presence of a keratinized covering. *Dicynodon*, *Lystrosaurus*, and *Kannemeyeria* also possess rugose palatines with nutritive foramina, although they differ from the those of taxa such as *Oudenodon* in two important respects. First, the

rugosity is not as distinctly developed as in the posterior area of *Oudenodon*. Second, the surface rugosity is evenly developed over the entire palatal surface, instead of being more rugose posteriorly and less so anteriorly.

The palatines of most specimens of *Myosaurus* lack nutritive foramina, and Cluver (1974b) interpreted this as evidence for the absence of a keratinized covering. One of the co-types of this taxon (SAM 3526a) bears a few small pits on the surface of the palatine. However, I do not think these pits provide sufficient evidence to overturn Cluver's hypothesis because this specimen was acid prepared and the pits could easily be artifacts of preparation. The palatines of *Kingoria* are notably reduced compared to those of most other dicynodont taxa and have a relatively smooth surface. I have coded *Kingoria* as "?" in this data set because none of the specimens I have examined have had the palatines sufficiently well-prepared to say decisively whether nutritive foramina were present or absent.

- 23) Nasal bosses absent (0), present as a single median swelling (1), present as paired swellings near the dorsal or posterodorsal margin of external nares (2), present as paired swellings that meet in the midline to form a swollen anterodorsal surface on the snout (3).

The nasals of *Patranomodon* and *Otsheria* are relatively smooth and do not show evidence of a boss. The surface of the nasals is not well preserved in either of the co-types of *Myosaurus* (SAM 3526, SAM 3526a), making it difficult to definitely determine whether nasal bosses were present in either specimen. However, this area is well preserved in another specimen (BP/1/2690), and a nasal boss is clearly absent.

Diictodon, *Robertia*, *Eodicynodon*, *Emydops*, *Kingoria*, and *Pristerodon* all possess a single, median, oval-shaped swelling on the nasals that is covered with numerous small, nutritive foramina, likely indicating the presence of a keratinized covering in life. A similar boss is also present in *Cistecephalus*, although it tends to be smaller and more weakly developed than in the other taxa.

Chelydontops, *Oudenodon*, *Tropidostoma*, *Aulacephalodon*, *Pelanomodon*, *Rhachiocephalus*, and *Dicynodon* possess paired nasal bosses that tend to be located over the dorsal or posterodorsal margin of the external nares and do not meet along the mid-line of the skull. The exact morphology of the bosses varies among the included taxa (compare e.g. *Oudenodon*, *Aulacephalodon*, *Rhachiocephalus*, and *Dicynodon*), as well as within them in some cases (e.g., Tollman *et al.*, 1980 described sexually dimorphic and ontogenetic variation in the size and shape of the bosses of *Aulacephalodon*). *Endothiodon* also possesses paired nasal bosses, although these tend to be more elongate and ridge-like than in the other taxa, and a median ridge is often present between them. Paired nasal bosses occur in at least some species of *Lystrosaurus* (Cluver 1971), although the unusual downturn of the snout in that genus makes them appear less obvious. In all of these taxa the bosses bear numerous nutritive foramina, likely indicating the presence of a keratinized covering in life. I have coded all of these taxa with a single character state because they all share paired bosses that do not meet along the mid-line of the skull. Further subdivision of this character, while theoretically possible, would be difficult because of the minor variations in boss morphology that occur among individual specimens.

The nasal bosses of *Kannemeyeria* are unique among the taxa included in this analysis. Although it has paired bosses, these are anteroposteriorly elongated, rugose, and meet along the midline of the skull, giving the entire dorsal surface of the snout a raised, swollen appearance. Nutritive foramina also are present, indicating that this entire surface likely possessed a keratinized covering in life.

- 24) Foramen present on the palatal surface of the palatine (1) or absent (0).

The majority of anomodont taxa do not possess a palatal foramen. The palatal foramen is present in *Myosaurus* and *Cistecephalus*. It is most distinct in *Myosaurus*, where it is relatively large, round, and passes entirely through palatal surface of the palatine. It is clearly distinct from the nutritive foramina found on palatines of many dicynodonts because the nutritive foramina tend to be much smaller and do not pass completely through the surface of the bone. The foramen is relatively smaller in *Cistecephalus*. Although not included in this analysis, at least two other dicynodonts appear to possess this feature. The holotype of *Cistecephaloidea* (SAM 6243) may possess a palatal foramen, although the palatal surface of the palatines in that specimen is not well preserved, making it difficult to determine if the apparent foramen is a real feature or postmortem damage. Cox (1972) also figures what may be a palatal foramen in *Kawingasaurus*, although in that genus it is near the anterior end of the palatine and bounded anteriorly by the maxilla.

- 25) Anterior margin of orbit extended posteromedially to partly close off the snout from the rest of the skull (1) or snout open to back of the skull (0).

In the majority of dicynodonts and non-dicynodont anomodonts a wide orbitonasal opening leading into the back of the snout is present. However, in *Myosaurus* the frontal, prefrontal, and lacrimal extend medially and posteriorly so that the front of the orbits nearly completely closes off the snout from the rest of the skull (Cluver 1974b). A similar, though less extreme condition is present in *Cistecephalus* and *Cistecephaloidea* (although the latter genus is not included in this analysis). In these taxa the front of the orbits also extend posteriorly and medially, but a relatively wide orbitonasal opening remains between them.

- 26) Pineal foramen flush or nearly flush with dorsal surface of skull (0), surrounded by a strong, rugose boss (1), or surrounded by a thin, smooth, chimney-like boss. (2).

Nearly all dicynodonts and non-dicynodont anomodonts possess a pineal foramen on the dorsal surface of the skull (*Kawingasaurus* and *Kombuisia* are exceptions and lack a pineal foramen; Cox 1972; Hotton 1974). In the majority of the taxa included in this analysis the pineal foramen is flush with the dorsal surface of the skull or surrounded by a thin, slightly

raised rim. I have not distinguished between these morphologies in my coding of this character because they are very similar and the rim can be lost easily if the skull roof is weathered or damaged.

Endothiodon, *Chelydontops*, *Aulacephalodon*, and *Rhachiocephalus* all possess a prominent, rugose, bony boss around the pineal foramen. The bosses of *Chelydontops* and *Endothiodon* have a dome-shaped morphology, while that of *Rhachiocephalus* is more cylindrical. The pineal boss of *Aulacephalodon* appears to be an ontogenetically variable character, with large specimens tending to have much more pronounced bosses. The morphology of the boss in *Aulacephalodon* is generally intermediate between the more dome-shaped and cylindrical forms. A pineal boss is also present in the non-dicynodont anomodonts *Otsheria*, *Ulemica* and *Suminia*. However, in these taxa the boss has a slightly tapered, chimney-like morphology, with thin, smooth walls. I consider this morphology to be sufficiently distinct from the morphology of taxa such as *Rhachiocephalus* to warrant a separate character state. Although a pineal foramen is absent in *Kawingasaurus* and *Kombuisia*, I have omitted an "absent" character state because neither of these taxa were included in this analysis.

- 27) Anterior portion of palatine contacts the premaxilla (1) or does not contact the premaxilla (0).

All of the taxa included in this analysis possess an anterior portion of the palatine that contacts the maxilla on the ventral surface of the skull. In *Otsheria*, *Chelydontops*, *Pristerodon*, *Emydops*, *Cistecephalus*, *Myosaurus*, *Tropidostoma*, *Oudenodon*, *Aulacephalodon*, *Pelanomodon*, *Rhachiocephalus*, *Kannemeyeria*, and *Dicynodon* the palatine also contacts the posterior edge of the premaxilla. Although there is minor variation in the exact morphology and extent of the contact between the palatine and premaxilla, I have chosen not to subdivide the states of this character further because factors such as weathering or damage from preparation can easily alter the details of the contact (Keyser 1993).

- 28) Postcaniniform crest present (1) or absent (0).

Tropidostoma, *Rhachiocephalus*, *Oudenodon*, and *Pelanomodon* possess a postcaniniform crest. The crest has a sharp ventral edge, a smoothly-sloping lateral surface, bears teeth in *Tropidostoma*, and arises from the posteromedial side of the caniniform process. The degree of development of the crest varies slightly among taxa and among specimens within a given taxon, but this variation is not great enough to warrant different character states. The postcaniniform crest can be distinguished from the postcaniniform keel (Character 1) because the keel has a rounded ventral edge, a steep, wall-like lateral surface, and is formed from a continuation of the lateral palatal rim posterior to the caniniform process. I have coded taxa that lack a distinct caniniform process as "?" because this character is not directly applicable to them.

- 29) Stapedial foramen absent (1) or present (0).

The presence of a stapedial foramen characterizes several synapsid clades. *Patranomodon*, the most basal anomodont for which a stapes is known, lacks a stapedial foramen, although a dorsal process that contacts the paroccipital process is present (Rubidge & Hopson 1996). A stapes is not known in *Otsheria*, but the stapes of *Suminia* also lacks a foramen. Some specimens of *Eodicynodon* (e.g., NM QR2989, ROZ 9) possess a stapedial foramen that is completely or nearly completely enclosed, whereas other specimens (e.g., NM QR2912) lack a distinct stapedial foramen. Although the significance of this variation is not well understood, I have chosen to code *Eodicynodon* as possessing a stapedial foramen in this analysis (= the globally basal condition for Synapsida). A fully enclosed stapedial foramen is consistently present in *Cistecephalus* and *Kawingasaurus* (Cox 1972), although the latter taxon is not included in this analysis. All other taxa examined here lack a stapedial foramen.

- 30) Proximal articular surface of humerus a slightly convex area on proximal surface of bone without much expansion onto the dorsal surface (0), somewhat expanded with some encroachment onto the dorsal surface (1), or strongly developed and set off from rest of humerus by a weak neck (2).

A humerus is not preserved for *Patranomodon* or *Otsheria*. However, other non-dicynodont anomodonts (e.g., *Galepus*, *Suminia*) possess humeral heads that are a slightly raised, rounded swellings with the articular surface limited to the proximal end of the bone, establishing polarity for this character. *Eodicynodon*, *Robertia*, *Diictodon*, and *Pristerodon* also possess humeral heads of this morphology. The humeral heads of most of the other included taxa are present as sub-hemispherical swellings in which the articular surface has some encroachment on the dorsal surface of the humerus. The degree to which the head is developed is somewhat variable among these taxa (e.g., it is limited in *Oudenodon* but more distinct in *Kingoria*), but I have not divided this state up further because it also appears to be susceptible to alteration by postmortem weathering or damage as well as ontogenetic factors. *Cistecephalus* and *Kawingasaurus* possess strongly developed humeral heads that are set off from the shaft of the bone by a weak but distinct neck.

I coded *Chelydontops* and *Pelanomodon* as "?" because humeri that definitely can be attributed to these taxa are not known. At least one specimen of *Myosaurus* (BP/1/4269) includes partial humeri, but I also coded this taxon as "?" because the articular surfaces are currently imbedded in matrix and could not be examined.

- 31) Proximal articular surface of femur present as a weak swelling that is mostly limited to the proximal surface of the bone (0), present as a more rounded, hemispherical swelling that has some encroachment on the anterior surface of the femur (1), or present as a rounded, hemispherical to subspherical swelling that is set off from the proximal surface by a neck (2).

In non-dicynodont anomodonts, *Eodicynodon*, *Robertia*, *Diictodon*, *Pristerodon*, and *Endothiodon* the femoral head is present as a weak, rounded swelling of the anterior corner of the proximal surface of the bone (assuming that the femur is positioned in a "sprawling" orientation). The articular surface does not extend onto the anterior surface of bone, and it is not separated from the rest of the proximal surface by a distinct neck. The majority of the other taxa included in this analysis possess femoral heads that are rounded to subspherical, with articular surfaces that encroach upon the anterior surface of

the bone (again assuming a "sprawling" posture). The degree of development of the femoral head is variable in these taxa (e.g., the head in *Kingoria* is more spherical than in most other taxa), but none possess a distinct neck that separates the head from the dorsal surface of the femur. *Cistecephalus* is unique among the included taxa because a well-developed neck separates the head from the rest of the femur. The head is also highly spherical in this taxon. Although not included in this analysis, a femoral neck also has been reported in some Triassic dicynodonts (e.g., *Placerias*, Camp and Welles, 1956). Well-preserved femora that can definitely be assigned to the taxa coded "?" are not known.

- 32) Squamosal with a distinct dorsolateral notch in posterior view (1) or with a relatively straight contour (0).

The zygomatic and occipital portions of the squamosal of *Emydops*, *Cistecephalus*, *Myosaurus*, *Otsheria*, and *Patranomodon* meet at roughly a right angle, giving the lateral margins of the skull a relatively straight contour in posterior view. In the other taxa included in this analysis, the lateral edge of the occipital portion of the squamosal ventral to the zygomatic portion bows laterally before curving medially to meet the zygomatic portion. This lateral convexity gives the lateral margin of the skull a distinctly notched appearance just below the zygomatic branch of the squamosal in posterior view. Although these character states are unmistakable in well-preserved specimens, they are easily altered if a specimen has undergone plastic deformation. Dorsoventral crushing tends to make unnotched taxa appear as if a notch was present, whereas lateral compression can make notched specimens appear to have a much straighter contour.

- 33) Interpterygoid vacuity relatively short and does not reach the level of the palatal exposure of the palatines (0), relatively long but does not reach the level of the palatal exposure of the palatines (1), long and reaches the level of the palatal exposure of the palatines (2), or absent (3).

In non-dicynodont anomodonts, the interpterygoid vacuity is relatively short compared to the length of the skull, completely enclosed by the pterygoids, and does not extend forward to the level of the portions of the palatines that contact the maxillae. The interpterygoid vacuities of *Dicynodon*, *Lystrosaurus*, and *Kannemeyeria* also are relatively short and do not reach the level of the portions of the palatines that meet the maxillae (and premaxillae in some taxa). However, in these taxa the anterior margin of the vacuity is formed by the vomers. I have not distinguished between these morphologies in coding this character because I am only concerned with the relative length of the vacuity, not the bones that contribute to its formation.

In *Eodicynodon*, *Robertia*, *Diictodon*, *Chelydontops*, *Pristerodon*, *Emydops*, *Kingoria*, *Rhachiocephalus*, and *Aulacephalodon* the interpterygoid vacuity is relatively long compared to the length of the skull but does not reach the level of the anterior portions of the palatines that contact the maxillae and premaxillae. *Tropidostoma*, *Oudenodon*, and *Pelanomodon* also possess relatively long interpterygoid vacuities, but in these taxa the vacuity does reach the level of the anterior portions of the palatines that contact the maxillae and premaxillae. In both groups of taxa the vomers form the anterior margin of the vacuity. *Cistecephalus* is unique among the included taxa in lacking an interpterygoid vacuity.

The majority of the specimens referable to *Endothiodon* that I have had the opportunity to examine do not preserve this area well. Of these specimens, BP/1/1659 possess the best interpterygoid vacuity, which appears likely to have been relatively short and not to have reached the level of the anterior portion of the palatines. However, because of the poor preservation of the feature in this specimen and my inability to confirm or disconfirm the observation in other specimens, I have chosen to code *Endothiodon* as "?". I coded *Myosaurus* as "?" because the co-type specimens (SAM 3525 and SAM 3526a) conflict in regard to this character. In SAM 3526a, which is slightly better preserved, the vacuity is long, but does not reach the anterior portion of the palatines. In SAM 3526 the vacuity is long and does appear to reach the anterior portion of the palatines. The other specimens of *Myosaurus* that I have had the opportunity to examine do not preserve the feature well enough to allow confident resolution of the conflict.

- 34) Anterior portion of squamosal contacts maxilla (1) or does not contact maxilla (0).

In *Patranomodon*, *Otsheria*, *Eodicynodon*, *Endothiodon*, *Kingoria*, and *Myosaurus* the zygomatic branch of the squamosal is separated from the maxilla by the jugal. In all other taxa included in this analysis, the anterior end of the zygomatic branch of the squamosal contacts the maxilla. I have coded *Chelydontops* as "?" because neither the holotype (SAM 11558) or referred specimen (SAM 12259) preserve the zygomatic branch of the squamosal.

- 35) Lateral palatal foramen present at level of the anterior, expanded palatal exposure of the palatines (1), present posterior and dorsal to the level of the anterior, expanded palatal exposure of the palatines (2), or absent (0).

Most of the taxa included in this analysis possess a small foramen located between the palatine and the anterior pterygoid ramus. The exact size and shape of this foramen varies, but in most cases it is at the same level as the expanded, anterior portion of the palatine that meets the maxilla (and premaxilla in some taxa). Many specimens of *Emydops* do not show good evidence of this foramen, but it is present in some specimens (e.g., SAM K1671, SAM K6623). The foramen tends to be very small in these individuals, suggesting that it would easily be lost if even minor lateral compression of the skull occurred.

A lateral palatal foramen, bounded by the palatine and the anterior pterygoid ramus, is also present in *Pristerodon* and *Endothiodon*, although its location is notably different. In these taxa, the foramen is located posterior and somewhat dorsal to the expanded, anterior portion of the palatine so that it is more a part of the dorsolateral wall of the choana than the palatal surface of the skull.

The non-dicynodont anomodonts *Ulemica* and *Otsheria* do not possess a lateral palatal foramen, but the foramen is present in *Suminia* (Rybczynski 2000). A small foramen bounded by the pterygoid and palatine is present on the right side of the skull in the holotype of *Patranomodon* (NM QR3000). Although this foramen is a potential positional homologue of the lateral palatal fenestra, I have not coded it as such because a corresponding foramen is not present on the left side of the skull.

Because the holotype is the only known specimen of *Patranomodon*, it is difficult to determine whether the foramen is a real feature or the result of postmortem damage, individual variation, or pathology. If additional specimens of *Patranomodon* that also possess this foramen are discovered, a reassessment of the homologies of the lateral palatal foramen may be necessary.

36) Three (0), four (1), five (2) or six (3) sacral vertebrae present.

The number of sacral vertebrae is most accurately counted in specimens in which the sacrum and pelvis are articulated. However, counts can also be made in disarticulated specimens by observing the number of vertebrae that possess expanded sacral ribs or the number of facets for sacral vertebrae on the medial side of the ilium. The latter methods can be less accurate because the last sacral vertebra sometimes has relatively small ribs, and the facets often have a complex morphology that makes them difficult to count (DeFauw 1986).

Three sacral vertebrae are present in *Patranomodon*, *Eodicynodon*, *Robertia*, and *Cistecephalus*. Four are present in *Diictodon*, *Endothiodon*, and *Kingoria*. Most of the other taxa included in this analysis possess five sacral vertebrae, but six are present in *Lystrosaurus* and *Kannemeyeria*. I have coded *Otsheria*, *Chelydontops*, *Emydops*, *Tropidostoma*, *Myosaurus*, and *Pelanomodon* as “?” because sacra that can definitely be referred to these taxa are not known.

37) Transverse flange of the anterior pterygoid process well-developed (0) or reduced (1).

The transverse flange of the anterior pterygoid process is large and laterally directed in non-dicynodont anomodonts, although it is unusual among therapsids in not descending below the level of the palate (Rubidge and Hopson 1996). A well-developed transverse flange of the pterygoid is also present in *Eodicynodon* as well as several undescribed specimens collected in the lower *Tapinocephalus* Assemblage Zone (Rubidge, personal communication, 2000). However, in these forms the flange is ventrally directed. I have not distinguished between these morphologies in coding this character because I am concerned only with the relative size of the flange. Modesto *et al.* (1999) and Rybczynski (2000) subdivided this state, but their analyses included additional non-dicynodont anomodonts as well as several non-anomodont outgroups. Similar subdivision of this state also may be desirable in future analyses that include a greater number of lower *Tapinocephalus* Assemblage Zone dicynodonts.

The transverse flange of the pterygoid is ventrally directed and highly reduced in all other taxa included in this analysis. Some taxa possess small, plate-like extensions (e.g., *Kingoria*) or keels (e.g., *Diictodon*) on the ventral surface of the anterior pterygoid ramus, but these features are of notably different morphologies and never as large as the flange in *Eodicynodon*.

38) Ectepicondylar foramen on humerus present (1) or absent (0).

The presence of an ectepicondylar foramen characterizes several clades of synapsids, and the reconstruction of the ancestral character states for Anomodontia on many recent cladograms (e.g., Sidor and Hopson 1998) suggests that the foramen was present in the common ancestor of all anomodonts. Humeri are not known for *Anomocephalus*, *Patranomodon*, *Otsheria*, or *Ulemica*, but an ectepicondylar foramen has been reported in *Galepus* and *Galechirus* (Brinkman 1981). The foramen is absent in *Galeops* and *Suminia* (Brinkman 1981; personal observation). If *Galepus* and *Galechirus* represent a grade of anomodont evolution more basal than either *Galeops* or the venyukovioids (*sensu* Modesto *et al.*, 1999; Rybczynski 2000), then it is likely the phylogenetic inference is correct and the presence of an ectepicondylar foramen is the basal state for anomodonts. However, because *Galepus* and *Galechirus* have not been included in any of the recent cladistic analyses of anomodonts, this hypothesis has yet to be rigorously tested. The discovery of humeri referable to a greater number of basal anomodonts also will help to resolve this issue.

King (1981b) noted the presence of a probable ectepicondylar foramen in *Robertia*, and DeFauw (1986) hypothesized that the foramen was likely present in *Kingoria* based on her examination of a damaged specimen. I have been able to confirm King's (1981b) observation regarding the foramen in *Robertia* (e.g., SAM 11885). In addition, I also have observed an ectepicondylar foramen in *Diictodon* (e.g., SAMK1633, UCMPV3691/42053), *Emydops* (e.g., SAMK10009), and *Cistecephalus* (e.g., BP/1/696, BP/1/2915), indicating that this feature is more widely distributed among dicynodonts than previously recognized. All other taxa included in this analysis lack an ectepicondylar foramen. Well-preserved humeri that can definitely be attributed to the taxa coded “?” are not known. I have included *Kingoria* in this group because the only report of an ectepicondylar foramen in that taxon is based on a specimen that is damaged in the region of the foramen (DeFauw 1986).

39) Cleithrum present (1) or absent (0).

The pectoral girdles of most non-dicynodont anomodonts are very poorly known, making the polarity of this character difficult to establish for Anomodontia. Cleithra appear to be absent in *Galeops* and *Suminia* (Brinkman 1981; personal observation), but the pectoral girdles of other basal anomodonts are either unknown or too poorly preserved to be informative. Reconstruction of the ancestral state for this character based on recent cladograms of Synapsida suggests a cleithrum was present in the common ancestor of all anomodonts.

Cleithra have been reported in several dicynodont taxa, including *Oudenodon*, *Kannemeyeria*, and *Rhachiocephalus*, but most of these accounts are incorrect (DeFauw 1986; personal observation). Cluver (1978) and DeFauw (1986) noted that a cleithrum was present in *Cistecephalus* and *Diictodon* respectively, and I have been able to confirm these observations. There is also strong evidence of a cleithrum in *Robertia* (SAM 11885, cast 3 of King 1981b). A cleithrum is likely present in *Kawingasaurus* (Cox, 1972), although this taxon is not included in this analysis. All other taxa examined here for which pectoral girdles are known do not possess a cleithrum. Well preserved pectoral girdles that can definitely be attributed to taxa coded “?” are not known.

- 40) Transverse ridge across snout at level of prefrontals present (1) or absent (0).

Several dicynodont taxa (e.g., *Rhachiocephalus*, *Oudenodon*, *Aulacephalodon*) possess prefrontal bosses of some type. In the majority of these taxa, the dorsal surface of the snout between these bosses is relatively smooth and flat. *Aulacephalodon* and *Pelanomodon* possess a low, rounded, transverse ridge that connects the prefrontal bosses on the dorsal surface of the snout. Some species of *Lystrosaurus* (e.g., *L. declivis*, *L. murrayi*) also possess a transverse ridge in a similar position on the skull (the frontonasal ridge of Cluver 1971), but the pronounced downturning of the snout in that taxon gives it a slightly different appearance. I have given *Lystrosaurus* the same coding as *Aulacephalodon* and *Pelanomodon* because the ridge is present in nearly the same location (i.e., between the prefrontals, near the nasal-frontal suture), making a strong positional argument for homology. In all other taxa included in this analysis the surface of the snout lacks a distinct transverse ridge between the prefrontals.

Stratigraphic character

- 41) First occurrence in *Eodicynodon* Assemblage Zone (0), *Tapinocephalus* Assemblage Zone (1), *Pristerognathus* Assemblage Zone (2), *Tropidostoma* Assemblage Zone (3), *Cistecephalus* Assemblage Zone (4), *Dicynodon* Assemblage Zone (5), *Lystrosaurus* Assemblage Zone (6), or *Cynognathus* Assemblage Zone (7).

The stratigraphic data used to code this character are based on those presented in King (1988) and Rubidge (1995a). Most of the data were taken directly from these sources, but my treatment of three taxa that are known from very limited material necessitates some explanation.

Otsheria is represented by a single specimen from the Ocher Subassemblage of the Dinocephalian Fauna of Golubev (2000). This fauna is likely of Late Kazanian to Early Tartarian age (Golubev 2000). Rubidge (1995b) suggests a Kazanian age for the *Eodicynodon* Assemblage Zone of South Africa, and Smith and Keyser (1995) propose an early Tartarian age for the *Tapinocephalus* Assemblage Zone. The Upper Permian strata of Russia are not well correlated with those of South Africa, and I have chosen to include *Otsheria* as a point occurrence in the upper *Eodicynodon* Assemblage Zone. However, this should be regarded as an approximation, and including *Otsheria* in the *Tapinocephalus* Assemblage Zone does not significantly alter the results of the stratigraphic analysis.

Patranomodon is also represented by a single specimen, but this was collected in the *Eodicynodon* Assemblage Zone of South Africa, eliminating correlation problems. Because only one specimen exists, the range of *Patranomodon* is not well constrained at this time and I have chosen to represent it as a point occurrence in Figure 2.

