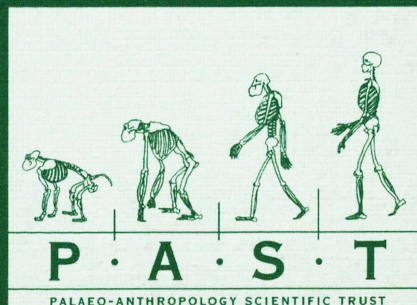


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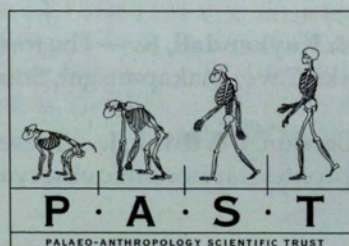
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A review of Robert Broom's therapsid holotypes: have they survived the test of time?

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While still a medical student in Scotland in the late 1880s, Robert Broom had already identified the principal aim of his scientific career as being 'to solve the problem of the origin of the mammals'. In Australia, between 1892 and 1896, his work on extant and fossil marsupials and monotremes established that, contrary to the then prevailing scientific opinion which supported a polyphyletic origin for mammals from a diverse range of amphibians and reptiles, the most important living class had been monophyletically derived, most likely from a lineage of Karoo therapsid reptiles. Later, on a trip to the United States in 1909/10 he revived the theory which proposed the existence of a close relationship between the South African therapsids and the Permian 'pelycosaur' reptiles of North America. The third, and most extensive element of Broom's task was carried out almost exclusively in South Africa over a period spanning more than half a century during which he created 369 therapsid holotypes, 168 of which were allocated to new genera. This paper establishes that of those holotypes, approximately 57% currently remain valid according to the parameters defined herein. While such a figure may initially seem to support Broom's reputation as an 'arch splitter', it may equally be reflective of the fragmentary state of therapsid systematics at the time when Broom carried out the majority of his research. Today, Broom is most widely-remembered for the celebrated series of fossil hominid discoveries which he made towards the end of his life in the limestone caves of the Transvaal. However, because the task of unravelling the story of the evolution of the mammals was the one which first motivated his interest in science and which formed the single continuous thread running throughout a long and otherwise varied career, it is perhaps still more accurate to view Broom principally as one of the great Karoo (and, in particular, therapsid) palaeontologists.

Keywords: Robert Broom, Therapsida, therapsid holotypes, validity, mammalian evolution.

INTRODUCTION

'The mammal-like reptiles of South Africa may be safely regarded as the most important fossil animals ever discovered, and their importance lies chiefly in the fact that there is little or no doubt that among them we have the ancestors of the mammals, and the remote ancestors of man. Even in the forms that cannot be directly ancestral, we have evidences of the most interesting collateral branches, the study of which throws the most instructive light on the processes of evolution' (Broom 1932).

So begins Robert Broom's monograph, *'The Mammal-like Reptiles of South Africa and the Origin of Mammals'*, one of the first and certainly the most extensive of the early reviews of therapsid systematics. Within this branch of palaeontology the Karoo Basin of South Africa is uniquely positioned in that it provides an almost complete evolutionary story of the creatures which present 'the best documented example in the fossil record of an evolutionary sequence connecting two major structural grades' (Hopson 1987), an 80-million year period during which the various lineages of 'mammal-like reptiles' progressively bridged the transition between the primitive, reptilian state and the advanced, mammalian condition.

From Broom's perspective the therapsid lineage was particularly intriguing in that he saw behind its development the presence of an evolutionary force of a 'different type which appears to have foreseen the future' (Broom 1932) and thus the perfect justification for the anti-evolutionary (or, to be more exact, anti-Darwinian) views of the prominent Victorian palaeontologist Richard Owen and his own somewhat contrived theory of 'creative evolution' (Findlay 1972). Although Broom's metaphysical position

has since fallen out of favour (if, indeed, it was ever seriously regarded – see, for example, Strkalj (1996)) his work in documenting the entire history of mammalian evolution remains, in a purely palaeontological sense, an epic undertaking.

As early as 1885, when acting as secretary for his local natural history society in Glasgow, Broom had evinced an interest in the Karoo reptiles, and by the late 1880s, while still a medical student at the University of Glasgow, he had already identified the principal objective of his scientific career as being to 'solve the problem of the origin of the mammals' (Findlay 1972). In 1892, his quest took him to Australia where in addition to intermittent bouts of duty as a *locum tenens*, he intensively studied the anatomy of both extant and fossil marsupials and monotremes, (the latter being recovered mainly from the important Wombeyan Cave site which Broom himself had discovered in 1893) (Findlay 1972). In a series of articles (*inter alia*, Broom 1895, 1896, 1899a) despatched from various New South Wales mining towns, Broom established, to his own satisfaction at least, the monophyletic origin of the mammals, thereby rebutting the then prevailing theory that the most important living class had been polyphyletically derived from a diverse range of reptiles and amphibians.

Two decades later, on an infamous trip to the United States in 1909/10, during which he sold to the American Museum of Natural History a series of exquisite therapsid specimens which he viewed as his own personal property but which Louis Péringuey, then the Director of the South African Museum, considered part of the country's

national heritage, Broom had the opportunity to study the AMNH's extensive collection of reptile fossils which had been obtained from the Permian beds of North America (Findlay 1972). In a resulting paper (Broom 1910), described by Watson (1952) as 'the most important he ever wrote', Broom resuscitated the theory, first propounded by Cope in 1881 (Broom 1938b), which established a close affinity between the North American 'pelycosaurs' and the South African therapsids. Subsequently, Broom identified the varanopseid 'pelycosaur' *Elliotsmithia longiceps* from an undescribed specimen which had been discovered by van Hoepen 20 years earlier at Abrahamskraal, near Prince Albert (Broom 1937b). To date, *Elliotsmithia longiceps* remains the only 'pelycosaur' taxon attributable to the Karoo Basin of South Africa (see also Modesto *et al.* 2001).

Long since convinced that the most ancient origins of the mammals were to be found not in the hills of New South Wales but rather in the rich fossiliferous beds of the Karoo Basin, Broom had left Australia in 1896 and travelled to South Africa. It was there, between the time of his first arrival in the country in 1897 and his death in 1951 that he carried out the most extensive element of his task. During that 54-year period he described several hundred therapsid holotypes, a significant proportion of which were allocated to new genera. The purpose of the present paper is to enumerate, more than half a century after Broom's death, the current validity of those holotypes, at both the specific and generic levels, and thus also to attempt to place Broom's scientific contribution in an appropriate historical context and to evaluate the extent of the continuing influence of his research on therapsid palaeontology.

SOURCES AND TECHNIQUES

Each of Broom's therapsid holotypes is described in the Appendix. Holotypes described up to 1932 are established by reference to the 1932 monograph, although the publication in which the holotype was originally described is also specified. Post-1932 holotypes are established by reference to the individual publication in which the relevant holotype was first described and each such publication is also specified in the Appendix.

Broom's now archaic model of therapsid systematics, which he established in 1932, whereby the Therapsida were divided into five orders (Dinocephalia, Therocephalia, Gorgonopsia, Anomodontia and Cynodontia) and six suborders (Bauriamorpha, Burnetiamorpha, Dromasauria, Ictidosauria, Rubidgea and Rubidginoidea), is not retained here. However, where the context requires, archaic spellings (such as '*Aulacocephalodon*', '*Udenodon*' and 'Karoo') are retained.

For holotypes described up to 1932, only generic names accepted by Broom on or prior to that date are given in the Appendix. Where a generic name change has first been proposed by an authority other than Broom, that authority is not specified in the Appendix but can be traced by reference to the relevant source publication. Similarly, where a post-1932 holotype has undergone more than one subsequent generic name change, only the

most recently established generic name is specified in the Appendix, although again the full generic history may be identified by referring to the relevant source publication.

Unless otherwise noted in the Appendix, the continuing validity or invalidity of a holotype has been established, primarily, by reference to the following sources:

Dinocephalia – King 1988.

Therocephalia – van den Heever 1987; Brink 1988; J.A.

Hopson, pers. comm., 2002.

Gorgonopsia – Sigogneau-Russell 1989.

Anomodontia – King 1988.

Cynodontia – Hopson & Kitching 1972; J.A. Hopson, pers. comm., 2002.

Biarmosuchia – Sigogneau-Russell 1989.

From the abovementioned primary sources it is apparent that the review of both Broom's anomodont and therocephalian holotypes has been particularly fragmentary. Accordingly, with respect to those orders, unless a specific authority responsible for synonymizing a particular holotype is actually quoted, or a specific authority is referred to as providing a complete or extensive review of the synonymies in a particular area, only the primary source is referred to in the Appendix and the full taxonomic history may be identified by reference to the bibliography contained therein.

The parameters applied to establish whether or not a particular holotype continues to be valid have been liberally set. Owing primarily to the effects of diagenetic distortion, a considerable number of Broom's holotypes are currently regarded as indeterminate or otherwise called into question. However, unless a particular holotype has been positively 'sunk', either by Broom himself or by another authority, into an alternative species and/or genus it is regarded herein as valid, with any doubt which has been expressed concerning the holotype being referred to in the relevant comments section in the Appendix.

RESULTS AND ANALYSIS

By reference to the sources detailed in the preceding section it can be established that Broom described a total of 369 therapsid holotypes, of which 210 continue to be valid according to the applicable definition; a continuing validity rate of 56.91%. Those holotypes include a total of 168 genotypes, of which 93 continue to be valid according to the applicable definition; a continuing validity rate of 55.36%. A more detailed breakdown of continuing validity, by reference to the individual orders, follows:

Order	Total HT*	Valid HT	Validity (%)	Total GT*	Valid GT	Validity (%)
Dinocephalia	25	13	52	18	8	44.44
Therocephalia	79	49	62.02	58	42	72.41
Gorgonopsia	57	44	77.19	29	17	58.62
Anomodontia	162	94	58.02	31	17	54.84
Cynodontia	39	4	10.26	27	4	14.81
Biarmosuchia	7	6	85.70	5	5	100

*HT = holotypes; GT = genotypes.

It can be seen from the table that the continuing validity rates for those orders (such as the Therocephalia and the Gorgonopsia) which to date have not been subject to a high degree of taxonomic revision are significantly higher than the rates for those orders (such as the Anomodontia and, in particular, the Cynodontia) that have been more intensively studied. This strongly suggests that, over time, the aggregate validity rate for Broom's therapsid holotypes will decline even further as more and more currently poorly understood taxa become better known.

An alternative method of analysis also reveals that whereas Broom's main influence as a therapsid palaeontologist has traditionally been regarded to have come to an end with his move from the Northern Cape Province to Pretoria in 1934, 177 of his therapsid holotypes, or approximately 48%, were actually described between 1934 and 1951, almost exclusively as a result of his close connection with the amateur collector Sidney Rubidge and the particularly fossil-rich localities surrounding Rubidge's farm at Wellwood near Graaff-Reinet in the Eastern Cape Province. Those two periods may also be summarized in terms of continuing validity rates as follows:

Period	Total HT*	Valid HT	Validity (%)	Total GT*	Valid GT	Validity (%)
1897–1932	192	117	60.94	102	62	60.78
1934–1951	177	93	52.54	66	31	46.97

*HT = holotypes; GT = genotypes.

Although only around 37% (66 of 177) of the holotypes which Broom described between 1934 and 1951 were allocated to new genera (compared to more than 53% for the period 1897–1932), the continuing validity rates attributable to the latter period actually decrease *vis-à-vis* the earlier period in terms of both holotypes and genotypes. These figures are somewhat ambiguous; but when they are considered in conjunction with the fact that between 1934 and 1951 Broom was also creating numerous new hominid and other mammalian taxa from Sterkfontein and its related sites (Broom & Schepers 1946; Broom & Robinson 1950, 1952), many of which are now regarded as superfluous, they do not offer any evidence that Broom progressively adopted a more conservative method of classification even though by that time therapsid palaeontology itself had achieved a much greater degree of systematic resolution.

CONCLUSIONS

It has been shown in the preceding section that of the total of 369 therapsid holotypes which Broom described during his career (in itself a prodigious number), 168 (or approximately 45.5%) were allocated to new genera. Further, if the order Anomodontia (the order which was by far the best described by 19th century palaeontologists and thus the one on which Broom was least able to stamp his own brand of diversity) is removed from the analysis the ratio of new genera rises to 66.2% (137 new genera from a total of 207 holotypes). Of the total number of

holotypes slightly less than 57% currently remain valid (a figure which is likely to decline even further in the coming years), and in one remarkable instance, no fewer than 21 of Broom's *Dicynodon* holotypes have since been ascribed to a single species of anomodont – *Oudenodon baini* Owen (King 1988).

While the above figures would appear to justify Broom's reputation, attributed to him from various sources, as an 'arch splitter' (Findlay 1972), and while it would be naïve to assume that in adopting such an approach he did not have at least one eye on posterity, it is also arguable that Broom's method of classification was the most practicable one available to a palaeontologist working, as he did, in the early stages of the twentieth century, in rudimentary conditions and with a very sparse initial database. In the absence of an integrated overall picture, 'Occam's razor' is a difficult instrument to wield, and consolidation in any science tends to be a discipline best carried out by those with more sophisticated methods of analysis and greater resources of reference material at their disposal.

Today, Broom is chiefly remembered for the internationally-renowned discoveries of hominid fossils which he made in the limestone caves of the Transvaal between 1936 and 1951 and which, along with the finds of the Leakey family in East Africa and Eugene Dubois in south-east Asia, still set the basic parameters in the story of human origins. However, while Broom was of course well aware of the publicity value of the material emerging from Sterkfontein, Swartkrans and Kromdraai during those years and the potency of the story of human evolution that they revealed, his belated entry into palaeoanthropology does seem to contain something of an opportunistic air, predicated as it was upon his resentment of the generally hostile reception afforded outside South Africa to Raymond Dart's discovery of the 'Taung Child' in 1925 (Dart 1951) as well as the desperate financial straits which he found himself in immediately before his appointment as chief palaeontologist at the Transvaal Museum in 1934 (Findlay 1972).

Conversely, it was the task of shedding light on the story of the evolution of the mammals, and in particular of the therapsid lineage, that first motivated Broom's interest in palaeontology and formed the subject matter of the vast majority of his 450 publications throughout every stage of a long and otherwise varied career. This, arguably, marks the pinnacle of his scientific achievements. All of these facts, taken together, lead inevitably to the conclusion that Broom began as, and remained for the rest of his life, a Karoo palaeontologist at heart. It is appropriate, therefore, that *The Mammal-like Reptiles of South Africa* ends with a homage to the notable Karoo fossil hunters of the past. In its concluding chapter Andrew Geddes Bain, William Atherstone, Joseph Orpen, Alfred 'Gogga' Brown, Dr D.V. Kannemeyer and the Revd J.H. Whaits, to name but a few, are all afforded their due recognition. These are still the great pioneering names of South African palaeontology. That list, at least, has survived the test of time; except that now, of course, it must also include Robert Broom.

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APPENDIX: Robert Broom's therapsid holotypes

DINOCEPHALIA

(*Titanosuchus*) *Jonkeria cloetei* (new species)

Holotype described: Broom 1903c

Validity: Species valid

Comments: Genus reassigned to *Jonkeria* van Hoepen (Broom 1929); Boonstra (1969) considers the specimen indeterminate

Scaptonodon duplessisi (new genus and species)

Holotype described: Broom 1904d

Validity: Genus and species invalid

Comments: Synonymized with *Titanosuchus ferox* Owen (Boonstra 1969)

Archaeosuchus cairncrossi (new genus and species)

Holotype described: Broom 1905c

Validity: Genus and species valid

Comments: Originally classified by Broom as a therocephalian; Boonstra (1969) considered the holotype a *nomen nudum*

- Pelosuchus priscus* (new genus and species)
Holotype described: Broom 1905c
Validity: Genus and species invalid
Comments: Synonymized with *Keratocephalus moloch* von Huene (Boonstra 1969)
- Eccasaurus priscus* (new genus and species)
Holotype described: Broom 1909
Validity: Genus and species valid
Comments: Boonstra (1969) considers the specimen determinable only as an anteosaurid
- Moschops capensis* (new genus and species)
Holotype described: Broom 1911b
Validity: Genus and species valid
- Moschognathus whaitsi* (new genus and species)
Holotype described: Broom 1914b
Validity: Genus invalid; species valid
Comments: Genus reassigned to *Moschops* Broom (Boonstra 1969)
- Dinartamus vanderbyli* (new genus and species)
Holotype described: Broom 1923
Validity: Genus and species valid
Comments: Boonstra (1969) considered the specimen indeterminate
- Dinophoneus ingens* (new genus and species)
Holotype described: Broom 1923
Validity: Genus invalid; species valid
Comments: Genus reassigned to *Jonkeria* van Hoepen (Boonstra 1969)
- Enobius strubeni* (new genus and species)
Holotype described: Broom 1923
Validity: Genus and species valid
Comments: Boonstra (1969) considered the specimen indeterminate
- Criocephalus vanderbyli* (new genus and species)
Holotype described: Broom 1928b
Validity: Genus and species valid
- Taurocephalus lerouxi* (new genus and species)
Holotype described: Broom 1928b
Validity: Genus and species valid
- Anteosaurus minor* (new species)
Holotype described: Broom 1929
Validity: Species invalid
Comments: Synonymized with *Anteosaurus magnificus* Watson (Boonstra 1969)
- Dinosphageus haughtoni* (new genus and species)
Holotype described: Broom 1929
Validity: Genus invalid; species valid
Comments: Genus reassigned to *Jonkeria* van Hoepen (Boonstra 1969)
- Dinocynodon dubius* (new genus)
Holotype described: Broom 1929
Validity: Genus invalid
Comments: Original classification as genus *Titanosuchus* Owen retained (King 1988); Boonstra (1969) considered the specimen indeterminate
- Jonkeria crassus* (new species)
Holotype described: Broom 1929
Validity: Species invalid
Comments: Synonymized with *Jonkeria haughtoni* Broom (Boonstra 1969)
- Jonkeria pugnax* (new species)
Holotype described: Broom 1929
Validity: Species invalid
Comments: Synonymized with *Jonkeria ingens* Broom (Boonstra 1969)
- Jonkeria vanderbyli* (new species)
Holotype described: Broom 1929
Validity: Species valid
- Phoneosuchus angusticeps* (new genus and species)
Holotype described: Broom 1929
Validity: Genus and species invalid
Comments: Synonymized with *Jonkeria truculenta* van Hoepen (Boonstra 1969)
- Scullya gigas* (new genus and species)
Holotype described: Broom 1929
Validity: Genus and species valid
Comments: Boonstra (1969) considered the specimen indeterminate
- Taurops macrodon* (new genus and species)
Holotype described: Broom 1932
Validity: Genus and species invalid
Comments: Synonymized with *Tapinocephalus atherstonei* Owen (Boonstra 1969)
- Dinoplus atrox* (new genus and species)
Holotype described: Broom 1936a
Validity: Genus and species invalid
Comments: Synonymized with *Jonkeria truculenta* van Hoepen (Boonstra 1969)
- Dinosuchus vorsteri* (new genus and species)
Holotype described: Broom 1936a
Validity: Genus and species invalid
Comments: Synonymized with *Anteosaurus magnificus* Watson (Boonstra 1969)
- Struthiocephalus milleri* (new species) (with E.C.Olson)
Holotype described: Broom & Olson 1937
Validity: Species invalid
Comments: Synonymized with *Struthiocephalus whaitsi* Haughton (Boonstra 1969)
- Struthiocephalus rheederi* (new species)
Holotype described: Broom 1937b
Validity: Species invalid
Comments: Synonymized with *Struthiocephalus whaitsi* Haughton (Boonstra 1969)
- THEROCEPHALIA**
- Ictidosuchus primaevus* (new genus and species)
Holotype described: Broom 1900
Validity: Genus and species valid
- Ictidosaurus angusticeps* (new genus and species)
Holotype described: Broom 1903d
Validity: Genus and species valid
- Lycosuchus vanderrieti* (new genus and species)
Holotype described: Broom 1903a
Validity: Genus and species valid
- Lycosuchus mackayi* (new species)
Holotype described: Broom 1903d
Validity: Species valid
Comments: Determinable only to the level of an early therocephalian or gorgonopsian (van den Heever 1987)
- Scylacosaurus sclateri* (new genus and species)
Holotype described: Broom 1903d
Validity: Genus and species valid

Scymnosaurus ferox (new genus and species)
 Holotype described: Broom 1903d
 Validity: Genus and species valid
 Comments: Determinable only to the level of a lycosuchid (van den Heever 1987)

Glanosuchus macrops (new genus and species)
 Holotype described: Broom 1904f
 Validity: Genus and species valid

Priesterognathus baini (new species)
 Holotype described: Broom 1904f
 Validity: Species invalid
 Comments: Synonymized with *Glanosuchus macrops* Broom (van den Heever 1987)

Melinodon simus (new genus and species)
 Holotype described: Broom 1905b
 Validity: Genus and species valid
 Comments: Originally classified by Broom as a bauriamorph

Aelurosuchus browni (new genus and species)
 Holotype described: Broom 1906
 Validity: Genus and species valid
 Comments: Originally classified by Broom as a bauriamorph; may ultimately be synonymized with *Bauria cynops* Broom (J.A. Hopson, pers. comm., 2002)

Arnognathus parvidens (new genus and species)
 Holotype described: Broom 1907c
 Validity: Genus and species valid
 Comments: Determinable only to the level of a scylacosaurid (van den Heever 1987)

(*Scymnosaurus*) *Moschorhinus warreni* (new genus and species)
 Holotype described: Broom 1907a
 Validity: Genus and species invalid
 Comments: Genus reassigned to *Moschorhinus* Broom (Broom 1932); synonymized with *Tigrisuchus simus* Owen (J.A. Hopson, pers. comm., 2002)

Alopecodon priscus (new genus and species)
 Holotype described: Broom 1908
 Validity: Genus and species valid

Alopecodon rugosus (new species)
 Holotype described: Broom 1908
 Validity: Species invalid
 Comments: Synonymized with *Alopecodon priscus* Broom (van den Heever 1987)

Hyaenosuchus whaitsi (new genus and species)
 Holotype described: Broom 1908
 Validity: Genus and species invalid
 Comments: Synonymized with *Lycosuchus vanderrieti* Broom (van den Heever 1987)

Pardosuchus whaitsi (new genus and species)
 Holotype described: Broom 1908
 Validity: Genus and species valid

Trochosuchus acutus (new genus and species)
 Holotype described: Broom 1908
 Validity: Genus and species valid
 Comments: Determinable only to the level of a lycosuchid (van den Heever 1987)

Bauria cynops (new genus and species)
 Holotype described: Broom 1909
 Validity: Genus and species valid
 Comments: Originally classified by Broom as a bauriamorph

Arctosuchus tigrinus (new genus)
 Holotype described: Broom 1911b

Validity: Genus valid
 Comments: Genus reassigned from *Lycosaurus* Owen; specimen possibly a gorgonopsian (Sigogneau-Russell 1989)

Eriphostoma microdon (new genus and species)
 Holotype described: Broom 1911b
 Validity: Genus and species valid
 Comments: Specimen possibly a gorgonopsian (Sigogneau-Russell 1989)

Ictidognathus parvidens (new genus and species)
 Holotype described: Broom 1911b
 Validity: Genus and species valid

Alopecorhinus parvidens (new genus and species)
 Holotype described: Broom 1912b
 Validity: Genus and species valid
 Comments: Holotype considered a *nomen dubium* (van den Heever 1987)

(*Ictidognathus*) *Ictidostoma hemburyi* (new genus and species)
 Holotype described: Broom 1912b
 Validity: Genus and species valid
 Comments: Genus reassigned to *Ictidostoma* Broom (Broom 1930b)

(*Priesterognathus*) *Cynariognathus platyrhinus* (new genus and species)
 Holotype described: Broom 1912b
 Validity: Genus and species valid
 Comments: Genus reassigned to *Cynariognathus* Broom (Broom 1932); determinable only to the level of a scylacosaurid (van den Heever 1987)

Bauria watsoni (new species)
 Holotype described: Broom 1914a
 Validity: Species invalid
 Comments: Originally classified by Broom as a bauriamorph; synonymized with *Bauria cynops* Broom (J.A. Hopson, pers. comm., 2002)