Chelydontops is known from two specimens. The holotype was collected on the farm Die Cypher, near Beaufort West South Africa (Cluver 1975). Kitching (1977) places this locality in the lower *Tapinocephalus* Assemblage Zone. The second specimen was discovered on the farm Beukesplaas, near Fraserburg, which is close to the *Tapinocephalus*/*Pristerognathus* Assemblage Zone boundary in Figure 1 of Rubidge *et al.* (1995). *Chelydontops* is not included among the taxa for which ranges are given in Smith and Keyser (1995), and the lack of material suggests its range may not be well constrained. I have chosen to represent it as having a short range in the middle of the *Tapinocephalus* Zone, but it may be possible to extend its range to encompass most of the zone. Such a range extension does not have a significant effect on the stratigraphic analysis other than necessitating a shorter ghost range for *Endothiodon*.

APPENDIX 2

Data matrix showing codings for characters and taxa used in this analysis.

Patranomodon and *Otsheria* are outgroups.

<i>Patranomodon</i>	?000000?0	000?000000	0000000?1?	0000000??0	0
<i>Otsheria</i>	?0000000??	11?????00	0000?21???	?0000?0??0	0
<i>Eodicynodon</i>	0200010100	0000103300	1110000000	0110100000	0
<i>Robertia</i>	0211021101	1000201100	1110000010	0111101110	1
<i>Diictodon</i>	0213?21102	1110201101	1110000010	0111111110	1
<i>Endothiodon</i>	?112100221	100?012204	1220010?10	01?0211000	2
<i>Chelydontops</i>	0211110121	1100111100	122001001?	?11?1?1??0	1
<i>Pristerodon</i>	0211011121	1000113100	1210001010	0111221000	1
<i>Emydops</i>	1211010111	1111013300	1210001010	?0111?11?0	3
<i>Kingoria</i>	1213?102?2	1101003301	1?10000011	1110111?00	4
<i>Cistecephalus</i>	1213?10212	1111013300	1211101002	2031101110	3
<i>Myosaurus</i>	1213?10212	1111003300	100110101?	?0?01?1?0	6
<i>Tropidostoma</i>	0211012221	1100311101	1320001111	11211?1000	3
<i>Oudenodon</i>	0213?12222	1110311101	1320001111	1121121000	4
<i>Rhachiocephalus</i>	0213?12222	1110311103	1320011111	1111121000	3
<i>Pelanomodon</i>	0213?1022?	1110????12	13200011??	?1211?1?1	5
<i>Aulacephalodon</i>	0213?12222	1100311112	1320011011	1111121001	4
<i>Dicynodon</i>	0213?12222	1110311113	1420001011	1101121000	4
<i>Lystrosaurus</i>	0213?12222	1110311410	1420000011	1101131001	6
<i>Kannemeyeria</i>	0213?12222	1110311414	1430001011	1101131000	7

APPENDIX 3

Reference Specimens

<i>Patranomodon</i> :	NM QR3000
<i>Otsheria</i> :	PIN 1758/5
<i>Eodicynodon</i> :	NM QR2902, NM QR2904, NM QR2905, NM QR2906, NM QR2909, NM QR2911, NM QR2912, NM QR2978, NM QR2989, NM QR2990, NM QR2991, NM QR 3002, NM QR3007, NM QR3014, NM QR3153, NM QR3154, NM QR3155, NM QR3157, NM QR3158, ROZ 1, ROZ 9, ROZ 11, SAM 11879
<i>Robertia</i> :	SAM 11461, SAM 11761, SAM 11885, SAM K7807
<i>Diictodon</i> :	AMNH 5532, AMNH 5533, AMNH 5609, GSP STH36, GSP T72, SAM 1242, SAM 10086, SAM K1633, SAM K5105, SAM K7725, TM 253, UCMP V3504/32131, UCMP V3504/32125, UCMP V3504/42837, UCMP V3691/41791, UCMP V3691/42053, V3691/42057, UCMP V3694/42396
<i>Endothiodon</i> :	AMNH 5562, AMNH 5565, AMNH 5570, AMNH, 5572, AMNH 5573, AMNH 5574, AMNH 5603, BP/1/1659, BP/1/5743, BP/1/5744, BP/1/5747, BP/1/5748, BP/1/5751, BP/1/5754, BP/1/5756, SAM 629, SAM 2676, SAM K7252
<i>Chelydontops</i> :	SAM 11558, SAM 12259
<i>Pristerodon</i> :	AM 2825, AMNH 5507, BP/1/241, BP/1/2642, GSP FL102, GSP M336, GSP WB106, SAM 10141, SAM 10161, SAM K1658, TM 313, UCMP V3694/42396
<i>Emydops</i> :	AMNH 8209, BP/1/262, BP/1/2366, GSP M1000, SAM 3721, SAM 10153, SAM 10172, SAM 10009, SAM 11060, SAM K1671, SAM K5974, SAM K6623, SAM K10009, TM 242
<i>Kingoria</i> :	BP/1/1562, BP/1/3858, NM QR479, SAM 3723, SAM 6043, SAM 10666, SAM K1260a, SAM K8620, SAM K8069
<i>Cistecephalus</i> :	BP/1/696, BP/1/2915, BP/1/31, BP/1/506, BP/1/1696, BP/1/2450, BP/1/2915, BP/1/4086, GSP RMS410, SAM 10664, SAM 10665, SAM K6814
<i>Myosaurus</i> :	BP/1/2690, BP/1/2701b, BP/1/4269, SAM 3526, SAM 3526a
<i>Tropidostoma</i> :	BMNH R860, BMNH R866, BMNH R868, GSP RMS183, GSP RMS631, GSP RS327, SAM K8633, SAM K9960, TM 249, TM 250, TM 383, TM 384, TM 385
<i>Oudenodon</i> :	AM 4545, AMNH 5300, AMNH 5313, AMNH 5635, BP/1/749, BP/1/788, GSP M208, GSP M845, GSP MIF133, SAM 6045, SAM 10066, SAM 11114, SAM K5227, SAM K7688
<i>Rhachiocephalus</i> :	BP/1/1512, BP/1/2548a, BP/1/2889, GSP C82, GSP RS240, SAM K1393
<i>Pelanomodon</i> :	GSP AF9183
<i>Aulacephalodon</i> :	AMNH 5562, BP/1/304, BP/1/634, BP/1/766, BP/1/2460, GSP CBT53, GSP MJF129, NM QR1478, SAM 8789, SAM K6404, SAM K7158
<i>Dicynodon</i> :	BP/1/2188, BP/1/2784, BP/1/5287, GSP AF9683, SAM K1191, SAM K7011, SAM K7591, SAM K7806, UCMP V36102/33431
<i>Lystrosaurus</i> :	AM 404, AM 2731, AM 4040, AM 5009, NM C150, NM C 299, NM C6547, SAM K1469, TM 37, TM 4050, SAM 4523, UCMP V65341/31363, UCMP V76019/42870
<i>Kannemeyeria</i> :	AM 5008, BP/1/1168, BP/1/2902, BP/1/3638, BP/1/4523, BP/1/4524, BP/1/5624, BP/1/4550, NM QR1127, SAM 10555, UCMP V36113/38373, UCMP V47047/42916

CRANIAL DESCRIPTION AND TAXONOMIC RE-EVALUATION OF *KANNEMEYERIA ARGENTINENSIS* (THERAPSIDA: DICYNODONTIA)

by

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ABSTRACT

Examination of the holotype skull of the Triassic dicynodont *Kannemeyeria argentinensis* Bonaparte reveals that many of its purported diagnostic characters are distortion-related. A redescription of the holotype indicates that its inclusion in the genus *Kannemeyeria* cannot be supported. Several characters are, however, identical to the Argentine taxon *Vinceria*, and we suggest that the two taxa may be congeneric. This finding challenges the validity of a global *Kannemeyeria*-biochron, but not necessarily the relationship of tetrapod faunal groups in South America and Africa.

KEYWORDS: Triassic, dicynodont, Argentina, *Kannemeyeria*, *Vinceria*

INTRODUCTION

From 1964 to 1967 the Triassic-aged basins of Argentina yielded a number of important tetrapod fossils (Bonaparte 1967a,b). These discoveries prompted researchers, especially Cox (1965), Romer (1966) and Bonaparte (1967b), to propose a tetrapod faunal complex based on the recognition of several Argentine Triassic 'reptile faunal groups'. The identification of a new species of the African dicynodont *Kannemeyeria* Weithofer (1888) lay at the centre of the interpretation and supposed faunal succession, and established a kannemeyeriid fauna in South America. Bonaparte (1966) described the new taxon as *Kannemeyeria argentinensis*, based on a skull and some postcranial remains from the upper levels of the Puesto Viejo Formation of Argentina.

Bonaparte (1966, 1967b) argued for the inclusion of specimen PVL3465 (Figure 1 & 2) within *Kannemeyeria* based largely on its affinity to the then recognised species *Kannemeyeria erithrea* Houghton 1915 (= *Kannemeyeria simocephalus*, Broom 1937; Renaut 2000). Characters used to support this referral were the narrow, pointed snout, the high parietal crest, and the sunken pineal foramen. Bonaparte (1966) saw little to differentiate this specimen from *Kannemeyeria*; the few differences, including the more bowed-out zygomatic arches, more ventral development of the caniniform, and minor sutural differences, were considered to be species-level apomorphies. Keyser & Cruickshank (1979) referred to the synonymy between *Kannemeyeria erithrea* and *Kannemeyeria simocephalus*, and speculated that PVL3465 may be a juvenile specimen of *Kannemeyeria simocephalus*. Lucas & Wild (1995) adopted a similar approach, but

assumed *Kannemeyeria argentinensis* to be conspecific with *Kannemeyeria cristarhynchus* Keyser & Cruickshank (1979).

Regardless of its specific designation, this specimen has been used to establish the presence of *Kannemeyeria* in South America. This, in turn, was used to propose a global *Kannemeyeria*-biochron (Lucas & Wild 1995), which has become crucial to understanding kannemeyeriid (and Triassic dicynodont) biogeography and adaptive radiations. None of these taxonomic investigations have involved a formal comparative study of the relevant taxa or morphotypes. Consequently, the following description examines and compares these taxa in detail, and is based on first hand observations of the original material of all relevant taxa. The holotype specimen of *Kannemeyeria argentinensis* has been severely bilaterally compressed, and some elements of the description are therefore based on two referred specimens, MACN18.871 and PVL3471 (Bonaparte 1971), which quantitatively and qualitatively agree on crucial aspects with specimen PVL3465.

Materials

Our description of *Kannemeyeria argentinensis* is based primarily on the skull and lower jaw of the holotype, PVL3465, from the upper levels of the Puesto Viejo Formation, Las Malvinas, San Rafael, Mendoza Province, Argentina (Bonaparte 1966). Both the skull and lower jaw have experienced considerable lateral compression. The right side of the skull has been damaged and is currently embedded in plaster. The bilateral compression of the skull during preservation has abnormally narrowed the snout and interorbital

region. The compacted median elements of the occiput, and the narrow foramen magnum and occipital condyle, indicate that the occiput has been unnaturally elevated. The parietal flange of the squamosal has an extreme vertical orientation, the sphenethmoid region has been flattened, and the tusks have been forced closer together. The lower jaw rami have been completely compressed to form thin plates. Much of the dentary symphysis is missing, and the articular condyle is damaged.

Both referred specimens (MACN18.871 and PVL3471) were recovered from the same locality as the

holotype. Although Bonaparte (1971) recognised that these specimens agree closely with the general and detailed morphology of the holotype, they have never been described. To examine this taxon properly it was necessary to compare it with other dicynodonts of similar size, morphology and age, such as the genotype of the Triassic taxon *Vinceria* Bonaparte (PVL3831), and a specimen of a southern African shansiodont (BP/1/5532, Hancox 1998) housed at the Bernard Price Institute. Included in the comparative sample was a lower jaw of *Aulacephalodon* (BP/1/766) and referred specimens of *Kannemeyeria*, including BP/1/4532, a

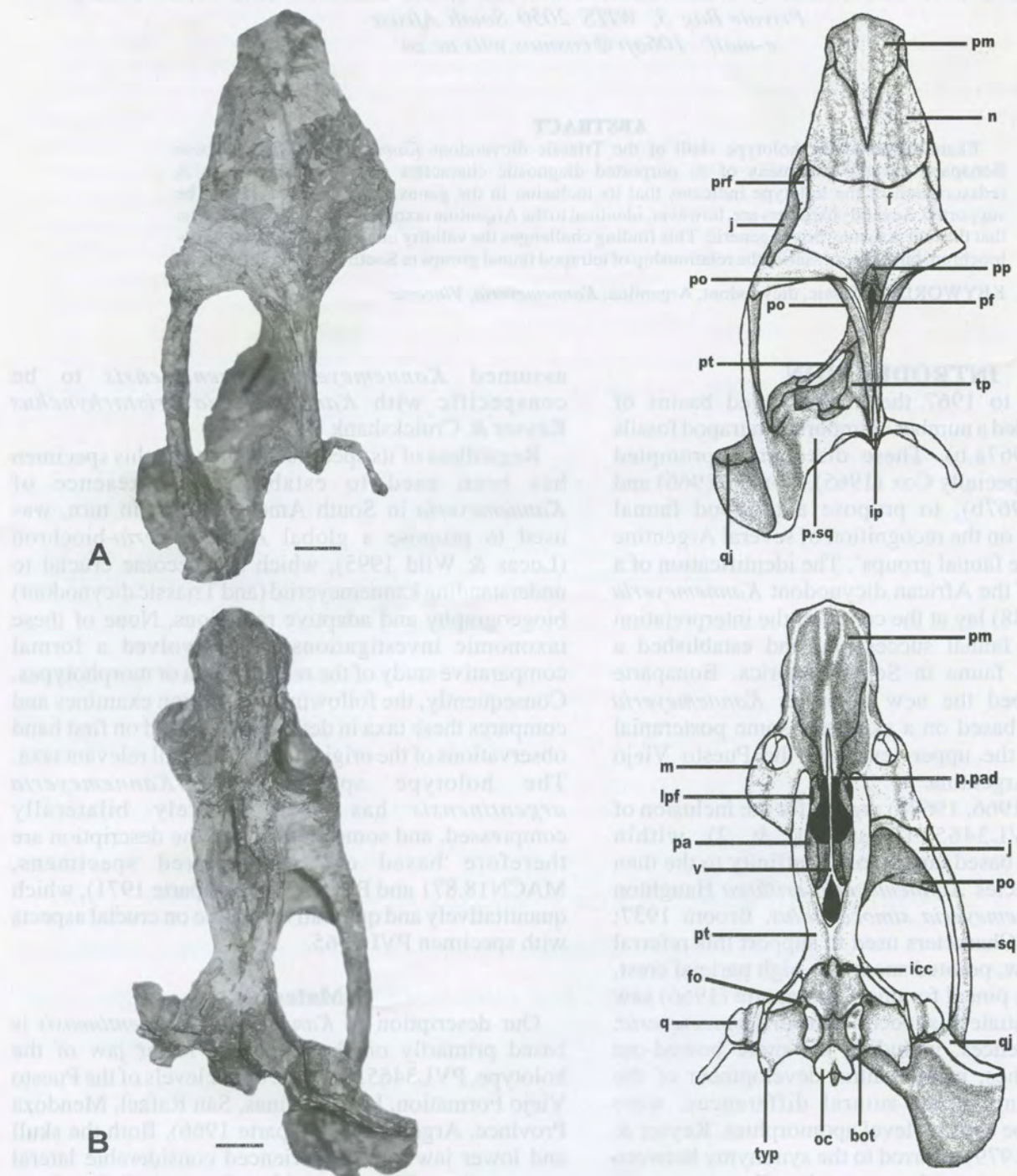


Figure 1. Photographs and partially reconstructed drawings of the dorsal, A, and ventral, B, views of the skull of specimen PVL3465 (*'Kannemeyeria argentinensis'*). Scale bar represents 25mm. (See p.90 for abbreviations)

sub-adult specimen BP/1/2992, and the sub-adult specimen SAMPK3017 (ex-holotype of *Kannemeyeria* "erithrea" Haughton 1915).

DESCRIPTION

General description

Specimen PVL3465 (Figure 1, 2) is a small to medium Triassic dicynodont, similar in size to the referred specimen of *Kannemeyeria argentinensis* (PVL3471) and the holotype specimen of the Triassic genus *Vinceria* (PVL3831), but the various bone elements are slender and not as robust as in the other specimens. PVL3465 is without doubt an adult individual because it shows none of the characteristic features of sub-adult dicynodonts determined by Cruickshank (1965). Adult features of this skull include well ossified sutures with extensive overlapping of the various bones, large well-developed tusks with considerable wear, and extensive ossification of the braincase and sphenethmoid region. The extremely large orbits of this taxon may give the

impression that this is a juvenile specimen. Taken in isolation, this feature is insufficient to establish a sub-adult condition, and such huge orbits relative to the adult skull are characteristic of some shansiodonts (Cox & Li 1983; Keyser & Cruickshank 1979; King 1988) including *Shansiodon* (Yeh 1959) and *Vinceria* (PVL3831).

The skull (Figure 1) appears elongated because it is abnormally narrow, and the total skull length exceeds the total width over the squamosals. Although the pre-orbital length is considerably less than the post-orbital length, the relative pre-caniniform distance is markedly greater than in *Kannemeyeria* specimens. PVL3465 superficially resembles *Kannemeyeria* in dorsal view by the long and thin parietal crest, the narrow skull, the posteriorly and laterally flared squamosal wings, and slight lateral projection of the maxilla and caniniform process away from the snout. The entire snout region is extremely narrow, and ends in a pointed tip. In lateral view (Figure 2) the specimen has a greater resemblance

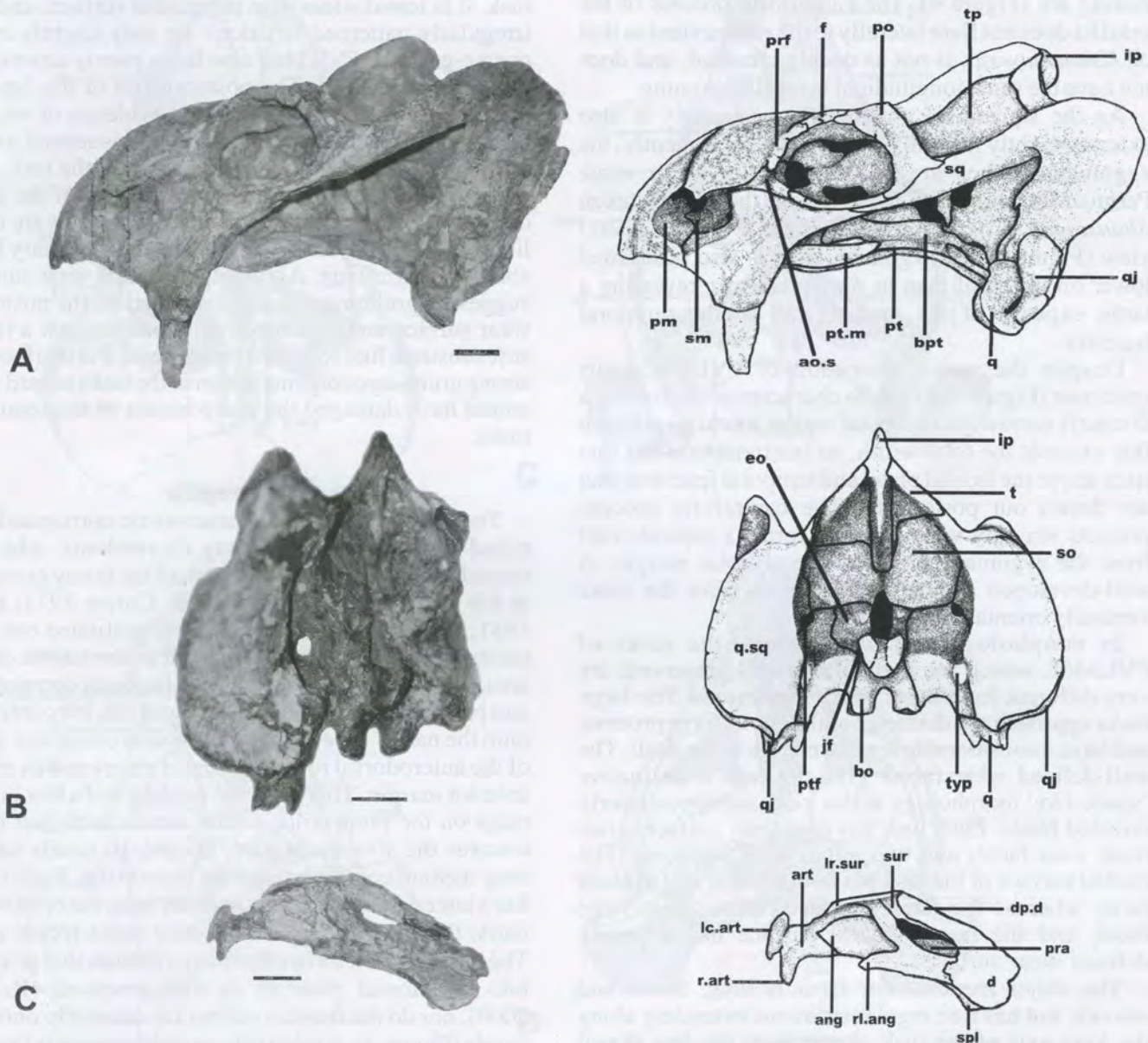


Figure 2. Photographs and partially reconstructed drawings of the left lateral, A, and occipital, B, views of the skull, and the right lateral, C, view of the lower jaw of specimen PVL3465 (*"Kannemeyeria argentinensis"*). Scale bar represents 25mm. (See p.90 for abbreviations)

to *Kannemeyeria* because the dorsally projecting parietal crest forms a sharp angle with the frontal plate. Both views exhibit a marked median dorsal ridge on the snout, which seems to extend onto the frontal plate as well.

The extreme bilateral compression of this specimen is probably responsible for much of the slender appearance of the skull, including the 'pointed snout'. On close inspection of the dorsal skull roof it is clear that the medial edges of these bones have been forced against each other, and were raised above the rest of the skull surface. Consequently, the apparent median ridge differs in appearance from the genuine feature in *Kannemeyeria*, confirming that it is the result of compressive distortion.

The large nasal recess dominates the pre-orbital region, and is far larger, relative to the skull, than in *Kannemeyeria* specimens. In front of the recess the anterior alveolar edge is relatively longer than in *Kannemeyeria*, and describes a shallow anteroventral cutting arc (Figure 4). The caniniform process of the maxilla does not flare laterally to the same extent as that of *Kannemeyeria*, is not as deeply crenated, and does not have the same longitudinal ventral thickening.

As the squamosal projects far posteriorly it also extends slightly medially (Figure 3). Consequently, the zygomatic arches are bowed laterally as in some Permian dicynodonts (King 1988) and the Triassic taxon *Shansiodon* (Cox & Li 1983; King 1988). In lateral view (Figure 4) the zygomatic arch is also positioned lower on the skull than in *Kannemeyeria*, revealing a large expanse of the medial wall of the temporal fenestra.

Despite the severe distortion of PVL3465, this specimen (Figure 3, 4) can be characterised as having a distinctly narrow intertemporal region, a total skull length that exceeds the total width, an intertemporal bar that rises above the frontal plate, and temporal fenestrae that are drawn out posteriorly. The caniniform process projects strongly ventrally, and forms a separate unit from the zygomatic arch and the alveolar margin. A well-developed canine tusk emerges from the more vertically orientated caniniform.

In morphology and wear facets, the tusks of PVL3465, which are particularly well preserved, are very different from those of *Kannemeyeria*. The large tusks approach the diameter of the caniniform process, and have a considerable length relative to the skull. The well-defined wear facets give the tusk a distinctive 'spade-like' morphology with a long, anteroposteriorly directed blade. Each tusk has four wear surfaces (two main wear facets and two minor wear surfaces). The medial surface of the tusk has both a major and a minor facet, whereas the lateral surface has a single large facet, and the posterolateral surface has a poorly defined wear surface.

The major medial wear facet is long, broad and smooth, but has fine regular striations extending along the long axis of the tusk. Apart from the low dorsal margin of the facet, level with the outer rim of the caniniform process, all other edges are sharp and well

defined. This wear facet undoubtedly marks the shearing of the horn-covered dentary symphysis against the tusk during depression and elevation of the lower jaw. A minor wear facet occurs about halfway down the large medial facet. This elongate almost triangular minor wear surface occurs along the anterior edge of the large facet, and at a slightly oblique angle to the main surface. Although the minor wear surface has a blunt posterior margin, its anterior rim has been double-honed to a very sharp edge. The fine diagonal striations on this smooth surface extend posteroventrally from the outer rim. This anteromedial wear facet probably resulted from the passage of the lateral margin of the horn-covered dentary symphysis during the 'jaw-mill' cycles of the second phase of mastication (Crompton & Hotton 1967; Renaut 2000).

On the outer surface of the tusk, the second large wear facet occurs lateral and slightly anterior to the inner wear facet. Although not as long as the medial facet, this equally broad wear surface has its dorsal margin about two-thirds down the exposed length of the tusk. It is less distinct than the medial surface, and the irregularly patterned striations are only slightly more coarse-grained. PVL3465 also has a poorly developed posterior wear facet. The posterior rim of the 'spade-like' tusk is slightly indented, and evidence of wear is observed just above this indentation. This second minor wear surface occurs quite far dorsally on the tusk, and may indicate a backward and upward pull of the head during food acquisition. Both outer wear facets are most likely related to the substrate in which the primary food source was growing. Although the lateral wear surface suggests a grubbing and digging function, the posterior wear surface and fine outer striations suggest a fairly soft substrate like soft mud or wet sand. Furthermore, a strong grubbing or digging action of the tusks in hard soils would have damaged the sharp blades of the spatulate tusks.

Snout region

The snout exhibits the characteristic corrugated and pitted surface texture of many dicynodonts, which is considered to represent the extent of the horny covering in life (Crompton & Hotton 1967; Cluver 1971; King 1981; 1988). This surface texture is continued onto the palatal surface of the snout as well as the lateral cheek area, largely occupied by the maxilla. Such corrugation and pitting is not limited to the premaxilla, but continues onto the nasals. The narrow premaxilla comprises most of the anterodorsal roof of the nasal recess and its entire anterior margin. There is some evidence of a low lateral ridge on the premaxilla, which curves with that bone towards the alveolar border. The robust nasals have a long median contact behind the premaxilla. Each nasal has a lateral thickening that extends from the orbit to the naris, thereby forming a thickened nasal recess roof. The nasals do not form a median extension that projects into the frontal plate as in *Kannemeyeria* (Renaut 2000), nor do the frontals extend far anteriorly onto the nasals (Figure 3). A relatively straight contact is formed between the frontal and nasal bones, extending anterolaterally.

The maxilla forms a well-defined ledge along the ventral border of the wide nasal recess. Immediately above that ledge, a large vertically orientated septomaxilla fills the entire area of the recess. At the posterodorsal corner of the nasal recess the septomaxilla contacts a narrow anterior splint of lacrimal. Although the wedge-shaped lacrimal is quite small, it extends far anteriorly and separates the nasal and maxilla. The lacrimal forms the dorsal end of the ventral orbital ridge, and much of the floor of a well-developed antorbital sulcus (Figure 4). The slender forward projecting lacrimal and the antorbital sulcus are similar to *Vinceria andina* (holotype PVL3831) and the South African shansiodont taxon represented by BP/1/5532.

Although the caniniform process is not well developed, the maxilla has a broad ventral surface. Several low irregular ridges, and scattered pits and foramina, occur on the wide lateral cheek-plate of the

maxilla. This is unlike the small uniform surface of the cheek-plate in *Kannemeyeria* and more reminiscent of shansiodont specimens (such as BP/1/5532). From its broad ventral surface the maxilla sends a thick posterior extension onto the suborbital bar between the jugal and squamosal. The posterior projection of the maxilla does not intervene between the squamosal and jugal, and thus does not form the characteristic *Kannemeyeria*-type of interdigitation (Figure 4) of these elements in the suborbital bar (Renaut 2000).

Anterior palate

The secondary palate (Figure 3) is trough-shaped with high sidewalls, and has approximately the same length as the pterygoid girder. As in *Kannemeyeria* most of the anterior palate is composed of a thin sheet of premaxilla overlapping the maxilla, with a thick and well-developed median ridge. The posterior median palatal ridge is largely composed of the fused vomers

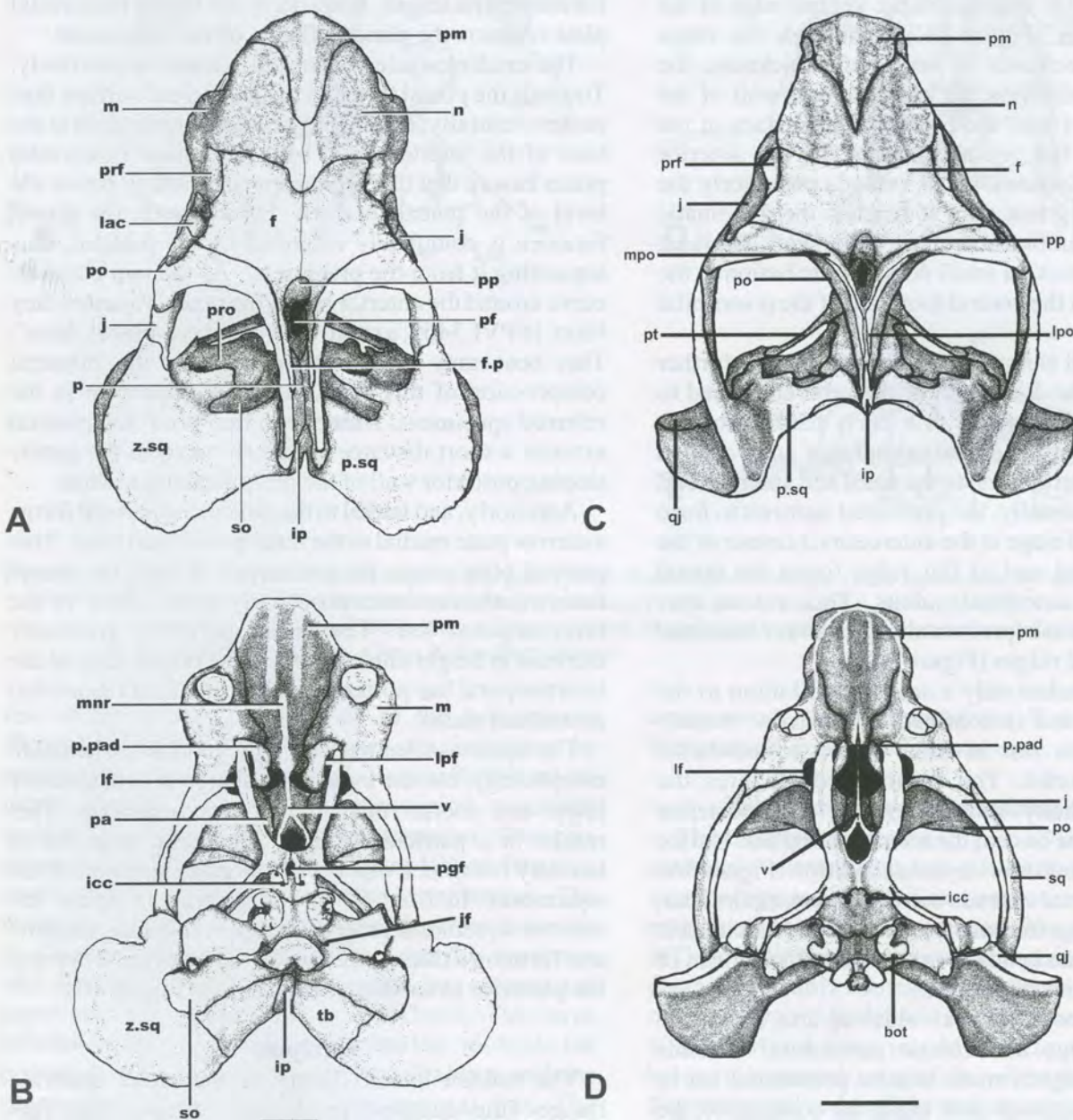


Figure 3. Composite cranial reconstructions of the genotype of *Kannemeyeria* and the taxon represented by specimens PVL3465, MACN18.871 and PVL3471 ("*Kannemeyeria argentinensis*" Bonaparte). Dorsal, A, and ventral, B, views of *Kannemeyeria simocephalus* (after Renaut 2000). Dorsal, C, and ventral, D, views of the reconstructions of holotype PVL3465. Scale bars represent 50mm. (See p.90 for abbreviations)

overlapped by the premaxilla. The bilateral compression of specimen PVL3465 has ventrally displaced the anterior margins of the internal choana. It therefore seems that the premaxilla fails to reach the high choanal margin (Figure 1B), and is excluded by the intervening palatine and maxilla contacting the vomer. Examination of the referred specimens confirmed that this condition is primarily due to distortion. Although the medially projecting maxilla restricts the premaxilla to a thin strip on either side of the median palatal ridge, this splint of premaxilla just reaches the anterior choanal margin (Figure 3D). The bilateral compression of specimen PVL3465 (Figure 1B) has closed both labial fossae, but the referred specimens show a large fossa level with the lateral palatal foramen.

Skull roof

From the anterior rim of the orbit, the jugal ventrally continues the ridge that marks the ventral edge of the antorbital sulcus (Figure 4C). Although the ridge progressively decreases in height and thickness, the jugal widens and forms the anteroventral wall of the orbit. The jugal forms the broad dorsal surface of the suborbital bar, but remains medial to the anterior extension of the squamosal. It extends posteriorly the length of the zygoma until it reaches the zygomatic flange of the squamosal at the back of the skull. The jugal does, however, make a small dorsal contribution to the postorbital bar at the ventral footplate of the postorbital bone.

The prefrontal is not very large, but extends further posteriorly on the dorsal rim of the orbit compared to *Kannemeyeria*. Composed of a fairly narrow strip, it comprises most of the dorsal orbital roof and crenated rim, located posterolateral to the nasal and anterolateral to the frontal. Laterally, the prefrontal narrows to form the dorsal orbital ridge at the anterodorsal corner of the orbit. The ventral end of this ridge forms the dorsal margin of the antorbital sulcus. This sulcus thus separates the dorsal (prefrontal) and ventral (lacrimal and jugal) orbital ridges (Figure 3C).

The frontal makes only a small contribution to the orbital margin, and is confined to a narrow, weakly crenated segment just in front of the posterodorsal corner of the orbit. The frontal accompanies the postorbital medially and posteriorly as a posterior extension onto the base of the intertemporal bar. Unlike the characteristic *Kannemeyeria* condition (Figure 3A) in which the frontal extends onto the intertemporal bar, the broad posterior frontal projection of this specimen is extremely short and ends in front of the anterior rim of the pineal foramen (Figure 3C).

From the posterodorsal side of the orbit the particularly large and robust postorbital extends ventrally as a slightly more slender postorbital bar to contact the squamosal and jugal. In contrast to the shortened postorbital footplate in *Kannemeyeria*, the postorbital footplate of this dicynodont extends anteriorly between the jugal and squamosal. Posterodorsal to the orbit, the medially extending broad

bar of the postorbital rapidly narrows until it turns posteriorly to form the lateral surface of the intertemporal bar. This morphology is common for most dicynodonts with narrow intertemporal regions, but this taxon has an unusual postorbital morphology (Figure 3C), particularly when compared with *Kannemeyeria*. At the base of the intertemporal bar the postorbital twists 90° proximally, so that its ventral surface faces laterally to form the medial border of the temporal fenestra, and the dorsal surface faces medially to contact the parietal. As it twists the postorbital also narrows, but the medial and lateral surfaces retain their integrity. As a result, the postorbital comprises two consecutive plates lateral to the parietal. The relatively thick medial plate (mpo; Figure 3C) attenuates dorsoventrally to a thick splint that contacts its opposite about two-thirds along the intertemporal bar. The thin lateral plate (lpo; Figure 3C) forms the dorsolateral surface of the interparietal region for most of its length. Posteriorly the lateral postorbital plate contacts the parietal flange of the squamosal.

The small elongate preparietal extends far anteriorly. Towards the pineal foramen the preparietal surface dips posteroventrally, forming a pre-pineal depression at the base of the intertemporal bar. The raised postorbital plates ensure that this region appears sunken below the level of the pineal foramen. Furthermore, the pineal foramen is completely encircled by the parietal, thus separating it from the preparietal. As the two parietals curve around the anterior rim of the pineal foramen they form, in PVL3465, a small bifurcated pre-pineal 'boss'. This boss may have been caused by the bilateral compression of this skull, and is not apparent in the referred specimens. Anterior to the 'boss' the parietal extends a short distance anteriorly to form the gently sloping posterior wall of the pre-pineal depression.

Anteriorly, and lateral to the pineal, the parietal forms a narrow plate medial to the inner postorbital plate. This parietal plate meets its counterpart behind the pineal foramen and continues posteriorly as the 'floor' of the intertemporal bar. The fused parietals gradually increase in height until they form the dorsal edge of the intertemporal bar posterior to the contact of the medial postorbital plates.

The squamosal has the typical dicynodont tri-laminate morphology, but the zygomatic flange is considerably lower and shorter than that of *Kannemeyeria*. This results in a particularly long zygomatic arch that is laterally composed of a broad anterior extension of the squamosal. In front of the postorbital footplate the anterior squamosal projection tapers in a long shallow arc, forming a thick splint below the jugal and covering the posterior extension of the maxilla (Figure 4C).

Occiput

The sudden lateral flaring of the broad quadrate flange of the squamosal results in a sunken occiput. This occipital morphology (Figure 4) is different from the 'bowl-shaped' occiput of *Kannemeyeria simocephalus* and the more 'plate-like' morphology of *Kannemeyeria cristarhynchus* (Renaut 2000). The

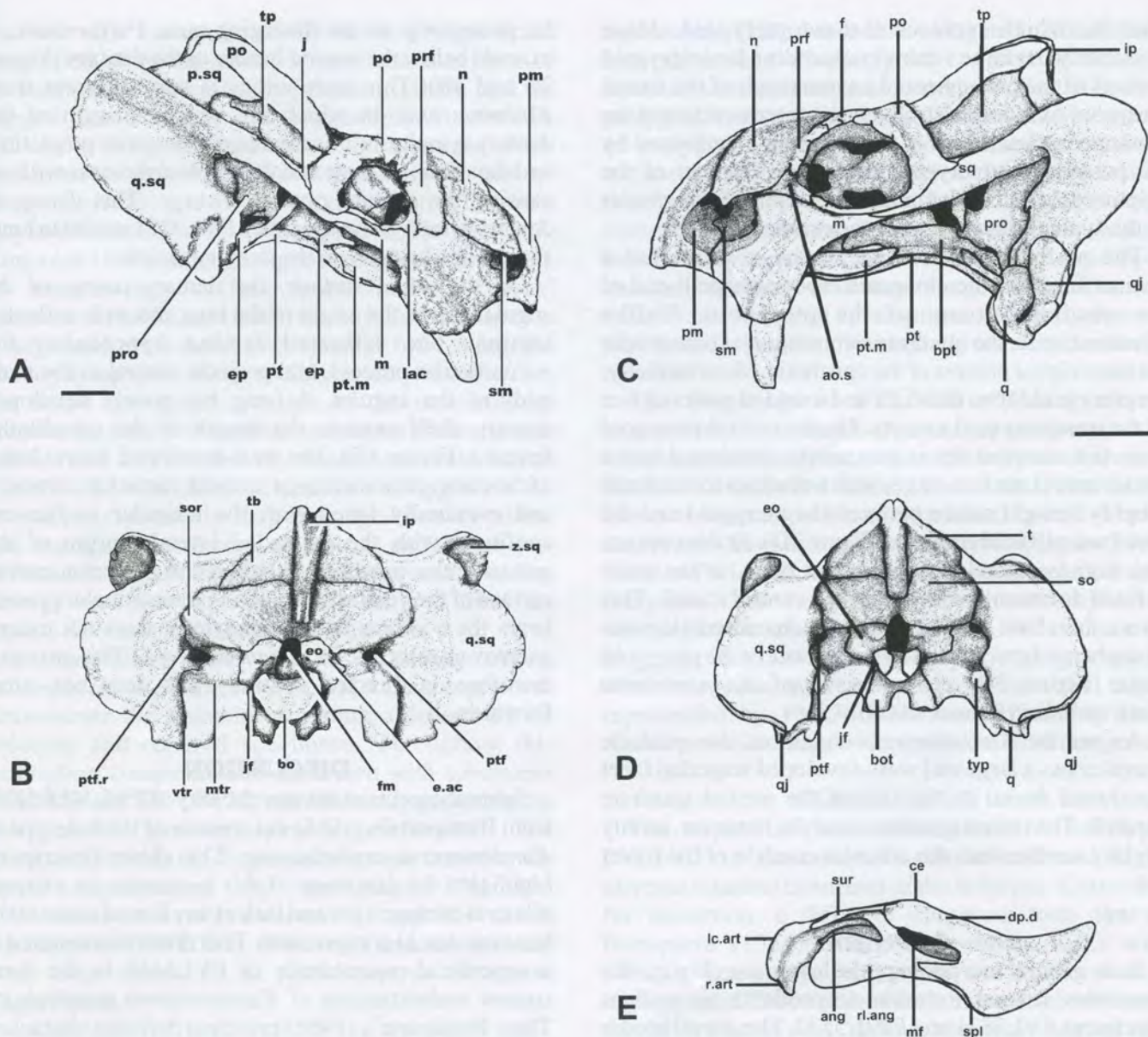


Figure 4. Composite cranial reconstructions of the genotype of *Kannemeyeria* and the taxon represented by specimens PVL3465, MACN18.871 and PVL3471 ("*Kannemeyeria argentinensis*" Bonaparte). Lateral, A, and occipital, B, views of *Kannemeyeria simocephalus* (after Renault 2000). Lateral, C, and occipital, D, views and lower jaw of the reconstructions of holotype PVL3465. Scale bars represent 50mm. (See p.90 for abbreviations)

rest of the general morphology of the neurocranial elements are similar to *Kannemeyeria*, including the prominent 'tympanic processes' (Renaut 2000) and the tubera composed entirely of basioccipital, anteriorly supported by the para-basisphenoid complex. The open, elongated tubera in PVL3465 (Figure 1B) are largely a result of the post-mortem bilateral compression. The occipital condyle has a slight central depression similar to *Kannemeyeria*. Differences between this specimen and *Kannemeyeria* include a broader, less striated and lower supraoccipital ridge in PVL3465. The large tabular makes a distinct contribution to both the posterodorsal rim of the temporal fenestra and the posterolateral end of the intertemporal bar. The interparietal has only a short anterior extension into the bar between the tabulars, and then between the parietals. Furthermore, the interparietal seems to have a single dorsal nuchal ridge, but this may correspond to the

compressed lateral arms of the V-shaped posterior interparietal crest in *Kannemeyeria*.

Palatal region and quadrate complex

The entire palatal region (Figure 3D) is generally long and fairly narrow, and has a fundamentally different morphology to that of *Kannemeyeria*. At the anterior margin of the choana the narrow, elongated palatal pad of Cox (1998) has a slightly wider anterior expansion, but is otherwise fairly constant in height and rugosity. Most of the pterygoid girder has a marked ventral extension. It extends as a long, roughly horizontal 'blade' well below the general level of the other palatal elements. The pterygoid is therefore well developed ventrally, as well as medially, and forms part of the sidewall of the choana. Laterally, however, the exposure of the anterior pterygoid ramus (Figure 4C) is reduced to a thin strip of bone by the wide and thin pterygoid process of the

maxilla, which replaces the ectopterygoid. More posteriorly the large ventrally extending basipterygoid process of the parasphenoid covers much of the lateral pterygoid surface. It also covers the anterior origin of the quadrate ramus, which is then laterally overlapped by the posterior epipterygoid footplate. The rest of the epipterygoid and basicranial axis morphology is similar to the typical *Kannemeyeria* anatomical pattern.

The posteromedial surface of the quadrate has a distinct facet for the elongated 'spoon-shaped' end of the quadrate ramus of the pterygoid. Unlike *Kannemeyeria*, the quadrate ramus has no contact with the paroccipital process of the opisthotic. More medially, the pterygoid forms the thick and rounded posterior rim of the interpterygoid vacuity. On the central pterygoid body this rounded rim is posteriorly developed into a broad ventral median ridge, which declines towards the roughly straight suture between the pterygoid and the para-basisphenoid complex (Figure 3D). At this contact, and slightly lateral to the median ridge, is the well-defined foramen for the internal carotid canal. This taxon, therefore, does not have the characteristic para-basisphenoid groove of *Kannemeyeria*, or the pterygoid fossa (Figure 3B) characteristic of *Kannemeyeria simocephalus* (Renaut 2000).

As per the *Kannemeyeria* condition, the quadrate complex has a large and well-developed stapedial facet positioned dorsal to the rim of the medial quadrate condyle. The lateral quadrate condyle, however, is only slightly smaller than the articular condyle of the lower jaw.

Lower jaw

In its general morphology the lower jaw (Figure 4E) resembles several Permian dicynodonts as well as specimens PVL3831 and BP/1/5532. The dorsal border has a characteristic and pronounced coronoid eminence (Cox 1998), which extends a particularly long distance on both the dorsal dentary bar and the surangular. Behind the dorsal peak of the eminence the dorsal rim of the jaw slopes sharply posteroventrally. This slope is continuous with the long articular recess. Such morphology is almost identical to that of specimen PVL3831 (*Vinceria andina*), as well as that of BP/1/5532 (a shansiodont specimen). Much of the lateral articular condyle and retroarticular process has been damaged in the holotype (Figure 2C) and the referred specimens, but the direction of extension of the reflected lamina, and remnants of the lateral rim of the retroarticular process, indicate a posteroventral orientation for the condyle similar to a specimen of *Aulacephalodon* (BP/1/766), and *Vinceria* (PVL3831).

The dentary symphysis of specimen PVL3471 is large and well developed, and generally continues the ventral border of the angular, and the dorsal border of the surangular. Ventrally, the wide splenial recess has deeply bifurcated the dentary symphysis, splitting it into its dentary rami. The splenial thus has a considerable exposure on the buccal surface of the jaw, and extends

far posteriorly on the diverging rami. Furthermore, it extends below the ventral border of the dentary (Figure 2C and 4E). This morphology is very different from *Kannemeyeria*, in which the ventral margin of the dentary symphysis has an extensive posterior projection, and thus forms a large and deep splenial recess without causing the dentary rami to diverge. This divergent dentary symphysis in specimen PVL3471 results in long, sharp-edged ridges on the dentary tables.

On the labial surface, the dentary recess of the angular marks the origin of the long and wide reflected lamina. The reflected lamina approaches the retroarticular process, and projects ventral to the main body of the angular. A long, but poorly developed dentary shelf extends the length of the mandibular fenestra (Figure 4E). The well-developed lateral ledge of the surangular increases in width farther posteriorly, and eventually fuses with the articular to become confluent with the expanded lateral margin of the retroarticular process. Although the posterior curved surface of the ventrally projecting retroarticular process bears the concave lateral condyle, it does not extend anteroventrally as in *Kannemeyeria*. The process, therefore, is directed ventrally and does not curve forwards.

DISCUSSION

Several aspects of the morphology of PVL3465 differ from Bonaparte's (1966) description of the holotype of *Kannemeyeria argentinensis*. The above description highlights the distortion of this specimen: its extreme bilateral compression and lack of any lateral shear of the bones or dorsal compression. This distortion resulted in a superficial resemblance of PVL3465 to the then-current understanding of *Kannemeyeria* morphology. Thus, Bonaparte's (1966) principal defining characters of this taxon are merely distortion-related (such as the narrow skull, high parietal crest, mid-nasal ridge, and pointed snout). Noticing this apparent resemblance to *Kannemeyeria*, Bonaparte (1966) chose to base his descriptions on a comparison with the well-preserved holotype specimen of *Kannemeyeria "erithrea"*, SAMPK3017 (Haughton 1915, 1917). However, the description and allometric analysis of SAMPK3017 by Renaut (2000) clearly demonstrated that it is a sub-adult individual of *Kannemeyeria simocephalus*, whereas PVL3465 is an adult individual. Similarities that they share include the large lacrimal and prefrontal bones (which are overgrown and reduced in adult *Kannemeyeria* specimens), as well as the weak caniniform process and a large reflected lamina (distinctive of a sub-adult condition in *Kannemeyeria*). Many of the unusual features of SAMPK3017 are ontogenetic (Renaut 2000), and consequently the comparison of the features of these two specimens is invalid.

Our description has isolated several critical differences between the South American specimens and the African genus *Kannemeyeria*. These differences are not limited to specific autapomorphies,

because this taxon does not show a significant proportion of the diagnostic generic characteristics of *Kannemeyeria* determined by Renaut (2000), and we suggest that "*Kannemeyeria argentinensis*" cannot be included in that genus. Furthermore, the lower jaw of this specimen is fundamentally different from that of *Kannemeyeria* and has a characteristic Permian dicynodont morphology (Crompton & Hotton 1967; King *et al.* 1989), although slightly modified and adapted. Its morphology differs from that of typical *Kannemeyeria* (Renaut 2000) in the following aspects: a large and well-developed splenial bifurcating the dentary symphysis, a long and high coronoid eminence, the shape and anterior extent of the retroarticular process, the distinct horizontal orientation of the articular recess (and the functionally more horizontal lateral condyle), the large reflected lamina extending below the ventral jaw rim, and the long and ridged dentary tables. The significant numbers of cranial and lower jaw differences suggest that this taxon possessed a feeding strategy and jaw physiology that differed from the typical *Kannemeyeria* anatomical pattern.

It is insufficient to show that this taxon may not be a valid species of *Kannemeyeria*, and it is appropriate to demonstrate the possible taxonomic relations of the holotype and referred specimens. Throughout this description comparisons were drawn with specimens PVL3831 and BP/1/5532, which closely resemble the holotype of "*Kannemeyeria argentinensis*". The characters listed in the diagnosis below are shared by the taxon represented by specimen PVL3465 ("*Kannemeyeria argentinensis*"), and the taxon represented by PVL3831 (*Vinceria*), and are different from those shared by all *Kannemeyeria* specimens (Figure 3, 4).

Revised diagnosis of the taxon represented by PVL3465

A small to medium sized Triassic dicynodont. Large orbits relative to the skull. Narrow intertemporal region that projects posterodorsally, but less so than in *Kannemeyeria*. Large nasal recess relative to total snout size. Preorbital length less than postorbital length. Well-developed caniniform processes directed ventrally, but without lateral or ventral expansions. Ventrally directed, large, spatulate tusks with multiple wear facets. Median dorsal nasal ridge present, but reduced, and no dorsal thickening. Zygomatic arches bowed laterally, and extend far posteriorly so that the zygomatic flange of the squamosal is reduced. Squamosal projects much farther posteriorly than does intertemporal region. Lacrimal extends anteriorly to contact septomaxilla, and separates nasal from maxilla. Prefrontal limited to the orbit margin. Well-developed antorbital sulcus on lacrimal between prefrontal and jugal orbital ridges. Frontal does not extend onto intertemporal bar. Preparietal separated from pineal foramen by anterior extensions of parietal. Lateral surface of intertemporal bar formed by two plates of postorbital. Posterior projection of postorbital contacts

squamosal. Thin, weak and elongated palatal pads. Lateral surface of pterygoid covered by maxilla anteriorly and basipterygoid posteriorly. Central body of pterygoid forms median ventral ridge. Quadrate ramus of pterygoid contacts the posteromedial quadrate surface. Lateral quadrate condyle only slightly smaller than lateral articular condyle. Lower jaw forms large mandibular fenestra. Dentary symphysis widely bifurcated by large splenial at mentum. Well-developed and long coronoid eminence. Large reflected lamina with extensive ventral development. Ventrally directed retroarticular process. Horizontally orientated articular recess.

The diagnosis of PVL3456 ("*Kannemeyeria argentinensis*") is based on a unique combination of observed plesiomorphic and synapomorphic characters that best describe this taxon. Most of these characters, however, draw a specific comparison (Figure 3, 4) with the revised diagnosis of *Kannemeyeria* (Renaut 2000) because PVL3465 had previously been included with that genus. These comparisons show that the majority of the diagnostic characters for PVL3465 cannot be accommodated within the generic diagnosis of *Kannemeyeria*, and we propose that the taxon represented by PVL3465 differs sufficiently from *Kannemeyeria* to suggest its exclusion from that genus.