Alopecognathus angusticeps (new genus and species)
 Holotype described: Broom 1915
 Validity: Genus and species invalid
 Comments: Synonymized with *Glanosuchus macrops* Broom (van den Heever 1987)

Cerodon tenuidens (new genus and species)
 Holotype described: Broom 1915c
 Validity: Genus and species valid
 Comments: Determinable only as an early therocephalian (van den Heever 1987)

Icticephalus polycynodon (new genus and species)
 Holotype described: Broom 1915b
 Validity: Genus and species valid
 Comments: Determinable only to the level of an ictidosuchid (van den Heever 1987)

Simorhinella baini (new genus and species)
 Holotype described: Broom 1915b
 Validity: Genus and species valid

Scylacoides ferox (new genus and species)
 Holotype described: Broom 1915c
 Validity: Genus and species valid
 Comments: Specimen is possibly a gorgonopsian (van den Heever 1987)

Scylacorhinus falkenbachii (new genus and species)
 Holotype described: Broom 1915c
 Validity: Genus and species invalid
 Comments: Synonymized with *Scylacosaurus sclateri* Broom (van den Heever 1987)

Scymnosaurus watsoni (new species)

Holotype described: Broom 1915b

Validity: Species valid

Comments: Determinable only to the level of a scylacosaurid (van den Heever 1987)

(*Trochosuchus*) *Trochosaurus major* (new species)

Holotype described: Broom 1915c

Validity: Species valid

Comments: Genus reassigned to *Trochosaurus* Haughton (Broom 1932); determinable only to the level of a lycosuchid (van den Heever 1987)

Alopecopsis atavus (new genus and species)

Holotype described: Broom 1920

Validity: Genus and species invalid

Comments: Synonymized with *Theriognathus microps* Owen (J.A. Hopson, pers. comm., 2002)

(*Ictidosuchus*) *Ictidosuchoides longiceps* (new genus and species)

Holotype described: Broom 1920

Validity: Genus and species valid

Comments: Genus reassigned to *Ictidosuchoides* Broom (Broom 1930b)

Moschorhinus kitchingi (new species)

Holotype described: Broom 1920

Validity: Species invalid

Comments: Synonymized with *Tigrisuchus simus* Owen (J.A. Hopson, pers. comm., 2002)

Alopecodon minor (new species)

Holotype described: Broom 1925

Validity: Species invalid

Comments: Synonymized with *Alopecodon priscus* Broom (van den Heever 1987)

Baurioides watsoni (new genus and species)

Holotype described: Broom 1925

Validity: Genus and species invalid

Comments: Originally described by Broom as a bauriamorph; synonymized with *Bauria cynops* Broom (juvenile specimen) (J.A. Hopson, pers. comm., 2002)

Ictidoparia brevirostris (new genus and species)

Holotype described: Broom 1925

Validity: Genus and species valid

Comments: Indeterminable – type specimen is lost (van den Heever 1987)

Notosollasia laticeps (new genus and species)

Holotype described: Broom 1925

Validity: Genus and species invalid

Comments: Synonymized with *Theriognathus microps* Owen (J.A. Hopson, pers. comm., 2002)

Pristerognathus vanderbyli (new species)

Holotype described: Broom 1925

Validity: Species invalid

Comments: Synonymized with *Glanosuchus macrops* Broom (van den Heever 1987)

Pristerognathus vanwyki (new species)

Holotype described: Broom 1925

Validity: Species invalid

Comments: Synonymized with *Pristerognathus minor* Haughton (Broom 1932); synonymized with *Glanosuchus macrops* Broom (van den Heever 1987)

Euchambersia mirabilis (new genus and species)

Holotype described: Broom 1930b

Validity: Genus and species valid

Lycideops longiceps (new genus and species)

Holotype described: Broom 1930b

Validity: Genus and species valid

Whaitsia major (new species)

Holotype described: Broom 1930b

Validity: Species invalid

Comments: Synonymized with *Theriognathus microps* Owen (J.A. Hopson, pers. comm., 2002)

Microhelodon eumerus (new genus)

Holotype described: Broom 1931

Validity: Genus invalid

Comments: Originally described as *Microgomphodon eumerus* Seeley (Cynodontia); originally classified by Broom as a bauriamorph; classified as a cynodont by Hopson & Kitching (1972); tentatively identified as a juvenile specimen of *Bauria cynops* (J.A. Hopson, pers. comm., 2003)

Alopecideops gracilis (new genus and species)

Holotype described: Broom 1932

Validity: Genus and species valid

Comments: Determinable only to the level of a scylacosaurid (van den Heever 1987)

Hofmeyria atavusi (new genus and species)

Holotype described: Broom 1935c

Validity: Genus and species valid

Hyenosaurus platyceps (new genus and species)

Holotype described: Broom 1935c

Validity: Genus and species invalid

Comments: Synonymized with *Theriognathus microps* Owen (J.A. Hopson, pers. comm., 2002)

Lycedops scholtzi (new genus and species)

Holotype described: Broom 1935b

Validity: Genus and species valid

Comments: Determinable only to the level of a scylacosaurid (van den Heever 1987)

Cerdosuchoides brevidens (new genus and species)

Holotype described: Broom 1936a

Validity: Genus and species valid

Cerdosuchus aulodon (new genus and species)

Holotype described: Broom 1936a

Validity: Genus and species invalid

Comments: Synonymized with *Notaelurodon kitchingi* Broom (J.A. Hopson, pers. comm., 2002)

Cynariognathus gallowayi (new species)

Holotype described: Broom 1936a

Validity: Species invalid

Comments: Synonymized with *Glanosuchus macrops* Broom (van den Heever 1987)

Moschorhinus minor (new species)

Holotype described: Broom 1936a

Validity: Species invalid

Comments: Synonymized with *Tigrisuchus simus* Owen (J.A. Hopson, pers. comm., 2002)

Moschorhynchus latirostris (new genus and species)

Holotype described: Broom 1936a

Validity: Genus and species invalid

Comments: Synonymized with *Theriognathus microps* Owen (J.A. Hopson, pers. comm., 2002)

Notaelurodon kitchingi (new genus and species)

Holotype described: Broom 1936a

Validity: Genus and species valid

Comments: Determinable only to the level of an akidnognathid (van den Heever 1987)

Notaelurops paucidens (new genus and species)
 Holotype described: Broom 1936a
 Validity: Genus and species invalid
 Comments: Synonymized with *Theriognathus microps* Owen (Brink 1988)

Notosollasia luckhoffi (new species)
 Holotype described: Broom 1936a
 Validity: Species invalid
 Comments: Synonymized with *Theriognathus microps* Owen (J.A. Hopson, pers. comm., 2002)

Trochorhinus vanhoepeni (new genus and species)
 Holotype described: Broom 1936a
 Validity: Genus and species valid
 Comments: Determinable only to the level of a lycosuchid (van den Heever 1987)

Trochosaurus dirus (new species)
 Holotype described: Broom 1936b
 Validity: Genus and species valid

Alopecognathus megalops (new species)
 Holotype described: Broom 1937a
 Validity: Species valid
 Comments: Determinable only to the level of a scylacosaurid (van den Heever 1987)

Ictidosuchoides rubidgei (new species)
 Holotype described: Broom 1937a
 Validity: Species valid
 Comments: Genus reassigned to *Ictidosuchops* Broom (J.A. Hopson, pers. comm., 2002)

Ictidosuchoides intermedius (new species)
 Holotype described: Broom 1938c
 Validity: Species valid
 Comments: Genus reassigned to *Ictidosuchops* Broom (Brink 1988)

Ictidosuchops bauroides (new genus and species)
 Holotype described: Broom 1940b
 Validity: Genus and species valid

Moschorhinus esterhuyseni (new species)
 Holotype described: Broom 1940b
 Validity: Species invalid
 Comments: Synonymized with *Tigrisuchus simus* Owen (J.A. Hopson, pers. comm., 2002)

Nanictidops kitchingi (new genus and species)
 Holotype described: Broom 1940b
 Validity: Genus and species valid

Nanictocephalus richardi (new genus and species)
 Holotype described: Broom 1940a
 Validity: Genus and species valid

Octocynodon elegans (new genus and species)
 Holotype described: Broom 1940b
 Validity: Genus invalid (but see below); species valid
 Comments: Genus reassigned to *Polycynodon* Broom & Robinson (Brink 1988)

Pelictosuchus paucidens (new genus and species)
 Holotype described: Broom 1940b
 Validity: Genus and species invalid
 Comments: Synonymized with *Akidnognathus parvus* Haughton (J.A. Hopson, pers. comm., 2002)

Scaloposuchus rubidgei (new genus and species)
 Holotype described: Broom 1940a
 Validity: Genus and species valid

Ictidosuchops watermeyeri (new species)
 Holotype described: Broom 1941
 Validity: Species invalid
 Comments: Synonymized with *Ictidosuchops intermedius* Broom (Brink 1988)

Aneugomphius ictidoceps (new genus and species) (with J.T. Robinson)
 Holotype described: Broom & Robinson 1948b
 Validity: Genus and species invalid
 Comments: Synonymized with *Theriognathus microps* Owen (J.A. Hopson, pers. comm., 2002)

Cerdops burgheri (new genus and species)
 Holotype described: Broom 1948a
 Validity: Genus and species invalid
 Comments: Synonymized with *Cerdosuchoides brevidens* Broom (J.A. Hopson, pers. comm., 2002)

Ictidochampsia platyceps (new genus and species)
 Holotype described: Broom 1948a
 Validity: Genus and species valid

Ictidodracops longiceps (new genus and species) (with J.T. Robinson)
 Holotype described: Broom & Robinson 1948b
 Validity: Genus and species valid

Silpholestes jackae (new genus and species)
 Holotype described: Broom 1948b
 Validity: Genus and species valid

Tetracynodon tenuis (new genus and species) (with J.T. Robinson)
 Holotype described: Broom & Robinson 1948b
 Validity: Genus and species valid

Whaitsia pricei (new species) (with J.T. Robinson)
 Holotype described: Broom & Robinson 1948b
 Validity: Species invalid
 Comments: Synonymized with *Theriognathus microps* Owen (J.A. Hopson, pers. comm., 2002)

Sesamodontoides pauli (new genus and species)
 Holotype described: Broom 1950b
 Validity: Genus and species invalid
 Comments: Synonymized with *Microgomphodon oligocynus* Seeley (J.A. Hopson, pers. comm., 2002)

GORGONOPSIA

Aloposaurus gracilis (new genus and species)
 Holotype described: Broom 1910
 Validity: Genus and species valid

Aelurosaurus tenuirostris (new species)
 Holotype described: Broom 1911b
 Validity: Species invalid
 Comments: Synonymized with *Aelurosaurus* cf. *felinus* Owen (Boonstra 1935)

Aelurosaurus whaitsi (new species)
 Holotype described: Broom 1911b
 Validity: Species valid

Arctognathus curvimola (new genus)
 Holotype described: Broom 1911b
 Validity: Genus valid
 Comments: Genus reassigned from *Lycosaurus* Owen

Aelurosaurus striatidens (new species)
 Holotype described: Broom 1912b
 Validity: Species invalid
 Comments: Synonymized with *Aelurosaurus felinus* Owen (Sigogneau 1970)

Scymnognathus whaitsi (new genus and species)
 Holotype described: Broom 1912b

- Validity: Genus invalid (but see *Scymnognathus parvus*); species valid
 Comments: Genus reassigned to *Gorgonops* Owen (Sigogneau 1970)
- Scylacognathus parvus* (new genus and species)
 Holotype described: Broom 1913a
 Validity: Genus and species valid
- Scylacops capensis* (new genus and species)
 Holotype described: Broom 1913b
 Validity: Genus and species valid
- (*Scymnognathus*) *Lycaenoides angusticeps* (new genus and species)
 Holotype described: Broom 1913e
 Validity: Genus invalid; species valid
 Comments: Genus reassigned to *Lycaenoides* Broom (Broom 1932); genus reassigned to *Lycaenops* Broom (Sigogneau 1970)
- (*Scymnognathus*) *Aelurognathus tigriceps* (new species) (with S.H. Haughton)
 Holotype described: Broom & Haughton 1913a
 Validity: Species valid
 Comments: Genus reassigned to *Aelurognathus* Haughton (Broom 1932)
- Scymnognathus minor* (new species)
 Holotype described: Broom 1913e
 Validity: Species invalid
 Comments: Synonymized with *Lycaenops angusticeps* Broom (Sigogneau 1970)
- (*Scymnorhinus*) *Broomisaurus planiceps* (new genus and species)
 Holotype described: Broom 1913a
 Validity: Genus and species valid
 Comments: Reassigned from preoccupied genus *Scymnorhinus* (Broom 1932)
- (*Asthenognathus*) *Delphaciognathus paucidens* (new genus and species)
 Holotype described: Broom 1915c
 Validity: Genus and species valid
 Comments: Reassigned from preoccupied genus *Asthenognathus* (Broom 1932); pending review (Sigogneau-Russell 1989)
- Cerdognathus grayi* (new genus and species)
 Holotype described: Broom 1915b
 Validity: Genus and species valid
 Comments: Pending review (Sigogneau-Russell 1989)
- Cyniscodon lydekkeri* (new genus and species)
 Holotype described: Broom 1915b
 Validity: Genus and species valid
 Comments: Pending review (Sigogneau-Russell 1989)
- Scymnognathus parvus* (new species)
 Holotype described: Broom 1915b
 Validity: Species valid
 Comments: Currently the only valid species of the genus *Scymnognathus* Broom; pending review (Sigogneau-Russell 1989)
- Cynarioides tenuis* (new genus and species)
 Holotype described: Broom 1925
 Validity: Genus invalid; species valid
 Comments: Reassigned to the genus cf. *Aloposaurus* Broom (Sigogneau 1970)
- Cynariops robustus* (new genus and species)
 Holotype described: Broom 1925
 Validity: Genus invalid; species valid
 Comments: Reassigned to the genus *Scylacognathus* (Sigogneau 1970)
- Lycaenops ornatus* (new genus and species)
 Holotype described: Broom 1925
 Validity: Genus and species valid
- Aelurosaurus breviceps* (new species)
 Holotype described: Broom 1930a
 Validity: Species invalid
 Comments: Synonymized with *Aelurosaurus whaitsi* Broom (Sigogneau 1970)
- Cynarioides gracilis* (new species)
 Holotype described: Broom 1930a
 Validity: Species valid
 Comments: Pending review (Sigogneau-Russell 1989)
- Cynarioides grimbeeki* (new species)
 Holotype described: Broom 1935b
 Validity: Species valid
 Comments: Reassigned to genus *Scylacognathus* Broom (Sigogneau 1970)
- Cynarioides laticeps* (new species)
 Holotype described: Broom 1935b
 Validity: Species invalid
 Comments: Synonymized with *Scylacognathus grimbeeki* Broom (Sigogneau 1970)
- Galerhinus polyodon* (new genus and species)
 Holotype described: Broom 1935c
 Validity: Genus invalid; species valid
 Comments: Reassigned to genus *Aelurosaurus* Owen (Sigogneau 1970)
- Scylacognathus major* (new species)
 Holotype described: Broom 1935c
 Validity: Species invalid
 Comments: Synonymized with *Scylacognathus parvus* Broom (Sigogneau 1970)
- Cerdorhinus parvidens* (new genus and species)
 Holotype described: Broom 1936a
 Validity: Genus and species valid
- Dinogorgon rubidgei* (new genus and species)
 Holotype described: Broom 1936a
 Validity: Genus and species valid
- Galerhinus rubidgei* (new species)
 Holotype described: Broom 1936a
 Validity: Species valid
 Comments: Genus reassigned to *Paragalerhinus* Sigogneau (Sigogneau 1970)
- Cyniscops rubidgei* (new genus and species)
 Holotype described: Broom 1937a
 Validity: Genus invalid; species valid
 Comments: Genus reassigned to *Cyonosaurus* Olson (Sigogneau 1970)
- Galerhynchus rubidgei* (new genus and species)
 Holotype described: Broom 1937b
 Validity: Genus invalid; species valid
 Comments: Genus reassigned to *Cerdorhinus* Broom (Sigogneau 1970)
- Gorgorhinus luckhoffi* (new genus and species)
 Holotype described: Broom 1937a
 Validity: Genus and species valid
 Comments: Pending review (Sigogneau-Russell 1989)
- Scymnognathus major* (new species) (with E.C. Olson)
 Holotype described: Broom & Olson 1937
 Validity: Species invalid
 Comments: Synonymized with *Lycaenops* cf. *angusticeps* Broom (Sigogneau 1970)

- Rubidgea atrox* (new genus and species)
Holotype described: Broom 1938e
Validity: Genus and species valid
Comments: Originally classified by Broom as suborder Rubidgea
- Rubidgea kitchingi* (new species)
Holotype described: Broom 1938e
Validity: Species valid
Comments: Originally classified by Broom as suborder Rubidgea; pending review but genus not considered *Rubidgea* Broom (Sigogneau-Russell 1989)
- Aelurosauroides wilmanae* (new species)
Holotype described: Broom 1940b
Validity: Species valid
Comments: Genus reassigned to *Aelurosaurus* Owen (Sigogneau 1970)
- Broomisaurus rubidgei* (new species)
Holotype described: Broom 1940a
Validity: Species valid
Comments: Genus reassigned to *Leontocephalus* Broom (Sigogneau 1970)
- Leontocephalus cadlei* (new genus and species)
Holotype described: Broom 1940b
Validity: Genus and species valid
- Prorubidgea maccabei* (new genus and species)
Holotype described: Broom 1940b
Validity: Genus and species valid
- Rubidgea laticeps* (new species)
Holotype described: Broom 1940b
Validity: Species valid
Comments: Originally classified by Broom as suborder Rubidgea; genus reassigned to *Broomicephalus* Brink & Kitching (Brink & Kitching 1953)
- Scylacocephalus watermeyer* (new species)
Holotype described: Broom 1940a
Validity: Species valid
Comments: Genus reassigned to *Aelurosaurus* Owen (Sigogneau 1970)
- Cyniscops longiceps* (new species)
Holotype described: Broom 1941
Validity: Species invalid
Comments: Synonymized with *Cyonosaurus longiceps* Olson (Sigogneau 1970)
- Sycosaurus brodiei* (new species)
Holotype described: Broom 1941
Validity: Species valid
Comments: Genus reassigned to *Prorubidgea* Broom (Sigogneau 1970)
- Aelurosaurus brevirostris* (new species)
Holotype described: Broom 1948a
Validity: Species valid
Comments: Indeterminable; type specimen is lost (Sigogneau 1970)
- Clelandina rubidgei* (new genus and species)
Holotype described: Broom 1948a
Validity: Genus and species valid
- Clelandina major* (new species)
Holotype described: Broom 1948a
Validity: Species valid
Comments: Pending review (Sigogneau-Russell 1989)
- Cyniscops cookei* (new species)
Holotype described: Broom 1948a
Validity: Species valid
Comments: Genus reassigned to *Arctognathus* Broom (Sigogneau 1970)
- Cyniscops kitchingi* (new species)
Holotype described: Broom 1948a
Validity: Species valid
Comments: Genus reassigned to *Cyonosaurus* Olson (Sigogneau 1970)
- Gorgorhinus minor* (new species)
Holotype described: Broom 1948a
Validity: Species valid
Comments: Genus reassigned to *Arctops* Watson (Sigogneau 1970)
- Lycaenops pricei* (new species) (with J.T. Robinson)
Holotype described: Broom & Robinson 1948a
Validity: Species invalid
Comments: Synonymized with *Arctognathus cf. curvimola* Owen (Sigogneau 1970)
- Nanogorgon gracilis* (new genus and species) (with J.T. Robinson)
Holotype described: Broom & Robinson 1948a
Validity: Genus and species invalid
Comments: Synonymized with *Cyonosaurus* sp. (juvenile form) (Sigogneau 1970)
- Pardocephalus wallacei* (new genus and species)
Holotype described: Broom 1948a
Validity: Genus and species invalid
Comments: Synonymized with *Arctops ferox* Broom (Sigogneau 1970)
- Scymnognathus holmesi* (new species)
Holotype described: Broom 1948a
Validity: Species invalid
Comments: Synonymized with *Aelurognathus sollasi* Broili & Schroeder (Sigogneau 1970)
- Smilesaurus ferox* (new genus and species)
Holotype described: Broom 1948a
Validity: Genus invalid; species valid
Comments: Genus reassigned to *Arctops* Watson (Sigogneau 1970)
- Smilesaurus maccabei* (new species)
Holotype described: Broom 1948a
Validity: Species invalid
Comments: Synonymized with *Arctops ferox* Broom (Sigogneau 1970)
- Tigricephalus kingwilli* (new genus and species)
Holotype described: Broom 1948a
Validity: Genus invalid; species valid
Comments: Genus assigned to *Lycaenops* Broom (Sigogneau 1970)
- Leontosaurus vanderhorsti* (new genus and species) (with M. George)
Holotype described: Broom & George 1950a
Validity: Genus invalid; species valid
Comments: Genus reassigned to *Sycosaurus* Haughton (Sigogneau 1970)
- Tigrisaurus pricei* (new genus and species) (with M. George)
Holotype described: Broom & George 1950a
Validity: Genus invalid; species valid
Comments: Genus reassigned to *Dinogorgon* Broom (Sigogneau 1970)

ANOMODONTIA

(*Dicynodon*) *Kannemeyeria latifrons* (new species)

Holotype described: Broom 1899b

Validity: Species invalid

Comments: Genus reassigned to *Kannemeyeria* Seeley (Broom 1932); synonymized with *Kannemeyeria simocephalus* Weithofer (Cruickshank 1965; King 1988)

Oudenodon truncatus (new species)

Holotype described: Broom 1899b

Validity: Species invalid

Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975)

(*Udenodon*) *Dicynodon gracilis* (new species)

Holotype described: Broom 1901

Validity: Species valid

Comments: Genus reassigned to *Dicynodon* Owen (Broom 1932); also described as *Kingoria gracilis* Broom (Cluver & Hotton 1981)

Chelyoposaurus williamsi (new genus and species)

Holotype described: Broom 1904

Validity: Genus and species valid

Comments: Considered a *nomen nudum* (King & Rubidge 1993)

Prodicynodon pearstonensis (new genus and species)

Holotype described: Broom 1904a

Validity: Genus and species invalid

Comments: Synonymized with *Endothiodon* sp. (King 1988)

(*Oudenodon*) *Dicynodon megalorhinus* (new species)

Holotype described: Broom 1904c

Validity: Species valid

Comments: Genus reassigned to *Dicynodon* Owen (Broom 1932)

(*Oudenodon*) *Emydopsis trigoniceps* (new species)

Holotype described: Broom 1904b

Validity: Species valid

Comments: Genus reassigned to *Emydopsis* Broom (Broom 1921); Genus reassigned to *Emydops* Broom (Toerien 1953)

Dicynodon jouberti (new species)

Holotype described: Broom 1905c

Validity: Species invalid

Comments: Genus reassigned to *Diictodon* Broom (Cluver & Hotton 1981); synonymized with *Diictodon galeops* Broom (King 1993)

(*Opisthoctenodon*) *Pristerodon agilis* (new species)

Holotype described: Broom 1905a

Validity: Species valid

Comments: Genus reassigned to *Pristerodon* Broom (Broom 1915a)

(*Opisthoctenodon*) *Pristerodon brachyops* (new species)

Holotype described: Broom 1905a

Validity: Species invalid

Comments: Genus reassigned to *Pristerodon* Broom (Broom 1915a); synonymized with *Emydops* sp. (Cluver & King 1983)

Dicynodon ingens (new species)

Holotype described: Broom 1907a

Validity: Species valid

Galechirus scholtzi (new genus and species)

Holotype described: Broom 1907c

Validity: Genus and species valid

Comments: Originally classified by Broom as a dromasaur

Lystrosaurus andersoni (new species)

Holotype described: Broom 1907b

Validity: Species invalid

Comments: Synonymized with *Lystrosaurus platyceps* Seeley (King 1988)

Galepus jouberti (new genus and species)

Holotype described: Broom 1910

Validity: Genus and species valid

Comments: Originally classified by Broom as a dromasaur

Diaelurodon whaitsi (new genus and species)

Holotype described: Broom 1911b

Validity: Genus invalid; species valid

Comments: Genus reassigned to *Pristerodon* Broom (Toerien 1953)

(*Oudenodon*) *Dicynodon bolorhinus* (new species)

Holotype described: Broom 1911b

Validity: Species valid

Comments: Genus reassigned to *Dicynodon* Owen (Broom 1932)

Taognathus megalodon (new genus and species)

Holotype described: Broom 1911b

Validity: Genus and species valid

Comments: Considered a *nomen nudum* (King & Rubidge 1993)

(*Dicynodon*) (*Bainia*) *Aulacocephalodon laticeps* (new species)

Holotype described: Broom 1912b

Validity: Species invalid

Comments: Genus reassigned (*Bainia* Broom 1921; *Aulacocephalodon* Broom 1932); synonymized with *Aulacephalodon baini* Owen (Keyser 1972)

Dicynodon lutriceps (new species)

Holotype described: Broom 1912b

Validity: Species invalid

Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)

Dicynodon psittacops (new species)

Holotype described: Broom 1912b

Validity: Species valid

Comments: Genus reassigned to *Diictodon* Broom (Cluver & Hotton 1981); King (1993) suggested that the specimen should be synonymized with *Diictodon galeops* Broom

Emydops minor (new genus and species)

Holotype described: Broom 1912b

Validity: Genus and species valid

(*Endothiodon*) *Esoterodon whaitsi* (new species)

Holotype described: Broom 1912b

Validity: Species valid

Comments: Genus reassigned to *Esoterodon* Seeley (Broom 1932); genus reassigned to *Endothiodon* Owen (Cox 1964)

(*Endothiodon*) *Emydochampsia platyceps* (new genus and species)

Holotype described: Broom 1912b

Validity: Genus and species invalid

Comments: Genus reassigned to *Emydochampsia* (Broom 1915c); synonymized with *Endothiodon uniseries* Owen (Cluver & King 1983; King 1988)

Galeops whaitsi (new genus and species)

Holotype described: Broom 1912b

Validity: Genus and species valid

Comments: Originally classified by Broom as a dromasaur

(*Oudenodon*) (*Diictodon*) *Dicynodon kolbei* (new species)

Holotype described: Broom 1912c

Validity: Species invalid

Comments: Genus reassigned (*Diictodon* Broom 1913c; *Dicynodon* Broom 1913f); synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)

Prodicynodon beaufortensis (new species)

Holotype described: Broom 1912b

Validity: Species invalid

Comments: Synonymized with *Endothiodon* sp. (King 1988)

- Dicynodon alticeps* (new species) (with S.H. Haughton)
Holotype described: Broom & Haughton 1913b
Validity: Species valid
- Dicynodon ictidops* (new species)
Holotype described: Broom 1913c
Validity: Species valid
Comments: Genus reassigned to *Diictodon* Broom (Cluver & Hotton 1981); King (1993) suggested that the specimen should be synonymized with *Diictodon galeops* Broom
- Dicynodon leontops* (new species)
Holotype described: Broom 1913c
Validity: Species valid
- Dicynodon lissops* (new species)
Holotype described: Broom 1913c
Validity: Species valid
- (*Dicynodon*) *Aulacocephalodon moschops* (new species)
Holotype described: Broom 1913c
Validity: Species valid
Comments: Genus reassigned to *Aulacocephalodon* Owen (Broom 1932); genus reassigned to *Pelanomodon* Broom (Cluver & King 1983)
- Dicynodon planus* (new species)
Holotype described: Broom 1913c
Validity: Species invalid
Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)
- Dicynodon platyceps* (new species)
Holotype described: Broom 1913c
Validity: Species invalid
Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)
- (*Dicynodon*) *Prolystrosaurus strigops* (new species)
Holotype described: Broom 1913a
Validity: Species invalid
Comments: Genus reassigned to *Prolystrosaurus* Haughton (Broom 1932); synonymized with *Lystrosaurus murrayi* Huxley (King 1988)
- Dicynodon testudirostris* (new species) (with S.H. Haughton)
Holotype described: Broom & Haughton 1913b
Validity: Species valid
Comments: Genus reassigned to *Diictodon* Broom (Cluver & Hotton 1981); King (1993) suggested that the specimen should be synonymized with *Diictodon galeops* Broom
- Dicynodon tylorhinus* (new species)
Holotype described: Broom 1913c
Validity: Species valid
Comments: Genus reassigned to *Propelanomodon* Toerien (Keyser 1972)
- Dicynodon whaitsi* (new species)
Holotype described: Broom 1913c
Validity: Species valid
- Diictodon galeops* (new genus and species)
Holotype described: Broom 1913c
Validity: Genus and species valid
- Emydopsis longiceps* (new genus and species)
Holotype described: Broom 1913c
Validity: Genus invalid; species valid
Comments: Genus reassigned to *Emydops* Broom (Cluver & King 1983)
- Emydorhynchus palustris* (new genus and species)
Holotype described: Broom 1913c
Validity: Genus invalid (but see *Emydorhynchus formosus* below); species valid
Comments: Genus reassigned to *Diictodon* Broom (Cluver & Hotton 1981); King (1993) suggested that the specimen should be synonymized with *Diictodon galeops* Broom
- Eocyclops longus* (new genus and species)
Holotype described: Broom 1913c
Validity: Genus invalid; Species valid
Comments: Genus reassigned to *Rhachiocephalus* Owen (Cluver & King 1983)
- (*Endothiodon*) *Esoterodon paucidens* (new species)
Holotype described: Broom 1915c
Validity: Species invalid
Comments: Genus reassigned to *Esoterodon* Seeley (Broom 1932); synonymized with *Endothiodon uniseries* Owen (Cluver & King 1983; King 1988)
- Endothiodon seeleyi* (new species)
Holotype described: Broom 1915c
Validity: Species invalid
Comments: Synonymized with *Endothiodon uniseries* Owen (Cluver & King 1983; King 1988)
- Esoterodon angusticeps* (new species)
Holotype described: Broom 1915c
Validity: Species invalid
Comments: Synonymized with *Endothiodon uniseries* Owen (Cluver & King 1983; King 1988)
- Dicynodon cavifrons* (new species) (with S.H. Haughton)
Holotype described: Broom & Haughton 1917
Validity: Species valid
- Dicynodon corstorphine* (new species) (with S.H. Haughton)
Holotype described: Broom & Haughton 1917
Validity: Species invalid
Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)
- Dicynodon pygmaeus* (new species) (with S.H. Haughton)
Holotype described: Broom & Haughton 1917
Validity: Species invalid
Comments: Synonymized with *Diictodon testudirostris* Broom & Haughton (Cluver & Hotton 1981); King (1993) suggested that the specimen should be synonymized with *Diictodon galeops* Broom
- Dicynodon rogersi* (new species) (with S.H. Haughton)
Holotype described: Broom & Haughton 1917
Validity: Species valid
- (*Emydops*) *Emydopsis platyceps* (new species) (with S.H. Haughton)
Holotype described: Broom & Haughton 1917
Validity: Species valid
Comments: Genus reassigned to *Emydopsis* Broom (Broom 1921); genus reassigned to *Emydops* Broom (Cluver & King 1983)
- Dicynodon schwarzi* (new species)
Holotype described: Broom 1919a
Validity: Species invalid
Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)
- (*Bainia*) *Aulacocephalodon haughtoni* (new genus and species)
Holotype described: Broom 1921
Validity: Genus and species invalid
Comments: Genus reassigned to *Aulacocephalodon* Owen (Broom 1932); synonymized with *Aulacocephalodon baini* Owen (Keyser 1972)

(*Bainia*) *Aulacocephalodon peavoti* (new species)

Holotype described: Broom 1921

Validity: Species invalid

Comments: Genus reassigned to *Aulacocephalodon* Owen (Broom 1932); synonymized with *Aulacephalodon baini* Owen (Keyser 1972)

Dicynodon andrewsi (new species)

Holotype described: Broom 1921

Validity: Species invalid

Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)

Dicynodon curtus (new species)

Holotype described: Broom 1921

Validity: Species invalid

Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1972; Cluver & Hotton 1981)

Dicynodon ictinops (new species)

Holotype described: Broom 1921

Validity: Species valid

Dicynodon macrorhynchus (new species)

Holotype described: Broom 1921

Validity: Species invalid

Comments: Genus reassigned to *Diictodon* Broom (Cluver & Hotton 1981); synonymized with *Diictodon galeops* Broom (King 1993)

Dicynodon osborni (new species)

Holotype described: Broom 1921

Validity: Species valid

Dicynodon sollasi (new species)

Holotype described: Broom 1921

Validity: Species valid

Comments: Genus reassigned to *Diictodon* Broom (Cluver & Hotton 1981); King (1993) suggested that the specimen should be synonymized with *Diictodon galeops* Broom

Dicynodon watsoni (new species)

Holotype described: Broom 1921

Validity: Species valid

Dicynodon woodwardi (new species)

Holotype described: Broom 1921

Validity: Species valid

Emydops parvus (new species)

Holotype described: Broom 1921

Validity: Species valid

Emydopsis longus (new species)

Holotype described: Broom 1921

Validity: Species valid

Comments: Genus reassigned to *Emydops* Broom (Toerien 1953)

(*Emydopsis*) *Emydorhinus sciuroides* (new genus and species)

Holotype described: Broom 1921

Validity: Genus and species valid

Comments: Genus reassigned to *Emydorhinus* Broom (Broom 1935)

Emyduranus platyops (new genus and species)

Holotype described: Broom 1921

Validity: Genus invalid; species valid

Comments: Genus reassigned to *Pristerodon* Broom (King & Rubidge 1993)

(*Endothiodon*) *Endogomphodon crassus* (new genus and species)

Holotype described: Broom 1921

Validity: Genus and species invalid

Comments: Genus reassigned to *Endogomphodon* Broom (Broom

1932); synonymized with *Endothiodon whaitsi* Broom (Cluver & King 1983; King 1988)

Eosimops newtoni (new genus and species)

Holotype described: Broom 1921

Validity: Genus and species valid

Comments: Indeterminate (Cluver & King 1983)

Palemydops platysoma (new genus and species)

Holotype described: Broom 1921

Validity: Genus and species valid

Dicynodon milletti (new species)

Holotype described: Broom 1928a

Validity: Species invalid

Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)

Dicynodon vanderbyli (new species)

Holotype described: Broom 1928a

Validity: Species invalid

Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)

Dicynodon wilmanae (new species)

Holotype described: Broom 1928a

Validity: Species invalid

Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)

Cerataelurus mirabilis (new genus and species)

Holotype described: Broom 1930b

Validity: Genus and species valid

Comments: Indeterminate (Cluver & King 1983)

Megacyclops whaitsi (new genus and species)

Holotype described: Broom 1930b

Validity: Genus invalid; species valid

Comments: Genus reassigned to *Rhachiocephalus* Owen (Cluver & King 1983)

Aulacocephalodon latissimus (new species)

Holotype described: Broom 1932

Validity: Species invalid

Comments: Synonymized with *Aulacephalodon baini* Owen (Keyser 1972)

Cistecephalus angusticeps (new species)

Holotype described: Broom 1932

Validity: Species invalid

Comments: Synonymized with *Cistecephalus microrhinus* Owen (Keyser 1973)

Dicynodon gilli (new species)

Holotype described: Broom 1932

Validity: Species valid

Dicynodon latirostris (new species)

Holotype described: Broom 1932

Validity: Species invalid

Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)

Dicynodon platyfrons (new species)

Holotype described: Broom 1932

Validity: Species invalid

Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)

Dicynodon robustus (new species)

Holotype described: Broom 1932

Validity: Species valid

Dicynodon rubidgei (new species)

Holotype described: Broom 1932

- Validity: Species valid
Comments: Genus reassigned to *Diictodon* Broom (Cluver & Hotton 1981); King (1993) suggested that the specimen should be synonymized with *Diictodon galeops* Broom
- Dicynodon taylori* (new species)
Holotype described: Broom 1932
Validity: Species valid
- Endogomphodon minor* (new species)
Holotype described: Broom 1932
Validity: Species invalid
Comments: Synonymized with *Endothiodon uniseries* Owen (Cluver & King 1983; King 1988)
- Platycyclops haughtoni* (new genus and species)
Holotype described: Broom 1932
Validity: Genus invalid; species valid
Comments: Genus reassigned to *Rhachiocephalus* Owen (Cluver & King 1983)
- Cteniosaurus platyceps* (new genus and species)
Holotype described: Broom 1935c
Validity: Genus and species valid
- Dicynodon acutirostris* (new species)
Holotype described: Broom 1935c
Validity: Species valid
- Dicynodon grimbeeki* (new species)
Holotype described: Broom 1935b
Validity: Species valid
Comments: Genus reassigned to *Diictodon* Broom (Cluver & Hotton 1981); King (1993) suggested that the specimen should be synonymized with *Diictodon galeops* Broom
- Dicynodon validus* (new species)
Holotype described: Broom 1935c
Validity: Species valid
- Dicynodon venteri* (new species)
Holotype described: Broom 1935c
Validity: Species valid
- Emydopsis minimus* (new species)
Holotype described: Broom 1935b
Validity: Species valid
Comments: Genus reassigned to *Emydops* Broom (Toerien 1953)
- Emydorhinus fragilis* (new species)
Holotype described: Broom 1935c
Validity: Species invalid
Comments: Synonymized with *Emydorhinus sciuroides* Broom (Kitching 1977)
- Emydorhynchus formosus* (new species)
Holotype described: Broom 1935b
Validity: Species valid
Comments: Currently the only valid species of the genus *Emydorhynchus* Broom
- Emyduranus gracilis* (new species)
Holotype described: Broom 1935c
Validity: Species valid
Comments: Genus reassigned to *Pristerodon* Broom (King & Rubidge 1993)
- Eumantellia mirus* (new genus and species)
Holotype described: Broom 1935a
Validity: Genus invalid; species valid
Comments: Genus reassigned to *Pristerodon* Broom (King & Rubidge 1993)
- Palemydops minor* (new species)
Holotype described: Broom 1935c
- Validity: Species valid
Aulacocephalodon nesemanni (new species)
Holotype described: Broom 1936a
Validity: Species invalid
Comments: Synonymized with *Aulacephalodon baini* Owen (Keyser 1972)
- Dicynonodon microdon* (new species)
Holotype described: Broom 1936a
Validity: Species valid
- Dicynodon nanus* (new species)
Holotype described: Broom 1936a
Validity: Species valid
- Dicynodon wellwoodensis* (new species)
Holotype described: Broom 1936a
Validity: Species invalid
Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)
- Emydopsis microdon* (new species)
Holotype described: Broom 1936a
Validity: Species valid
Comments: Genus reassigned to *Emydops* Broom (Toerien 1953)
- Aulacocephalodon hartzenbergi* (new species)
Holotype described: Broom 1937b
Validity: Species invalid
Comments: Synonymized with *Aulacephalodon baini* Owen (Keyser 1972)
- Aulacocephalodon luckhoffi* (new species)
Holotype described: Broom 1937b
Validity: Species invalid
Comments: Synonymized with *Aulacephalodon baini* Owen (Keyser 1972)
- Dicynodon dutoiti* (new species) (with G.W.H. Schepers)
Holotype described: Broom & Schepers 1937
Validity: Species valid
- Dicynodon gamkaensis* (new species)
Holotype described: Broom 1937b
Validity: Species valid
- Dicynodon kitchingi* (new species)
Holotype described: Broom 1937a
Validity: Species valid
- Dicynodon luckhoffi* (new species)
Holotype described: Broom 1937b
Validity: Species valid
- Kannemeyeria wilsoni* (new species)
Holotype described: Broom 1937b
Validity: Species valid
- Newtonella platyceps* (new genus and species)
Holotype described: Broom 1937b
Validity: Genus invalid; species valid
Comments: Genus reassigned to *Pristerodon* Broom (King & Rubidge 1993)
- Palemydops rubidgeae* (new species)
Holotype described: Broom 1937a
Validity: Species valid
- Rhachiocephalus angusticeps* (new species)
Holotype described: Broom 1937b
Validity: Species invalid
Comments: Synonymized with *Rhachiocephalus magnus* Owen (Cluver & King 1983; King 1988)

- Dinanomodon rubidgei* (new genus and species)
Holotype described: Broom 1938a
Validity: Genus and species valid
- Pelanomodon rubidgei* (new genus and species)
Holotype described: Broom 1938a
Validity: Genus and species valid
- Aulacocephalodon rubidgei* (new species)
Holotype described: Broom 1940a
Validity: Species invalid
Comments: Synonymized with *Aulacephalodon baini* Owen (Keyser 1972)
- Dicynodon allani* (new species)
Holotype described: Broom 1940b
Validity: Species invalid
Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)
- Dicynodon anneae* (new species)
Holotype described: Broom 1940b
Validity: Species invalid
Comments: Synonymized with *Diictodon whitsonae* Toerien (Cluver & Hotton 1981); King (1993) suggested that the specimen should be synonymized with *Diictodon galeops* Broom
- Dicynodon cadlei* (new species)
Holotype described: Broom 1940a
Validity: Species valid
- Dicynodon calverleyi* (new species)
Holotype described: Broom 1940b
Validity: Species valid
- Dicynodon graafi* (new species)
Holotype described: Broom 1940b
Validity: Species valid
- Dicynodon grahami* (new species)
Holotype described: Broom 1940b
Validity: Species valid
Comments: Genus reassigned to *Kingoria* Cox (Cluver & Hotton 1981)
- Dicynodon hartzenbergi* (new species)
Holotype described: Broom 1940b
Validity: Species valid
- Dicynodon maccabei* (new species)
Holotype described: Broom 1940b
Validity: Species invalid
Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)
- Dicynodon macrodon* (new species)
Holotype described: Broom 1940a
Validity: Species valid
- Dicynodon nesemanni* (new species)
Holotype described: Broom 1940a
Validity: Species valid
- Dicynodon richardi* (new species)
Holotype described: Broom 1940b
Validity: Species valid
- Dicynodon sidneyi* (new species)
Holotype described: Broom 1940b
Validity: Species valid
Comments: Genus may be *Pelanomodon* Broom (Cluver & King 1983) or *Propelanomodon* Toerien (K.D. Angielczyk, pers. comm., 2002)
- Dicynodon swierstrai* (new species)
Holotype described: Broom 1940b
- Validity: Species valid
- Dicynodon trigonocephalus* (new species)
Holotype described: Broom 1940b
Validity: Species valid
- Dicynodontoides parringtoni* (new genus and species)
Holotype described: Broom 1940b
Validity: Genus and species valid
- Dinanomodon gigas* (new species)
Holotype described: Broom 1940b
Validity: Species valid
- Lystrosaurus rubidgei* (new species)
Holotype described: Broom 1940b
Validity: Species invalid
Comments: Synonymized with *Lystrosaurus murrayi* Huxley (King 1988)
- Platycyclops latirhinus* (new species)
Holotype described: Broom 1940a
Validity: Species invalid
Comments: Synonymized with *Rhachiocephalus haughtoni* Broom (Cluver & King 1983)
- Platycyclops rubidgei* (new species)
Holotype described: Broom 1940a
Validity: Species invalid
Comments: Synonymized with *Rhachiocephalus haughtoni* Broom (Cluver & King 1983)
- Aulacocephalodon brodiei* (new species)
Holotype described: Broom 1941
Validity: Species invalid
Comments: Synonymized with *Aulacephalodon baini* Owen (Keyser 1972)
- Aulacocephalodon coatoni* (new species)
Holotype described: Broom 1941
Validity: Species invalid
Comments: Synonymized with *Aulacephalodon baini* Owen (Keyser 1972)
- Dicynodon weatherbyi* (new species)
Holotype described: Broom 1941
Validity: Species valid
- Lystrosaurus bothai* (new species)
Holotype described: Broom 1941
Validity: Species invalid
Comments: Synonymized with *Lystrosaurus murrayi* Huxley (King 1988)
- Myosauroides minnaari* (new genus and species)
Holotype described: Broom 1941
Validity: Genus and species valid
- Aulacocephalodon cadlei* (new species)
Holotype described: Broom 1948a
Validity: Species invalid
Comments: Synonymized with *Aulacephalodon baini* Owen (Keyser 1972)
- Cistecephalus major* (new species)
Holotype described: Broom 1948a
Validity: Species invalid
Comments: Synonymized with *Cistecephalus microrhinus* Owen (Keyser 1973)
- Cistecephalus platyfrons* (new species)
Holotype described: Broom 1948a
Validity: Species invalid
Comments: Synonymized with *Cistecephalus microrhinus* Owen (Keyser 1973)

Cistecephalus rubidgei (new species)
 Holotype described: Broom 1948a
 Validity: Species invalid
 Comments: Synonymized with *Cistecephalus microrhinus* Owen (Keyser 1973)

Dicynodon aetoramphus (new species)
 Holotype described: Broom 1948a
 Validity: Species valid

Dicynodon benjamini (new species)
 Holotype described: Broom 1948a
 Validity: Species valid

Dicynodon brachyrhynchus (new species)
 Holotype described: Broom 1948a
 Validity: Species invalid
 Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)

Dicynodon duvenhagei (new species)
 Holotype described: Broom 1948a
 Validity: Species valid
 Comments: Genus reassigned to *Kingoria* Cox (Cluver & Hotton 1981)

Dicynodon galecephalus (new species) (with J.T. Robinson)
 Holotype described: Broom & Robinson 1948a
 Validity: Species valid
 Comments: Genus reassigned to *Kingoria galecephala* Broom & Robinson (Cluver & Hotton 1981)

Dicynodon glaucops (new species)
 Holotype described: Broom 1948a
 Validity: Species invalid
 Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)

Dicynodon howardi (new species)
 Holotype described: Broom 1948a
 Validity: Species valid
 Comments: Genus reassigned to *Kingoria* Cox (Cluver & Hotton 1981)

Dicynodon moutonae (new species)
 Holotype described: Broom 1948a
 Validity: Species invalid
 Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)

Dicynodon robertsi (new species)
 Holotype described: Broom 1948a
 Validity: Species invalid
 Comments: Synonymized with *Oudenodon baini* Owen (Keyser 1975; Cluver & Hotton 1981)

Dicynodon scheepersi (new species)
 Holotype described: Broom 1948a
 Validity: Species valid

Digalodon rubidgei (new genus and species) (with J.T. Robinson)
 Holotype described: Broom & Robinson 1948a
 Validity: Genus and species invalid
 Comments: Synonymized with *Aulacephalodon baini* Owen (Cluver & King 1983)

Pelanomodon wesselsi (new species)
 Holotype described: Broom 1948a
 Validity: Species valid
 Comments: Genus reassigned to *Rhachiocephalus* Owen (Keyser 1972)

Platycyclops crassus (new species)
 Holotype described: Broom 1948a

Validity: Species invalid
 Comments: Synonymized with *Rhachiocephalus haughtoni* Broom (Cluver & King 1983)

Platycyclops richardi (new species)
 Holotype described: Broom 1948a
 Validity: Species invalid
 Comments: Synonymized with *Rhachiocephalus haughtoni* Broom (Cluver & King 1983)

Aulacocephalodon pricei (new species) (with M. George)
 Holotype described: Broom & George 1950b
 Validity: Species invalid
 Comments: Synonymized with *Aulacephalodon baini* Owen (Keyser 1972)

Aulacocephalodon vanderhorsti (new species) (with M. George)
 Holotype described: Broom & George 1950b
 Validity: Species invalid
 Comments: Synonymized with *Aulacephalodon baini* Owen (Keyser 1972)

Dicynodon clarencei (new species)
 Holotype described: Broom 1950a
 Validity: Species valid

Dicynodon leontocephalus (new species)
 Holotype described: Broom 1950a
 Validity: Species valid

Kitchingia planifrons (new genus and species) (with M. George)
 Holotype described: Broom & George 1950b
 Validity: Genus and species invalid
 Comments: Synonymized with *Rhachiocephalus magnus* Owen (Kitching 1977)

Pelanomodon halli (new species)
 Holotype described: Broom 1950a
 Validity: Species invalid
 Comments: Synonymized with *Pelanomodon moschops* Broom (Keyser 1972)