CONCLUSION

The superficial resemblance of the holotype, PVL3465, to *Kannemeyeria* can be attributed to the extreme bilateral distortion of the holotype. Correcting for distortion, a different diagnosis from that of Bonaparte (1966) emerges. Spatulate tusks with multiple wear-facets, long palatal and dentary pads, a high coronoid eminence, and the horizontal orientation of the articular recess define the anatomy of the masticatory mechanism of specimen PVL3465. These characters are completely different from those of *Kannemeyeria*. Although the anatomy of the masticatory mechanism of PVL3465 is similar to that of many Permian dicynodonts (Crompton & Hotton 1967; King *et al.* 1989), it does have many unique features. In terms of functional anatomy, the angle of articulation at the recess and the reverse angle in front of the coronoid eminence, imply that the dentary tables were pulled in a long shearing action against the secondary palate. The action of such a jaw cycle would not have followed the *Kannemeyeria* type, which relied on heavy crushing and grinding actions (Renaut 2000).

Several diagnostic characters shared between PVL3465 ("*Kannemeyeria argentinensis*") and PVL3831 (*Vinceria*) constitute fundamental differences between these two taxa and *Kannemeyeria*. These include the shorter prefrontal length, the more vertically orientated occiput, the preparietal separated from the pineal, and the separation of the nasal and maxilla by the lacrimal. Unlike *Kannemeyeria*, which has a long posterior projection of the frontal, PVL3465 and *Vinceria* share short parietal extensions of the frontal. Both PVL3465 and *Vinceria*

have a marked antorbital sulcus, and a peculiar 'double-plate' morphology of the postorbital. These differences extend to the palatal region, where both taxa exhibit several characters that are directly opposed to the typical *Kannemeyeria* condition.

Our study has shown conclusively that the taxon represented by PVL3465 exhibits a different jaw morphology and mechanism to *Kannemeyeria*. Moreover, it has a large number of cranial characters that are different from those of *Kannemeyeria* and instead closely resemble those of the Argentine taxon *Vinceria*. Although it appears that PVL3465 is closely related to *Vinceria*, it is inappropriate to examine this relationship until the authors have completed a phylogenetic analysis of *Vinceria*. Nevertheless, we can conclude that based on the revised diagnosis of PVL3465, *Kannemeyeria* cannot be considered to occur in South America, and a global *Kannemeyeria*-biochron, as proposed by Lucas & Wild (1995), cannot be supported by the current fossil evidence.

ABBREVIATIONS

Cranial

ang	angular
ao.s	antorbital sulcus
bo	basioccipital
bot	basioccipital tubera
bpt	basipterygoid of the parasphenoid
ce	coronoid eminence
dp.d	dorsal plate of the dentary
eo	exoccipital
f	frontal
fm	foramen magnum
f.p	parietal projection of the frontal
icc	foramen for internal carotid canal
ip	interparietal
j	jugal
jf	jugular foramen
lac	lacrima
lc.art	lateral condyle of the articular
lpo	lateral postorbital plate
lf	labial fossa
mf	mandibular fenestra
mpo	medial postorbital plate
mtr	medial tympanic ridge
n	nasal
p	parietal
pgf	pterygoid fossa
p.pad	palatal pad

pm	premaxilla
po	postorbital
pp	preparietal
prf	prefrontal
pro	prootic
pt	pterygoid
p.sq	parietal flange of the squamosal
pt.m	pterygoid process of the maxilla
ptf	post temporal fenestra
ptf.r	recess of the post temporal foramen
q	quadrate
q.sq	quadrate flange of the squamosal
qj	quadratojugal
r.art	retroarticular process
rl.ang	reflected lamina of the angular
sm	septomaxilla
so	supraoccipital
sor	supraoccipital ridge
spl	splenia
sq	squamosal
sur	surangular
t/tb	tabular
tp	temporal plate of the parietal
typ	ympanic process of the opisthotic
v	vomer
vtr	ventral tympanic ridge

Institutional

BP	Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa
MACN	Muséo Argentino de Ciencias Naturales, Buenos Aires, Argentina
PVL	Instituto Miguel Lillo, Tucuman, Argentina
SAM	South African Museum, Cape Town, South Africa

ACKNOWLEDGEMENTS

We thank Dr. J.F. Bonaparte (Muséo Argentino de Ciencias Naturales, Buenos Aires, Argentina) and Dr. J. Powell (Instituto M. Lillo, Tucuman, Argentina) for permitting us free access to their respective dicynodont collections. We are also indebted to Dr. R. Herbst and family (Instituto M. Lillo, Tucuman) for their wonderful hospitality and assistance, and Drs. R. Damiani and K. Padian, and C. Sullivan and K. Angielczyk for their comments on earlier versions of the manuscript. This study was supported by travel grants from the University of the Witwatersrand, and the National Research Foundation of South Africa.

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A PARTIAL SKELETON OF THE TRITHELEDONTID *PACHYGENELUS* (THERAPSIDA: CYNODONTIA)

by

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ABSTRACT

Tritheledontids are advanced cynodonts that are considered the sister group of Mammalia. To date the postcranial skeleton has remained largely unknown, so that cladistic analyses are based on cranial characters only. This paper describes a specimen of the tritheledontid *Pachygenelus* which has most of the skull and vertebral column, a complete shoulder girdle, and most of the forelimb. The girdle and limb are closely comparable to those of *Massetognathus* and *Eozostrodon*, and unlike these elements in tritylodontids, which are more derived for fossorial specialisations.

KEYWORDS: Therapsida, *Pachygenelus*, postcranial skeleton.

INTRODUCTION

Recent cladistic analyses favour tritheledontids as the sister taxon to Triassic mammals (Hopson 1994; Luo 1994). The morphology of tritheledontids is still poorly known, however, and virtually nothing has been published on the postcranial skeleton. The specimen described here goes some way to fill this gap, and supports the above relationship; *Pachygenelus* is less derived than the contemporary tritylodontids, which are specialised fossorial herbivores.

MATERIAL AND METHODS

Pachygenelus is the most common tritheledontid. The specimen described herein has enough of the skull preserved, including the dentition, for positive identification and to establish skull length. It also preserves much of the vertebral column and ribs, a nearly complete pectoral girdle, and the left forelimb excluding the distal phalanges. Some unusual aspects of the skull are noted below.

The specimen was collected from the Upper Elliot Formation, now generally considered of Lower Jurassic age (Benton 1994), on Clarens townlands. It was encased in a fine grained sandy matrix cemented with calcium carbonate, and containing hard caliche nodules. The latter imply that lithification was a slow process, which may account for some of the peculiarities of the specimen noted below. A thin, fairly soft ferruginous layer surrounded most of the bone and was separated from it by a very thin amorphous calcitic layer. The specimen was prepared mechanically.

DESCRIPTION

Only the anterior portion of the skull is preserved (Figure 1); this shows the internarial process of premaxilla making contact with the nasal. The skull roof, braincase and occiput have been lost through weathering: a skull length of 50 ± 5 mm is indicated by

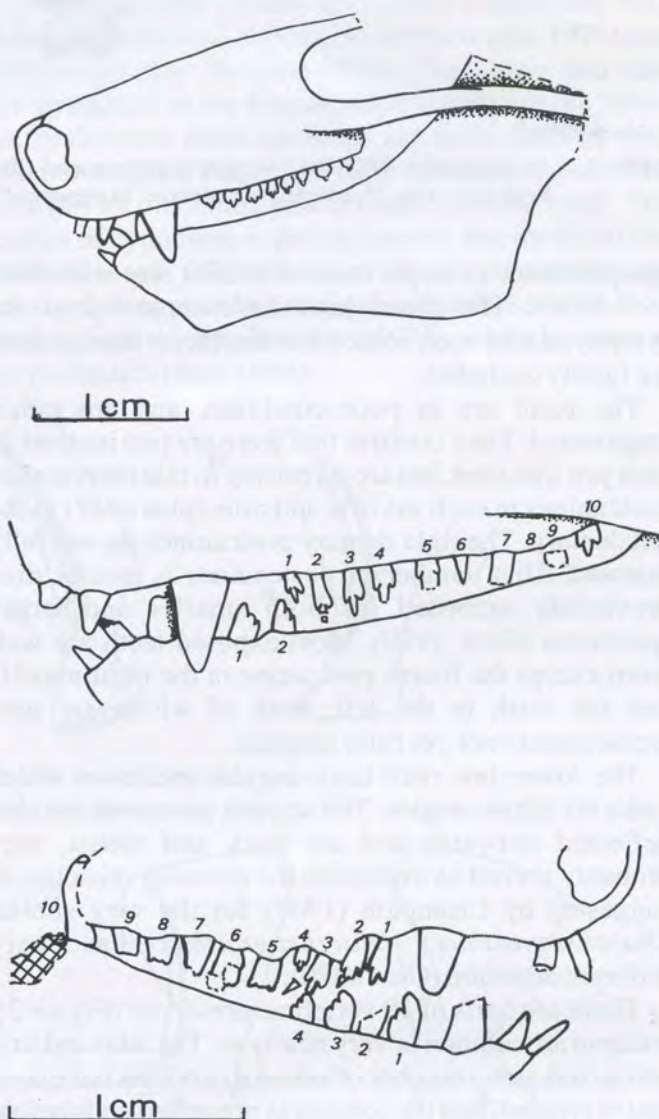


Figure 1. *Pachygenelus* BP/1/5623. Left lateral view of skull as preserved, detail of left and right dentitions. Scale bars = 1 cm.



Figure 2. *Pachygenelus* BP/1/5623 Vertebral column and ribs. Scale bar = 1 cm. Numbering of vertebrae "as preserved".

comparison with a specimen of similar size with skull roof intact. The lower jaws have separated at the symphysis and been somewhat displaced, though they are tightly occluded.

The teeth are in poor condition, and are rather fragmented. They confirm that there are two incisors in each jaw quadrant, but are surprising in that there are ten postcanines in each maxilla and nine (plus one?) in the left dentary. The right dentary postcanines are not fully exposed. This number of postcanines is greater than previously recorded for both smaller and larger specimens (Gow 1980). Most exposed teeth are well worn except the fourth postcanine in the right maxilla and the sixth in the left, both of which are new replacements not yet fully erupted.

The lower jaw rami have angular processes which make 90 degree angles. The angular processes are also deflected outwards and are thick and robust, they probably served as insertions for masseter muscles, as suggested by Crompton (1963) for the very similar *Diarthrognathus*. *Diarthrognathus* has very different dentition (Gow 1980).

There are parts of 19 vertebrae preserved (Figure 2), either in articulation or very nearly so. The atlas and axis and an unknown number of anterior cervicals have been lost to erosion, and the column as preserved ends before the lumbar region. The centra are quite well preserved, increasing in length along the column from cervical to posterior dorsal region. The neural arches are poorly represented and there is no trace of neural spines. This

is mostly the result of erosion, but also due to poor preservation. The young age of the individual is also a contributing factor.

Several of the more anterior ribs are present, but are generally badly eroded. They are circular to slightly ovoid in section, with poor differentiation of tuberculum and capitulum. There is no sign of the ribs that were attached to the last five vertebral centra, but the neural arches bear prominent rib facets.

Due to the young age of the individual, the elements of the pectoral girdle were not fused and have become slightly separated (Figure 3). Only the lower half of the right scapula remains and this includes the acromion process. Of the left scapula only the dorsal margin is missing, but the acromion region is badly preserved (a shed maxillary tooth lies beside it on the blade). The scapula is tall and narrow with a deeply concave external surface, the acromion is thickened, with a flat surface for articulation of the clavicle; it is very similar to the scapula of *Eozostrodon* figured by Jenkins and Parrington (1976), and thus more derived than the scapula of earlier cynodonts and totally lacking the pronounced specialisations of tritylodontids (Sues

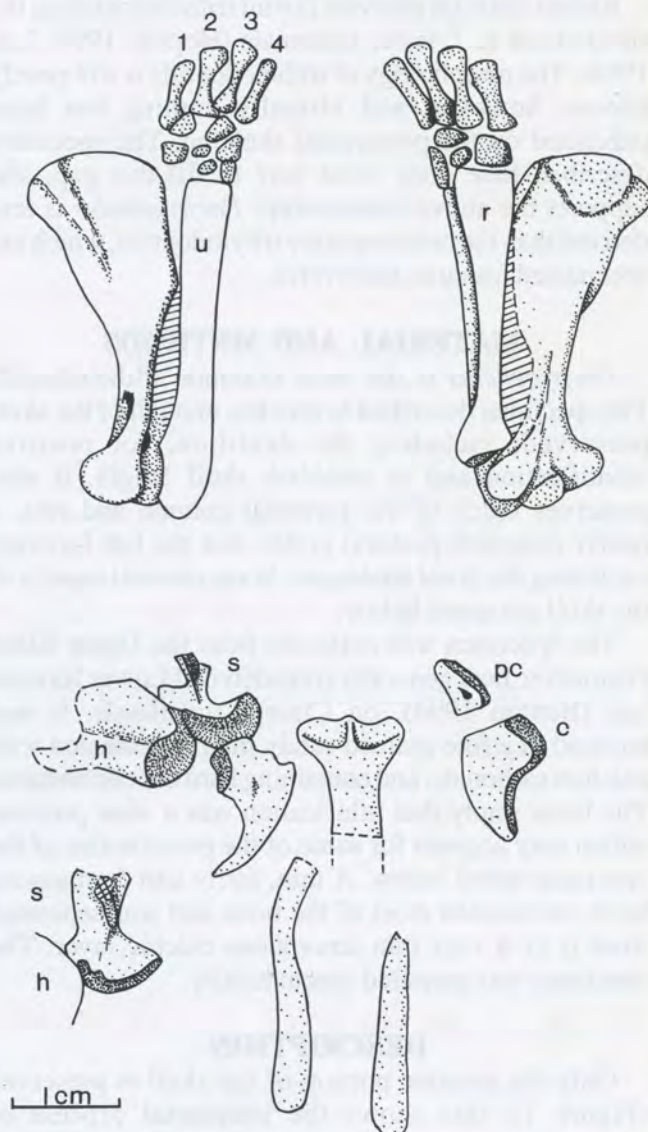


Figure 3. *Pachygenelus* BP/1/5623. Pectoral girdle and forelimb. Scale bar = 1 cm.

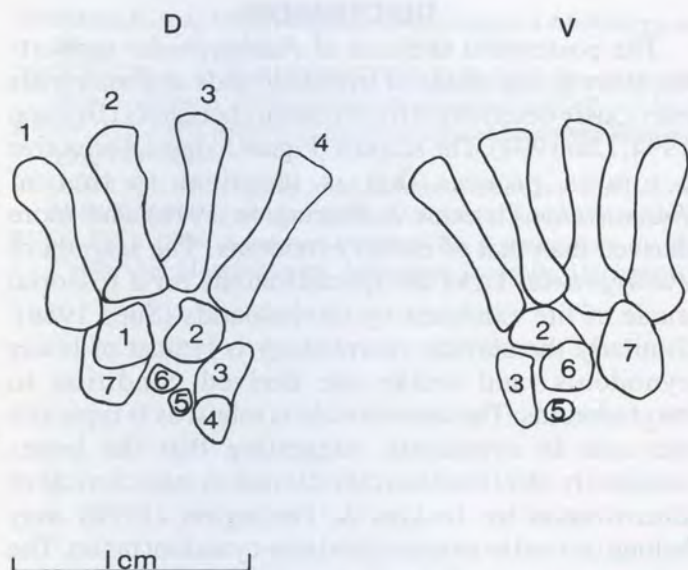


Figure 4. *Pachygenelus* BP/1/5623. Wrist detail, dorsal and ventral. Scale bar = 1 cm. Note bones are still supported by matrix.

1986).

Both coracoids are present; these are typical of cynodonts, having a straight suture for the procoracoid (damaged on the right coracoid). Only one procoracoid with a coracoid foramen is preserved, and this appears to be the right element; comparison with the specimen of *Cynognathus* figured by Jenkins (1971) suggests the orientation and relationship with the coracoid depicted here (Figure 3). Both clavicles are present, slightly incomplete, and a little distorted. Their morphology is plesiomorphic for cynodonts and unlike the highly derived condition seen in tritylodontids (Sues 1986). The

interclavicle is robust; its broad posterior projection had broken off and could not be found. The cross piece of the T that bears the facets for the clavicles is deflected upwards relative to the shaft of the T through an angle of approximately 44 degrees. This bone is so robust as to cast doubt on the identity of the interclavicle tentatively assigned to *Eozostrodon* by Jenkins and Parrington (1976), which is far more delicate, and which Evans (1981) suggests may belong to the rhynchocephalian *Gephyrosaurus*. The facets on the interclavicle which received the clavicles are finished in smooth periosteal bone, suggesting that movement was possible at these joints.

Of the right forelimb only the proximal head of the humerus is preserved. The articulated left forelimb comprises humerus, radius and ulna, seven largely indeterminate wrist elements (Figure 4), two of which are the radiale and ulnare (but these lack the intricate morphology of equivalent elements in Triassic mammals), and four proximal metacarpals (the fifth is missing), one of which is damaged. The metacarpals are numbered according to their relationship to the carpal elements. The limb bones are closely comparable with those of *Eozostrodon* (Jenkins & Parrington 1976) and *Massetognathus* (Jenkins 1970). The radius and ulna are straight as in the former, not curved as in the latter. In tritylodonts these elements are more derived with autapomorphies related to their fossorial habits. The ulna has an olecranon process and sigmoid notch. The carpus of cynodonts is poorly known, but the proximal phalanges of this specimen of *Pachygenelus* are relatively longer and more slender than those of Triassic forms figured by Jenkins (1971) and the coeval tritylodontids (Sues 1986).

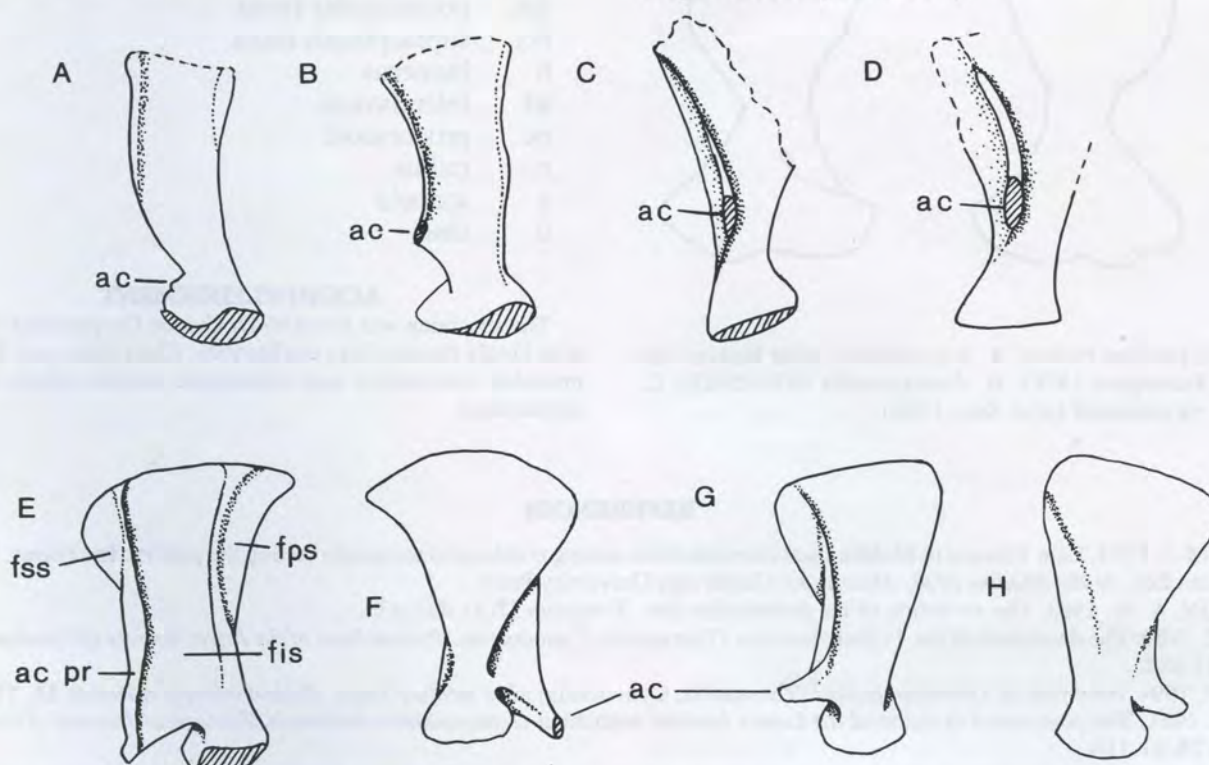


Figure 5. Cynodont scapulae. A, *Cynognathus* (after Jenkins 1971), B, *Luangwa* (after Kemp 1980), C, *Pachygenelus* (BP/1/5623), D, *Megazostrodon* (after Jenkins & Parrington 1976), E & F *Kayentatherium wellsi* (after Sues 1986), G & H, *Tritylodon longaevus* (BP/1/5167).

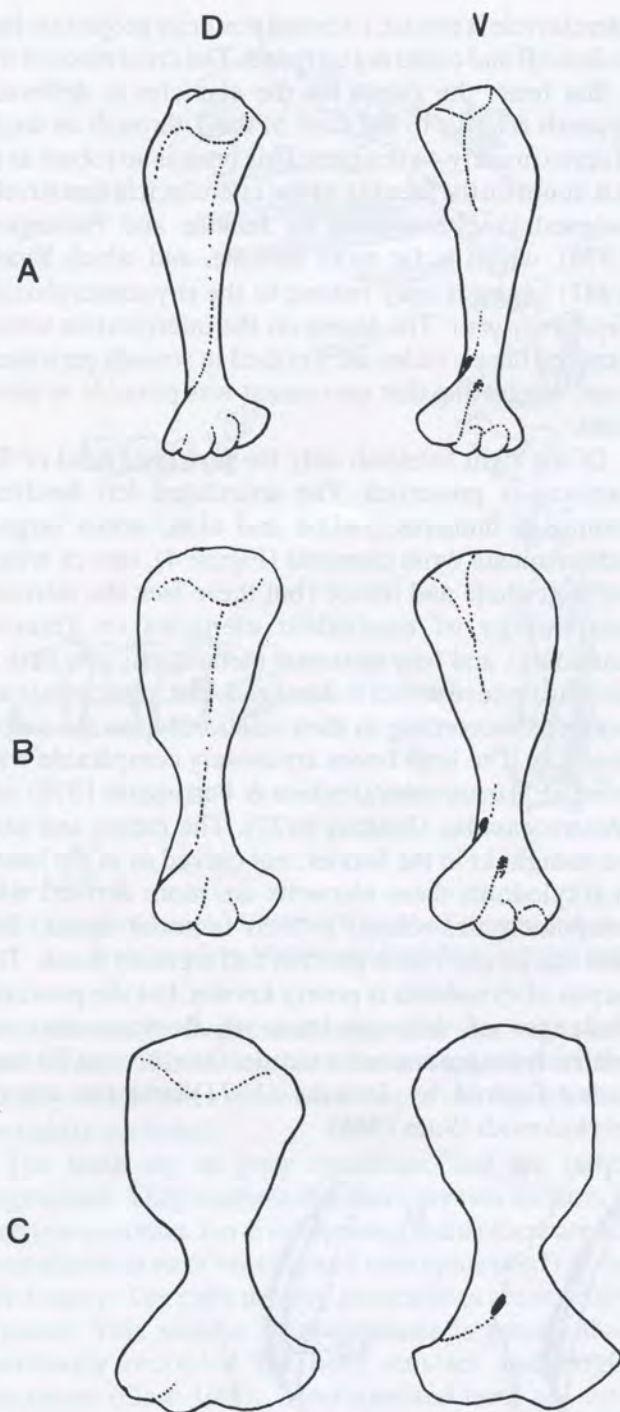


Figure 6. Cynodont humeri. A, *Eozostrodon* (after Jenkins and Parrington 1976), B, *Pachygenelus* (BP/1/5623), C, tritylodontid (after Sues 1986).

DISCUSSION

The postcranial skeleton of *Pachygenelus* supports the sister group status of tritheledontids and mammals previously determined from cranial characters (Hopson 1994; Luo 1994). The scapula (Figure 5) has a distinctive acromion process that is identical to that of *Eozostrodon* (Jenkins & Parrington 1976) and more derived than that of earlier cynodonts. The scapula of *Pachygenelus* lacks the specialisations for a fossorial mode of life exhibited by tritylodontids (Sues 1986). Similarly the clavicle morphology is typical of lower cynodonts, and unlike the derived condition in tritylodontids. The interclavicle is robust as is typically the case in cynodonts, suggesting that the bones tentatively identified as a clavicle and an interclavicle of *Eozostrodon* by Jenkins & Parrington (1976) may belong instead to an associated non-cynodont taxon. The humerus (Figure 6), radius, and ulna are essentially identical to those of *Eozostrodon* and lack the specialisations seen in tritylodontids. The wrist elements are more plesiomorphic than those of Triassic mammals. The preserved metacarpals are relatively longer and more slender than those of Triassic cynodonts and tritylodontids. The skull confirms the presence of only two incisors in each jaw quadrant, and compared with previously described dentitions (Gow 1980), suggests that the number of postcanines varied intraspecifically.

ABBREVIATIONS

ac	acromion
ac pr	acromion process
c	coracoid
cl	clavicle
fis	infraspinous fossa
fps	postscapular fossa
fss	supraspinous fossa
h	humerus
icl	interclavicle
pc	procoracoid
r	radius
s	scapula
u	ulna

ACKNOWLEDGEMENT

The specimen was found by Dr Gideon Groenewald of Clarens who kindly donated it to this Institute. Chris Sidor and Zhexi Luo provided constructive and enthusiastic reviews which are much appreciated.

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ABSTRACT

A new genus and species of viverrid of modern type, *Orangicelis gariepensis*, is described from the basal Middle Miocene locality of Arrisdrift in southern Namibia. It is the earliest known representative of the subfamily Viverrinae from Africa. Detailed examination of the morphology-like carnivorans of the early Miocene of Africa, hitherto all assigned to the family Viverridae, reveals that most of them are related to this group.