Pelanomodon kitchingi (new species) (with M. George)
 Holotype described: Broom & George 1950
 Validity: Species invalid
 Comments: Synonymized with *Pelanomodon rubidgei* Broom (Keyser 1972)

Platycyclops acutirostris (new species) (with M. George)
 Holotype described: Broom & George 1950b
 Validity: Species invalid
 Comments: Synonymized with *Rhachiocephalus haughtoni* Broom (Kitching 1977; Cluver & King 1983)

Platycyclops pricei (new species) (with M. George)
 Holotype described: Broom & George 1950b
 Validity: Species invalid
 Comments: Synonymized with *Rhachiocephalus haughtoni* Broom (Cluver & King 1988)

CYNODONTIA

Karoomys browni (new genus and species)
 Holotype described: Broom 1903b
 Validity: Genus and species invalid
 Comments: Originally classified by Broom as an ictidosaur; synonymized with *Cynognathus crateronotus* Seeley (Hopson & Kitching 1972)

Sesamodon browni (new genus and species)
 Holotype described: Broom 1905b
 Validity: Genus and species invalid
 Comments: Originally classified by Broom as a bauriamorph; synonymized with *Microgomphodon oligocynus* Seeley (J.A. Hopson, pers. comm., 2002)

- Trirachodon minor* (new species)
Holotype described: Broom 1905b
Validity: Species invalid
Comments: Synonymized with *Trirachodon berryi* Seeley (Hopson & Kitching 1972)
- Gomphognathus minor* (new species)
Holotype described: Broom 1911a
Validity: Species invalid
Comments: Synonymized with *Gomphognathus browni* Seeley (Broom 1919); synonymized with *Diademodon tetragonus* Seeley (Hopson & Kitching 1972)
- Ictidopsis elegans* (new genus and species)
Holotype described: Broom 1912
Validity: Genus and species invalid
Comments: Synonymized with *Thrinaxodon liorhinus* Seeley (Broom 1932)
- Nythosaurus browni* (new species)
Holotype described: Broom 1912b
Validity: Species invalid
Comments: Synonymized with *Cynognathus crateronotus* Seeley (Hopson & Kitching 1972)
- Tritheledon riconoi* (new genus and species)
Holotype described: Broom 1912a
Validity: Genus and species valid
Comments: Originally classified by Broom as an ictidosaur (*Diademodon*) *Cyclogomphodon platyrhinus* (new genus and species)
Holotype described: Broom 1913d
Validity: Genus and species invalid
Comments: Genus reassigned to *Cyclogomphodon* Broom (Broom 1919b); synonymized with *Diademodon tetragonus* Seeley (Hopson & Kitching 1972)
- (*Lycognathus*) *Lycochampsa ferox* (new genus and species)
Holotype described: Broom 1913e
Validity: Genus and species invalid
Comments: Genus reassigned to *Lycochampsa* (Broom 1915c); synonymized with *Cynognathus crateronotus* Seeley (Hopson & Kitching 1972)
- Octogomphus woodi* (new genus and species)
Holotype described: Broom 1919b
Validity: Genus and species invalid
Comments: Synonymized with *Diademodon tetragonus* Seeley (Hopson & Kitching 1972)
- Lycanognathus platyceps* (new genus)
Holotype described: Broom 1925
Validity: Genus invalid
Comments: Synonymized with *Cynognathus crateronotus* Seeley (Hopson & Kitching 1972)
- Cyrbasiodon boycei* (new genus and species)
Holotype described: Broom 1930b
Validity: Genus and species invalid
Comments: Originally classified by Broom as a therocephalian; synonymized with *Procynosuchus delaharpeae* Broom (Hopson & Kitching 1972)
- Cynosuchoides whaitsi* (new genus)
Holotype described: Broom 1931
Validity: Genus invalid
Comments: Synonymized with *Cynosaurus suppostus* Owen (Hopson & Kitching 1972)
- Lycanognathus kannemeyeria* (new species)
Holotype described: Broom 1931
Validity: Species invalid
Comments: Synonymized with *Cynognathus crateronotus* Seeley (Hopson & Kitching 1972)
- Cynogomphius berryi* (new genus)
Holotype described: Broom 1932
Validity: Genus invalid
Comments: Synonymized with *Cynognathus berryi* Seeley (Hopson & Kitching 1972)
- Thrinaxodon putterilli* (new species)
Holotype described: Broom 1932
Validity: Species invalid
Comments: Synonymized with *Thrinaxodon liorhinus* Seeley (Hopson & Kitching 1972)
- Trirachodon browni* (new species)
Holotype described: Broom 1932
Validity: Species invalid
Comments: Synonymized with *Diademodon tetragonus* Seeley (Hopson & Kitching 1972)
- Trirachodontoides berryi* (new genus)
Holotype described: Broom 1932
Validity: Genus invalid
Comments: Synonymized with *Trirachodon berryi* Seeley (Hopson & Kitching 1972)
- Nanictosaurus kitchingi* (new genus and species)
Holotype described: Broom 1936a
Validity: Genus and species valid
Comments: Originally synonymized with *Cynosaurus suppostus* Owen (Hopson & Kitching 1972); restored to valid genus and species (J.A. Hopson, pers. comm., 2002)
- Nanictosuchus kitchingi* (new genus and species)
Holotype described: Broom 1936a
Validity: Genus and species valid
Comments: Originally classified by Broom as a therocephalian; *N. melinodon* (which Broom (1940a) also established as a new genus (in error)) has been synonymized with *Procynosuchus delaharpeae* Broom (Hopson & Kitching 1972)
- Notictosaurus luckhoffi* (new genus and species)
Holotype described: Broom 1936a
Validity: Genus and species invalid
Comments: Synonymized with *Thrinaxodon liorhinus* Seeley (Hopson & Kitching 1972)
- Micrictodon marionae* (new genus and species)
Holotype described: Broom 1937b
Validity: Genus and species invalid
Comments: Synonymized with *Thrinaxodon liorhinus* Seeley (Hopson & Kitching 1972)
- Procynosuchus delaharpeae* (new genus and species)
Holotype described: Broom 1937b
Validity: Genus and species valid
- Procynosuchus rubidgei* (new species)
Holotype described: Broom 1938d
Validity: Species invalid
Comments: Synonymized with *Procynosuchus delaharpeae* Broom (Hopson & Kitching 1972)
- Nanictosaurus robustus* (new species)
Holotype described: Broom 1940b
Validity: Species invalid
Comments: Synonymized with *Procynosuchus delaharpeae* Broom (Hopson & Kitching 1972)
- Nanictosaurus rubidgei* (new species)
Holotype described: Broom 1940b
Validity: Species invalid
Comments: Regarded as a junior synonym of *Nanictosaurus kitchingi* Broom (J.A. Hopson, pers. comm., 2002)

Nanictosuchus melinodon (new genus and species)

Holotype described: Broom 1940a

Validity: Genus and species invalid

Comments: Synonymized with *Procynosuchus delaharpeae* Broom (Hopson & Kitching 1972)

Paracynosuchus rubidgei (new genus and species)

Holotype described: Broom 1940a

Validity: Genus and species invalid

Comments: Synonymized with *Procynosuchus delaharpeae* Broom (Hopson & Kitching 1972)

Mygalesaurus platyceps (new genus and species)

Holotype described: Broom 1942

Validity: Species invalid

Comments: Originally classified by Broom as suborder Rubidginidea; synonymized with *Procynosuchus delaharpeae* Broom (Hopson & Kitching 1972)

Mygalesuchus peggyae (new genus and species)

Holotype described: Broom 1942

Validity: Species invalid

Comments: Originally classified by Broom as suborder Rubidginidea; synonymized with *Cynosaurus suppostus* Owen (Hopson & Kitching 1972)

Aelurodraco microps (new genus and species) (with J.T. Robinson)

Holotype described: Broom & Robinson 1948b

Validity: Genus and species invalid

Comments: Synonymized with *Procynosuchus delaharpeae* Broom (Hopson & Kitching 1972)

Galecranium liorhynchus (new genus and species)

Holotype described: Broom 1948a

Validity: Genus and species invalid

Comments: Synonymized with *Procynosuchus delaharpeae* Broom (Hopson & Kitching 1972)

Galeophrys kitchingi (new genus and species)

Holotype described: Broom 1948a

Validity: Genus and species invalid

Comments: Synonymized with *Procynosuchus delaharpeae* Broom (Hopson & Kitching 1972)

Leavachia duvenhagei (new genus and species)

Holotype described: Broom 1948a

Validity: Genus and species invalid

Comments: Synonymized with *Procynosuchus delaharpeae* Broom (Hopson & Kitching 1972)

Notictosaurus gracilis (new species) (with J.T. Robinson)

Holotype described: Broom & Robinson 1948a

Validity: Species invalid

Comments: Synonymized with *Galesaurus planiceps* Owen (Hopson & Kitching 1972)

Protocynodon pricei (new genus and species)

Holotype described: Broom 1949

Validity: Genus and species invalid

Comments: Synonymized with *Procynosuchus delaharpeae* Broom

(Hopson & Kitching 1972)

Silphedestes polyodon (new genus and species)

Holotype described: Broom 1949

Validity: Genus and species invalid

Comments: Originally classified by Broom as a therocephalian; synonymized with *Procynosuchus delaharpeae* Broom (Hopson & Kitching 1972)

Protacmon reubsameni (new species)

Holotype described: Broom 1950b

Validity: Species invalid

Comments: Synonymized with *Diademodon tetragonus* Seeley (Hopson & Kitching 1972)

Sysphinctostoma gracilis (new species)

Holotype described: Broom 1950b

Validity: Species invalid

Comments: Synonymized with *Diademodon tetragonus* Seeley (Hopson & Kitching 1972); reassigned to *Trirachodon kannemeyeri* Seeley (J.A. Hopson, pers. comm., 2002)

BIARMOSUCHIA

Ictidorhinus martinsi (new genus and species)

Holotype described: Broom 1913c

Validity: Genus and species valid

Comments: Originally classified by Broom as a gorgonopsian

Burnetia mirabilis (new genus and species)

Holotype described: Broom 1923

Validity: Genus and species valid

Comments: Originally classified by Broom as a burnetiamorph

Lycaenodon longiceps (new genus and species)

Holotype described: Broom 1925

Validity: Genus and species valid

Comments: Originally classified by Broom as a gorgonopsian

Hipposaurus rubidgei (new species)

Holotype described: Broom 1940a

Validity: Species invalid

Comments: Originally classified by Broom as a gorgonopsian; synonymized with *Lycaenodon longiceps* Broom (Sigogneau 1970)

Rubidgina angusticeps (new genus and species)

Holotype described: Broom 1942

Validity: Genus and species valid

Comments: Originally classified by Broom as a rubidginoid

Hipposaurus kitchingi (new species)

Holotype described: Broom 1948a

Validity: Species valid

Comments: Originally classified by Broom as a gorgonopsian; indeterminate – type specimen is lost (Sigogneau 1970)

Lemurosaurus pricei (new genus and species)

Holotype described: Broom 1949

Validity: Genus and species valid

Comments: Originally classified by Broom as a gorgonopsian

A review of the South African temnospondyl amphibian record

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The Karoo of South Africa preserves a near-unbroken sequence of sedimentary rocks and associated vertebrate fauna from the Late Carboniferous to the Middle Jurassic periods. These rocks host a rich temnospondyl amphibian record from the Late Permian to the Early Jurassic. This record is amongst the most diverse temnospondyl record in the world and comprises 10 higher-level taxa, most of which occur in the Triassic part of the sequence and which is dominated by members of the Stereospondyli, with lesser representation by two Palaeozoic lineages. This paper presents a synthesis of the South African temnospondyl amphibian record and highlights the most recent advances in their taxonomy and biostratigraphic placement.

Keywords: South Africa, Karoo, temnospondyls, stereospondyls.

INTRODUCTION

The Karoo Basin of South Africa preserves a continuous sequence of sedimentary rocks from the Late Carboniferous through to the Middle Jurassic periods (Smith 1990). Within this thick succession, the Permo-Triassic Beaufort Group and overlying Triassic-Jurassic Stormberg Group preserve a rich fossil biota that documents the evolution of terrestrial life during the late Palaeozoic and early to middle Mesozoic eras. These rocks are world renowned primarily for their therapsid ('mammal-like reptile') fauna, the diversity and abundance of which have allowed for the biostratigraphic subdivision of the sequence (Kitching 1977; Kitching & Raath 1984; Rubidge 1995). Less well known amongst Karoo fossil vertebrates are the temnospondyl amphibians, which are surpassed only by therapsids in terms of diversity and abundance.

The Temnospondyli was the largest, most diverse and most successful group of fossil amphibians, ranging in time from the Early Carboniferous to the Early Cretaceous (Milner 1990). Temnospondyls were superficially salamander-like in appearance with a total body length that varied from below 1 m to 6 m or more, most being above 1 m. They have also been widely linked to the origin of some or all of the modern lissamphibian groups (e.g. Milner 1988; Bolt 1991; Trueb & Cloutier 1991). Temnospondyls have been recovered from all continents and are near-ubiquitous components of non-marine sedimentary rocks of Permian and Triassic age. This abundance has led to their playing an important and sometimes critical role in local biostratigraphy and global correlation of non-marine strata of Triassic age (e.g. Hancox *et al.* 1995; Ivakhnenko *et al.* 1997; Ochev & Shishkin 1989; Lucas 1998).

In the Karoo the temnospondyl fauna is dominated by members of the great Mesozoic radiation of temnospondyls known as the Stereospondyli (Milner 1990; Yates & Warren 2000), with members of the Palaeozoic lineages Dvino-sauria and Dissorophoidea making up the non-stereo-

spondyl component. The Permo-Triassic Beaufort Group contains all but one of the higher-level temnospondyl taxa known from the Karoo, with most of these occurring in the Triassic part of the Group. The overlying Triassic-Jurassic 'Stormberg Group' has received far less attention palaeontologically, a fact reflected in the considerably lower diversity of tetrapods, including temnospondyls (Kitching & Raath 1984). Despite this overall rich temnospondyl record, relatively little research has been directed towards Karoo temnospondyls. In recent years, however, there has been a resurgence of interest in South African temnospondyls, especially in taxonomic studies (see review below), their role in interpreting the basin development of the Karoo (Hancox & Rubidge 1997; Hancox 1998), and in local biostratigraphy and correlation of non-marine tetrapod faunas (Hancox *et al.* 1995; Shishkin *et al.* 1995; Lucas 1998; Damiani 1999; Hancox *et al.* 2000; Shishkin 2000).

The only previous review of Karoo temnospondyls was that of Kitching (1978), a paper which was concerned primarily with documenting the total numbers and stratigraphic distribution of the temnospondyl fauna of the Beaufort Group. Since then, a significant number of new temnospondyl taxa have been described, additional information has been obtained through redescription of older material, and stratigraphic and biostratigraphic advances have been made. The aim of this paper is to summarize the taxonomy as well as stratigraphic occurrence of all known temnospondyls from the Karoo. It is not the intention here to critically reassess the relationships of each temnospondyl species discussed, although we provide a brief summary of the taxonomic history of those species whose relationships have been controversial. In the review below, higher-level taxa are arranged in alphabetical order, whereas individual species within each higher-level taxon are listed in chronological order of description. Synonymy lists include only those references in which a change in a taxon name has occurred. Note that the relationships of the Brachyopidae and Chigutisauridae

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within the Temnospondyli remain controversial (Shishkin 1991; Schoch & Milner 2000; Yates & Warren 2000; Damiani & Kitching 2003), and are here listed under the Stereospondyli merely for convenience. We precede our review with a brief outline of the Palaeozoic and Mesozoic geology of the Karoo in order to provide the necessary stratigraphic and biostratigraphic framework. Photographs of the skulls of Karoo temnospondyls, in dorsal view, are presented in Figs 1–3. A chart illustrating the biostratigraphic distribution of Beaufort Group temnospondyls is presented elsewhere (Damiani, in press), and is not repeated here.

Institutional abbreviations in the text are as follows: AM, Albany Museum, Grahamstown; BMNH, Natural History Museum, London; BP, Bernard Price Institute for Palaeontological Research, Johannesburg; BSP, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich; CGP, Council for Geoscience, Pretoria; MA, Museum Africa, Johannesburg; FMNH, Field Museum of Natural History, Chicago; GPIT, Institut und Museum für Geologie und Paläontologie, Tübingen; MGM, MacGregor Museum, Kimberley; NM, National Museum, Bloemfontein; RC, Rubidge Collection, Wellwood, Graaff-Reinet; SAM, South African Museum, Cape Town; TM, Transvaal Museum, Pretoria; UCMP, University of California Museum of Paleontology, Berkeley; UMZC, University Museum of Zoology, Cambridge.

GEOLOGICAL SETTING

The Karoo Basin of South Africa preserves a 12 km thick succession of mainly sedimentary rocks that accumulated in a retroarc foreland basin during the Late Carboniferous to Early Jurassic in southwestern Gondwana (Johnson *et al.* 1997; Catuneanu *et al.* 1998). These rocks reflect changing depositional environments including glacial, deep marine, deltaic, fluvial and aeolian (Smith 1990), and have yielded a diverse fossil biota consisting of plants, vertebrates, invertebrates, and trace fossils (Hancox & Rubidge 1997).

Lithostratigraphically the Karoo Supergroup is subdivided into five main groups. These are, in ascending stratigraphic order, the Dwyka, Ecce, Beaufort, 'Stormberg' and Drakensberg groups, broadly representing deposition in glacial (Dwyka), marine (Ecce) and terrestrial (Beaufort and Stormberg) environments (Smith 1990). This sedimentary sequence is capped by the Drakensberg volcanics which terminated sedimentation in the basin in the Middle Jurassic (Smith 1990). Vertebrate fossils in this sequence are known from the Ecce, Beaufort and 'Stormberg' groups.

The Early to Late Permian-aged Ecce Group consists of 16 different formations in the various parts of the basin (Johnson *et al.* 1997). In terms of vertebrate fossils, actinopterygian fish are common in several of these formations. The mesosaurid reptiles *Mesosaurus* and *Stereosternum* are the only tetrapods from the Ecce (Oelofsen 1981, 1987; Modesto 1996), and are confined to the Early Permian Whitehill Formation, a white-weathering, black carbonaceous shale considered to have been deposited in a deep-water, anoxic environment

(Oelofsen 1987; Catuneanu *et al.* 1998). *Mesosaurus* and *Stereosternum* are of particular importance as representing the oldest known amniotes from Gondwana.

The Beaufort Group conformably overlies the Ecce Group and the lithological contact between these groups is thought to coincide with the position of the 'palaeo-shoreline' (Rubidge *et al.* 2000). Its strata are fluvially derived and typically consist of alternating mudstone and sandstone units with characteristic upward-fining textures, red and purple colours, abundant vertebrate fossils, dessication cracks and palaeosol horizons, suggesting sediment accumulation on vast, semi-arid alluvial plains by floodplain aggradation (Smith 1990). The Beaufort Group preserves a complete Late Permian to early Middle Triassic (Rubidge 1995) sedimentary sequence and associated vertebrate fauna, and has long been recognized as the global standard for the non-marine Permo-Triassic (Romer 1975; Cosgriff 1984; Lucas 1998). This abundant and diverse vertebrate fauna is dominated by therapsids (Kitching 1977) which, combined with the paucity of basin-wide lithostratigraphic markers, have been used for the biostratigraphic subdivision of the group and stratigraphic correlation with faunas elsewhere (Kitching 1977; Keyser & Smith 1979; Rubidge 1995).

The current biostratigraphic scheme of the Beaufort Group consists of eight assemblage zones (Rubidge 1995); these have been broadly linked to the lithostratigraphy which comprises many formational names in the various parts of the basin (Keyser & Smith 1979; Rubidge 1995). These biozones are, in ascending order from oldest to youngest, the *Eodicynodon*, *Tapinocephalus*, *Pristerognathus*, *Tropidostoma*, *Cistecephalus*, *Dicynodon*, *Lystrosaurus* and *Cynognathus* Assemblage zones. The first six of these biozones are of Late Permian age (Rubidge 1995), the *Lystrosaurus* Assemblage Zone is broadly Early Triassic in age (Groenewald & Kitching 1995; Hancox 2000), and the *Cynognathus* Assemblage Zone is of Early-Middle Triassic age (Hancox 2000). Thus contrary to previous opinion which held that the *Cynognathus* biozone was either of Early (e.g. Anderson & Cruickshank 1978; Cosgriff 1984) or Middle Triassic (e.g. Ochev & Shishkin 1989) age, it is now considered to straddle the Early-Middle Triassic boundary. The Permo-Triassic boundary in the Karoo Basin is currently held to occur within the lowest part of the *Lystrosaurus* Assemblage Zone, and is defined by the last appearance of the dicynodont *Dicynodon* (Smith 1995). At present there are no formal subdivisions of the various Beaufort biozones although the *Cynognathus* Assemblage Zone has been subdivided into a lower 'A' zone (upper Olenekian), a middle 'B' zone (early Anisian), and an upper 'C' zone (late Anisian) (Hancox *et al.* 1995; Shishkin *et al.* 1995; Hancox & Rubidge 1997).

The 'Stormberg Group' unconformably overlies the Beaufort Group and is separated from it by a time gap representing the entire late Middle Triassic (Ladinian) (Hancox 2000). The 'Stormberg Group' consists of, in ascending stratigraphic order, the Molteno, Elliot and Clarens formations. The Molteno Formation is of Late Triassic (possibly Carnian) age (Hancox 2000); it hosts a diverse insect and plant assemblage, but as of yet the only

vertebrate body fossils are of fish (Anderson & Anderson 1984). The overlying Lower Elliot Formation is regarded by some workers to be a coeval, distal equivalent of the uppermost Molteno Formation (Cairncross *et al.* 1995; Anderson *et al.* 1998). It hosts a relatively meagre vertebrate fauna (Anderson *et al.* 1998) that has been assigned to the *Euskelosaurus* Range Zone (Kitching & Raath 1984) and used to support a Late Triassic age (Kitching & Raath 1984; Olsen & Galton 1984). The middle and upper parts of the Elliot Formation host a more diverse and abundant vertebrate fauna (Kitching & Raath 1984; Anderson *et al.* 1998) that, along with the lower part of the overlying Clarens Formation, has been assigned to the *Massospondylus* Range Zone (Kitching & Raath 1984) and used to support an Early Jurassic age (Smith & Kitching 1997; Anderson *et al.* 1998). Finally, the Clarens Formation hosts a meagre vertebrate record consisting primarily of elements of the underlying Upper Elliot Formation (Kitching & Raath 1984), and is of Early-Middle Jurassic age. Although vertebrate fossils are considerably less abundant in the Stormberg than in the Beaufort Group, this is compensated for by the presence of some of the earliest dinosaurs and mammals in the world (Kitching & Raath 1984). The Elliot Formation also preserves the last known temnospondyls from the Karoo (Warren & Damiani 1999).

REVIEW OF SOUTH AFRICAN TEMNOSPONDYLS

Temnospondyli Zittel 1887–1890

Dissorophoidea Boulenger 1902

Amphibamidae Moodie 1910

Micropholis stowii Huxley 1859, Fig. 1A

Petrophryne granulata Owen 1876a

Micropholis granulata Lydekker 1890b

Holotype. BMNH R4382, a skull, partially preserved as an internal mould, with attached lower jaw and partial pectoral girdle.

Locality and horizon. Given by Huxley (1859) as the 'foot of the Rhenosterberg', and by Watson (1913) as 'Rhenosterberg (north-west of New Bethesda), District Graaff-Reinet, Cape Colony', although the Rhenosterberg Range lies mainly in the southwest of the adjacent Middelburg District; *Lystrosaurus* Assemblage Zone, Early Triassic.

Referred material. BMNH R510, the holotype skull of '*Petrophryne granulata*' Owen (Watson 1913); BMNH R510a, a skull (Watson 1913); BSP 1934 VIII 42 and BSP 1934 VIII 43, three and five near-complete skeletons in sandstone nodules, respectively (Broili & Schröder 1937a). All specimens from the farm Donnybrook, Queenstown District, Eastern Cape Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Remarks. The somewhat enigmatic small temnospondyl *Micropholis stowii* was initially placed in its own higher-level taxon, the Micropholidae (Watson 1919), which was accepted by most subsequent workers (Haughton 1925; Kuhn 1933; Romer 1947; Huene 1956; Milner 1990; Warren & Hutchinson 1990). However, it is also widely referred to the Dissorophidae (Carroll & Winer 1977; Cosgriff 1984). Most recently, Daly (1994) recognized an assemblage of

primitive dissorophoids, including *M. stowii*, which she transferred to the Amphibamidae. *M. stowii* is of particular importance as representing the last surviving member of the dissorophoid temnospondyls. The species was redescribed by Boy (1985) on the basis of Broili & Schröder's (1937a) material, and new material is currently under description by Schoch & Rubidge. Van Heerden (1974) described a supposed skin impression of the reptile *Procolophon*, which was reinterpreted by Gow (1977) as the cast of a temnospondyl skull roof. Schoch & Milner (2000) attributed that specimen, NM QR1597, to *Lydekkerina*, but the presence of nodular ornament, large orbits, and a large otic notch (*cf.* Gow 1977) is identical to *M. stowii* and unlike *Lydekkerina*.

Dvinosauria Yates & Warren 2000

Tupilakosauridae Kuhn 1960

Thabanchuia oomie Warren 1999, Fig. 1B

Holotype. UCMP 42780, a near-complete skull with attached mandibular rami, and associated postcranial elements.

Locality and horizon. UCMP locality V4744, near Thaba N'chu, Free State Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Referred material. UCMP 42777, UCMP 42781, partial skulls and associated postcranial elements, and UCMP 42778, a string of articulated vertebrae with some ribs (Warren 1999); locality and horizon as for holotype.

Remarks. *Thabanchuia oomie* represents the fourth member of the rare higher-level taxon Tupilakosauridae, alongside *Tupilakosaurus heilmanni* from the Early Triassic of East Greenland (Nielson 1954), *Tupilakosaurus wetlugensis* from the Early Triassic of Russia (Shishkin 1961), and possibly *Kourerpeton bradyi* from the ?Late Permian of North America (Olsen & Lammers 1976; Warren 1999). The Tupilakosauridae represent relict survivors of the Palaeozoic Dvinosauria (Warren 1999; Yates & Warren 2000).

Stereospondyli Zittel 1887–1890

Brachyopidae Lydekker 1885

Batrachosuchus browni Broom 1903, Fig. 1C

Holotype. SAM-PK-5868, a near-complete skull.

Locality and horizon. An unknown locality in the Aliwal North District, Eastern Cape Province; the horizon is presumably the *Cynognathus* Assemblage Zone, which is widely exposed in the Aliwal North District.

Referred material. None.

Remarks. The holotype and only known specimen was collected by Mr Alfred Brown of Aliwal North, and described in an exceedingly brief note by Broom. An attempt was made to trace the type locality from Brown's extensive personal diaries held at the South African Museum, but there was nothing on record about its collection. Additional descriptions of *Batrachosuchus browni* have been provided by Haughton (1925), Watson (1956), Welles & Estes (1969) and Chernin (1977).

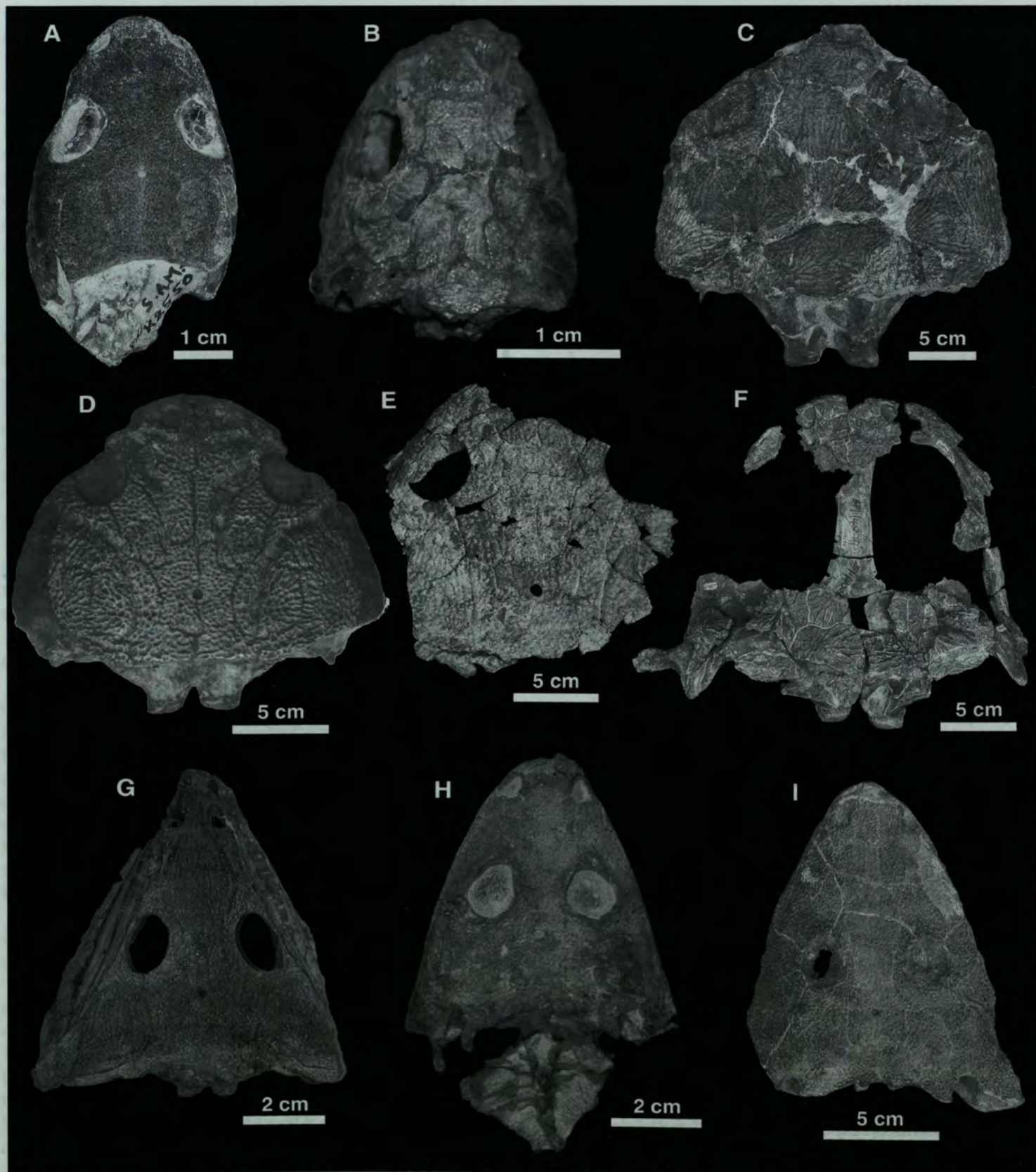


Figure 1. Photographs (in dorsal view) of the skulls of South African temnospondyls. **A**, *Micropholis stowii*, SAM-PK-K8550; **B**, *Thabanchuia oomie*, holotype, UCMP 42780; **C**, *Batrachosuchus browni*, holotype, SAM-PK-5868; **D**, *Bathignathus watsoni*, holotype, BMNH R3589; **E**, *Bathignathus poikilops*, holotype, BP/1/5790; **F**, *Vanastega plurimidens*, holotype, BP/1/4004; **G**, *Laidleria gracilis*, holotype, AM 4313; **H**, *Lydekkerina huxleyi*, holotype, BMNH R507; **I**, *Eolydekkerina magna*, holotype, BP/1/5079.

***Batrachosuchus* sp.**

Material. UMZC T194, a mandibular fragment, and UMZC T193, an atlas (Watson 1956). UCMP 42856 and UCMP 80859–60, assorted cranial and postcranial remains

(Welles & Estes 1969), now renumbered as follows: UCMP 42856, cranial and vertebral remains; UCMP 140568–69, 140571–72, 140575–78 and 140586, skull fragments; UCMP 140587–92, mandibular fragments; UCMP 80857–58,

140580, 140584, 140570, 140573–74, 140583, 140585 and 80859–60, postcranial remains.

Locality and horizon. UMZC material from the farm Luiperkop (not 'Luiper Kop' of Watson (1956) or 'Luiperdskop' of Kitching (1963)), Burgersdorp District, Eastern Cape Province (not 'Orange Free State' of Warren & Marsicano (2000)); *Cynognathus* Assemblage Zone, Early-Middle Triassic. UCMP material from the farm Slookraal, Rouxville District, Free State Province; Subzone B of the *Cynognathus* Assemblage Zone, early Anisian. Note that Welles & Estes (1969) ascribe the UCMP material to the farm Bethel; however, the locality from which the material was recovered actually belongs to the farm Slookraal (Renaut, pers. comm.).

Remarks. Further descriptions of some of the UCMP material have been provided by Colbert & Cosgriff (1974) and Warren & Marsicano (2000). Although this material has been referred to *Batrachosuchus*, there seems no reason why some of this material should not pertain to another brachyopid genus from the Karoo.

Bathignathus watsoni (Haughton) Damiani & Jeannot 2002, Fig. 1D

Batrachosuchus sp. Watson 1919

Batrachosuchus watsoni Haughton 1925

Holotype. BMNH R3589, a near-complete skull.

Locality and horizon. Unknown, but presumed by Watson (1956) to have come from the Burgersdorp District, Eastern Cape Province, and thus from the *Cynognathus* Assemblage Zone which is widely exposed in this district.

Referred material. None.

Remarks. Redescribed by Watson (1956) and Welles & Estes (1969), who separated the species from *Batrachosuchus browni* largely on skull proportions. Chernin (1977) listed further morphological differences and, following Welles & Estes (1969), suggested that '*Batrachosuchus*' *watsoni* may be sufficiently distinct from *B. browni* to warrant generic separation. However, Warren & Marsicano (2000) suggested that the species may be conspecific. Damiani & Jeannot (2002) listed further morphological differences and erected a new genus, *Bathignathus*, for '*B.*' *watsoni*.

Bathignathus poikilops Damiani & Jeannot 2002, Fig. 1E

Holotype. BP/1/5790, a partial skull roof and part of an occiput.

Locality and horizon. Farm Driefontein, Paul Roux District, Free State Province; Subzone A of the *Cynognathus* Assemblage Zone, upper Olenekian.

Referred material. BP/1/5883, a complete right mandibular ramus (Damiani & Jeannot 2002); locality and horizon as for holotype.

Remarks. This brachyopid shows phenetic similarities to both *Batrachosuchus browni* and *Bathignathus* ('*Batrachosuchus*') *watsoni*, but was argued (Damiani & Jeannot 2002) to show closest affinities with the latter.

Vanastega plurimidens Damiani & Kitching 2003, Fig. 1F

Holotype. BP/1/4004, a partial skull and associated cranial fragments, and a near-complete left mandibular ramus.

Paratype. BP/1/5831, a partial left mandibular ramus.

Locality and horizon. Farm Nooitgedacht, Burgersdorp District, Eastern Cape Province; Subzone B of the *Cynognathus* Assemblage Zone, early Anisian.

Referred material. None.

Remarks. A brachyopid remarkable for apparently being most closely related to the North American *Vigilius wellesi* (Welles & Estes 1969; Warren & Marsicano 2000), a species suggested (Shishkin 1991; Warren & Marsicano 2000) to be a dvinosaurian.

Chigutisauridae Rusconi 1949

cf. *Siderops* sp. Warren & Damiani 1999

Material. BP/1/5092, a partial skull with attached partial mandibular rami.

Locality and horizon. Farm Vastrap, Ladybrand District, Free State Province; Upper Elliot Formation, Early Jurassic.

Remarks. This and the material described below as Chigutisauridae indet. from the Late Triassic-Early Jurassic Elliot Formation represent the last known temnospondyls from the Karoo and the undoubted post-Triassic stereospondyls from Africa. Significantly, all well-known post-Triassic stereospondyl remains from Gondwana appear to be chigutisaurid, including the Elliot material. This material had previously been mentioned by Kitching & Raath (1984), Olsen & Galton (1984) and Hopson (1984), with the Lower Elliot material being referred to as capitosaurid and the Upper Elliot material as brachyopid. All of this material was examined by Warren & Damiani (1999) and found to be chigutisaurid.

Chigutisauridae indet.

Material. BP/1/4750, fragmentary cranial and postcranial remains from the farm Friesland West, Bethlehem District, Free State Province; Lower Elliot Formation, Late Triassic (Warren & Damiani 1999).

BP/1/5111, a partial left mandible with attached skull remains, articulated and disarticulated vertebrae, detached partial ribs, and a fragment of interclavicle from the farm Broken Slopes (an annexe of the farm Vastrap), Ladybrand District, Free State Province; Upper Elliot Formation, Early Jurassic (Warren & Damiani 1999).

BP/1/5252, partial left and right mandibular rami with associated cranial material from the farm Hollywood, Lady Grey District, Eastern Cape Province; Lower Elliot Formation, Late Triassic (Warren & Damiani 1999).

BP/1/5406, fragments of a skull with attached mandibular fragments, vertebral elements and a partial femur from the farm Vastrap, Ladybrand District, Free State Province; Upper Elliot Formation, Early Jurassic (Warren & Damiani 1999).

Laidleriidae Kitching 1957

Laidleria gracilis Kitching 1957, Fig. 1G

Holotype. AM 4313, an articulated skeleton comprising a complete skull with attached partial lower jaw, and presacral postcranial skeleton.

Locality and horizon. Elucwecwe, Engcobo District, East-

ern Cape Province; *Cynognathus* Assemblage Zone, Early-Middle Triassic.

Referred material. None.

Remarks. Kitching (1957) tentatively placed *Laidleria gracilis* in the Trematosauridae, but suggested that the species may in future be referred to a new 'family', the Laidleriidae. The species was retained in the monotypic Laidleriidae by some workers and considered closely related to the Rhytidosteidae (Cosgriff 1965; Warren 1998), but placed directly in the Rhytidosteidae by others (Warren & Black 1985; Milner 1990; Schoch & Milner 2000). Cosgriff & Zawiskie (1979) considered the Laidleriidae as *incertae sedis* within the Temnospondyli, while Yates & Warren (2000) allied *Laidleria* with the enigmatic Plagiosauridae. The holotype skull was redescribed in detail by Warren (1998).

Lydekkerinidae Watson 1919

Lydekkerina huxleyi (Lydekker) Broom 1915, Fig. 1H

Bothriceps huxleyi Lydekker 1889

Putterillia platyceps Broom 1930

Limnoiketes paludinatans Parrington 1948

Lydekkerina sp. Parrington 1948

Holotype. BMNH R507, a complete skull.

Locality and horizon. An unknown locality near Edenburg, Free State Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Referred material. BMNH R504–506, R508, cranial and postcranial remains in sandstone nodules (Lydekker 1890b); locality and horizon as for holotype. SAM-PK-3525, a partial skull (Haughton 1925); BSP 1934 VIII 44, three skulls with associated partial postcranial skeletons in a sandstone nodule (Broili & Schröder 1937b); UMZC T238, a skull and associated cervical vertebrae (Parrington 1948); a partial skull and associated postcrania described as *Lydekkerina* sp. by Parrington (1948); UMZC T214, the holotype (a skull and pectoral girdle) of *Limnoiketes paludinatans* Parrington (Shishkin *et al.* 1996); TM 168, TM 88, the holotype (a skull) and paratype (a dermal shoulder girdle and lower jaw), respectively, of *Putterillia platyceps* Broom (Shishkin *et al.* 1996). All material except for BMNH specimens are from the Harrismith Commonage, Free State Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Remarks. Watson (1912, 1919) provided a redescription of some of the British Museum material, while Shishkin *et al.* (1996) provide additional data based on specimens from the TM, BPI and NM. Despite a wealth of specimens, the ontogeny and morphological variation within *Lydekkerina huxleyi* has never been studied, and forms the basis of a current research project by A.M. Jeannot. This study will also determine if only one species of *Lydekkerina* is present, as is universally assumed.

Broomulus dutoiti (Broom) Romer 1947

Lydekkerina dutoiti Broom 1930

Holotype. MGM 4285, a poorly preserved skull with associated lower jaws and partial pectoral girdle.

Locality and horizon. Harrismith Commonage, Free State

Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Referred material. None.

Remarks. Various considered a valid species, indeterminate, or a junior synonym of *Lydekkerina huxleyi*. The species was redescribed following additional preparation by Shishkin *et al.* (1996) who confirmed its status as a valid taxon differing from *L. huxleyi* by a suite of characters.

Eolydekkerina magna Shishkin *et al.* 1996, Fig. 1I

Holotype. BP/1/5079, a near-complete skull.

Locality and horizon. Farm Fairydale, Bethulie District, Free State Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Referred material. None.

Mastodontosauridae Lydekker 1885 *sensu* Damiani 2001a

Xenotosuchus africanus (Broom) Morales & Shishkin 2002, Fig. 2A

Capitosaurus africanus Broom 1909 *nomen nudum*

Capitosaurus africanus (Broom) Haughton 1925

Parotosaurus africanus (Broom) Watson 1962

Parotosuchus africanus (Broom) Chernin 1978

Wellesaurus africanus (Broom) Damiani 2001a

Lectotype. SAM-PK-2360, the posterior half of a skull and a partial left mandible; designated type by Haughton (1925), since Broom (1909) did not designate a holotype.

Locality and horizon. Farm Vaalbank, Burgersdorp District, Eastern Cape Province; Subzone B of the *Cynognathus* Assemblage Zone, early Anisian.

Referred material. SAM-PK-3008, a poorly preserved skull (Haughton 1925); farm Winaarsbaken, Burgersdorp District, Eastern Cape Province. UCMP 41286, a near-complete skull and lower jaws (Morales & Shishkin 2002); farm Matabele, Rouxville District, Free State Province. Both specimens from Subzone B of the *Cynognathus* Assemblage Zone; early Anisian.

Remarks. Welles & Cosgriff (1965) considered '*Capitosaurus*' *africanus* a *nomen 'vanum'* since Broom (1909) did not figure the skull and provided only a cursory description. Chernin (1978) figured and redescribed the lectotype and transferred the species to the catch-all genus *Parotosuchus*. Shishkin *et al.* (1995), Maryanska & Shishkin (1996) and Damiani (2001a) suggested that '*Parotosuchus*' *africanus* may be related to *Wellesaurus peabodyi* (Welles & Cosgriff 1965; Damiani 2001a), and Damiani (2001a) transferred '*P.*' *africanus* to *Wellesaurus*. Most recently, Morales & Shishkin (2002) described a new specimen of *W. africanus* and transferred the species to a new genus, *Xenotosuchus*, but conceded that the species showed closest affinities to 'stenosaurids' (including *Wellesaurus*).

Parotosuchus haughtoni (Broili & Schröder) Chernin 1978, Fig. 2B

Capitosaurus haughtoni Broili & Schröder 1937c

Parotosaurus haughtoni (Broili & Schröder) Romer 1947

Karoosuchus haughtoni (Broili & Schröder) Ochev 1966

Holotype. BSP 1934 VIII 50, a fragmentary skull, apparently destroyed during World War II. *Neotype:*

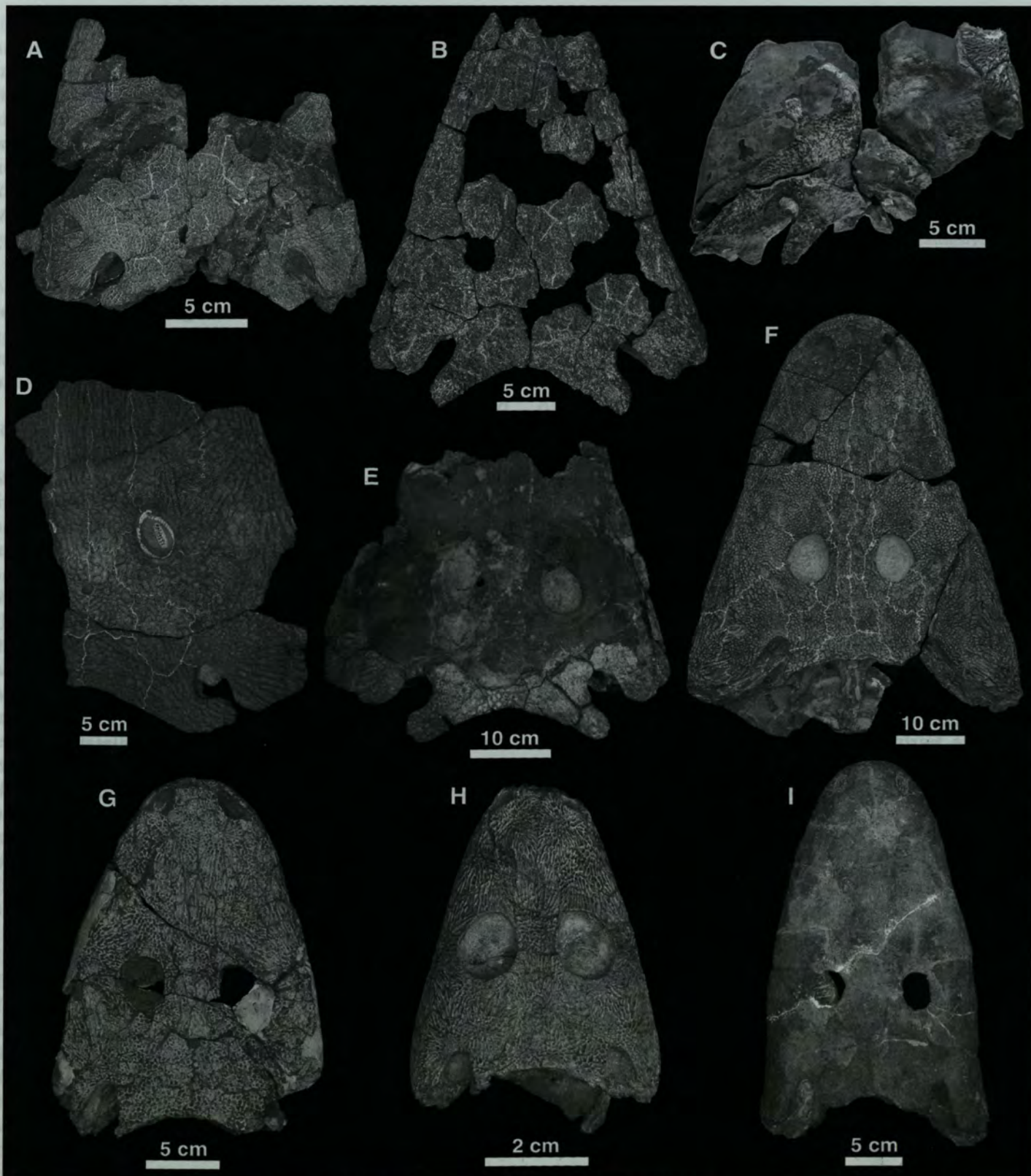


Figure 2. Photographs (in dorsal view) of the skulls of South African temnospondyls. A, *Xenotosuchus africanus*, holotype, SAM-PK-2360; B, *Parotosuchus haughtoni*, neotype, BP/1/5673; C, *Watsonisuchus magnus*, holotype, UMZC T173; D, *Paracyclotosaurus morganorum*, holotype, BP/1/5551; E, *Jammerbergia formops*, holotype, NM QR1436; F, *Uranocentron senekalensis*, referred specimen, NM QR1483; G, *Laccosaurus watsoni*, referred specimen, BP/1/213; H, *Broomistega putterilli*, referred specimen, BP/1/5058; I, *Rhinesuchoides tenuiceps*, holotype, FMNH UC 1519.

BP/1/5673, a partial skull and lower jaws, and associated intercentra (Damiani 2001b), designated neotype by Damiani (2001a).

Locality and horizon. Holotype: farm Kaaimansgat, Rouxville District, Free State Province; Subzone A of the *Cynognathus* Assemblage Zone, upper Olenekian. *Neo-*

type: Farm Driefontein, Paul Roux District, Free State Province; Subzone A of the *Cynognathus* Assemblage Zone, upper Olenekian.

Referred material. None.