KEYWORDS: Middle Miocene, Namibia, Viverridae, Carnivora, Arrisdrift

INTRODUCTION

In a recent publication, Morales *et al.* (1998) described the carnivore fauna from Arrisdrift, Namibia. Excavations that were undertaken in the past few years have led to the discovery of additional taxa which were not represented in the earlier assemblage. The aim of this paper is to describe a new genus of viverrid from this early Middle Miocene site.

SYSTEMATIC DESCRIPTION

Family Viverridae Gray, 1821

Subfamily Viverrinae Gill, 1872

Genus *Orangicelis* nov.

Species *Orangicelis gariepensis* nov.

Etymology: The genus is named for the Orange River with the suffix *-celis* which is often used in composing the names of small carnivores. *Gariep* is the Khoi name for the Orange River.

Holotype: AD 613'98, hemi-mandible with C-M₂ (Figure 1), housed at the Geological Survey of Namibia Museum, Windhoek.

Paratype: AD 119'98, right mandible with C-M₁ (Figure 2), housed at the Geological Survey of Namibia Museum, Windhoek.

Diagnosis: Primitive viverrine intermediate in size between *Viverricula indica* and *Viverra zibetha*. Robust dentition: P₂ with greatly reduced anterior cusplet, M₁ short with high and closed trigonid, in which the metaconid is important and the paraconid is in a very lingual position. Small talonid with very well developed entoconid, attaining the height of the hypoconid. M₂ relatively large, with open trigonid in that there remains

a small paraconid and the metaconid is slightly higher than the protoconid, the cuspids are distinctly more rounded than of M₁, but the hypoconid is higher than the entoconid and is separated from it and the hypoconid.

Type locality: Arrisdrift, Spangkop, Namibia.

Age: Basal Middle Miocene (Faunal Set P 61a) (approximately MN 4) ca 17.5 Ma.

DESCRIPTION OF THE HOLOTYPE

The canine is poorly preserved, but would have been robust with an oval section. The P₁ is unisulcate and very reduced. The P₂ has a voluminous main cusp, a small low anterior cusplet and a small but high distal cusplet, and there is a small basal cingulum posteriorly (Figure 1). The P₃ is similar to the P₂ but the cusps and cingulum are better developed. The P₄ is more robust than the other premolars and possesses a large posterior cusp in a more buccal position, and an enlarged posterior cingulum which lingually develops two medium sized cusplets. The anterior cusplet is small. The M₁ is slightly conoid on its external wall at the height of the hypoconid and on the internal wall of the paraconid. Nevertheless, the structure of the tooth is clearly visible. The trigonid has an av-shaped occlusal morphology with a high, voluminous metaconid situated close to the protoconid which occupies a very lingual position. The talonid is well developed, possessing a strong entoconid which is possibly slightly lower than the hypoconid, but in any case almost the same height as it. The entoconid is joined to the hypoconid by a low but well developed hypoconulid which closes the posterior margin of the talonid. The entoconid is clearly separated from the metaconid, in much so that a small, low, cusp-like exists between them. The lingual wall of the hypoconid is oblique to the axis of the tooth, being oriented towards

NEW VIVERRINAE (CARNIVORA: MAMMALIA) FROM THE BASAL MIDDLE MIOCENE OF ARRISDRIFT, NAMIBIA

by

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a small paraconid and the metaconid is slightly higher than the protoconid, the talonid is deeply excavated like that of M₁, but the hypoconulid is higher than the entoconid and is separated from it and the hypoconid.

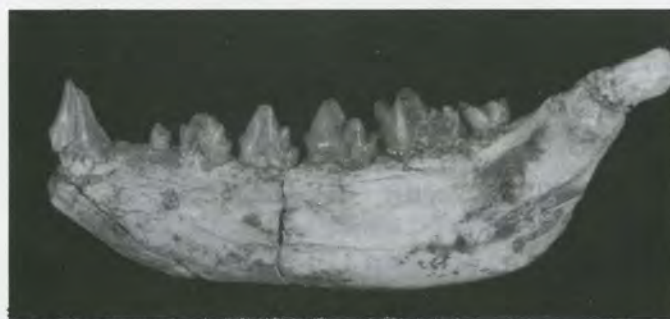
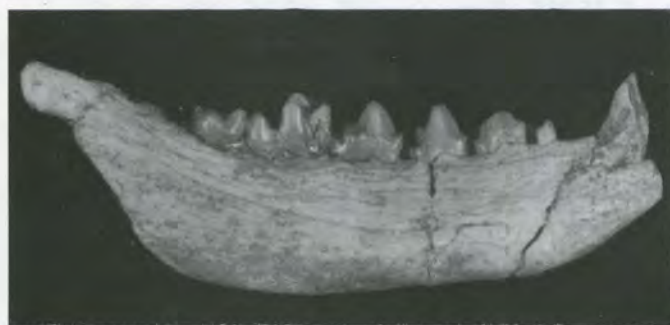
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the contact between the metaconid and protoconid. The talonid valley is closed only on its buccal side and appears to be deeply excavated. The M_2 is well developed, the trigonid being formed of a high, conical metaconid and a lower, more elongated protoconid, and a minute paraconid can be detected. The strong talonid is limited anteriorly by the posterior cristids of the metaconid and protoconid, and like the M_1 , is deeply excavated, but the hypoconulid is higher than the entoconid and is separated from it and the hypoconid. The mandibular body is high and wide with a robust symphysis marked by strong rugosities.



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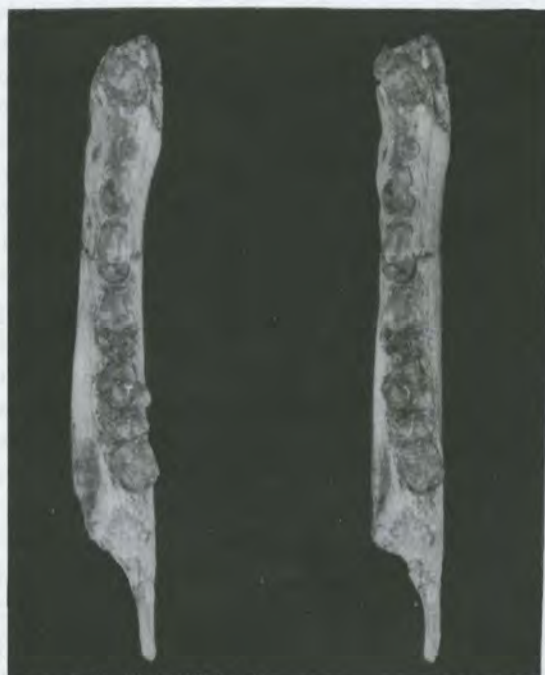


Figure 1. *Orangictis gariensis* nov. gen., sp. from Arrisdrift, Early Middle Miocene, Namibia. AD 613'98, holotype left mandible with C- M_2 ; top: longual view, middle: labial view, bottom: occlusal view (stereo). (Scale bar: 10mm).



Figure 2. *Orangictis gariensis* nov. gen., nov. sp. from Arrisdrift, Early Middle Miocene, Namibia. AD 119'98, paratype right mandible with C- M_1 in occlusal view (stereo). (Scale bar: 10mm).

Measurements: (Length-width in mm) P_2 5.1 x 3; P_3 6.3 x 3.9; P_4 7.0 x 4.4; M_1 ca 8.5 x 5.0; M_2 5.2 x 4.1.

Referred material. AD 429'97, a left mandible and AD 119'98 a right hemi-mandible (Figure 2). These specimens show a similar, quite advanced stage of wear of the teeth. Judging from the size and the similar dental wear stage, the two pieces may well belong to a single individual. Differences from the holotype are minor. There is no P_1 . In the P_4 the posterior cingulum on the postero-internal side of the tooth does not form any lingual cusps. The M_1 has a well developed wear facet parallel to the occlusal surface, revealing that this tooth is robust as a consequence of the increased width of the trigonid, which is widest at the level of the protoconid-metaconid. There is an alveolus for the M_2 , indicating that the tooth possessed two poorly fused roots.

Measurements: (Length-width in mm). AD 421'97, P_2 4.8 x 2.7; P_3 5.5 x 3.5; P_4 7.1 x 4.5; M_1 ca 9.2 x 5.8; AD 119'98, C_1 6 x 4.7; P_2 5.1 x 2.9; P_3 6 x 3.5; P_4 7.4 x 4.5; M_1 9.9 x 5.8.

COMPARISONS

Orangictis shares with extant Viverrinae (*Viverra*, *Viverricula* and *Civettictis*) the structure of the talonid of the lower molars in which the entoconid is well developed and separated from the neighbouring cusps. This morphology is typical of Viverrinae and primitive Hyaenidae (*Protictitherium*) and differs greatly from *Genetta* or *Herpestes*, in which the entoconid is either weaker or is fused with the hypoconulid, forming a cutting crest. In Hemigalinae there is a similar construction of the talonid, but the structure of the molars is very different. In Paradoxurinae as well, there is a strong entoconid in the talonid of M_1 , but the dentition is more bunodont and the M_2 more reduced. Among the known fossil forms from the Early Miocene of East Africa (Schmidt-Kittler 1987) only *Kichechia zamanae* Savage (1965) possesses similar characters to *Orangictis*. The new genus is not close to *Legetetia* (by reduction of the M_2 among other characters) nor to

Herpestides aequatorialis and *Leptoplesictis rangwai* (by the morphology of the talonid of the M_1 and M_2). These two forms appear to be highly derived in the direction of *Leptoplesictis aurelianensis*, and for the same reasons away from the Viverrinae.

Orangictis shares with *Kichechia* the general robusticity of the dentition, the morphology of the premolars and the construction of the trigonid of the M_1 . However, the morphology of the M_1 of *Orangictis* is very advanced and similar to that encountered in Viverrinae, showing that *Kichechia* is clearly primitive. Comparisons between second molars are not possible on account of the doubts expressed by Schmidt-Kittler (1987) concerning the identification of the Songhor mandible previously attributed to *Kichechia* by Savage (1965).

Among the fossil forms known from the Early Miocene only *Herpestides antiquus* from western Europe (Beaumont, 1967) shows a comparable structure of the talonid of M_1 and M_2 , but the development of the cuspids is weaker. In addition, the structure of the trigonid in *Herpestides antiquus* is much more secodont and its dentition is relatively closer to that of *Protictitherium*.

Special mention should be made of *Plioviverrops collectus* from the Early Miocene of Laugnac, France, described by Bonis (1973) as *Herpestides collectus*. *Plioviverrops*, the type species of which is *Plioviverrops orbigny*, is known from the Turolian of Pikermi. The genus is not well known before the Late Miocene. The form from Laugnac, *Plioviverrops collectus*, shows important differences from typical *Plioviverrops* from the Late Miocene, including the height of the entoconid of M_1 (which in *Plioviverrops* reaches the height of the metaconid), the reduction of the M_2 , the morphology of the P_4 (which is more robust with a conical protoconid) and the absence of cingula in the M_1 . *Plioviverrops collectus* is clearly different from *Herpestides antiquus*, as was shown by Bonis (1995), but it is not possible to classify it in *Plioviverrops*. It differs at least at the generic level from both *Herpestides* and *Plioviverrops*, but is closer in several features to *Leptoplesictis aurelianensis* from La Grive (Viret 1951; Beaumont 1973).

Orangictis and the Laugnac form differ in the amount of reduction of the M_2 , being more advanced in the French form, which instead possesses a more elongated and gracile M_1 , and in the structure of the talonid of the molars which is more excavated in *Orangictis* than in the Laugnac species. An important difference resides in the degree of separation of the entoconid, which in *Laugnictis* is almost indistinguishable from the hypoconulid, whereas in *Orangictis* it is clearly separated from it.

SYSTEMATIC STATUS OF *ORANGICTIS*

The separation between the families Herpestidae and Viverridae has been a major problem to palaeontologists due to the fact that the distinction of the extant representatives of the two families is based on

characters related to the soft anatomy - not observable in the fossil record - and/or to the morphology of the auditory region - scarce in the fossil record - (Wozencraft 1989; Wyss & Flynn 1993; Hunt & Tedford 1993; Véron 1995).

The most relevant characters for diagnosing *Orangictis* are related to the structure of the lower molar talonid, especially the strong development of the entoconid, which reaches the size of the hypoconid. Probably the important size of the entoconid could be considered as a derived character not shared with the extant Herpestidae. The representatives of this family have a different talonid configuration, without entoconid or with a keeled prolongation of the hypoconid that reaches the position of the entoconid. Hypocarnivorous members of Viverridae such as *Viverra* and *Civettictis* share this talonid construction with *Orangictis*, but hypercarnivorous genera of the same family such as *Genetta*, *Prionodon*, *Poiana*, and others have a more simple talonid quite close to some Herpestidae. The existence of two different dental patterns within the Viverridae is evident and it is questionable whether the family is a monophyletic group, as suggested by Véron (1995).

The lower molar pattern that occurs in *Orangictis* can also be seen in the subfamily Hemigalinae, which is normally included in the Viverridae, as well as in some fossil genera such as *Herpestides* which is considered either to be the oldest known fossil Viverridae (Hunt 1991) or a viverrid probably related with the hyaenid stem group (Beaumont 1967), and *Protictitherium* considered to be a primitive hyaenid (Schmidt-Kittler 1976). The possible phylogenetic relationship between Herpestidae and Hyaenidae (Hunt & Tedford 1993; Véron 1995) is not supported by the dental morphology of these two fossil genera, which show a dental pattern closer to Viverridae than to any other feloid, including Herpestidae.

In conclusion, *Orangictis* is closely related to some modern Viverrinae. None of the early Miocene East African carnivores described by Schmidt-Kittler (1987) are related to this group, meaning that the new genus is the earliest known Viverrinae in Africa. Attention is called to the fact that in such a diverse group of "viverrids" as those described by Schmidt-Kittler from the early Miocene of East Africa, there is no form related to the hypocarnivorous Viverrinae or with the primitive Hyaenidae. On the contrary, the East African forms are either more primitive, the case with *Legetetia* and *Kichechia*, or they present characters derived in the direction of hypercarnivorous Viverridae or Herpestidae.

ACKNOWLEDGEMENTS

We thank the Museo Nacional de Ciencias Naturales, CSIC, Madrid DGICYT projects PB 95-0113 and PB95-0014 and the Spanish Agency for International Cooperation (AECI). Thanks are also due to Professor Y. Coppens (Collège de France), Professor Ph. Taquet and Dr B. Senut (Laboratoire de Paléontologie), Mr R. Burrell and Dr J. Ward (Namdeb, Namibia), Messrs G. Hoveka and A. Vogt (National Monuments Council of Namibia) and Dr G. Schneider (Geological Survey of Namibia).

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NEW EVIDENCE OF THE GIANT HYAENA, *PACHYCROCUTA BREVIROSTRIS* (CARNIVORA, HYAENIDAE), FROM THE GLADYSVALE CAVE DEPOSIT (PLIO-PLEISTOCENE, JOHN NASH NATURE RESERVE, GAUTENG, SOUTH AFRICA)

by

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ABSTRACT

A well preserved cranium which represents the most complete skull of *Pachycrocuta brevirostris* (Carnivora, Hyaenidae) discovered in Africa, and a maxillary fragment from the Gladysvale Cave Deposit (John Nash Nature Reserve, Gauteng, South Africa) are described and compared to other fossil and extant hyaenid specimens from South Africa and Europe. In addition, some aspects of functional morphology in the hyaenid dentition are reconsidered and suggested to be directly related to the palaeoecological role of *P. brevirostris*.

KEYWORDS: Plio-Pleistocene, *Pachycrocuta brevirostris*, morphology, functional morphology, palaeoecology, South Africa, Europe.

INTRODUCTION

In 1954, Ewer described the fairly complete cranium KA-55 from the Kromdraai A Deposit and named the new species *Hyaena bellax* (Ewer 1954b). Sixteen years later the suggestion was made that this specimen be assigned rather to the genus *Pachycrocuta* (Ficcarelli & Torre 1970), known from several sites in Eurasia. At least two species of *Pachycrocuta* are known in Europe, *P. brevirostris* and *P. perrieri* (Werdelin & Solounias 1991; Guérin & Patou-Mathis 1996), and the two taxa are distinguished by metric tooth features (Werdelin & Solounias 1991: 22). Howell & Petter (1980) have pointed out close affinities between *P. bellax* and the comparatively well known Eurasian specimens of *P. brevirostris* and *P. perrieri*. This view was also supported by Turner (1986, 1987, 1988, 1990; Turner & Anton 1996), who had originally postulated close affinities between *Pachycrocuta* and *Hyaena*. Howell & Petter (1980) favored a two-lineage theory: *P. pyrenaica* – *P. perrieri* | *P. brevirostris* | *H. hyaena*. Ficcarelli & Torre had proposed a similar theory in 1970, although their analysis relied on different features. Further studies including all hyaenids (Werdelin & Solounias 1991) led to *H. brunnea* being placed in the new genus, *Parahyaena*, because of the lack of shared synapomorphies with *H. hyaena*.

Currently, research interests have shifted to the question of attributing a palaeoecological role to the giant hyaena *Pachycrocuta* in the Plio-Pleistocene. Turner & Anton (1996) have offered initial concrete conclusions from its fossil record. From this same perspective, an initial comprehensive study of new East

African material (Turkana Basin, Kenya) has contributed interesting insights (see Werdelin 1999). On the basis of new material from the Gladysvale Cave Deposit (Gauteng, South Africa) assigned to *P. brevirostris*, we examine and review certain morphological aspects and discuss the palaeoecological implications.

MATERIAL AND METHODS

(List of abbreviations on page xxx)

BPI: GV 3914 *Pachycrocuta brevirostris* (fairly complete cranium with dentition: P², P³, P⁴, M¹ sin. et dext.), dump 8, block 1, collected 28.4.1996.

BPI: GV 4264 *Pachycrocuta brevirostris* (left maxillary fragment with dentition: P², P³, fragmentary P⁴), dump 8, collected 9.10.1996.

Locality: Gladysvale Cave Deposit (John Nash Nature Reserve, Gauteng, South Africa)

Age: approximately 1.0 million years

Comparative fossil material

NMB: Se 279 *Pliocrocuta perrieri* (Croizet & Jobert 1828) (skull and dentition: P¹, P², M¹ dext., P³, M¹ sin.). St.V. 974 *Euryboas* sp. (cranium, dentition: P², P³, P⁴, M¹ sin. et dext., upper C, I¹, I², I³ dext.), V.A. 2005 *Pachycrocuta brevirostris* (*Hyaena robusta* LeVille 1921: cranium, dentition: P¹, P², P³, P⁴, M¹ sin. et dext.). V.A. 65 *Pachycrocuta brevirostris* (*Hyaena robusta* LeVille 1921: cranium, dentition: I³, P¹, P², P³, P⁴, M¹ dext., upper C sin. fragmentary, I³ sin. fragm. P³ sin. fragm.)

TM: KA 55 *Pachycrocuta brevirostris* (*Hyaena bellax* Ewer 1954b) (left half of a cranium with articulated mandible, right maxillary fragment, dentition).

BPI: M 2530 *Parahyaena brunnea*. M 2567 cf. *Chasmaporthetes*. M 299, M 8348, M 245, M 248, M 254, M 8297, M 8925, M 2560, M 2587, M 8295, M 253 *Hyaena makapani*.

TM: KA 56 *Crocuta spelaea capensis*, KA 58 and KA 60 *Crocuta ultra*, SK 314 *Hyaenictis*, SK 326 *Parahyaena brunnea dispar*, Sts 128 *Crocuta crocuta*, Sts 129 hyaenid indet., Sts 135 *Euryboas silberbergi*, SF 376 *Pachycrocuta brevirostris*.

Comparative extant material

Hyaena hyaena

ZMUZ: 10155, 10156, 10157, 17510. FIS: 1158, 1356, 4273, 4578, 6729, 4644, 4645, 1158, 1356, 15687, 15689, 15690, 15691, 32782, 63952, 15687 (juvenile).

Parahyaena brunnea

FIS: 15684, 6926.

Crocuta crocuta

ZMUZ: 12258, 13096, 13097, 13098. SI: 4579, 16358 (juvenile). MS: ZA 1147M9, 162 (juvenile).

Measurements were taken with calipers to the nearest 0.1 millimeter several times and averaged each time. Where possible, measurements were taken buccally. Terminology follows current literature.



SYSTEMATIC PALAEOONTOLOGY

Order CARNIVORA Bowditch, 1821

Family HYAENIDAE Gray, 1869

Genus *Pachycrocuta* Kretzoi, 1938

Pachycrocuta brevirostris (Aymard, 1846)

Synonymy: see Werdelin & Solounias (1991: 23), Turner & Anton (1996) and Werdelin (1999).

DESCRIPTION

GV 3914 (Figures 1-5, measurements see Table 1)

The cranium

The cranium consists of a large and broad hyaenid skull belonging to a relatively old individual (Figures 1-4). The upper jaws, the anterior portion of the cranium and the left zygomatic arch are preserved. The latter increases considerably in depth and massiveness while projecting dorsolaterally. In ventral view, the zygomatic arch appears trapezoidal in outline (Figure 2). The posterior portion of the frontals and the palate, plus a major part of the left maxilla, including the infraorbital foramen, are penetrated, distorted, shifted or destroyed by calcite crystals containing breccia infill. The original vaulting of the palate cannot be directly observed, but there are longitudinal crevices on the left and right palatine, suggesting that considerable vaulting was originally present and was at least comparable to the condition usually stated for *C. crocuta*.

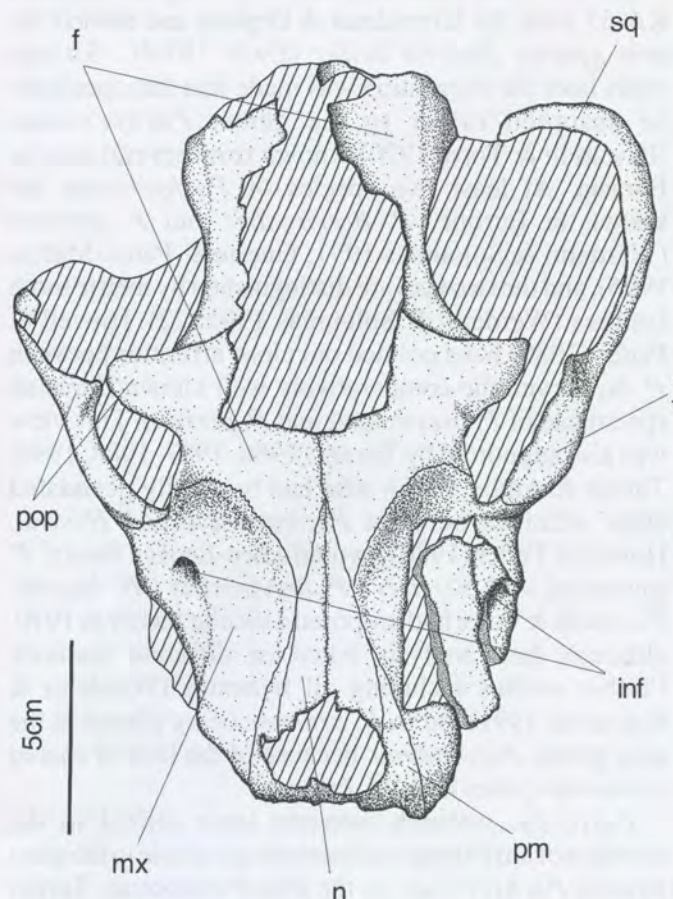


Figure 1A, B. Dorsal view of the skull of *Pachycrocuta brevirostris* (GV 3914). Hatch lines indicate breccia infill. The scale bar equals 5 cm.

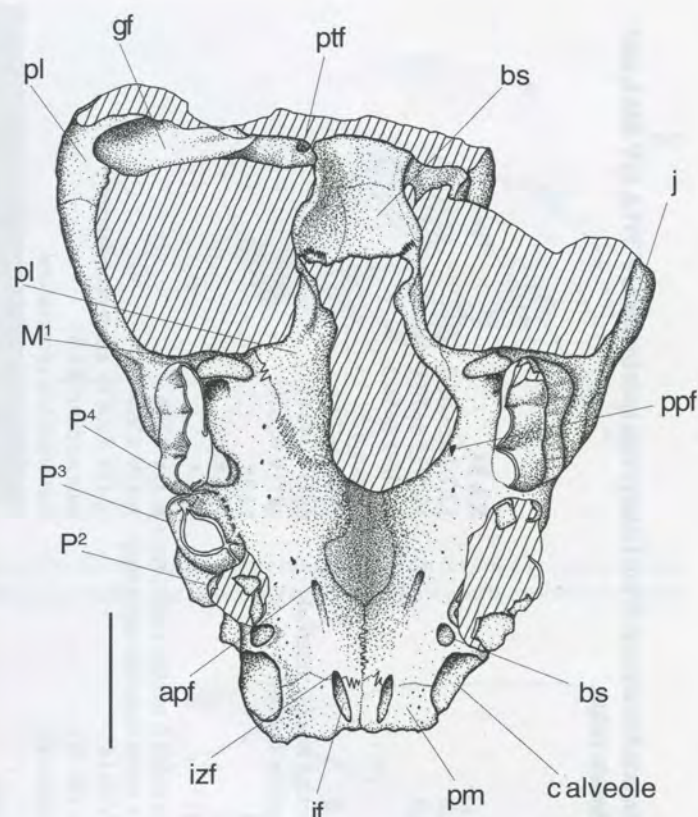


Figure 2A,B. *Pachycrocuta brevirostris* skull (GV 3914) in ventral view. Stippled lines indicate the probable course of the sutures. Wear facets are blank (Figure B). The scale bar equals 5 cm.

The postorbital processes of the jugals are large, oriented vertically and project slightly forwards rather than backwards. Below the orbit, the dorsal border of the jugal is flat and sloped, and reaches far anteroventrally.

All sutures in the specimen differ in accordance with their state of preservation or, in some cases, because of their ontogenetic development. Although some sutures in the forehead can be traced easily, their preservation in the palate is such that it is often impossible to distinguish between bone margins and fine cracks. Nevertheless, we include their most probable courses, using dotted lines (Figure 4). The maxilla-frontal suture reaches further posteriorly than in extant hyaenids. Unfortunately, the nasals are too imperfectly preserved to be measured accurately; they are comparatively long and broad relative to the width of the skull. In lateral view, the frontals slope down less abruptly than in extant hyaenids and the face is characterized by an upwardly tilted forehead.

The posterior portion of the maxilla and the posterior part of the jugal form the well developed cheek region, which bears a conspicuous impression between the roots of the upper P^4 (dented area of at least one square centimetre, compare Qiu 1987: 53).

The incisive foramina lie at the level of the anterior portion of the canine alveole and the incisive fossa reaches almost as far to the posterior as the hindmost point of the root of the second premolar. Premaxilla-maxilla sutures pass near the posterior end of the incisive foramen. The foramen incisivum is narrow at its posterior end, compared to extant *Hyaena* and

Crocuta. An index of the foramen palatinum anterior length versus fossa palatina length would be advantageous, but cannot be given. Judged from the position of the foramen palatinum anterior, there is greater similarity to the 'crocutoid' than to the 'hyaenid' type (compare Qiu 1987: 62).

The jugal-maxilla suture describes a regular curve some distance from the orbita in the rostral portion. The posterior course is more difficult to trace, but both features seem to be 'crocutoid'.

The dentition (Figure 5)

All teeth are heavily worn. M^1 is placed obliquely rather than perpendicularly in relation to the longitudinal axis of P^4 . From P^4 to P^2 the buccal outline describes a regularly curved line. The long axes of the two fourth premolars are almost parallel to each other.

M^1

Three distinct cusps have probably been developed. The upper first molars were worn down to a considerable extent by the talonid of M_1 , and their overall state of preservation is too imperfect to allow detailed description.

P^4

The P^4 is relatively broad; the metastyle blade runs just offline from the longitudinal tooth axis. It forms nearly a right angle with the longitudinal axis of the comparatively large protocone. The protocone is large and shorter than the parastyle, which in turn is not as long as the metastyle (see Table 1). The paracone cusp

TABLE 1.

Summary of comparative measurements in the skull and upper dentition (in mm), taken from *Pachycrocuta brevirostris* from Gladysvale specimens GV 3914, GV 4264, and from Kromdraai specimen KA 55. * = approximate value.

	GV 3914	GV 4264	KA 55
P ² w/l=ratio x100	11.9/19.0=62.8	12.0/17.5=68.6	12.7/18.5=68.7
P ³ w/l=ratio x100	17.9*/26.7=67.0	17.0/26.0=65.0	18.0/25.4=70.9
P ⁴ w/l=ratio x100	22.5/38.4=58.6	21.9/?	21.4/39.3=54.5
P ⁴ protocone diameter	at root 6.9	at root 5.7	at root 6.5
P ⁴ protocone w/l=ratio x100	7.6/9.1=83.5	6.0*/8.0*=75.0	7.0/9.2=76.1
P ⁴ protocone shape	massive, projecting far anteriorly	slender, projecting less far anteriorly	as GV 3914
P ⁴ parastyle	less massive than GV 4264 (wear?)	massive, anteriorly swollen	as GV 4264
P ⁴ parastyle length	12.0*	not preserved	11.1*
P ⁴ paracone length	12.4*	not preserved	13.1*
P ⁴ metastyle length	14.0*	not preserved	15.1*
P ² anterior cusp	no notch, less prominent than GV 4264	separated by a notch from the main cusp	as GV 4264
P ³ anterior cusp	no notch, more or less incorporated into main cusp	separated by a notch from the main cusp	as GV 4264
P ³ posterior cusp	distinct, but smaller than GV 4264	larger than GV 3914	as GV 4264 or more pronounced
tooth row P ² -P ⁴ (length)	more curved than GV 4264 (81.2)	faintly curved (80.0*)	intermediate (81.5)
P ² cingulum lingual	curvature pronounced	curvature pronounced	curvature less pronounced
shape of cingulum in general	intermediate	sharp edged	rounded
distance mx/j - P ⁴ alveole border	21.0*	30.0*	23.0*
M ¹ w/l	6.9/19.9	M ¹ ?present	?/16.0*
distance inf - averaged alveole height P ³	25.5	26.3*	25
minimum width of snout	at height of P ¹	at height of P ²	at height of P ¹
depression above P ⁴	present	present	not present
position of inf	at height between roots of P ³	at height of posterior part of P ³	at height of posterior part of P ³
anterior vertical edge of P ³	faintly developed, more linguo-posterior	developed more anterior	as GV 3914
cingulum buccally	faintly developed	more prominent	as GV 4264
skull length (P ² - posterior end of zyg.)	170.0*	?	168
max. canine alveole diameter	21.0*	?	19.5*
distance orbit - alveole P ⁴	45.0*	?	37.0*
length of orbit (measured parallel to tooth row)	33.9*	?	37.6*

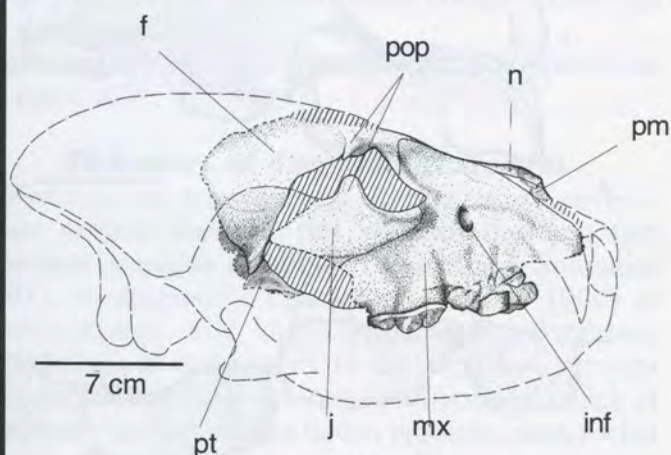


Figure 3A,B. Right lateral view of the skull of *Pachycrocota brevirostris* (GV 3914). Outline restoration based on recent *Crocota crocuta* specimens and on Turner & Anton (1996, Figure 2). Note the small orbit, the upwardly orientated face and the relatively short zygomatic arch. The scale bar equals 5 cm.

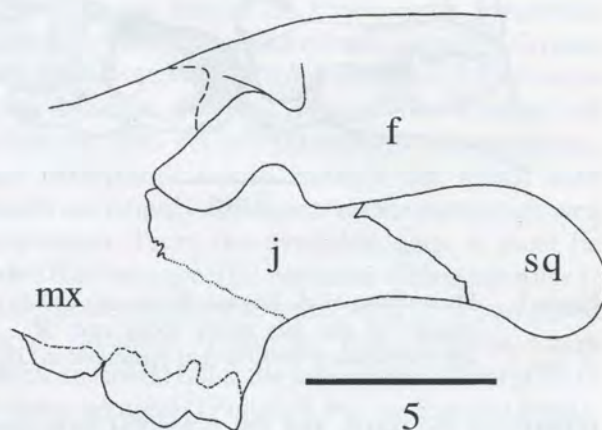


Figure 4A,B. Outline sketch of the skull of *Pachycrocota brevirostris* (GV 3914) in left lateral view, showing the reconstruction of the sutures on the zygomatic arch (Figure B). The scale bar equals 5 cm.

projects slightly posteriad. On the lingual wall of P⁴ the cingulum is weakly developed and, although worn off, appears to have persisted from the protocone to the posterior end of the metastyle. In buccal view the longitudinal grooves on the enamel diverge between metacone and paracone, paracone and parastyle. The anterior wear facet of the paracone of P⁴ (as described by Ewer 1954a: 189) is present and very small. The anterior obliquely inclined part of the wear facet of the protocone is worn down considerably by the paraconid and the main cusp of lower P⁴ (see Figure 5A,B).

P³

The P³ is rather slender, and within the tooth row its longitudinal axis forms an angle of about 25 degrees with the longitudinal axis of P⁴. The posterior cusp is clearly separated from the cingulum and moderately large. Between the main and the posterior cusp is a vestigial, oblique groove.

P²

The P² is fairly large and its longitudinal axis within the tooth row forms an angle of about 45 degrees with the longitudinal axis of P⁴. The posterior cusp is damaged, whereas the anterior is moderately developed and the lingual cingulum between the two roots is considerably curved (not figured).

Only the alveoli of P¹, not the teeth, are preserved (see Figure 2).

GV 4264 (Figures 6-8, measurements see Table 1)

This specimen consists of a left maxillary fragment belonging to an adult individual, including the infraorbital foramen and part of the dentition with P², P³ and a fragmentary P⁴ preserved (Figure 6-8).

On the maxilla above the roots of P⁴ is a depression similar to that in GV 3914. The minimum width of the snout is measured more toward the posterior (see Table 1). All teeth are less heavily worn than in GV 3914. Compared to GV 3914, the second premolar is smaller

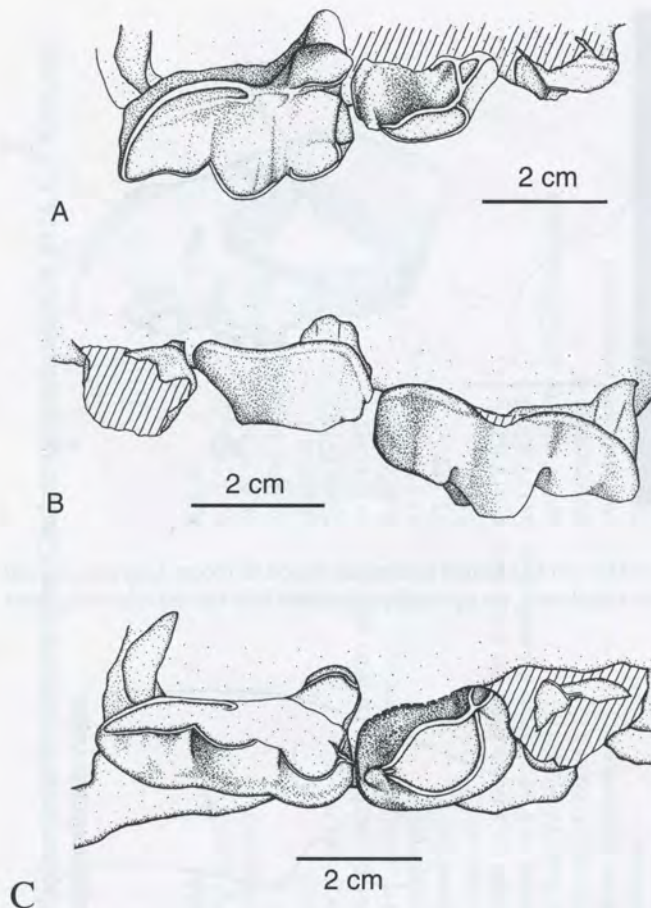


Figure 5. Illustrations of A. lingual, B. buccal, and C. occlusal aspects of the left upper tooth row (P^2 - M^1) of *Pachycrocuta brevirostris* as preserved in GV 3914.

relative to the third, and the premolar side cusps are much more prominent. When compared to the equivalent features in GV 3914, the P^4 extends further anteriorly, but this difference is probably due to wear in GV 3914 (Figures 7/8).

In the P^2 and P^3 , the lingual cingulum and all accessory cusps are more prominently developed than in GV 3914. The main cusp of the P^3 is more slender and smaller, while the anterior accessory cusp is positioned more anteriorly than mesially compared to GV 3914.

Only the P^4 protocone and parastyle are preserved. The parastyle appears to have been slightly smaller than in GV 3914, although no accurate measurements could be taken. The protocone is considerably smaller than in GV 3914 (see measurements in Table 1). In lateral view the infraorbital foramen lies exactly above P^3 , and the minimum width of the snout is measured across the anterior palatine foramina. Unfortunately, the fossae for the inferior oblique muscles are not preserved.

The curvature of the upper tooth row is much less pronounced in GV 4264 than in GV 3914.

In overall size, GV 3914 exceeds GV 4264 slightly.

Additional remarks

We did not observe the kind of wear facet preserved in GV 3914 protocone in any other fossil or extant specimen (Figures 5A and 5B). In KA-55, GV 3914, and GV 4264 the P^4 parastyle is worn off in various ways,

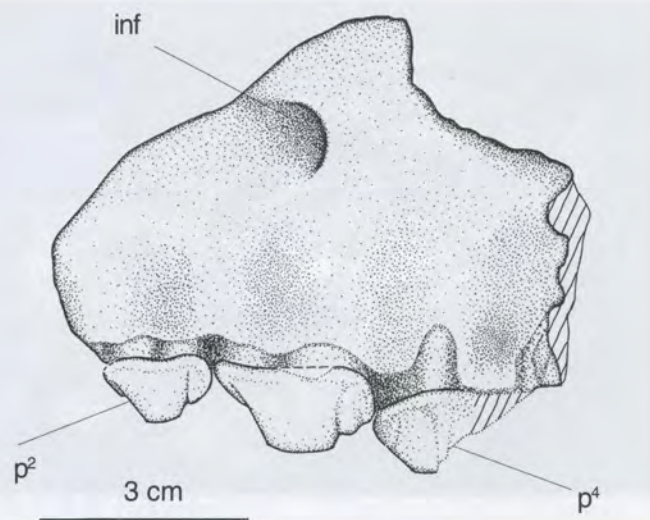


Figure 6. Lateral view of *Pachycrocuta brevirostris* maxillary fragment with P^2 , P^3 and anterior portion of P^4 in specimen GV 4264.

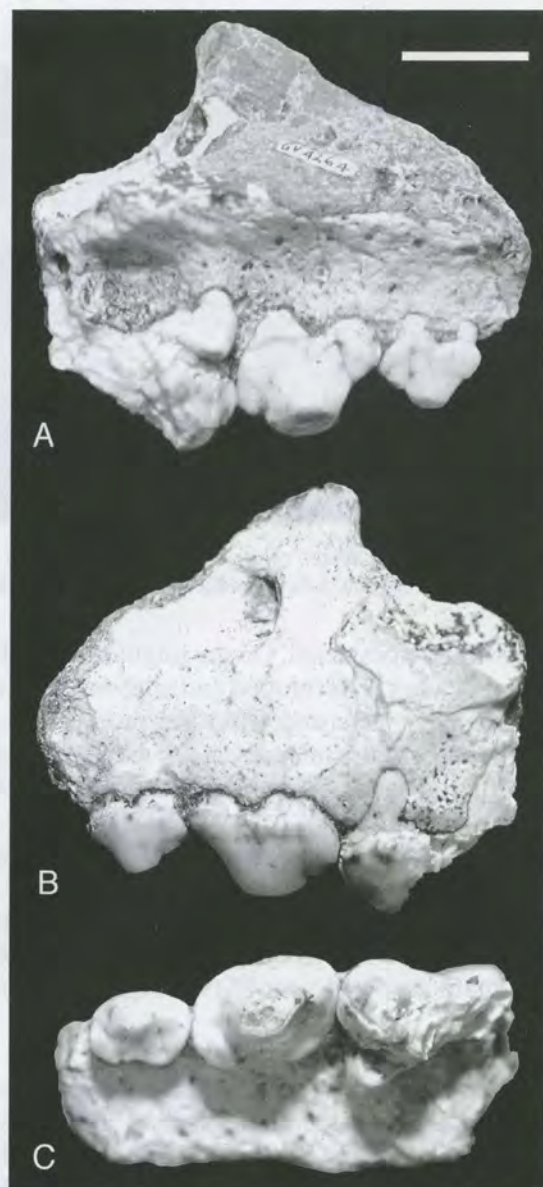


Figure 7. *Pachycrocuta brevirostris* (GV 4264), upper premolar tooth row as preserved in A. lingual, B. buccal, and C. occlusal views. The scale bar equals 2cm

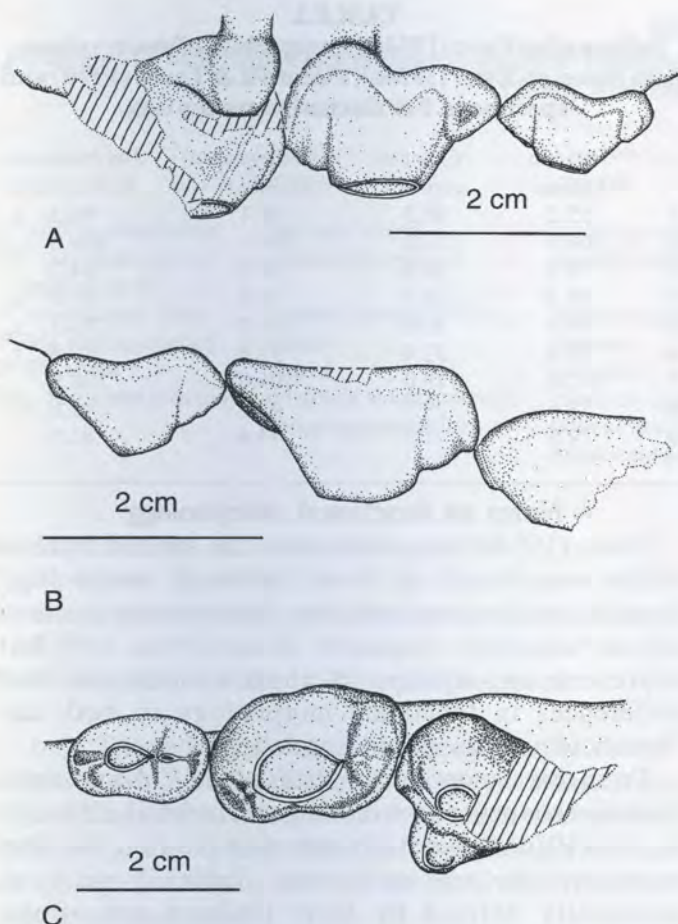


Figure 8. *Pachycrocuta brevirostris*. Line drawings of specimen GV 4264; upper premolar tooth row as preserved in A. lingual, B. buccal, and C. occlusal views. Note the size of the accessory cusps in relation to the main cusps in premolars 2 and 3.

making comparison difficult. In KA-55 the anterior wall is least worn off and therefore gives the impression of a comparatively large parastyle.

Non diagnostic characters in Gladysvale specimens attributed to *Pachycrocuta brevirostris*

There is a wide range of interpretations in the literature concerning the taxon-specific characters in fossil and extant hyaenids (see e.g. Qiu 1987: 59-67). Based on our comparative studies of fossil and extant hyaenids, we would suggest that, among the characters described in the South African specimens assigned to *Pachycrocuta brevirostris*, the following probably represent geographic or individual variation and should not be regarded as diagnostic features at the species level:

1. lingual cingulum is either sharply edged or rounded;
2. buccal cingulum variably pronounced;
3. varying massiveness of P² and P³ posterior side cusps (see Table 1);
4. P² and P³ anterior basal cusps variably distinct from paracones;
5. varying size of P⁴ protocone in relation to P⁴ parastyle;
6. varying curvature of tooth row;

7. varying distance between ventral border of orbit and alveolus of P⁴;
8. absence or presence of maxillary depression between roots of P⁴.

Discussion of diagnostic characters

Parahyaena brunnea and *Pachycrocuta perrieri* share certain features, but whether these in fact represent primitive retentions (Werdelin & Solounias 1991) or diagnostic characters (Turner 1990) is controversial, and the significance of certain morphological differences in the dentition remains unclear. Furthermore, taxonomic difficulties, which of course are directly related to this problem, render what would appear to be a simple generic assignment debatable (see e.g. Turner 1986: 208, 1987: 326).

Occasionally, in hyaenid taxonomy it may be a matter of interpretation whether to keep two samples in separate taxa or to unite them within the same taxon on the basis of considering 'only' dental characters. Examples can be found in *Pliohyaena pyrenaica orientalis* Qiu 1987 and *Pliocrocuta perrieri* (Croizet & Jobert, 1828) (see Werdelin & Solounias 1991; Guérin & Patou-Mathis 1996). The wide variety of interpretations also reflect taxonomic discrepancies, because groupings based merely on tooth size differences are heavily dependent on the sample chosen for comparison. From the available data, it must be concluded that intraspecific variation within samples is of considerable importance. Interestingly, if compared to other *P. brevirostris* samples from Eurasia, many South African fossils fall at the lower range of variability in tooth measurements (Figure 8, but see Randall 1981). It is in this context that the status of *P. perrieri* (see Kurtén 1956: 42) must be considered. *P. perrieri* is reported to be changing slightly in the course of its evolution and trending towards *Pachycrocuta brevirostris* (Werdelin & Solounias 1991: 22). Apart from absolute size, the only distinguishing feature between the two species is reported to be in the M₁ metaconid, which is always absent in *P. perrieri* (see Werdelin & Solounias 1991: 63). As already stated by Koufos (1992: 28), the length of the P⁴ metastyle is quite variable in *P. brevirostris*. Evidently, the taxonomic importance of what is most probably a polymorphic character has to be questioned in *P. brevirostris*, since this cusp is present in only four out of 29 specimens listed by Turner & Anton (1996); its mere presence therefore may indicate intraspecific variation. The solution to this problem may require reinvestigating the considerable dental variation within all *P. perrieri* samples – a task which is beyond the scope of the present study.

New east African remains from the Turkana Basin in Kenya were reported and compared to some of the known Eurasian *P. brevirostris* samples (Werdelin 1999). Interestingly, measurements of mandibular premolars 2,3 and 4 consolidate the taxonomic view adopted here on the basis of cranial and upper dentition features. Nonetheless, equivalent measurements of the upper premolar dentition in South African specimens

(Figure 9) remain within the extreme range of variability found in the Eurasian samples.

Revised diagnosis of *Pachycrocuta brevirostris* (Aymard, 1846)

Pachycrocuta brevirostris represents the largest known hyaenid, with an estimated skull length of around 300 mm (see Figure 1). According to Thackeray & Kieser (1992), an approximate body weight of 63 kg should be assumed based on lower carnassial length extrapolation. However, this weight appears to be underestimated, considering the fact that limb proportions indicate a shoulder height of 0.9 to 1 m (Turner & Anton 1996: 460). The size of the *Pachycrocuta* cranium presented in this paper suggests a markedly heavier body weight than proposed by Thackeray & Kieser (1992), but a lighter body weight than the approximately 125 kg of extant small female lions.

The skull is massive and broad, and the muzzle is comparatively short. Zygomatic arches are relatively short and broad. The tibia is proportionally shorter than the femur in comparison to extant hyaenids (Turner & Anton 1996: 460).

Not a single autapomorphic feature is currently held to be found in *P. brevirostris*. As a result of our analysis, we propose a group of presumably diagnostic dental characters:

1. P^1 normally present, occasionally small;
2. P^2 and P^3 proportionally similar to *Hyaena* and *Parahyaena*, less similar to *Crocota*;
3. M^1 present, large and only slightly obliquely positioned in relation to P^4 longitudinal axis.

Apart from its taxonomic weight, the hyaenid dentition reveals important information concerning functional morphology and allows conclusions about palaeoecology. Some suggestions have been brought forward in the literature, and in the following section we comment on some of these aspects concerning *P. brevirostris*.

TABLE 2.

Indices after Ewer (1954a). Comparison of mean values; data based on Ewer (1954a), Ficarelli & Torre (1970) and specimens. For discussion see the text.

	<i>Hyaena</i> <i>hyaena</i>	<i>Crocota</i> <i>crocota</i>	<i>Parahyaena</i> <i>brunnea</i>	<i>Pachycrocuta</i> <i>brevirostris</i>
1.	85.2	95.3	88.1	88.3
2.	104.0	133.0	104	109.8
3.	75.5	89.8	84.2	84.2
4.	33.3	44.7	35.2	37.9
5.	76.8	90.0	81.0	84.5
6.	52.8	72.4	53.8	62.5
7.	102.0	113.0	104.0	108.9
8.	43.5	29.7	47.7	42.6
9.	74.5	81.1	74.4	82.5

Notes on functional morphology

Ewer (1954a) has shown that the spotted hyaena differs considerably in dental functional morphology from its smaller extant relatives. The relevant features are not 'absolutely diagnostic' (Ewer 1954a: 189), but represent an attempt to show tendencies and differences in functional morphology in both the 'hyaenoid' and 'crocutoid' specializations.

From this standpoint, the status of the *P. brevirostris* dentition has never been investigated in detail, although Kurtén (1956) hinted at this important question. We here summarize the relevant features (Tables 2 and 3) as essentially defined by Ewer (indices 1-6 of the carnassial shear, indices 7-9 to show adaptation to crushing).

Comparison and interpretation of indices in Table 2

For the sake of clarifying ambiguity, the indices of functional significance as defined and applied by Ewer (1954a: 190-191) are:

1. P^4 length : combined lengths of P^2+P^3
2. M_1 length : P_4 length
3. Width across protocone : length of paracone + metacone of P^4
4. Metacone length : total length of P^4
5. Blade length of M_1 : total length of M_1

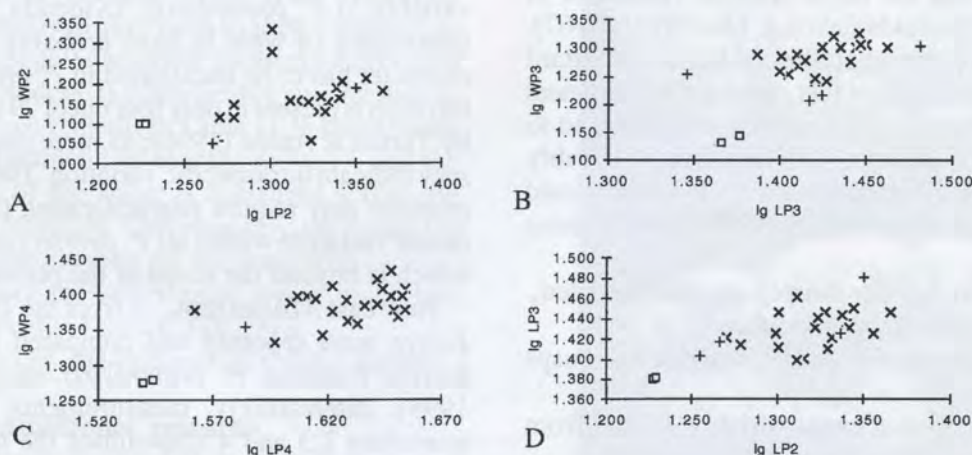


Figure 9 A-C. Bivariate plots of premolar length/width and D. length $P2/length P3$ ratio in lg (mm) of *Pachycrocuta brevirostris*. Taken from South African specimens (+: our data) and Eurasian specimens (x: from Turner & Anton 1996). Reference data is *Crocota crocuta* (squares), most of which is omitted for clarity of illustration. See also Werdelin (1999: 162-164).