Remarks. This species was long known from the holotype specimen only and was usually referred by most

workers to the catch-all genus *Parotosuchus* (= '*Capitosaurus*' and '*Parotosaurus*'), but placed in a new genus, *Karoosuchus*, by Ochev (1966). However, Damiani (1999, 2001b) described a new, near-complete specimen of *Parotosuchus haughtoni* which was made the neotype for the species (Damiani 2001a).

***Watsonisuchus magnus* (Watson) Ochev 1966, Fig. 2C**

Wetlugasaurus sp. Watson 1919

Wetlugasaurus magnus Watson 1962

Parotosaurus sp. Welles & Cosgriff 1965

Parotosuchus sp. Warren 1980

Holotype. UMZC T173, the posterior half of a skull split into several sections, and fragments of a right mandible.

Locality and horizon. Farm Watford, Burgersdorp District, Eastern Cape Province; Subzone A of the *Cynognathus* Assemblage Zone, upper Olenekian.

Referred material. None.

Remarks. Considered by Watson (1919, 1962) to most closely resemble the Laurasian taxon *Wetlugasaurus* in general skull morphology, later transferred to the catch-all taxon '*Parotosaurus*' by Welles & Cosgriff (1965), but shown by Ochev (1966) to pertain neither to *Wetlugasaurus* or '*Parotosaurus*' (= *Parotosuchus*).

***Watsonisuchus* sp. Damiani et al. 2001**

Material. CGP 1/60, the posterior portion of a right mandible.

Locality and horizon. Farm T'Zamenkomst 120, Venterstad District, Eastern Cape Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Remarks. This specimen represents the first undoubted record of a mastodonsaurid from the *Lystrosaurus* biozone.

***Paracyclotosaurus morganorum* Damiani & Hancox 2003, Fig. 2D**

Parotosuchus morgani Hancox & Rubidge 1997, *nomen nudum*

Paracyclotosaurus Hancox et al. 2000

Holotype. BP/1/5551, the right posterior portion of a skull.

Locality and horizon. Farm Wilgerkloof, Sterkstroom District, Eastern Cape Province; Subzone C of the *Cynognathus* Assemblage Zone, late Anisian.

Referred material. None.

***Jammerbergia formops* Damiani & Hancox 2003, Fig. 2E**

Holotype. NM QR1436, a partial skull.

Locality and horizon. Jammerberg, Wepener District, Free State Province; the horizon is presumably the *Cynognathus* Assemblage Zone (see discussion in Damiani & Hancox 2003).

Referred material. None.

Mastodonsauridae indet.

Cyclotosaurus albertyni* Broom 1904, *nomen dubium

Holotype. SAM-PK-K1876, fragments of a skull roof.

Locality and horizon. An unknown locality in the Rouxville District, Free State Province; the horizon is presumably the *Cynognathus* Assemblage Zone, which is

widely exposed in the Rouxville District.

Referred material. None.

Remarks. Broom (1904) stated that the frontal was included in the orbital margin and considered the otic notch to have been closed posteriorly, as in the Late Triassic *Cyclotosaurus*. The specimen is likely to be mastodonsaurid but the exceedingly brief description and lack of figures renders any taxonomic assignment uncertain. The holotype could not be located in the SAM collections and is evidently lost.

***Kestrosaurus dreyeri* Haughton 1925**

Holotype. SAM-PK-3452, a fragmentary skull, the fragments of which are set in plaster.

Locality and horizon. Farm Harmonia, Senekal District, Free State Province; Subzone A of the *Cynognathus* Assemblage Zone, upper Olenekian.

Referred material. A mandibular fragment said to be associated with the holotype skull (Chernin 1978).

Remarks. *Kestrosaurus dreyeri* was initially described (Haughton 1925) as possessing, amongst other peculiarities, paired anterior palatal vacuities, circular nostrils and an interfrontal. The presence of these characters was apparently corroborated by Chernin (1978), who redescribed the holotype skull as well as a referred mandibular fragment. *K. dreyeri* has been variously considered an aberrant 'capitosaurid' (Welles & Cosgriff 1965; Chernin 1978), closely related to *Benthosuchus* (Romer 1947), or closely related to *Mastodonsaurus* (Shishkin 1980; Milner et al. 1990), primarily on the basis of the alleged presence of paired anterior palatal vacuities. More recent workers (Hancox et al. 1995; Shishkin et al. 1995) consider *K. dreyeri* a typical 'capitosaurid' closely related to *Parotosuchus*. However, Damiani (2001a) considered the holotype skull an indeterminate mastodonsaurid as it was based largely on a plaster reconstruction within which non-diagnostic mastodonsaurid fragments had been embedded.

***Parotosuchus dirus* Chernin 1978**

Holotype. SAM-PK-434, fragments of a left and right lower jaw and associated cranial fragments.

Locality and horizon. An unknown locality near Aliwal North, Eastern Cape Province; the horizon is presumably the *Cynognathus* Assemblage Zone, which is widely exposed in the Aliwal North District.

Referred material. UMZC T167, a mastodonsaurid fragment from Aliwal North, Eastern Cape Province (Schoch & Milner 2000).

Remarks. The holotype pertains to a very large individual and is unusual in showing an additional row of teeth posterior to the usual post-symphyseal tooth row, and teeth on the anterior coronoid. The latter character is rare in stereospondyls but does occur in undescribed mandibles from the *Cynognathus* Assemblage Zone, probably referable to *Watsonisuchus* (RJD, pers. obs.). However, those mandibles are considerably smaller than that of *P. dirus*, differ significantly in the structure of the post-glenoid area, and usually lack any parasymphyseal teeth (RJD, pers. obs.). *Parotosuchus dirus* does not pertain

to *Parotosuchus* and probably represents a new genus, but additional material is required for a definitive diagnosis.

***Parotosaurus* sp.**

Material. UMZC T135, the posterior portion of a left mandible (Watson 1962).

Locality and horizon. Farm Winaarsbaken, Burgersdorp District (not 'Prince Albert District' of Schoch & Milner (2000)), Eastern Cape Province; Subzone B of the *Cynognathus* Assemblage Zone, early Anisian.

Remarks. As the crucial post-glenoid area of the mandible is damaged the specimen is largely generically indeterminate. However, it likely pertains to *Wellesaurus africanus* which is known from this locality and is the most common mastodontosaurid in Subzone B of the *Cynognathus* biozone.

Rhinesuchidae Watson 1919

***Rhinesuchus whaitsi* Broom 1908**

Rhinesuchus beaufortensis Boonstra 1940

Holotype. SAM-PK-1212, the basicranial region of a skull and associated cranial fragments.

Locality and horizon. Near Leeu-Gamka (formerly Fraserburg Road Station), Prince Albert District, Western Cape Province; *Tapinocephalus* Assemblage Zone, Late Permian.

Referred material. SAM-PK-3009, a near-complete skull and partial lower jaws (Haughton 1915b) from an unknown locality near Beaufort West, Western Cape Province. Skull fragments (unnumbered) from the farm Zeekoegat, Prince Albert District, Western Cape Province, mentioned by Broom (1908, 1912); *Tapinocephalus* Assemblage Zone, Late Permian. The posterior half of a skull from the farm Blaauw Krantz, Prince Albert District, Western Cape Province, mentioned by Haughton (1925); *Tapinocephalus* Assemblage Zone, Late Permian. SAM-PK-9135, the posterior end of a mandible (Watson 1962); farm Vogelfontein, Prince Albert District, *Tapinocephalus* Assemblage Zone, Late Permian. UMZC T64, a basicranial fragment (Watson 1962); farm Zeekoegat, Prince Albert District, Western Cape Province; *Tapinocephalus* Assemblage Zone, Late Permian.

Remarks. The Rhinesuchidae require a thorough morphological revision as inadequate data are available in the literature and most of the material is in need of preparation (RJD, pers. obs.). Consequently, the taxonomy and all accompanying remarks in this section are necessarily provisional pending a forthcoming revision by the authors. Haughton (1915b) briefly described a skull (SAM-PK-3009) which he referred to *R. whaitsi* but provided only photographs of the specimen and drawings of cross-sections through the left mandible. Watson (1919) figured the palate of *R. whaitsi* based on a sketch sent to him by Broom, and which Watson (1962) later considered to have probably been based on SAM-PK-3009. Haughton (1925) subsequently redescribed the holotype basicranial fragment and designated SAM-PK-3009 the 'paratype' for the species; however, this designation cannot hold as Broom (1908) did not designate a paratype.

SAM-PK-3009 was later designated the holotype for the new species *Rhinesuchus beaufortensis* (Boonstra 1940), with which Watson (1962) agreed but which is here and in Schoch & Milner (2000) considered a junior synonym of *R. whaitsi*.

***Uranocentrodon senekalensis* van Hoepen 1917, Fig. 2F**

Myriodon senekalensis van Hoepen 1911

Rhinesuchus major Broom 1912

Rhinesuchus senekalensis (van Hoepen) Haughton 1915b

Holotype. TM 75, the right side of a partial skull with attached lower jaw (van Hoepen 1911).

Locality and horizon. A sandstone quarry, the precise locality of which remains uncertain, near Senekal, Free State Province; *Dicynodon* Assemblage Zone, Late Permian.

Referred material. MA 60c1 and 60c1a, two partial skulls, described by Broom (1912) as *Rhinesuchus major*, and mentioned by van Hoepen (1911, 1915) as the specimens that had 'previously found their way to the Museum of the University College at Johannesburg'; three near-complete skeletons in numerous blocks of sandstone, all originally in the Transvaal Museum, Pretoria, and with which the holotype specimen, TM 75, is associated (van Hoepen 1915); NM QR1483, a near-complete skeleton in a sandstone block (Haughton 1915b); SAM-PK-2783, a partial left mandible with attached pieces of skull mentioned by Haughton (1915b); TM 185, a near-complete skull with attached lower jaw (Broom 1930). All known material of *Uranocentrodon senekalensis* is presumed to have come from the same unknown quarry near Senekal, a hypothesis supported by the similar lithology of the matrix associated with each specimen (Latimer *et al.* 2002).

Remarks. *Uranocentrodon senekalensis* was long considered from the Early Triassic *Lystrosaurus* Assemblage Zone (e.g. Kitching 1978) but has recently been shown (Latimer *et al.* 2002) to belong to the underlying *Dicynodon* Assemblage Zone, the assumption being that all of the known material was recovered from the same quarry near Senekal. In addition to the principal descriptions given by van Hoepen, Broom and Haughton, additional data on the species is provided by Watson (1962) and Findlay (1968).

***Laccosaurus watsoni* Haughton 1925, Fig. 2G**

Lydekkerina kitchingi Broom 1950

Muchocephalus muchos Watson 1962

Uranocentrodon watsoni (Haughton) Ochev 1966

Muchocephalus kitchingi (Broom) Schoch & Milner 2000

Holotype. SAM-PK-4010, a near-complete skull.

Locality and horizon. Farm Ferndale, Graaff-Reinet District, Eastern Cape Province; *Dicynodon* (formerly *Daptocephalus*) Assemblage Zone, Late Permian (Kitching 1978).

Referred material. BP/1/215, the holotype (a near-complete skull) of *Lydekkerina kitchingi* Broom. BP/1/213, the holotype (a near-complete skull) of *Muchocephalus muchos* Watson. Both specimens were found in close association on the farm Ringsfontein, Murraysburg District (Kitching 1978); *Dicynodon* (formerly *Daptocephalus*) Assemblage Zone, Late Permian. An additional

92 specimens (reposit in the BPI, Johannesburg) from the same horizon on the adjoining farm Beeldhouersfontein were referred to *L. kitchingi* by Kitching (1977, 1978).

Remarks. It appears likely that the holotypes of *Lydekkerina kitchingi* (Broom 1950), which is based on a small skull, and *Muchocephalus muchos* (Watson 1962), a much larger skull, represent juvenile and adult individuals of the same species as they were recovered in close association from the same locality. As the holotype of *M. muchos* appears morphologically indistinguishable from that of *Laccosaurus watsoni* (Haughton 1925), both *L. kitchingi* and *M. muchos* are here considered subjective junior synonyms of *L. watsoni*. As far as can be determined the 92 additional specimens of *L. kitchingi* reported by Kitching (1977, 1978) consist exclusively of small, probably juvenile, skulls (RJD, pers. obs.). Kitching (1978) also mentions a paratype specimen of *L. kitchingi* from Ringsfontein; however, Broom (1950) did not designate a paratype.

***Rhinesuchus capensis* Haughton 1925**

Rhinesuchus avenanti Boonstra 1940

Holotype. SAM-PK-7419, an incomplete skull.

Locality and horizon. Farm Spitzkop, Graaff-Reinet District, Eastern Cape Province; the horizon was given by Haughton (1925) as the 'Endothiodon zone' (now corresponding to the *Tropidostoma* Assemblage Zone), and by Broom (1948) and Kitching (1978) as the 'Cistecephalus zone', the latter now corresponding to both the *Tropidostoma* and *Cistecephalus* Assemblage zones (Rubidge 1995).

Referred material. SAM-PK-11489, the holotype (a skull) of *Rhinesuchus avenanti* Boonstra; farm Mynhardt's Kraal, Beaufort West District, Western Cape Province. The horizon is stated as the 'Tapinocephalus zone' by Boonstra (1940) and Kitching (1977), which now corresponds to both the *Tapinocephalus* and *Pristerognathus* Assemblage zones.

Remarks. The holotype of *R. capensis* is the largest known rhinesuchid skull with a high degree of ossification of the cranial bones (Haughton 1925). Consequently, sutures are poorly shown. Note that figures of *R. capensis* given by Haughton (1925) are inaccurate in that the skull is depicted as too short and broad, whereas it should be somewhat more slender and elongated (RJD, pers. obs.). The holotype of *R. avenanti* is considerably smaller but is otherwise very similar morphologically to *R. capensis*, and is here considered a junior synonym of the latter. In contrast, Watson (1962) and Schoch & Milner (2000) considered *R. avenanti* a junior synonym of *Rhinesuchoides tenuiceps* (Olson & Broom 1937), probably on the basis of having a similarly slender skull.

***Broomistega putterilli* (Broom) Shishkin & Rubidge 2000, Fig. 2H**

Lydekkerina putterilli Broom 1930

Holotype. TM 184, the posterior half of a skull and an associated mandibular fragment.

Locality and horizon. Harrismith Commonage, Free State Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Referred material. BP/1/5058, a complete skull with lower

jaw in articulation, and associated dermal pectoral girdle (Shishkin & Rubidge 2000); Ndanyane Hill, farm Hartebeest Spruit, Bergville District, KwaZulu-Natal. BP/1/3241, a partially disarticulated skeleton including skull and lower jaw (Shishkin & Rubidge 2000); farm Admiralty Estates, near Oliviershoek Pass, Bergville District, KwaZulu-Natal. Both specimens from the *Lystrosaurus* Assemblage Zone, Early Triassic.

Remarks. Described originally by Broom (1930) as a lydekkerinid closely related to *Lydekkerina huxleyi*, but shown by Shishkin & Rubidge (2000) to be a rhinesuchid and the only one known from the Triassic.

***Rhinesuchoides tenuiceps* Olson & Broom 1937, Fig. 2I**

Rhinesuchus rubidgei Broom 1948

Holotype. FMNH UC 1519, a skull and partial left lower jaw.

Locality and horizon. Stated by Olson & Broom (1937) as 'Tapinocephalus zone, 2 miles east of Stinkfontein'; this is probably the farm Stinkfontein located in the Prince Albert District, Western Cape Province, in which the *Tapinocephalus* Assemblage Zone is exposed (Kitching 1977).

Referred material. RC 73, the holotype (a skull) of *Rhinesuchus rubidgei* Broom (Schoch & Milner 2000); Farm Wimbledon (Welgevonden), Graaff-Reinet District, Eastern Cape Province; *Cistecephalus* Assemblage Zone, Late Permian.

Remarks. The synonymy of *Rhinesuchus rubidgei* and *Rhinesuchoides tenuiceps* was also accepted by Schoch & Milner (2000), both specimens being based on similarly sized skulls with near-identical proportions. Schoch & Milner (2000) also referred to *R. tenuiceps* three specimens, BP/1/2741, BP/1/2931 and BP/1/2958, which they state as pertaining to the *Tapinocephalus* Assemblage Zone. However, the latter two specimens are small rhinesuchid skulls associated with those collected by Kitching on the farm Beeldhouersfontein in the Murraysburg District (Kitching 1977, 1978), which were considered to belong to 'Lydekkerina' *kitchingi* (see *Laccosaurus watsoni*) and are from the *Dicynodon* Assemblage Zone. BP/1/2741 is a partial pelvis of the therapsid *Lystrosaurus* from the *Lystrosaurus* Assemblage Zone; the number as stated is probably a typographical error.

Rhinesuchidae indet.

***Eryops oweni* Lydekker 1890a, nomen dubium**

Eryops africanus Lydekker 1890b

Rhinesuchus africanus (Lydekker) Broom 1908

Holotype. BMNH R466, an incomplete right mandibular ramus.

Locality and horizon. An unknown locality in the Karoo.

Referred material. BMNH R470, an intercentrum (Lydekker 1890a); locality and horizon unknown but apparently associated with the holotype. SAM-PK-3010, a fragmentary skull and lower jaw (Haughton 1915b); farm Dunedin, Beaufort West District, Western Cape Province; the horizon was stated by Haughton (1915b) as 'Cistecephalus zone', although Kitching (1977) stated that the

locality pertains to the former 'Endothiodon zone', which now corresponds to the *Tropidostoma* Assemblage Zone (Rubidge 1995).

Remarks. The holotype specimen almost certainly pertains to a rhinesuchid because of the dense shagreen field covering the coronoid series and the slightly antero-posteriorly compressed marginal teeth. Haughton's (1915b) referred specimen includes a fragmentary and badly damaged skull and mandible; however, there is no reason to consider this specimen conspecific with Lydekker's holotype and the state of preservation of SAM-PK-3010 precludes any taxonomic referral.

Rhinesuchus broomianus von Huene 1931, *nomen dubium*

Holotype. GPIT Huene 1931 F.1, a partial skull.

Locality and horizon. Farm Kuilspoort, Beaufort West District, Western Cape Province; *Tropidostoma* (previously *Endothiodon*) Assemblage Zone, Late Permian.

Referred material. None.

Remarks. This species was considered valid by Schoch & Milner (2000) whose diagnosis was based principally on the skull being somewhat broader than in other rhinesuchids. However, the skull of *R. broomianus* has evidently undergone considerable dorso-ventral compaction and is poorly preserved, rendering any comparisons with other rhinesuchids difficult.

Rhytidosteidae Huene 1920

Rhytidosteus capensis Owen 1884

Holotype. BMNH R455, the antorbital portion of a skull with the anterior parts of the lower jaw in articulation, and the posterior part of the right mandible.

Locality and horizon. Given by Owen as 'Beersheba', Free State Province; Horizon unknown because of ambiguous locality details. Considered variably as from either the *Lystrosaurus* (Kitching 1978; Cosgriff & Zawiskie 1979; Shishkin 1994) or *Cynognathus* (Huene 1920; Romer 1947; Warren & Black 1985) Assemblage Zones.

Referred material. BMNH R503, an interotic fragment, a basicranial fragment, and a clavicular fragment (Lydekker 1890b), all considered by Lydekker to have been associated with the holotype; locality and horizon as for the holotype.

Remarks. Additional descriptions of *Rhytidosteus capensis* have been provided by Watson (1919), Huene (1920), Romer (1947) and Cosgriff (1965). Romer (1947) considered *R. capensis* conspecific with the trematosaurid *Microposaurus casei* (Haughton 1925), reconstructing the former using the outline of the latter and transferring *R. capensis* to the Trematosauridae. Cosgriff (1965) considered the association of *R. capensis* with *M. casei* to have been erroneous and returned the former to the Rhytidosteidae. Warren & Black (1985) suggested that *R. capensis* may be a composite of rhytidosteid and trematosaurid fragments, and left the species *incertae sedis* within the Trematosauroida (*sensu* Warren & Black 1985: Rhytidosteidae + Trematosauridae). However, most workers (Cosgriff 1984; Milner 1990; Shishkin 1994; Schoch & Milner 2000) consider *R. capensis* a valid

rhytidosteid. Schoch & Milner (2000) listed the fragmentary Russian species *Rhytidosteus uralensis* (Shishkin 1994) as a junior synonym of *R. capensis*. Although this assumption is reasonable, we prefer to leave *R. uralensis* as a separate species pending more complete material.

Pneumatostega potamia Cosgriff & Zawiskie 1979, Fig. 3A

Holotype. BP/1/981, a sandstone fragment containing the impression of a partial skull roof.

Locality and horizon. Farm Tafelberg, Middelburg District, Eastern Cape Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Referred material. SAM-PK-11188, associated fragments of a skull, lower jaw, dermal shoulder girdle and vertebral column (Cosgriff & Zawiskie 1979); farm Goede Hoop, Colesberg District, Eastern Cape Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Trematosauridae Watson 1919

Trematosuchus sobeyi (Haughton) Watson 1919, Fig. 3B

Trematosaurus sobeyi Haughton 1915a

Aphaneramma sp. Hammer 1987, in part.

Holotype. SAM-PK-2779, a complete skull.

Locality and horizon. Sobey's Quarry, Queenstown, Eastern Cape Province; Subzone A of the *Cynognathus* Assemblage Zone, upper Olenekian.

Referred material. SAM-PK-5136, the middle portion of a skull (Haughton 1925); locality and horizon as for the holotype. NM QR3263A and B, the anterior part of a snout and a palatal fragment, respectively (Shishkin & Welman 1994); farm Verdun, Paul Roux District, Free State Province; Subzone A of the *Cynognathus* Assemblage Zone, upper Olenekian.

Remarks. The referred specimen, SAM-PK-5136, was considered an indeterminate long-snouted (i.e. lonchorhynchine) trematosaurid and thus transferred to *Aphaneramma* sp. by Hammer (1987). However, SAM-PK-5136 comes from the same locality as the holotype of *Trematosuchus sobeyi* and is therefore reasonably considered referable to that taxon. The difficulty in placing SAM-PK-5136 taxonomically stems from the morphological similarity in postorbital skull morphology between short and long-snouted trematosaurids. A redescription of SAM-PK-5136 and all other supposed lonchorhynchines from the Karoo is in progress by the senior author.

Microposaurus casei Haughton 1925, Fig. 3C

Rhytidosteus casei Shishkin 1964

Holotype. SAM-PK-6556, a complete skull.

Locality and horizon. Exposures just above the Wonderboom Bridge, Burgersdorp District, Eastern Cape Province; Subzone B of the *Cynognathus* Assemblage Zone, early Anisian.

Referred material. None.

Remarks. Considered by Romer (1947) and Shishkin (1964) to be congeneric with the fragmentary rhytidosteid *Rhytidosteus capensis*, but shown by Cosgriff (1965) to be a trematosaurid. The species was later excluded from the Trematosauridae by Hammer (1987), but included by

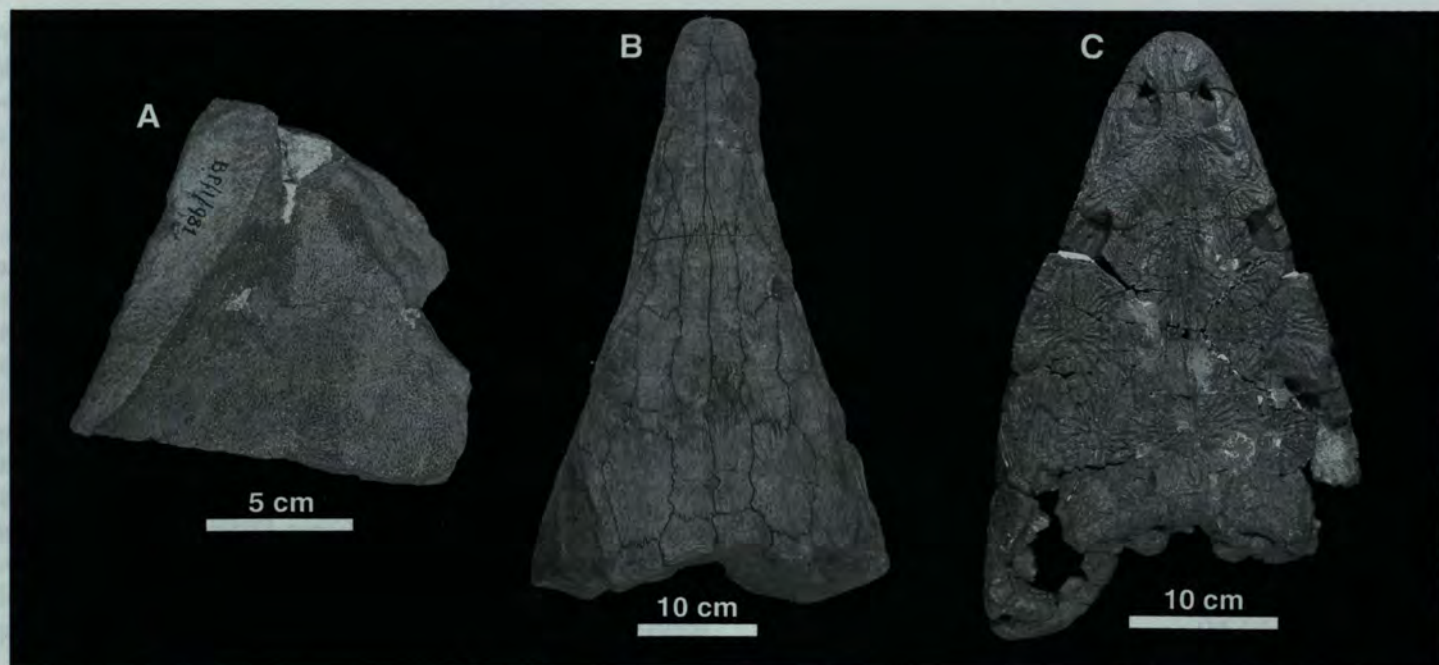


Figure 3. Photographs (in dorsal view) of the skulls of South African temnospondyls. **A**, *Pneumatostega potamia*, holotype, BP/1/981; **B**, *Trematosuchus sobeyi*, holotype, SAM-PK-2779; **C**, *Microposaurus casei*, holotype, SAM-PK-6556.

Warren & Black (1985), Hellrung (1987) and Schoch & Milner (2000). The latter authors suggested close affinities with *Tertrema* from the Early Triassic of Spitzbergen. However, the morphology of *M. casei*, currently being redescribed following additional preparation by the senior author, points strongly to affinities with the Russian 'platystegid' *Inflectosaurus amplus* (Shishkin 1960).

Trematosauridae indet.

Trematosaurus kannemeyeri Broom 1909, *nomen dubium*
Aphaneramma kannemeyeri (Broom) Huene 1920
Trematosuchus kannemeyeri (Broom) Zittel 1923
Gonioglyptus kannemeyeri (Broom) Huene 1925
Aphaneramma sp. Hammer 1987, in part
Holotype. SAM-PK-1329, a portion of the middle part of a badly weathered skull, including the orbits.

Locality and horizon. An unknown locality in the Free State Province, then known as the 'Orange River Colony' (Broom 1909); horizon unknown, but suggested as 'Upper Beaufort Beds' (equivalent to the *Cynognathus* Assemblage Zone) by Haughton (1925), and adopted by all subsequent workers.

Referred material. None.

Remarks. Widely considered an indeterminate, *Aphaneramma*-like lonchorhynchine by recent workers (Hammer 1987; Welles 1993; Shishkin & Welman 1994), and listed as a valid lonchorhynchine, *Aphaneramma kannemeyeri*, by Schoch & Milner (2000). In contrast, Damiani *et al.* (2000) considered *Trematosaurus kannemeyeri* referable to either a long or short-snouted trematosaurid, and declared the specimen a *nomen dubium*. Subsequent re-examination by the senior author has confirmed its lonchorhynchine affinities; however, its poor state of preservation precludes any further taxonomic placement and the species should remain a *nomen dubium*. A redescription is currently in progress by the senior author.

A recently discovered lonchorhynchine from the *Lystrosaurus* Assemblage Zone was reported by Damiani & Welman (2001) as representing an undoubted lonchorhynchine from that biozone. This specimen, NM QR3424, is represented by a partial snout and may belong to the same species as '*Trematosaurus*' *kannemeyeri*. A full description will be the subject of a forthcoming publication.

Trematosauridae gen. et. sp. indet.

Material. CGP 1/5, a complete but damaged right mandibular ramus (Damiani *et al.* 2000).

Locality and horizon. Farm Perdelaaagte (an annexe of the farm Heuningkrans 26), Burgersdorp District, Eastern Cape Province; *Lystrosaurus* Assemblage Zone, Early Triassic.

Remarks. This specimen appears to belong to a short-snouted trematosaurid such as *Trematosaurus* or *Trematosuchus*, and, along with NM QR3424, represents the second trematosaurid taxon from the *Lystrosaurus* Assemblage Zone. The specimen is of further importance as it comes from high in the *Lystrosaurus* Assemblage Zone, in strata which have been postulated to pertain to an 'intermediate' biozone between the *Lystrosaurus* and *Cynognathus* biozones (Neveling *et al.* 1999).

Stereospondyli indet.

Laccocephalus insperatus Watson 1919, *nomen dubium*

Holotype. BMNH R532, an incomplete skull in a sandstone nodule.

Locality and horizon. Stated by Watson (1919) as 'near Mr Hope's farm, Orange Free State'; horizon unknown.

Referred material. None.

Remarks. The poor preservation of *L. insperatus* renders any taxonomic assignment uncertain. However, in size and general outline the specimen is almost certainly a

stereospondyl. In particular, the presence of a *crista muscularis* of the parasphenoid and a median, raised area on the cultriform process, as alluded to by Watson (1919), suggest that *L. insperatus* may be a rhinesuchid or mastodonsaurid. However, there is neither sufficient morphological nor stratigraphic data to suggest that *L. insperatus* is synonymous with *Uranocentrodon senekalensis* (contra Schoch & Milner 2000).

Stereospondyli gen. et. sp. indet.

Material. BP/1/4935, a fragment of a mandibular ramus from the farm Mequatling, Clocolan District, Free State Province (Warren & Damiani 1999); Lower Elliot Formation, Late Triassic.

Remarks. Likely to pertain to a chigutisaurid, as with all of the other known temnospondyl material from the Elliot Formation (see Chigutisauridae).

Temnospondyli indet.

Petrophryne major Owen 1876b, *nomen dubium*

Bothriceps major (Owen) Lydekker 1890b

Holotype. BMNH R4145, a sandstone block containing a poorly preserved partial skull, largely as impression. Originally held in the museum of the Geological Society of London under the catalogue number S.A.119.

Locality and horizon. Collection data associated with the holotype states the horizon and locality as the 'Stormberg Beds', 'Southern margin of the Stormberg Range'.

Ptychosphenodon browni Seeley 1907, *nomen dubium*

Holotype. BMNH R3503, a mandibular fragment.

Locality and horizon. An unknown locality near Aliwal North, Eastern Cape Province; the horizon is presumably the *Cynognathus* Assemblage Zone, which is widely exposed in the Aliwal North District.

Syphonodon thecomastodon Seeley 1908, *nomen dubium*

Holotype. BMNH R3609, a large temnospondyl tooth.

Locality and horizon. Farm Wonderboom, Burgersdorp District, Eastern Cape Province; the horizon is presumably the *Cynognathus* Assemblage Zone, which is widely exposed in the Burgersdorp District.

Phrynosuchus whaitsi Broom 1913, *nomen dubium*

Rhinesuchus sp. Chernin & Kitching 1977

Holotype. SAM-PK-2357, a crushed, poorly preserved skull and articulated partial postcranial skeleton in a sandstone nodule.

Locality and horizon. Farm Droogvoets Fontein, Fraserburg District, Western Cape Province; Horizon uncertain, but suggested by Broom (1913) as 'upper part of the *Endothiodon* Zone', and more recently (Chernin & Kitching 1977) as either uppermost *Tapinocephalus* Zone or lowermost *Cistecephalus* Zone. These horizons now correspond, respectively, to the *Pristerognathus* and *Tropidostoma* Assemblage Zones, of Late Permian age.

Remarks. Broom (1913) made no attempt to place the specimen taxonomically, but it was later considered an indeterminate rhinesuchid by Chernin & Kitching (1977).

Schoch & Milner (2000) followed this assignment. However, re-examination of the specimen by the senior author failed to reveal any resemblance to rhinesuchids or any characters which could place the specimen taxonomically.

CONCLUSIONS

The Karoo of South Africa boasts a rich and varied temnospondyl fauna that is amongst the most diverse in the world, with 10 higher-level taxa recorded to date. This record is dominated by predominantly large temnospondyls of the clade Stereospondyli.

The Palaeozoic temnospondyl record in the Karoo is at present restricted to one higher-level taxon, the Rhinesuchidae, despite the fact that six of the eight biozones of the Beaufort Group are of Permian age. It is unclear, however, whether this reflects a true paucity (or absence) of other higher-level taxa or a preservational bias (Kitching 1978). Members of the Rhinesuchidae appear to be endemic to Gondwana, and have been recorded elsewhere from the Upper Permian of what is now Malawi (Watson 1962), India (Werneburg & Schneider 1996) and Brazil (Barberena 1998; Barberena & Dias 1998). However, the diversity of rhinesuchids is greater in the Karoo than anywhere else in Gondwana, and only in the Karoo are rhinesuchids known to have survived the end-Permian extinction event. These facts are significant because the Rhinesuchidae are widely regarded as the most basal stereospondyls (Milner 1990; Schoch & Milner 2000; Yates & Warren 2000).

The Mesozoic sequence plays host to all 10 higher-level temnospondyl taxa known from the Karoo, distributed as follows. The *Lystrosaurus* Assemblage Zone contains seven higher-level taxa, the Amphibamidae, Tupilakosauridae, Rhinesuchidae, Lydekkerinidae, Rhytidosteidae, Mastodonsauridae and Trematosauridae. The overlying *Cynognathus* Assemblage Zone hosts the last two of these taxa in addition to the Brachyopidae, Laidleriidae, and, possibly, the Rhytidosteidae. The now greater diversity of higher-level temnospondyl taxa in the *Lystrosaurus* biozone is noteworthy because of the previously held notion that the *Cynognathus* biozone contained a greater diversity of temnospondyls. This shift in diversity has occurred only recently, however, with the resurgence in studies of Beaufort Group temnospondyls. The remaining higher-level taxon, the Chigutisauridae, is at present known only from the Late Triassic–Early Jurassic Elliot Formation.

Finally, it is particularly noteworthy that the *Lystrosaurus* Assemblage Zone plays host to a relict member of the dvinosaurian radiation (*Thabanchuia*), the last surviving member of the Dissorophoidea (*Micropholis*), and the only Triassic rhinesuchid (*Broomistega*). These facts, combined with the high diversity of rhinesuchids in the Permian of the Karoo, lend strong support to the hypothesis that the initial radiation of the Stereospondyli occurred in a 'safe haven' that was located in Gondwana (Yates & Warren 2000; Warren *et al.* 2000). The evidence for a Gondwanan origin and radiation also suggests that the exact position of the 'safe haven' may have been southern Africa. However, it remains unclear whether the great stereospondyl

radiation began in the Late Permian (Yates & Warren 2000) or in the earliest Triassic (Milner 1990).

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Biological aspects of the Permian dicynodont *Oudenodon* (Therapsida: Dicynodontia) deduced from bone histology and cross-sectional geometry

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Bone histology and cross-sectional geometry were used to examine the growth patterns and lifestyle habits of the Late Permian dicynodont, *Oudenodon*. Several limb bones were analysed, revealing rapidly deposited fibro-lamellar bone, interrupted by annuli or sometimes Lines of Arrested Growth. Peripheral slowly deposited parallel-fibred bone was observed in several elements. It is suggested that the initial growth of *Oudenodon* was rapid during the favourable growing season, but decreased or sometimes ceased completely during the unfavourable season. Growth was cyclical and may have been sensitive to environmental fluctuations. The slowly forming parallel-fibred bone towards the sub-periosteal surface in several elements indicates a permanent transition to slow growth and may reflect the onset of sexual maturity. Bone cross-sectional geometry results reveal a markedly thick cortex, indicating a possible modification for digging. These cross-sectional geometry values, in conjunction with the limb morphology, suggest that *Oudenodon* was fossorial.

Keywords: Therapsida, *Oudenodon*, bone histology, growth patterns.

INTRODUCTION

The Dicynodontia are recognized as the most successful herbivorous therapsid group of the Late Permian (King 1990). They radiated into several, varied ecological niches and became the most numerous herbivorous tetrapods by the end of this period (Hotton 1986; King 1990). As a result of the highly varied and widespread nature of this group, the dicynodonts have received much attention in the literature, both systematically and morphologically (e.g. Angielczyk 2001; Cluver & Hotton 1983; Cluver & King 1983; Hotton 1986; Keyser 1975; Keyser & Cruickshank 1979; Rubidge & Sidor 2001). The focus of previous studies has been on cranial descriptions, locomotory modifications and masticatory systems (e.g. Cluver 1971; Cluver & Hotton 1983; Cluver & King 1983; Cox 1998; Kemp 1982; Keyser 1975; King 1996; King *et al.* 1989), while other biological traits, such as growth patterns and lifestyle habits, have been less extensively studied.

A few studies, such as those of Chinsamy & Rubidge (1993), Enlow & Brown (1957) and Ricqlès (1972, 1976, 1991), have used bone histology to deduce the growth patterns of several dicynodont genera. However, these studies were not comprehensive examinations and thus provided limited information. In addition, only one type of element was usually examined, making it difficult to deduce generic patterns of growth.

The lifestyle habits of a few dicynodonts such as *Lystrosaurus* (Brink 1951; Broom 1903; Groenewald 1991; King 1991; King & Cluver 1991), *Cistecephalus* (Cluver 1978) and *Diictodon* (Ray & Chinsamy 2003; Smith 1987) have been examined using burrow casts and functional anatomy to suggest specific modes of life.

Oudenodon was a medium-sized dicynodont (skull length from 100–300 mm) whose skeletal remains have been excavated from Late Permian deposits in South

Africa (Cluver & Hotton 1983). The morphology of the skull has been described in detail (Broom 1912; Cluver & Hotton 1983; Cluver & King 1983; Keyser 1975; Owen 1860) and distinctive features include a lack of teeth in both the upper and lower jaws, a deep and relatively narrow secondary palate, a sharp maxillary crest behind the caniniform process, the absence of maxillary tusks and narrow dentary tables on the dentaries (Cluver & Hotton 1983; Cluver & King 1983).

Although the cranial morphology of *Oudenodon* (Cluver & Hotton 1983; Cluver & King 1983; Keyser 1975;) and to a lesser extent the postcranial skeleton (Broom 1901), have been examined, little pertaining to the biology of this genus has been discussed. Thus, there is inadequate information regarding the growth patterns and lifestyle habits of *Oudenodon* for deducing its overall biology.

Bone histology is a well-established technique for examining growth patterns and lifestyle habits of extinct animals (e.g. Enlow & Brown 1957; Reid 1996; Ricqlès 1976, 1980). The bone histology of *Oudenodon* has previously been described by Ricqlès (1972) and Chinsamy & Rubidge (1993). Ricqlès (1972) examined a humerus and a femur, whereas Chinsamy & Rubidge (1993) used a humerus to interpret the growth patterns of *Oudenodon*. Although informative, both descriptions were brief and neither study considered inter-elemental histovariability. Although, Ricqlès (1972) examined a humerus and a femur, histological variation between the two elements was not discussed. It is becoming increasingly evident that inter-elemental histovariability should be considered when deducing the overall growth patterns of a genus (Botha 2002; Curry 1999; Horner *et al.* 1999, 2000; Starck & Chinsamy 2002; Ray *et al.*, in press).

A technique known as bone cross-sectional geometry can be used in conjunction with bone histology analysis to

Table 1. *Oudenodon* specimens used in this study and their localities. All specimens were recovered from the *Dicynodon* Assemblage Zone, Teekloof Formation, Beaufort Group of South Africa. SAM-PK-K refers to South African Museum, Iziko Museums of Cape Town, South Africa. SAM-PK-K4807 and SAM-PK-10019 consist of several disarticulated elements representing several individuals.

Locality	Specimen number	Skeletal element	Region sectioned
Richmond	SAM-PK-K4807a	Femur	Midshaft, proximal
	SAM-PK-K4807b	Femur	Midshaft, proximal
	SAM-PK-K4807c	Femur	Proximal
	SAM-PK-K4807d	Fibula	Midshaft, proximal
	SAM-PK-10019a	Femur	Midshaft, proximal
	SAM-PK-10019b	Tibia	Proximal
	SAM-PK-10019c	Fibula	Midshaft, proximal
	SAM-PK-10019d	Humerus	Distal
Murraysburg	SAM-PK-11141	Femur	Distal midshaft

provide information regarding an animal's lifestyle. Studies have shown that a direct relationship exists between an animal's lifestyle and the structural design of its bones (Bou *et al.* 1990; Fish 1993; Stein 1989; Wall 1983). For example, fossorial animals have thick, relatively short limb bones with a high force moment of their forelimb muscles for digging (Bou *et al.* 1990; Casinos *et al.* 1993). Equally, the bones of sirenians, cetaceans, crocodilians and certain aquatic birds have extremely high bone densities to counteract buoyancy (Buffrénil *et al.* 1990; Hua & Buffrénil 1996). Osteological modifications of an extinct animal can therefore provide valuable information for determining the type of habitat an animal occupied.

In a study conducted by Wall (1983), who examined the cortical thickness (bone wall) of 49 mammalian genera, it was found that most of the aquatic mammals studied had a significantly higher limb bone density than that of the terrestrial mammals. He proposed that if the compact bone wall exceeds 30% of the average diameter, the animal is aquatic or at least semi-aquatic, possibly as an adaptation to counteract buoyancy (Wall 1983).

Magwene (1993) studied the bone cross-sectional geometry of several crocodilian, lizard, non-mammalian therapsid and mammalian femora and found that, on average, non-mammalian therapsids and mammals have thinner bone walls compared to crocodilians and lizards. He argued that non-mammalian therapsids and mammals have lighter bones as a weight-saving modification because they are subject to greater bending and torsional stresses due to their higher activity levels. In contrast, crocodilian and lizard limb bones are more robust and stiff as they have less active lifestyles (Magwene 1993). Magwene examined each group collectively, but when the results are examined according to lifestyle, 75% of the semi-aquatic crocodilians and lizards and all of the arboreal/fossorial lizards studied had a cortical thickness of more than 30%. Similarly, 38% of the fossorial/arboreal mammals had a cortical thickness that exceeded 30%, while several of the other fossorial mammals had a cortical thickness that was at least 28%. Thus, Wall's '30%' threshold appears adequate for indicating the approximate minimum cortical thickness required for aquatic lifestyles, as well as for fossorial or arboreal lifestyles. Thus, bone cross-sectional geometry can be used to provide further information regarding the lifestyle habits of *Oudenodon*.

MATERIALS AND METHODS

The *Oudenodon* study elements, which were positively identified from associated cranial material, include several limb bones (humerus, femora, tibiae, fibulae). All specimens were recovered from the *Dicynodon* Assemblage Zone, Balfour/Teekloof Formation, Beaufort Group of South Africa (Rubidge 1995).

Limb bones were selected as they are the most readily preserved compared to other elements and they show the least secondary remodeling in the midshaft region (Francillon-Vieillot *et al.* 1990). Limb bones therefore provide the best record of the type of growth exhibited by the animal. Several different types of limb bones were included to ensure that inter-elemental histovariability was considered. The elements are from different individuals and represent various ontogenetic stages. Owing to their large size (approximate range between 90 and 160 mm in length) it is unlikely that any of the study elements represent juvenile individuals, they probably all represent subadult or adult individuals.

Most of the limb bones were transversely sectioned in the midshaft region. Proximal or distal regions were also sectioned where possible, depending on the particular element (Table 1). Each region of bone to be sectioned was embedded in the clear resin, Impset 21, to prevent the bone from disintegrating during the process. Once the resin had set, the area to be sectioned was cut using a Blanes diamond-tipped saw. The cut surface was polished until smooth using a Logitech LP50 lapping machine and then mounted onto a petrographic glass slide using the resin adhesive, Epotek. Pressure was then applied to the sections to eliminate any bubbles. A thin section, approximately 35 μ m thick, was then cut using a Logitech CS10 cut-off diamond-tipped saw. The resulting thin sections were polished until smooth with the Logitech LP50 lapping machine and examined using a Leitz Laborlux K compound microscope. The bone histology was photographed using a Nikon FinePix S1 Pro digital camera.

Thin sections were also used to measure the cortical thickness of the midshaft region of each bone. The cortical thickness was measured in microns at four equidistant radial positions using an eyepiece micrometer in the Leitz Laborlux K compound microscope at $\times 40$ magnification. The mean of these four measurements was divided by the mean bone diameter and the final value expressed as a percentage.

RESULTS

Bone histology

A comprehensive analysis of the bone histology of the *Oudenodon* postcrania revealed moderately vascularized fibro-lamellar bone tissue, becoming parallel-fibred towards the periphery in some cases. Interruptions by annuli of lamellar bone or Lines of Arrested Growth (LAGs) were noted throughout the cortex in all elements. Some variation was noted between the different types of elements and will be described in detail below.

Femur. (SAM-PK-11141, SAM-PK-K4807a, SAM-PK-K4807b, SAM-PK-K4807c, SAM-PK-10019a). The femora contain small medullary cavities, which are surrounded by notably thick cortices. The primary bone tissue is fibro-lamellar bone with longitudinally oriented primary osteons (Fig. 1A), but a laminar network is present in SAM-PK K4807b and SAM-PK-10019a (Fig. 1B). Annuli of lamellar bone or LAGs interrupt the fibro-lamellar bone at intervals. The globular osteocyte lacunae in the fibro-lamellar bone become flattened in the annuli. They have branched canaliculi, which radiate out in all directions. Vascularization is generally moderate, decreasing towards the periphery in femora SAM-PK-11141, SAM-PK-K4807a and SAM-PK-K4807c where the overall bone tissue organization becomes parallel-fibred bone (Fig. 1C). In these regions of parallel-fibred bone, the sparse vascular canals become simple and the annuli are sometimes multiple (i.e. several annuli clustered together). Secondary remodeling with numerous secondary osteons is observed surrounding the medullary cavity of femur SAM-PK-K4807b (Fig. 1D). Sharpey's fibres are observed in femur SAM-PK-K4807a (Fig. 1E).

Tibia. (SAM-PK-10019b). The tibia consists of a markedly thick cortex and a free medullary cavity is absent. Trabeculae, lined with endosteal lamellar bone, fill the entire medullary cavity. The primary tissue consists of highly vascularized fibro-lamellar bone, which is interrupted by annuli (Fig. 2). Large, longitudinally oriented primary osteons, which form a laminar network in places, decrease in diameter towards the sub-periosteal surface.

Fibula. (SAM-PK-10019c, SAM-PK-K4807d). The medullary cavities are completely filled with bony trabeculae (Fig. 3A). Secondary remodeling, with large resorption cavities is extensive. The moderately vascularized fibro-lamellar bone tissue contains distinct annuli of lamellar bone tissue, but becomes poorly vascularized parallel-fibred bone at the periphery of SAM-PK-10019c (Fig. 3B). Longitudinally oriented primary osteons in the fibro-lamellar bone are replaced by small, simple vascular canals that are sparsely distributed in the parallel-fibred region. Distinct Sharpey's fibres are noted in SAM-PK-10019c (Fig. 3B) and SAM-PK-K4807d.

Humerus. (SAM-PK-10019d). The bone tissue consists of fibro-lamellar bone interrupted by annuli, similar to the rest of the study elements (Fig. 4). LAGs are absent. The tissue is highly vascularized near the medullary cavity, but becomes moderately vascularized towards the sub-periosteal surface. Longitudinal primary osteons characterize the fibro-lamellar bone. Secondary remodel-

ing is extensive and a free medullary cavity is absent, which may be due to the section being taken from a more distal region compared to the other elements.