TABLE 3.
Functionally interpreted morphology in the bone-cracking hyaenid dentitions. Based on Ewer (1954a, 1954b) and Kurtén (1988). For discussion see the text.

	<i>Hyaena hyaena</i>	<i>Crocota crocota</i>	<i>Parahyaena brunnea</i>	<i>Pachycrocota brevirostris</i>
P ⁴ slicing adaptation	less specialized	highly specialized	less specialized	intermediate
M ¹ size reduction in relation to P ⁴	moderately reduced	strongly reduced	reduced	moderately reduced
P ⁴ orientation: bone	sagittal chewing efficacy	almost sagittal	sagittal	sagittal
P ⁴ /P ₄ sliding contact	absent	present	absent	present
P ³ /P ₄ shear	absent	present	absent	absent or present
M ₁ : form and function	relatively shorter: tabloid chopping mechanism	relatively longer: taloid functionless, metaconid lost	relatively shorter: taloid chopping mechanism	relatively shorter taloid reduced

6. Blade length of M₁ : total length of P⁴
7. P₃ width : P₄ width
8. Parastyle length : length of paracone + metacone of P⁴
9. Width of P³ : width of P⁴ across protocone

1-6: These indices characterize efficiency of the carnassial blade. In all these indices *P. brevirostris* comes closest to the condition observed in *P. brunnea*, indicating the double function morphology of the chopping and slicing mechanism involving posterior premolars and molar.

7: The premolar accessory cusps are usually well developed in *P. brevirostris*, but there is also evidence which suggests considerable intraspecific variation. *H. hyaena* and *P. brunnea* show signs of reduction in the anterior accessory cusp of P⁴ (Ewer 1954a: 191), whereas *C. crocota* does not. *P. brevirostris* has an intermediate character in this sense: the P⁴ works less efficiently as a crusher compared to *Hyaena* and *Parahyaena*, but more efficiently than in *C. crocota*.

8,9: These indices reveal that the crushing function of the upper premolar teeth is not as efficient as observed in *P. brunnea*, index 8 being closer to *H. hyaena* but still far from the specialized condition developed in *C. crocota*. Index 9 reveals an even higher value in *P. brevirostris* than in *C. crocota*.

Admittedly, indices 7 and 9 are less appropriate for comparison, because the third premolar reflects rather the evolutionary level, as it has not yet reached the 'larger relative width' developed in younger taxa, as recognized by Qiu (1987). In our opinion, this diminishes the functional significance of these two indices. We conclude from the above that *P. brevirostris* was an efficient bone crusher but a less efficient meat slicer, compared to extant bone-cracking hyaenids.

Notes on body size, palaeoecology and behavior

Some morphologies in the carnivore skull and dentition are known to be directly correlated with body size (Kurtén 1973; Werdelin & Solounias 1990) and can reflect its evolutionary changes (Soergel 1936; Kurtén 1965). On the one hand, the body mass of the hyaena has been shown to be closely related to climatic change (Klein & Scott 1989; Thackeray & Kieser 1992), while

on the other hand animal size is undoubtedly related to hunting ability and social behavior (Skinner, Davis & Ilani 1980; Hennig 1986). Considering its large size, dental morphology and limb proportions, the feeding habits of *P. brevirostris* may also be reconstructed on the basis of faunal analyses, which mirror the palaeoecological circumstances. Extant hyaenas are, aside from their opportunistic adaptation to scavenging, successful at killing prey. Bagged prey constitutes a variable but considerable percentage of their diet (see e.g. Tilson, Blotnitz & Henschel 1980; Skinner, Henschel & van Jaarsveld 1986; Cooper 1990; Henschel & Skinner 1990; Sillero-Zubiri & Gottelli 1992). Despite the fact that hyaenas are well known as taphonomic agents (e.g. Thenius 1961, 1976; Mills & Mills 1977; Lam 1992; Marean, Spencer, Blumenschine & Capaldo 1992), bones found in hyaena dens can be correlated with high accumulations of ungulate populations (Skinner, Henschel & van Jaarsveld 1986). On the basis of the fossil record, Werdelin (1989: 389) concluded from the relatively short distal limb bones that *P. brevirostris* was not adapted as a pursuit predator, and Turner & Anton (1996) suggested that the behavior of *P. brevirostris* may be comparable to *C. crocota* of the Late Pleistocene. In this context it is interesting that the Gladysvale D-8 deposits more frequently revealed equid remains than other early hominid-bearing sites in South Africa. This may possibly correspond with the occurrence of a bone-accumulating agent (Berger 1992, 1993), such as *P. brevirostris*.

This hypothesis is speculative at the present time, but it is testable through faunal analysis (see Sutcliffe 1970; Blumenschine 1988; Marean, Spencer, Blumenschine & Capaldo 1992) in a chronological framework provided by ESR-dating. By contrast, carnivore tooth attrition (Lindeque & Skinner 1984: 293) and an encephalization quotient (Sheppey & Bernard 1984) may be regarded as less promising approaches to the task of widening palaeoecological understanding.

ABBREVIATIONS

Institutions

- AIUZ Anthropologisches Institut der Universität
Zürich (Switzerland)
- BPI Bernard Price Institute for Palaeontological

	Research, University of the Witwatersrand, Johannesburg (South Africa)
NMB	Naturhistorisches Museum Basel (Switzerland)
PIMUZ	Paläontologisches Institut und Museum der Universität Zürich (Switzerland)
FIS	Forschungsinstitut Senckenberg, Frankfurt (Germany)
TMP	Transvaal Museum, Pretoria (South Africa)
ZMUZ	Zoologisches Museum der Universität Zürich (Switzerland)

Localities (South Africa)

BF	Bolt's Farm
GV	Gladysvale Cave
KA	Kromdraai
M	Makapansgat
SK	Swartkrans
Sts	Sterkfontein

Localities (France)

Se	Senèze
St.V.	St-Vallier

Locality (Italy)

V.A.	Val d'Arno
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Measurements

l, length; w, width.

Morphology

apf	anterior palatine foramen
bs	basisphenoid
c	canine

dext.	dextra
f	frontal
gf	glenoid fossa
if	incisive fossa
inf	infraorbital foramen
izf	incisive foramen
j	jugal
M	molar
mx	maxillary
n	nasal
P	premolar
pl	palatine
pm	premaxillary
pop	postorbital processes
ppf	posterior palatine foramen
pt	pterygoid
ptf	pterygoid foramen
sin.	sinistra
sq	squamosum
zyg.	zygomatic (arch)

ACKNOWLEDGEMENTS

We would like to thank Mike Raath (BPI), Francis Thackeray and Heidi Fourie (both TMP), Gustav Anzenberger and Martin Häusler (AIUZ), Burkhardt Engesser (NHB), and César Claude (ZMUS) for assistance and/or access to specimens in their care. We are greatly indebted to Karl-Alban Hünemann (Mellingen, Switzerland) and Michael Morlo (FIS) for expert advice and fruitful discussions. We also appreciate the support and patience of Hans Rieber and Thomas Bolliger (both PIMUZ), who commented on earlier versions of the manuscript. Misha Kavka kindly revised the English. The efforts of Ina Plug and Francis Thackeray are especially appreciated; certain errors would have been inevitable without their thorough review. This research was supported by the Swiss National Science Foundation (Grant No. 31-43584.95 to Peter Schmid), the Palaeo-Anthropological Scientific Trust, the National Geographic Society, the Adolph H. Schultz-Foundation, and the Georges & Antoine Claraz-Donation.

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LOCOMOTOR AND HABITAT CLASSIFICATIONS OF CERCOPITHECOID POSTCRANIAL MATERIAL FROM STERKFontein MEMBER 4, Bolt's Farm AND SWARTKRANS MEMBERS 1 AND 2, SOUTH AFRICA

by

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ABSTRACT

Much southern African cercopithecoid postcranial material is not associated with craniodental remains. Consequently, this postcranial material cannot be confidently assigned to a particular taxon, with the result that little is known about the locomotor strategies and habitat preferences of specific Plio-Pleistocene cercopithecoids from southern Africa. However, cercopithecoid postcrania can provide important information about habitats that were present at fossil sites, even when the material is not attributed to taxa. In this paper, ecomorphic analysis is used to assign cercopithecoid postcranial material from Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2 to one of three habitat/locomotor categories: forest-living arboreal quadrupeds ('forest arboreal'), open habitat terrestrial quadrupeds ('open terrestrial') and open habitat cercopithecoids using a mix of arboreal and terrestrial quadrupedalism ('open mixed'). Cercopithecoids representing all three habitat categories were found in the samples from Sterkfontein Member 4 and Bolt's Farm, suggesting that monkeys using a range of habitats and locomotor strategies were present at these sites. However, no 'forest arboreal' cercopithecoids were found in the samples from Swartkrans Members 1 and 2, indicating that cercopithecoids at these localities probably depended largely on open habitats. The habitat and locomotor strategy data were also used in combination with locality-based listings of fossil cercopithecoid craniodental remains to suggest possible locomotor strategies for several southern African Plio-Pleistocene cercopithecoid taxa, including *Parapapio broomi* (possibly 'forest arboreal'), *Parapapio jonesi* ('open terrestrial'), *Papio robinsoni* ('open terrestrial') and *Cercopithecoides williamsi* ('open mixed').

KEYWORDS: Cercopithecoidea, postcranial, Plio-Pleistocene, ecomorphology

INTRODUCTION

The Pliocene and early Pleistocene deposits of Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2 (Gauteng Province, South Africa) have yielded a wide variety and relatively large number of fossils from the Cercopithecoidea (Primates, Mammalia). However, much of the postcranial material is not associated with craniodental material, with the result that it cannot be confidently taxonomically assigned (Szalay & Delson 1979). The lack of association between the craniodental and postcranial remains has also resulted in uncertainty over the locomotor repertoires of many Pliocene and Pleistocene fossil cercopithecoids from southern Africa, including members of the genera *Parapapio* and *Papio* (Szalay & Delson 1979).

To date, there has been very little work on these fossil cercopithecoid postcranial specimens. The most comprehensive study of taxonomically unassigned postcrania from southern African cercopithecoids was that of Ciochon (1993), who used multivariate analysis to assign various fossil specimens to the most likely genus and/or species of Plio-Pleistocene monkey.

In this paper, the approach is somewhat different. Taxon-free multivariate analysis is used to assign the postcranial specimens to the most likely locomotor

strategies and habitat preferences. This gives important and useful information about the range of habitats that were present in or around Sterkfontein, Bolt's Farm and Swartkrans, which in turn helps to reconstruct the environment inhabited by early hominins. Furthermore, while no attempt is made to taxonomically assign the cercopithecoid postcrania, the results of the habitat and locomotor analysis are used here to reconstruct the most likely locomotor strategies of southern African cercopithecoids from the Plio-Pleistocene.

Cercopithecoids have been used in several reconstructions of the palaeohabitats of southern African Plio-Pleistocene sites (Butzer 1974; McKee 1991; Reed 1997; Kuman *et al.* 1997; Clarke *et al.* 1998; Kuman & Clarke 2000). However, given that craniodental material is more easily identified, and often more prevalent than postcranial remains, the reconstructions of the probable habitats of these cercopithecoids often rely on assumptions based on the ecology of the most closely-related extant Old World monkey species, and there has been very little investigation of habitat preferences as suggested by postcranial morphology. This has created contradictions in the way individual cercopithecoid taxa have been used in habitat reconstruction: colobines, for example, have been used to indicate woodland or forest

(e.g. Kuman *et al.* 1997; Kuman & Clarke 2000), despite other research in which it is suggested that at least one Plio-Pleistocene colobine species, *Cercopithecoides williamsi*, found at Sterkfontein Member 4, Swartkrans Member 2 and Bolt's Farm, was 'hyper-terrestrial' (Birchette 1982, but see below for further discussion of this). In light of the importance of cercopithecoids in the reconstruction of palaeohabitat, it is therefore necessary and useful to review the postcranial evidence for habitat use and locomotor strategies in cercopithecoids from southern African Plio-Pleistocene sites, attributing habitat and locomotor preferences to individual species wherever possible.

MATERIALS AND METHODS

The analytical method used in this study was an ecomorphic one, in which morphological features, such as bone shape and muscle lever arms, are used to distinguish between cercopithecoid groups of different habitat preferences and locomotor types. Assigning postcranial material to habitat-type and locomotor strategy in this way makes it possible to reconstruct the habitat of fossil species without having to rely on assumptions based on the ecology of the most closely related extant species (Plummer & Bishop 1994). Additionally, as specimens used in this type of analysis need not be taxonomically assigned (Plummer & Bishop 1994), this technique is especially useful in assigning the taxon-less southern African Plio-Pleistocene cercopithecoid postcranial specimens to the relevant habitat and locomotor categories.

The proximal and distal humerus, proximal ulna, and distal femur from nine extant African cercopithecoid species, representing three habitat and locomotor categories (described below) were included in the comparative sample (Table 1). All but 10 of the 194 specimens used in this sample were from wild-shot adult individuals without obvious skeletal pathology. Ten of the *Theropithecus gelada* sample were captive animals but were judged sufficiently similar to wild-shot individuals in univariate analysis to include in the multivariate study. Maturity was judged by the epiphyseal fusion of all

postcranial elements, and only adults with complete or near-complete fusion were measured. The sample was not separated by sex because none of the fossil specimens used in this study could be assigned to male or female.

The modern comparative sample was divided into three habitat types: forest-living arboreal quadrupeds ('forest arboreal'), open habitat terrestrial quadrupeds ('open terrestrial') and open habitat cercopithecoids using a mix of arboreal and terrestrial quadrupedalism ('open mixed'). These classifications are based on data on wild-living primates, taken from the literature (Napier & Napier 1967; Gebo & Chapman 1995; McGraw 1998a, 1998b) and have been designed to reflect the spectrum of habitat use and locomotion seen in the African cercopithecoids.

The fossil sample comprised 40 cercopithecoids from Plio-Pleistocene deposits at Sterkfontein, Bolt's Farm and Swartkrans, held in the collections at the Bernard Price Institute and Department of Anatomical Sciences, University of the Witwatersrand, and the Transvaal Museum, Pretoria (Appendix 1). The specimens included in the sample were all well preserved. They represented only a fraction of the total amount of cercopithecoid postcranial material found at the sites under discussion, much of which was too badly damaged to be used in the analyses described below.

Linear measurements (Appendix 2), adapted from Ciochon (1993) and Bishop (1994), were taken with digital calipers on both the modern and fossil specimens, and entered directly into a laptop computer using a caliper interface. Very few complete bones are found in the southern African fossil cercopithecoid postcranial sample, so in this study, morphological features from only the proximal and distal ends were quantified. Measurements were transformed into simple ratios (Appendix 3), to reflect both shape and functional lengths over which muscles act, and also to reduce the effects of differential size between individuals. To ensure that it was morphology rather than body mass that was determining habitat classification, each ratio was regressed against the relevant species and sex mean body mass, taken from Smith & Jungers (1997). If the

TABLE 1.
Monkeys in Extant Comparative Sample, Body Mass and Habitat/Locomotor Classification

Species	N	Male body mass (kg)	Female body mass (kg)	Habitat and locomotor category
<i>Cercopithecus neglectus</i>	16	7.35	4.13	Forest arboreal
<i>Lophocebus albigena</i>	16	8.25	6.02	Forest arboreal
<i>Colobus guereza</i>	30	13.5	9.2	Forest arboreal
<i>Cercopithecus aethiops</i>	28	4.26	2.98	Open mixed
<i>Papio cynocephalus</i>	28	21.8	12.3	Open mixed
<i>Papio anubis</i>	27	25.1	13.3	Open mixed
<i>Papio ursinus</i>	20	29.8	14.8	Open mixed
<i>Papio hamadryas</i>	12	21.0	11.4	Open terrestrial
<i>Theropithecus gelada</i>	17	19	11.7	Open terrestrial

Body mass data from Smith & Jungers (1997)

Habitat and locomotor data from sources cited in text

adjusted- r^2 value for the regression of body mass and the ratio exceeded 0.3, that ratio was excluded from further analysis.

A multivariate statistical technique, discriminant function analysis (DFA), was used to examine whether the morphology of each bony element could be used to distinguish between cercopithecoids of different habitat and locomotor preferences. The FORWARD STEPDISC routine from SAS 6.12 (SAS Institute Inc, 1996) was used to determine the most useful classificatory variables and to reduce intercorrelation between ratios. Once the best discriminatory variables had been selected, the quadratic DISCRIM procedure from SAS 6.12 was used to calculate the discriminant function for membership in each habitat group, which was then used to reassign each individual modern specimen to the most probable of the three habitat categories. The misclassification rates were estimated using the standard resubstitution procedure. These estimates form the basis for assessing the correctness and utility of the DFA for each dataset. The discriminant functions calculated using the modern cercopithecoid sample were then applied to the fossil sample, to assign each fossil specimen to the most likely habitat category. Only fossils with the complete suite of variables for each bony element were included in the analysis, as the computer program automatically excluded incomplete specimens.

RESULTS AND DISCUSSION

Discriminant function analysis: modern sample

Table 2 details the resubstitution results (indicating the utility of each bone in distinguishing between cercopithecoids of different habitat and locomotor categories) for the bones in the modern cercopithecoid sample. The four bony elements used in this study (proximal and distal humerus, proximal ulna and distal femur) were selected because of their relatively high resubstitution results, as at least 80% of each sample was re-assigned to the correct habitat and locomotor categories; these resubstitution results are very similar to the resubstitution results reported in ecomorphic studies of bovid postcrania (Plummer & Bishop 1994; Kappelman *et al.* 1997). Further analysis of cercopithecoid postcranial material has demonstrated that two of the other major long bones, the radius and the tibia, along with the distal ulna and proximal femur, do not discriminate between cercopithecoids of different habitat preferences and locomotor strategies as effectively as the bony elements used in this study (Elton 2000). Specimens in the 'open terrestrial' and 'forest arboreal'

categories were both mainly reclassified into 'open mixed', and neither were frequently or extensively reclassified into one another (Tables 3–6), demonstrating that the DFA distinguished effectively between the two locomotor extremes for all the bony elements. The modern cercopithecoid species assigned to the 'open mixed' category share morphological features with species in both the 'forest arboreal' and 'open terrestrial' categories. Thus, specimens in the open habitat mixed locomotion category did not discriminate as well as specimens in the other two habitat categories, and specimens included in 'open mixed' were reassigned to both the 'forest arboreal' and the 'open terrestrial' categories (Tables 3–6). Again, this is similar to the results of ecomorphic studies on bovids, in which 'intermediate' forms were more extensively misclassified than either of the more 'extreme' forms (Plummer & Bishop 1994; Kappelman *et al.* 1997).

Misclassification of the type reported here is an inevitable part of discriminant function analysis (Plummer & Bishop 1994). In the analyses of the cercopithecoid proximal and distal humerus, proximal ulna and distal femur, less than one half of each species group, including those species that originally formed part of the 'open mixed' sample, were incorrectly assigned to habitat and locomotor category (see Elton 2000, for further details). In other ecomorphic studies, it has been suggested that this degree of misclassification is likely to represent normal morphological variation (Plummer & Bishop 1994), a factor for which it is difficult to control. Thus, the results of the DFA for the modern cercopithecoid comparative sample appear to be sufficiently reliable to use the discriminant functions to classify the fossil specimens. However, although the misclassification that occurred in the modern cercopithecoid sample is not unusual for an ecomorphic analysis of this type, the species assigned to the 'open mixed' group were less successfully reclassified than those assigned to the other categories, and it is possible that there is a greater uncertainty over the reliability of the classification of the fossil specimens that are assigned to 'open mixed'. The implications of this for habitat reconstruction are discussed below.

Discriminant function analysis: fossil sample

20% of the total fossil sample was assigned to the 'forest arboreal' category, with 30% assigned to 'open terrestrial' and 50% to 'open mixed' (Table 7, Figure 1). Of the 25 specimens from Sterkfontein Member 4, four (16%) were assigned to 'forest arboreal', 15 (60%)

TABLE 2.
Total Percentage of Modern Specimens correctly assigned for each element

Element	Total percentage of modern specimens correctly assigned	
	Proximal	Distal
Humerus	84	81
Ulna	80	-
Femur	-	81

TABLE3.
Proximal humerus resubstitution Summary

From habitat	Number of observations and percent classified into habitat			Total
	Forest arboreal	Open mixed	Open terrestrial	
Forest arboreal	51 82%	6 10%	5 8%	62 100%
Open mixed	15 14%	78 76%	10 10%	103 100%
Open terrestrial	0 0%	2 7%	27 93%	29 100%

TABLE4.
Distal humerus resubstitution Summary

From habitat	Number of observations and percent classified into habitat			Total
	Forest arboreal	Open mixed	Open terrestrial	
Forest arboreal	54 87%	7 11%	1 2%	62 100%
Open mixed	9 9%	67 65%	27 26%	103 100%
Open terrestrial	0 0%	3 10%	26 90%	29 100%

TABLE5.
Proximal ulna resubstitution summary

From habitat	Number of observations and percent classified into habitat			Total
	Forest arboreal	Open mixed	Open terrestrial	
Forest arboreal	53 87%	5 8%	3 5%	61 100%
Open mixed	15 15%	65 63%	23 22%	103 100%
Open terrestrial	0 0%	3 10%	26 90%	29 100%

TABLE6.
Distal femur resubstitution Summary

From habitat	Number of observations and percent classified into habitat			Total
	Forest arboreal	Open mixed	Open terrestrial	
Forest arboreal	50 81%	10 16%	2 3%	62 100%
Open mixed	14 14%	71 69%	18 17%	103 100%
Open terrestrial	0 0%	2 7%	27 93%	29 100%

were assigned to 'open mixed' and six (24%) were assigned to 'open terrestrial'. Nine specimens from Bolt's Farm were analysed. Of these, four (44%) were assigned to the 'forest arboreal' category, four (44%) were assigned to 'open mixed' and one (12%) was assigned to 'open terrestrial'. Five specimens from the Swartkrans Member 1 Hanging Remnant were analysed, none of which were assigned to 'forest arboreal'. Four (80%) of these specimens were assigned to 'open terrestrial', with one assigned to 'open mixed'. Only one specimen from Swartkrans Member 2 was suitable for inclusion in the analysis, and was assigned to 'open terrestrial'.

Only a small proportion of the total fossil sample from Sterkfontein Member 4, Bolt's Farm and Swartkrans was used in analysis, because much of the cercopithecoid postcranial material recovered from these sites was too badly damaged to be included in DFA. Thus, any discussion of the habitat preferences of cercopithecoids present at these sites is based on a small number of fossils, with the possibility that certain cercopithecoid groups may not be represented in the sample. This is especially true for the Swartkrans assemblage, where only six postcranial specimens were suitable for analysis. Interpretation of the results is made more complex by the potential for errors in classification, particularly from and into the 'open mixed' category. Appendix 1 gives the posterior probabilities, indicating the likelihood of membership in each of the three habitat/locomotor categories, for the fossils included in the sample. These probabilities, in combination with the resubstitution results generated from the analysis of modern cercopithecoids (Tables 3–6), indicate that it is unlikely that 'forest arboreal' specimens have been misclassified as 'open terrestrial', and vice versa, but a small number of 'forest arboreal' and 'open terrestrial' fossils may have been misclassified as 'open mixed'. Specimens may also have been misclassified out of 'open mixed' into either 'forest arboreal' or 'open terrestrial'. If misclassification has occurred, the patterns evident at Sterkfontein Member 4 and Bolt's Farm are unlikely to be greatly altered, as all three cercopithecoid habitat categories are

represented. At Swartkrans, the small numbers of cercopithecoid fossils have been assigned predominantly to the 'open terrestrial' category. Thus, even with misclassification, the monkeys would still be included in one of the open habitat categories, as misclassification rarely occurs between the 'open terrestrial' and 'forest arboreal' categories. However, it is possible that the specimen assigned to 'open mixed' may have been misclassified from 'forest arboreal'. In which case, and given the small sample that represents this site, it cannot be discounted that some monkeys may have been dependent on forest, although it appears that cercopithecoids from Swartkrans exploited predominantly open habitats.

Habitat preferences of Plio-Pleistocene cercopithecoids

Cercopithecoids belonging to all three habitat categories are found at Sterkfontein Member 4. From this evidence, it appears that the cercopithecoids in and around Sterkfontein in Member 4 times inhabited forest, as well as open woodland/bushland habitats and grassland. The presence of fossilized lianas (*Dichapetalum mombuttense*), dependent on large trees, supports the view that there were some closed habitats present at Sterkfontein Member 4 (Bamford 1999). Vrba (1974) suggested that the environment at Sterkfontein initially supported bushland and water loving species, later altering to a more open habitat. A similar pattern, with open woodland and bushland in Member 4 and more open habitats in Member 5 has also been reconstructed by Reed (1997). These reconstructions are consistent with the relatively large proportion of 'forest arboreal' and 'open mixed' cercopithecoids found at Sterkfontein Member 4, but 'open terrestrial' species, likely to be dependent on more open, grassland, habitats, are also present in the cercopithecoid sample from Sterkfontein Member 4. Carnivores are likely to have been one of the accumulation agents for the Sterkfontein assemblage (Clarke *et al.* 1998), and it is possible that a proportion of the 'open terrestrial' specimens were carried from a considerable distance. However,

TABLE 7.
Habitat categories and locomotor preferences of cercopithecoids from Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2.

Site From habitat	Number of specimens and percentage classified into each habitat and locomotor category			Total
	Forest arboreal	Open mixed	Open terrestrial	
Sterkfontein Mbr 4	4 16%	15 60%	6 24%	25 100%
Bolt's Farm	4 44%	4 44%	1 12%	9 100%
Swartkrans Mbr 1	0 0%	1 20%	4 80%	5 100%
Swartkrans Mbr 2	0 0%	0 0%	1 100%	1 100%
Total	8 20%	20 50%	12 30%	40 100%

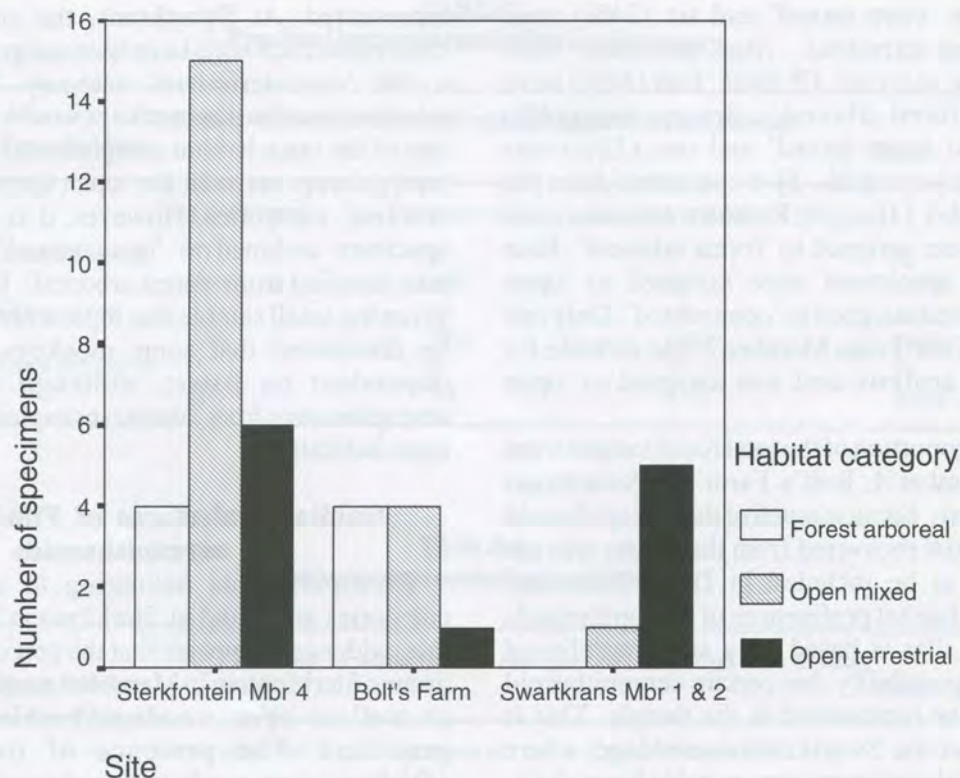


Figure 1. Habitat categories and locomotor preferences of cercopithecoids from Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2.

specimens assigned to 'open terrestrial' comprise very nearly one quarter of the total sample, and it is likely that this material does represent part of the habitat immediately surrounding the Sterkfontein site. Micromammal assemblages at Sterkfontein Members 4 and 5 appear to be variable, with evidence for riverine grassland species in both Members (Avery 2001), a result that corresponds well with the cercopithecoid-based habitat reconstructions.

Bolt's Farm is not a confirmed hominin site, and, to date, there has been very little research on its palaeohabitat. However, the site has yielded craniodental remains from at least three cercopithecoid species (Delson 1984), as well as taxonomically-unassigned cercopithecoid postcranial material, so the inclusion of the Bolt's Farm material gives useful information about the habitat and locomotor preferences of southern African monkeys. Bolt's Farm lies in close proximity to Sterkfontein and Swartkrans, and the cercopithecoid fauna is dated to around 2 Ma (Delson 1984). The inclusion of the Bolt's Farm cercopithecoids in the sample therefore complements the data derived from Sterkfontein Member 4 and Swartkrans Members 1 and 2. Cercopithecoids belonging to all three habitat types are in evidence in the Bolt's Farm sample, as is the case for Sterkfontein Member 4. This indicates that cercopithecoids inhabited grassland, bushland/open woodland, and forest environments at Bolt's Farm.

There were no 'forest arboreal' cercopithecoids in the sample from either Swartkrans Member 1 or Member 2, and as the majority of specimens were assigned to 'open terrestrial', it is probable that many of the Swartkrans cercopithecoids exploited relatively open habitats, such as grassland or open woodland, rather

than forest. Most reconstructions of the Swartkrans palaeohabitat show a predominantly open habitat (Vrba 1975; Watson 1993; Avery 1995; Reed 1997) with varying degrees of woodland or riverine forest surrounding the Blaaubank stream (Watson 1993; Avery 1995).

The Sterkfontein Member 4 and Bolt's Farm cercopithecoid samples contain a relatively large proportion of 'forest arboreal' specimens, which appear to be absent from the Swartkrans Member 1 and Member 2 sample (but see above for discussion of potential error associated with the habitat reconstructions). These results are in accordance with both Vrba (1975), who argued that, based on the representation of *Alcelaphini* and *Antelopini* relative to all other bovids, the Sterkfontein Type Site (Member 4) sampled more closed habitats whereas the Swartkrans sites contained more open habitat species, and Reed (1997), who also suggests that there are differences in tree cover and grassland at the two sites. Shipman & Harris (1988) concluded, however, that there is little significant habitat variability among the southern African cave sites. The results from the present study indicate that there were more closed habitat cercopithecoids at Sterkfontein and Bolt's Farm than there were at Swartkrans. However, further investigation into the habitat preferences of the Swartkrans cercopithecoids is necessary before this can be confirmed.

Probable locomotor behaviours of Plio-Pleistocene cercopithecoids from southern Africa

The primary aim of the research reported here was to assign Plio-Pleistocene cercopithecoid postcranial material to habitat and locomotor categories. However,

it is also possible, based on data from the present study, other data collected by the author (Elton 2000), and from sources that list the craniodental material found at the sites under investigation (Brain 1981; Delson 1984, 1988; Watson 1993; Turner *et al.* 1999), to make some suggestions as to possible locomotor strategies of southern African cercopithecoids. Such an exercise is necessarily tentative, particularly given the potential for sampling and classification errors, but may provide the foundation for more detailed investigation into the locomotor strategies of Plio-Pleistocene monkeys from southern Africa, an aspect of cercopithecoid palaeobiology that has been neglected to date.

Table 8 summarizes the occurrence data for primates found at Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2. Craniodental remains of *Cercopithecoides williamsi* have been identified from Sterkfontein Member 4, Bolt's Farm and Swartkrans Member 2. These sites have all yielded cercopithecoid postcrania assigned to at least one of the two open habitat categories ('open mixed' or 'open terrestrial'). Analysis of East African *C. williamsi* specimens (in particular, the partial skeleton KNM-ER 4420), has indicated that this species should be classified as 'open mixed' (Elton 2000), a result that is consistent with other, recent work on southern African *C. williamsi* locomotor behaviour (Ciochon 1993), although *C. williamsi* has also been described as 'hyper-terrestrial' (Birchette 1982). Thus, it is likely that *C. williamsi*, although a colobine, was not arboreal, and that its postcranial remains may form part of the open habitat sample at Sterkfontein, Bolt's Farm and Swartkrans.

P. robinsoni has been identified from craniodental material at all the sites included in this study (Delson 1984), although its presence at Sterkfontein Member 4 has been questioned (McKee 1993). It cannot be discounted that *P. robinsoni* was a forest-dweller, but it is more likely, based on both its high representation in the cercopithecoid craniodental assemblage at Swartkrans (Brain 1981) and the uncertainty over its presence at Sterkfontein Member 4, that it was an open

habitat monkey. Based on this reasoning, *P. ingens*, a very large cercopithecoid found at Swartkrans Member 1, may also have been an open habitat monkey. It is also worth noting that several postcranial specimens (SK 1506, SK 591d, SK unnumbered, and SK 591c) from Swartkrans Members 1 and 2, assigned to 'open terrestrial' in the present study, were classified in another multivariate study as *Papio cf. robinsoni* (Ciochon 1993), and may represent one or both of the *Papio* species at Swartkrans.

Based on the analysis of East African material, *T. oswaldi* is classified as 'open mixed' (Elton 2000). This reconstruction differs from traditional interpretations of the locomotor behaviour of this species, which has been argued to have a similar locomotor repertoire to the highly terrestrial *Theropithecus gelada* (Krentz 1993), although it shares postcranial features with both modern *Papio* and *Theropithecus* (Jolly 1972). However, it is possible that there is regional variation in habitat use and locomotion in such a geographically widespread taxon, so southern African forms of *T. oswaldi* may have been as terrestrial as the modern gelada.

The cercopithecoid species *C. williamsi*, *T. oswaldi*, *P. robinsoni* and *P. ingens* were argued above to be open habitat monkeys, using either a mix of arboreal and terrestrial locomotion, or being confined exclusively to terrestriality. However, both the Sterkfontein Member 4 and the Bolt's Farm samples contain postcranial specimens assigned to 'forest arboreal'. Thus, it is possible that some of the *Parapapio* species are forest living arboreal monkeys. One species of *Parapapio*, *P. broomi*, is known from Bolt's Farm, and as the other two species of cercopithecoid, *C. williamsi* and *P. robinsoni*, identified at this site are likely to have been open habitat monkeys, this indicates that *P. broomi*, in the absence of other, as yet undiscovered, cercopithecoid species, was a forest-living arboreal monkey. Three species of *Parapapio*, *P. broomi*, *P. whitei* and *P. jonesi*, have been discovered at Sterkfontein Member 4. *Parapapio* craniodental material, assigned to *P. jonesi*, has also been recovered from Swartkrans Member 1. If the small

TABLE 8.
Primates present at Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2.

	Sterkfontein Mbr 4	Bolt's Farm	Swartkrans Mbr 1	Swartkrans Mbr 2
<i>T. oswaldi</i>			✓	✓
<i>Pp. broomi</i>	✓	✓		
<i>Pp. jonesi</i>	✓		✓	
<i>Pp. whitei</i>	✓			
<i>P. izodi</i>	✓			
<i>P. robinsoni</i>	✓	✓	✓	✓
<i>C. williamsi</i>	✓	✓		✓
<i>Cercopithecoides</i> sp.			✓	
<i>P. ingens</i>			✓	
<i>Cercocebus</i> sp.			✓	
<i>A. africanus</i>	✓			
<i>P. robustus</i>			✓	✓

Data from Brain 1981; Delson 1984, 1988; Watson 1993; Turner *et al.* 1999

Swartkrans sample presented here is representative, 'forest arboreal' monkeys would be scarce, with the majority of cercopithecoids inhabiting open environments. Thus, it is plausible that *P. jonesi* was an open habitat monkey, possibly 'open terrestrial', inhabiting grassland at Sterkfontein and Swartkrans, and sympatric with arboreal *Parapapio* species at Sterkfontein. A degree of support for this scenario is provided by the results of another multivariate analysis of taxonomically-unassigned forelimb bones from southern African cercopithecoids, in which the specimens STS 377c and SWP 511 from Sterkfontein were attributed to *Parapapio* (Ciochon 1993). Both these specimens were assigned to the 'open terrestrial' category in the present study.

It is possible that different species within the genus *Parapapio* had different habitat preferences and locomotor strategies, with *P. broomi* being arboreal and *P. jonesi* terrestrial. Brain (1981 p.152) commented that it appeared 'remarkable' to find three synchronous species of *Parapapio* at Sterkfontein and other sites in southern Africa. However, there are several sympatric modern cercopithecoid taxa, such as species of *Cercopithecus* in West African forest habitats that forage in mixed-species groups (Fleagle 1988). *Cercopithecus* may provide an arboreal-habitat model for *Parapapio*, but if there was more significant variation in habitat use between *Parapapio* species, an apt ecological model may be *Macaca fascicularis* and *M. nemestrina* in Asia. These modern species are sympatric, with the secondary forest dwelling *M. fascicularis* being more arboreal than *M. nemestrina*, which often travels terrestrially, and inhabits upland and hilly areas (Fleagle 1988).

The taxon-free analysis of cercopithecoid postcranial specimens from Sterkfontein Member 4, Swartkrans Members 1 and 2, and Bolt's Farm indicated that there was variation in cercopithecoid habitat preferences and locomotor strategies within, and possibly between, these sites. In the absence of associated craniodental and postcranial material from southern African Plio-Pleistocene cercopithecoids, it is very difficult to assign postcranial material to a particular taxon, hindering investigation into their probable locomotor strategies. However, using a combination of occurrence data, the results of the ecomorphic analysis undertaken as part of this study, and other work on Plio-Pleistocene monkeys, it has been possible to make tentative suggestions as to the locomotor strategies of cercopithecoids from Sterkfontein Member 4, Swartkrans Members 1 and 2, and Bolt's Farm. Several of the cercopithecines, including *T. oswaldi*, *P. ingens*, *P. robinsoni* and *P. jonesi* may have been open habitat dwellers, with *T. oswaldi* argued to be best described as 'open mixed', and *P. jonesi* 'open terrestrial'. *P. robinsoni* may also have been 'open terrestrial'. Another cercopithecine, *P. broomi*, may have been a forest dwelling arboreal quadruped.

The one colobine represented by craniodental remains at the sites under discussion, *C. williamsi*, is likely to have been an open habitat monkey, described in this study as 'open mixed'. Thus, in the absence of other colobine species at Plio-Pleistocene sites in southern Africa, the presence of colobine craniodental remains does not necessarily indicate forest, although the presence of *P. broomi* specimens may do so.

CONCLUSIONS

The reconstructions of palaeohabitat from the cercopithecoid data for Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2 are generally consistent with other habitat reconstructions for these sites (Vrba 1974, 1975; Watson 1993; Avery 1995; Reed 1997; Bamford 1999; Kuman & Clarke 2000), although the presence of open habitat monkeys at Sterkfontein indicates that there might be more grassland in Member 4 times than is presently supposed. Monkeys assigned to all three habitat categories ('forest arboreal', 'open mixed' and 'open terrestrial') are present at the earlier sites of Sterkfontein Member 4 and Bolt's Farm, but the habitat preferences and locomotor repertoires of cercopithecoids appear to change during the Plio-Pleistocene, with a reduction of 'forest arboreal' monkeys at the more recent site of Swartkrans. This result corresponds well with the pattern of hominin occurrence at these sites: *A. africanus*, found at Sterkfontein Member 4, had an arboreal component to its locomotor behaviour (Wood & Richmond 2000), whereas *P. robustus*, found at the apparently much more open localities of Swartkrans Members 1 and 2, but not at Sterkfontein Member 4, appears to have no morphological features associated with arboreality (Wood & Richmond 2000).

ACKNOWLEDGEMENTS

I thank the Directors and staff of the Department of Anatomical Sciences, Medical School, University of the Witwatersrand, Johannesburg, and the Transvaal Museum, Pretoria, for permission to study the fossil cercopithecoid material in their care. Particular thanks are due to L. Berger, R. Clarke and L. Backwell at the University of the Witwatersrand and H. Fourie and F. Thackeray at the Transvaal Museum. I am also grateful for permission for, and help in, the study of modern cercopithecoid material at the Transvaal Museum, Pretoria; the South African Museum, Cape Town; the National Museums of Kenya, Nairobi; the Powell-Cotton Museum, Kent; the Natural History Museum, London; the National Museum of Natural History, Smithsonian Institution, Washington D.C.; the American Museum of Natural History, New York; the Museum of Central Africa, Tervuren, Belgium; the Musée d'Histoire Naturelle, Brussels; the Department of Anthropology, Zurich-Ifchel University; the Royal Museum of Scotland, Edinburgh; the Laboratory for Human Evolutionary Studies, University of California, Berkeley; and the Museum of Vertebrate Zoology, University of California, Berkeley. I thank two anonymous reviewers and L. Berger for their helpful and pertinent comments on this paper. Thanks also to B. Smith, C. Eagle, L. Bishop and B. Wood for invaluable comments on an earlier version of this work. The research was funded by a grant from The Wellcome Trust Bioarchaeology Panel.

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APPENDIX 1.
Southern African Taxonomically-unassigned postcranial specimens used in habitat analysis

Specimen	Site	Element	DFA posterior probabilities [†]			Habitat category
			FA	OM	OT	
SWP 1140	Sterkfontein Mbr 4	Distal humerus	0.000	0.998	0.002	Open mixed
SWP 1156	Sterkfontein Mbr 4	Proximal ulna	0.019	0.978	0.003	Open mixed
SWP 1176	Sterkfontein Mbr 4	Distal humerus	0.003	0.989	0.008	Open mixed
SWP 1211	Sterkfontein Mbr 4	Distal humerus	0.000	1.000	0.000	Open mixed
SWP 1262	Sterkfontein Mbr 4	Distal humerus	0.008	0.596	0.397	Open mixed
SWP 1271	Sterkfontein Mbr 4	Distal humerus	0.000	0.998	0.002	Open mixed
SWP 504	Sterkfontein Mbr 4	Proximal humerus	0.276	0.551	0.173	Open mixed
SWP 506	Sterkfontein Mbr 4	Distal humerus	0.000	0.915	0.085	Open mixed
SWP 509	Sterkfontein Mbr 4	Distal humerus	0.000	0.870	0.130	Open mixed
SWP 512	Sterkfontein Mbr 4	Distal humerus	0.000	0.676	0.324	Open mixed
SWP 525	Sterkfontein Mbr 4	Proximal ulna	0.020	0.961	0.019	Open mixed
SWP 962	Sterkfontein Mbr 4	Proximal humerus	0.257	0.735	0.008	Open mixed
STS 377c	Sterkfontein Mbr 4	Distal humerus	0.002	0.274	0.725	Open terrestrial
SWP 1287	Sterkfontein Mbr 4	Distal humerus	0.000	0.001	0.999	Open terrestrial
SWP 1572	Sterkfontein Mbr 4	Proximal ulna	0.000	0.077	0.923	Open terrestrial
SWP 510	Sterkfontein Mbr 4	Distal humerus	0.000	0.000	1.000	Open terrestrial
SWP 511	Sterkfontein Mbr 4	Distal humerus	0.039	0.365	0.597	Open terrestrial
STS 1905	Sterkfontein Mbr 4	Distal femur	0.968	0.018	0.014	Forest arboreal
SWP 1175	Sterkfontein Mbr 4	Distal femur	1.000	0.000	0.000	Forest arboreal
SWP 1535	Sterkfontein Mbr 4	Distal femur	1.000	0.000	0.000	Forest arboreal
SWP 1710	Sterkfontein Mbr 4	Distal femur	0.987	0.013	0.000	Forest arboreal
ST #?	Sterkfontein Mbr 4	Distal femur	0.157	0.842	0.002	Open mixed
SWP 1532	Sterkfontein Mbr 4	Distal femur	0.005	0.995	0.000	Open mixed
SWP 1717	Sterkfontein Mbr 4	Distal femur	0.052	0.777	0.172	Open mixed
STS 549	Sterkfontein Mbr 4	Distal femur	0.001	0.258	0.742	Open terrestrial
BF 47	Bolt's Farm	Distal humerus	0.079	0.921	0.000	Open mixed
BF 49	Bolt's Farm	Distal humerus	0.000	0.974	0.026	Open mixed
BF 55	Bolt's Farm	Proximal humerus	0.013	0.614	0.373	Open mixed
BF 56	Bolt's Farm	Distal humerus	0.003	0.678	0.319	Open mixed
BF 48	Bolt's Farm	Proximal humerus	0.001	0.076	0.923	Open terrestrial
BF 26	Bolt's Farm	Distal femur	1.000	0.000	0.000	Forest arboreal
BF 30	Bolt's Farm	Distal femur	0.998	0.002	0.000	Forest arboreal
BF 33 b	Bolt's Farm	Distal femur	1.000	0.000	0.000	Forest arboreal
BF 35 a	Bolt's Farm	Distal femur	0.997	0.003	0.000	Forest arboreal
SK 1506	Swartkrans Mbr 1*	Distal humerus	0.076	0.324	0.600	Open terrestrial
SK 591 d	Swartkrans Mbr 1*	Proximal ulna	0.000	0.056	0.944	Open terrestrial
SK #?	Swartkrans Mbr 1*	Distal humerus	0.004	0.056	0.940	Open terrestrial
SK 1500	Swartkrans Mbr 1*	Distal femur	0.317	0.636	0.047	Open mixed
SK 1817	Swartkrans Mbr 1*	Distal femur	0.073	0.309	0.618	Open terrestrial
SK 591c	Swartkrans Mbr 2	Distal humerus	0.000	0.012	0.988	Open terrestrial

* Swartkrans Mbr 1 specimens used in analysis are part of 'Hanging Remnant' assemblage

APPENDIX 2.1

Humerus measurements used in the analysis

Measurement	Description
Anteroposterior Head Diameter	Maximum diameter of the humeral head in the anteroposterior plane
Mediolateral Head Diameter	Maximum diameter of the humeral head in the mediolateral plane
Bicipital Groove Width	Minimum width of the bicipital groove at its centre
Bicipital Groove Depth	Maximum width of the bicipital groove at its centre
Greater Tuberosity Maximum Width	Maximum anteroposterior width of the greater tuberosity
Lesser Tuberosity Maximum Width	Maximum anteroposterior width of the lesser tuberosity
Biepicondylar Width	Maximum width across the distal humerus between the epicondyles
Mediolateral Articular Surface Width	Maximum mediolateral width of the articular surface across the anterior surface of the distal humerus
Medial Trochlea Distal Projection	Maximum distal projection of the medial side of the trochlea
Olecranon Fossa Depth	Greatest depth of the olecranon fossa
Olecranon Fossa Width	Maximum width of the olecranon fossa in the mediolateral plane
Posterior Trochlear Articular Surface Width	Greatest mediolateral width of the posterior trochlear articular surface
Trochlear Gutter Width	Maximum mediolateral width of the trochlear gutter on the posterior of the distal humerus

Measurements and descriptions adapted from Ciochon (1993)

APPENDIX 2.2

Ulna measurements used in the analysis

Measurement	Description
Radial Notch Width	Maximum linear width of the radial notch
Radial Notch Height	Maximum height of the radial notch
Trochlear Notch Midline Height	Minimum height of the trochlear notch at its midline
Trochlear Notch/Olecranon Length	Length of the olecranon process taken from the proximoposterior surface of the trochlear notch
Trochlear Notch/Olecranon Width	Maximum width of the olecranon process
Proximal Trochlear Notch Width	Maximum width of the proximal part of the trochlear notch articular surface
Distal Trochlear Notch Width	Maximum width of the distal part of the trochlear notch articular surface
Coronoid Process Projection	Maximum anterior projection of the coronoid process
Radial Notch Posterior Width	Minimum width of the shaft posterior to the radial notch
Trochlear Notch Posterior Width	Minimum width of the shaft posterior to the trochlear notch

Measurements and descriptions adapted from Ciochon (1993)

APPENDIX 2.3.

Femur measurements used in the analysis

Measurement	Description
Intercondylar notch to patellar groove	Minimum distance between the intercondylar notch and the patellar groove, measured anteroposteriorly
Patellar groove to posterior medial condyle	Maximum anteroposterior distance between the patellar groove and the posterior aspect of the medial condyle
Breadth of medial condyle	Maximum mediolateral breadth of the medial condyle
Breadth of lateral condyle	Maximum mediolateral breadth of the lateral condyle
Length of medial condyle	Maximum posterodistal length of the medial condyle
Length of lateral condyle	Maximum posterodistal length of the lateral condyle
Intercondylar distance	Maximum distance between the most medial extent of the lateral condyle and the most lateral extent of the medial condyle

Measurements adapted from Bishop (1994)

APPENDIX 3.1
Proximal humerus ratios used in the analysis

Ratio abbreviation	Composition	Demonstrates
HS	Anteroposterior head diameter x 100 / mediolateral head diameter	Humeral head shape
HP2	Maximum proximal head projection x 100 / mediolateral head diameter	Humeral head shape
BGS	Bicipital groove depth x 100 / bicipital groove width	Bicipital groove depth
BGW	Bicipital groove width x 100 / mediolateral head diameter	Bicipital groove width
GTUB	Greater tuberosity maximum width x 100 / anteroposterior head diameter	Greater tuberosity size
LTUB	Lesser tuberosity maximum width x 100 / anteroposterior head diameter	Lesser tuberosity size

APPENDIX 3.2
Distal humerus ratios used in the analysis

Ratio abbreviation	Composition	Demonstrates
TS	Anteroposterior lateral trochlea diameter x 100 / distal trochlea width	Trochlea shape
MTP	Trochlea projection x 100 / biepicondylar width	Extent of trochlea projection
OFD	Olecranon fossa depth x 100 / olecranon fossa width	Olecranon fossa shape
PTA1	Posterior trochlear articular surface width x 100 / biepicondylar width	Size of the posterior articular surface
PTA2	Posterior trochlear articular surface width x 100 / trochlear gutter width	Size of the posterior articular surface
PTA3	Posterior trochlear articular surface width x 100 / anteroposterior lateral trochlear diameter	Size of the posterior articular surface
TGW	Trochlear gutter width x 100 / biepicondylar width	Size of trochlear gutter

APPENDIX 3.3
Proximal ulna ratios used in the analysis

Ratio abbreviation	Composition	Demonstrates
RNS	Radial notch height x 100 / radial notch width	Radial notch shape
OH2	Trochlear notch-olecranon length x 100 / trochlear notch midline height	Olecranon height
OS	Trochlear notch-olecranon length x 100 / trochlear notch-olecranon width	Olecranon shape
TNS	Distal trochlear notch width x 100 / proximal trochlear notch width	Trochlear notch shape
RNW	Radial notch width x 100 / radial notch posterior width	Radial notch width
CPP	Coronoid process projection x 100 / trochlear notch posterior width	Coronoid process projection

APPENDIX 3.4
Distal femur ratios used in the analysis

Ratio abbreviation	Composition	Demonstrates
CL	Length lateral condyle x 100 / length medial condyle	Difference in condyle length
IFMC	Intercondylar notch to patellar groove distance x 100 / length medial condyle	Medial condyle length
SLC1	Breadth lateral condyle x 100 / length lateral condyle	Lateral condyle shape
SMC3	Length medial condyle x 100 / patellar groove to posterior medial condyle	Medial condyle shape
CB	Breadth lateral condyle x 100 / breadth medial condyle	Difference in condyle breadth
ICLB	Breadth lateral condyle x 100 / intercondylar distance	Lateral condyle breadth
ICD2	Intercondylar distance x 100 / patellar groove to posterior medial condyle	Intercondylar distance

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