Bone cross-sectional geometry

The femur SAM-PK-K4807a has a cortical thickness of 46% and the cortical thickness of both femora SAM-PK-K4807b and SAM-PK-10019a is 39%. A mid-diaphyseal region was not available for femur SAM-PK-K4807c. Although midshaft regions of the fibulae were available for study, the medullary cavities were completely filled with bony trabeculae, making it impossible to discern a distinct transition between trabeculae and compact bone. Thus, the midshaft cortical thickness of these elements was not measured. Similarly, a free medullary cavity was absent from tibia SAM-PK-10019b. The cortical thickness of the humerus SAM-PK-10019d was not measured as a midshaft region was unavailable.

DISCUSSION

Bone histology

Histological examination of the bones revealed rapidly deposited fibro-lamellar bone, indicating rapid growth. The primary bone tissue organization varied from laminar to longitudinally oriented primary osteons. Annuli of lamellar bone or LAGs were observed interrupting the fibro-lamellar bone, which indicates that growth slowed down or even ceased periodically. These observations agree with the findings of Ricqlès (1972) and Chinsamy & Rubidge (1993), although Ricqlès did not refer to any annuli or LAGs in the humerus. Ricqlès (1972) noted that the humerus used in his study was highly vascularized, which may indicate that this element was from a juvenile individual and growth may have been too rapid to exhibit growth rings.

Although the overall bone tissue pattern observed in this study agrees with the findings of Ricqlès (1972) and Chinsamy & Rubidge (1993) there are some variations not previously noted. The most marked and significant variation is the presence of slowly forming parallel-fibred bone at the periphery of several femora (SAM-PK-11141, SAM-PK-K4807a, SAM-PK-K4807c) and a fibula (SAM-PK-10019c). This bone tissue indicates a marked decrease in overall growth and represents a permanent transformation to slow growth. Ricqlès (1972) did not note parallel-fibred bone in his examination of the femur. A transition from rapidly to slowly forming bone tissue has been reported in the non-mammalian cynodonts *Procynosuchus* (Ray *et al.*, in press) and *Thrinaxodon* (Botha & Chinsamy, in press). Such a feature has been documented in extant animals as well and it is suggested that this transition represents the onset of sexual maturity (Castanet & Bæz 1991; Reid 1996; Sander 2000; Botha & Chinsamy, in press; Ray *et al.*, in press). The parallel-fibred bone in *Oudenodon* may represent the onset of sexual maturity whereby growth continued after sexual maturity was reached, but at a much slower rate.

It is suggested from the bone histology that femora SAM-PK-11141, SAM-PK-K4807a and SAM-PK-K4807c

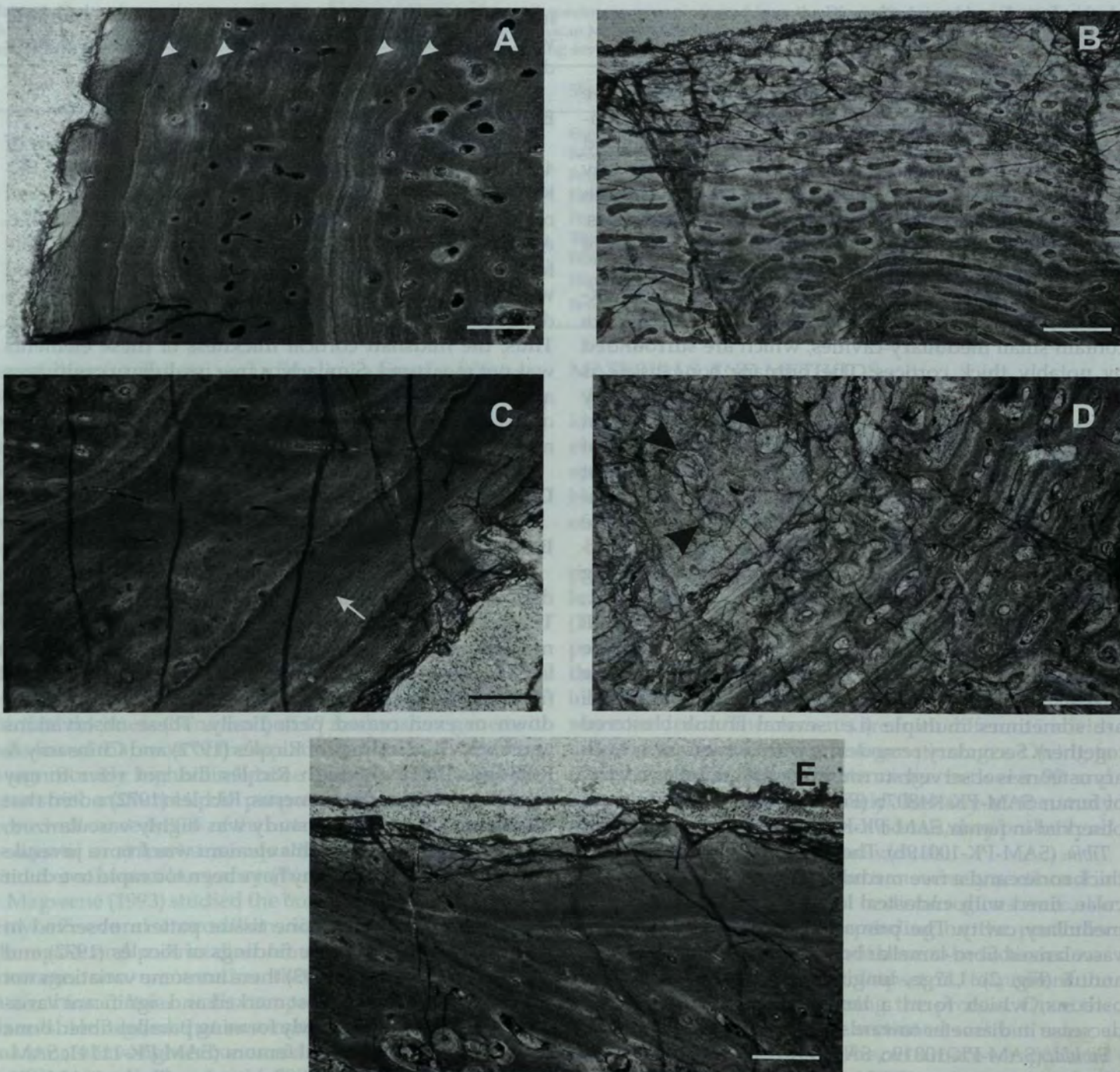


Figure 1. Bone histology of the *Oudenodon* femora. A, SAM-PK-K4807c, showing fibro-lamellar bone with longitudinally oriented primary osteons, interrupted by multiple annuli and LAGs (arrowheads). Parallel-fibred bone occurs at the periphery. Scale bar = 636 μ m. B, SAM-PK-10019a, showing fibro-lamellar bone in a laminar network. Scale bar = 636 μ m. C, SAM-PK-K4807a, showing fibro-lamellar bone becoming poorly vascularized parallel-fibred bone towards the sub-periosteal surface (arrow). Scale bar = 610 μ m. D, SAM-PK-K4807b, showing secondary osteons in the peri-medullary area (arrowheads). E, SAM-PK-K4807a, showing Sharpey's fibres. Scale bar = 635 μ m.

represent adult individuals, whereas femora SAM-PK-K4807b and SAM-PK-10019a represent subadult individuals. Parallel-fibred bone is absent from the latter two femora and although the vascularization is moderate, there is no decrease in vascularization towards the periphery, thus indicating continued active growth at the time of death. The moderate vascularization and abundant secondary osteons suggest that these two femora do not represent juvenile individuals, but the absence of peripheral, slowly forming parallel-fibred bone indicates that overall growth had not yet begun to slow down.

The highly vascularized primary tissue with abundant primary osteons and absence of parallel-fibred bone in tibia SAM-PK-10019b suggests that this element is representative of an early subadult. The fibulae exhibit extensive secondary remodeling and are moderately vascularized. Fibula SAM-PK-10019c exhibits peripheral parallel-fibred bone, indicating that the overall growth rate had begun to slow down. These characteristics suggest that this element represents an adult individual. As parallel-fibred bone is absent from fibula SAM-PK-K4807d, it is probably a subadult. There is a slight decrease in



Figure 2. *Oudenodon* tibia SAM-PEK-10019b, showing highly vascularized fibro-lamellar bone alternating with annuli of lamellar bone (arrowheads). Scale bar = 454 μm .

vascularization towards the sub-periosteal surface in humerus SAM-PEK-10019d, but LAGs and parallel-fibred bone are absent. The presence of annuli and absence of LAGs indicates that growth slowed down periodically, but did not cease. These characteristics suggest that the humerus represents a subadult.

Sharpey's fibres were observed in several of the femora and fibulae. Chinsamy & Rubidge (1993) also noted Sharpey's fibres in the *Oudenodon* humerus in their study. It is possible that the bones of *Oudenodon* had an unusually large proportion of Sharpey's fibres. As Sharpey's fibres represent areas of muscle insertion (Leeson & Leeson 1981), it is possible that *Oudenodon* had well-developed muscles to cope with digging. However, Chinsamy & Rubidge (1993) also noted Sharpey's fibres in all the dicynodont humeri in their study. Thus, it is also possible that distinct Sharpey's fibres are a common feature of dicynodont bone histology and most dicynodonts may have had particularly well-developed musculature to cope with their semi-erect posture. Such prominent Sharpey's fibres have not yet been noted in non-mammalian cynodonts (Botha 2002) or gorgonopsians and therocephalians (Ray *et al.*, in press). It is also possible that the larger dicynodonts in Chinsamy & Rubidge's (1993) study had substantial muscles and thus distinct Sharpey's fibres to cope with their large size. More studies on dicynodont bone histology, including multiple element analyses, are required to deduce whether this is the case.

Inter-elemental histovariability

It is becoming increasingly apparent, particularly from more recent studies including different types of elements, that inter-elemental histovariability has a significant effect on interpreting generic patterns of growth (Botha 2002; Curry 1999; Horner *et al.* 1999, 2000; Starck & Chinsamy 2002; Ray *et al.*, in press). It is therefore essential to include several different types of elements in a bone histological study, although it is recognized that this may prove difficult at times when fossil preservation is poor.

Although the overall bone tissue organization is similar between the different types of *Oudenodon* elements in this study, some inter-elemental histological variation was

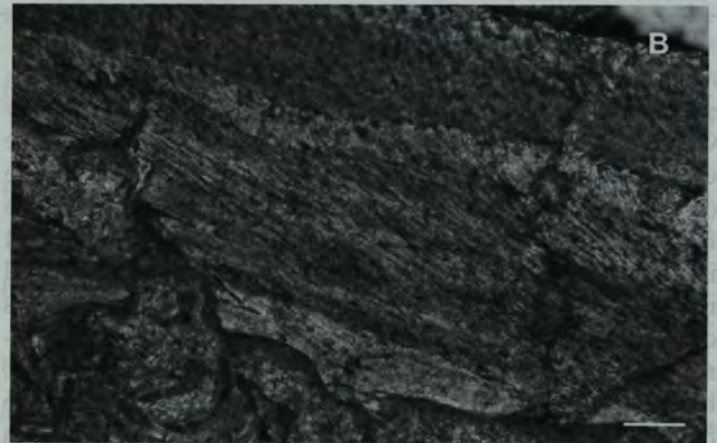


Figure 3. Bone tissue patterns of the *Oudenodon* fibulae. A, SAM-PEK-10019c, fibro-lamellar bone with longitudinally oriented primary osteons, becoming parallel-fibred bone with simple vascular canals towards the periphery. Scale bar = 434 μm . B, High magnification, showing prominent Sharpey's fibres. Scale bar = 163 μm .

noted. For example, parallel-fibred bone was not observed in the humerus SAM-PEK-10019d, but a midshaft region was not available for study and only the distal metaphyseal region could be examined. It is possible that the midshaft region, which would have exhibited more primary tissue, contained parallel-fibred bone. This is unlikely however, as the parallel-fibred bone occurs at the periphery, a region which could be observed in the humerus. Furthermore, Ricqlès (1972) did not document

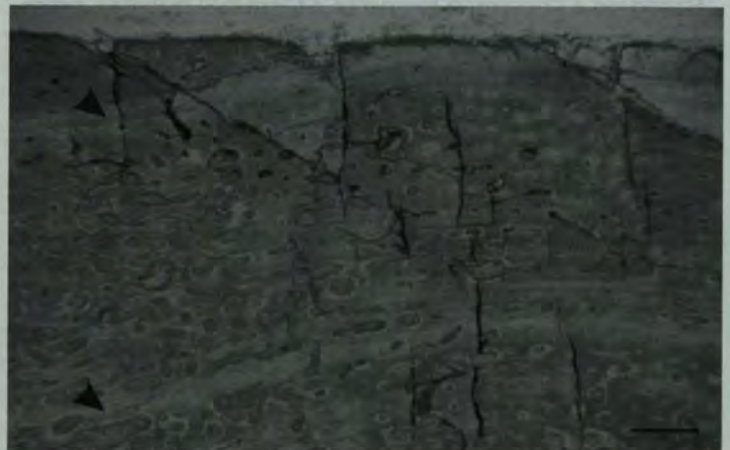


Figure 4. Bone histology of the *Oudenodon* humerus SAM-PEK-10019d, showing high vascularization in the inner and mid cortex, which decreases slightly at the sub-periosteal surface. Two annuli (arrowheads) can be seen interrupting the fibro-lamellar bone. Scale bar = 515 μm .

Table 2. Cortical thickness of the *Oudenodon* elements compared with other non-mammalian therapsids (represented as a percentage). *Scylacops* and *Pristerognathus* values were taken from Ray *et al.* (in press) and the *Aelurognathus* value was taken from Magwene (1993). Note that the *Pristerognathus* and *Aelurognathus* femora have a markedly lower cortical thickness compared to the *Oudenodon* femora. *Scylacops*, *Pristerognathus* and *Aelurognathus* were designated as adults (Magwene 1993; Ray *et al.*, in press).

Genus	Specimen number	Skeletal element	Cortical thickness (%)
<i>Oudenodon</i>	SAM-PK-10019a	Femur	39
	SAM-PK-K4807a	Femur	45
	SAM-PK-K4807b	Femur	39
<i>Scylacops</i>	SAM-PK-10188	Ulna	16
		Radius	24
<i>Pristerognathus</i>	SAM-PK-1157	Radius	18
		Femur	15
		Tibia	25
		Fibula	25
<i>Aelurognathus</i>		Femur	21

any parallel-fibred bone in the *Oudenodon* humerus in his study, neither was it noted in the study conducted by Chinsamy & Rubidge (1993). It is possible that both these elements as well as the humerus in this study were ontogenetically too young and thus depositing bone too fast to exhibit slowly forming parallel-fibred bone tissue. It is also possible that this may be an example of differential rates of bone growth between the various limb bones of a skeleton. It was noted in previous studies on non-mammalian cynodonts that proximal limb bones (i.e. humerus, femur) grew more quickly than distal limb bones (radius, ulna, tibia, fibula) (Botha 2002; Ray *et al.*, in press). Distal limb bones were less vascularized and annuli and/or LAGs were more numerous and distinct compared to those in the proximal limb bones. These characteristics indicate that the distal limb bones were growing more slowly than the proximal limb bones. Similarly, Starck & Chinsamy (2002), in a study on extant Japanese quail (*Coturnix japonica*), found that the mid-diaphyseal regions of the humerus and femur increased in cross-sectional thickness faster than the radius, ulna or tarsometatarsus. The humerus of *Oudenodon* may be the last limb bone within an individual to exhibit parallel-fibred bone.

Bone cross-sectional geometry

Based on a specimen found in a terminal burrow, previous studies have suggested that *Oudenodon* was fossorial. However, the suggestion was made on the basis of a juvenile specimen that had been recovered from a burrow at the base of the *Tropidostoma* Assemblage Zone, Teekloof Formation, Beaufort Group, South Africa (Smith 1987). The identification of this juvenile specimen is uncertain and *Oudenodon* is as yet, unknown from the *Tropidostoma* Assemblage Zone.

The bone cross-sectional geometry results in this study reveal a relatively thick cortex and may indicate a fossorial lifestyle. All the femoral cortical thickness values exceed 30%. Although the cortical thickness of the tibia and fibulae could not be quantified, the profusion of bony trabeculae within the medullary cavities would have provided extra strength and support to these elements. When comparing these results with other non-mammalian therapsids, *Oudenodon* exhibits a notably thick bone

wall (Table 2). Few cortical thickness values have been documented in the literature, which makes comparison difficult, but it can be seen from Table 2 that the cortical thickness of the *Oudenodon* femora is notably higher than that of the *Pristerognathus* (Ray *et al.*, in press) or *Aelurognathus* (Magwene 1993) femora. Although only ulna and radial values are available for the gorgonopsian *Scylacops*, neither value exceeds 30%. These results indicate that *Oudenodon* exhibits a particularly thick bone wall, possibly for a specific mode of life. If these results are examined in conjunction with the morphological modifications described by Broom (1901), they suggest that *Oudenodon* was fossorial. Broom (1901) described the postcranial skeleton of *Oudenodon* and it appears to exhibit modifications for a digging or fossorial lifestyle. The robust humerus has a well-developed delto-pectoral crest, the olecranon process on the ulna is greatly elongated and the radius and ulna are distally flattened. Furthermore, the broad, flat manus forms a large, flattened surface area and the phalanges end in large, distinct claws (Broom 1901). These morphological characteristics are typical of an animal that digs or burrows (Bargo *et al.* 2000; Yalden 1966). A positively identified specimen in a burrow complex could confirm this suggestion.

Implications for *Oudenodon* biology

The alternating bone tissue organization between rapidly deposited fibro-lamellar bone and slowly deposited lamellar bone within the annuli indicates that the growth of *Oudenodon* was cyclical. This bone tissue pattern is similar to those of *Dicynodon*, *Aulacephalodon*, *Endothiodon*, *Cistecephalus* and *Kannemeyeria* (Chinsamy & Rubidge 1993) as well as *Diictodon* (Ray & Chinsamy, in press). Experiments have revealed that seasonal fluctuations cause cyclical growth in extant reptiles (e.g. Castanet *et al.* 1993; Hutton 1986) and it is suggested that the cyclical growth patterns observed in these dicynodonts is due to a sensitivity to environmental fluctuations (Chinsamy & Rubidge 1993; Ray & Chinsamy, in press). As *Oudenodon* experienced a semi-arid climate with seasonal rainfall (Smith *et al.* 1993), it is possible that growth was influenced by seasonal fluctuations whereby the growth rate decreased or ceased during the unfavourable growing season. If *Oudenodon* was in fact fossorial, it may have

burrowed to escape harsh environmental conditions.

However, the peripheral parallel-fibred bone has not been noted previously in any dicynodont genus. Either this feature is unique to *Oudenodon* or it is generally found only in certain types of elements and will be revealed in other dicynodonts in future studies. It is also possible that previous studies have not examined elements that have been ontogenetically old enough to exhibit slowly forming parallel-fibred bone. Peripheral rest lines were not observed in any of the *Oudenodon* study elements, which suggests that growth continued throughout life, but at a much slower rate once sexual maturity was reached.

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The vertebrate fauna of the Upper Permian of Niger — II, Preliminary description of a new pareiasaur

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The skull of a new pareiasaur, *Bunostegos akokanensis* gen. et sp. nov., is described on the basis of a partial skull from the Upper Permian Moradi Formation of north-central Niger. Autapomorphies of the genus include the presence of three hemispherical bosses at the tip of the snout, an enlarged laterally projecting supraorbital boss positioned on each postfrontal, and additional, smaller bosses on the squamosal and supratemporal bones. *Bunostegos* is further characterized by a tab-like process of the nasal that articulates with the frontal, a pineal foramen located equidistant between the parietal-frontal and parietal-postparietal sutural contacts, a postparietal that is excluded from the caudal margin of the dorsal skull roof, and a blunt interpterygoid vacuity. The discovery of *Bunostegos* suggests an unsuspected degree of biogeographic endemism for central West Africa during the Late Permian.

Keywords: Permian, Moradi Formation, West Africa, Niger, Pareiasauria, Parareptilia.

INTRODUCTION

The Beaufort Group of South Africa chronicles an important period of vertebrate evolution — the assembly of an herbivore-based terrestrial ecosystem during the Middle and Late Permian (Olson 1962; Bakker 1972; Reisz & Sues 2000). Although perhaps best known for its therapsid ('mammal-like reptile') fauna (Hancox & Rubidge, 2001; Rubidge & Sidor, 2001), the Beaufort Group also enjoys the greatest diversity of pareiasaur taxa in the world. Rubidge (1995) conservatively listed four pareiasaur genera from South Africa, whereas Lee's (1997b) more recent taxonomic revision recognized at least eight genera comprising ten species. Importantly, the results of Lee's (1997b) study imply the sympatric co-occurrence of pareiasaur herbivores: three genera co-occur within the *Tapinocephalus* Assemblage Zone (AZ), four within the *Cistecephalus* AZ, and two within the *Dicynodon* AZ. Elsewhere in the world, pareiasaur remains are less abundant: three taxa are known from China, two taxa from Russia, and one each from Brazil, Germany, Morocco, Scotland and Zambia (Lee 1997b; Lee *et al.* 1997; Jalil 2001). Here we provide a preliminary description of an unusual new pareiasaur from the Republic of Niger that suggests a distinct biogeographic province for West Africa near the close of the Palaeozoic Era (Sidor *et al.* 2003).

The history of fossil discovery in the Moradi Formation of Niger was reviewed by de Ricqlès & Taquet (1982). Although they discussed the collection of abundant vertebrate remains on expeditions in 1966, 1967 and 1969, the only taxon to be formally named and described to date is the large captorhinomorph *Moradisaurus grandis* (Taquet 1969; de Ricqlès & Taquet, 1982). A pareiasaur skull from the Moradi Formation was figured by Taquet

(1972: pl. 1), but it was neither named nor described.

In November of 2000, a University of Chicago team led by P. Sereno revisited the Moradi Formation. They discovered a locality northwest of Agadez that produced the skulls of a new temnospondyl amphibian and the pareiasaur described in this contribution.

MATERIAL

The specimen was collected from an intraformational conglomeratic unit of the Moradi Formation. The skull was preserved palate-up and had been eroded down to the level of the orbit. As a consequence, the lower jaw is absent and much of the palate is preserved only as impression. The specimen was prepared at the Smithsonian Institution's National Museum of Natural History in Washington, D.C.

SYSTEMATIC PALAEONTOLOGY

Pareiasauria Seeley, 1888

Bunostegos akokanensis gen. et sp. nov.

Etymology. *Buno*, knobby (Greek); *stegos*, roof (Greek), referring to its identification as a pareiasaur and the knobby bosses that adorn the skull roof; *Akokan*, a town close to the type locality; *-ensis* (Latin), place or locality.

Diagnosis. Medium-sized pareiasaur with three hemispherical bosses located at the anterior end of the snout; nasal with a posterolateral tab-like process articulating with the frontal; elongate, laterally projecting postfrontal bosses overhanging orbits; hemispherical supratemporal boss located at posterolateral corner of skull roof; postfrontal and supratemporal bosses with neck separating globular head from skull roof; pineal foramen equidistant from frontoparietal and parietal-postparietal sutures.

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Holotype. MNN-MOR72, a nearly complete cranium that has been eroded ventrally.

Type Locality. Coordinates 18°47'01"N, 7°11'49"E, west of Arlit, Agadez Prefecture, Republic of Niger (Fig. 1). The locality lies in a conglomeratic layer of the Moradi Formation, which is believed to be uppermost Permian, based on biostratigraphic data (Taquet 1972).

DESCRIPTION

Preservation

MNN-MOR72 consists of a partial skull and several 'skins' of bone that preserve the external surface of the dorsal skull roof and temporal regions. Erosion has separated these 'skins' from the remainder of the skull by a gap of between 0–2 cm, leaving only an endocast of the skull in certain places. The conglomeratic nature of the surrounding matrix, coupled with the specimen's relatively spongy, pachyostotic bone, has made preparation and interpretation extremely difficult. In particular, this mode of preservation has limited our recognition of sutures between skull elements. Some sutures are visible on the internal surface of the 'skins' of bone, whereas others are visible on what remains of the skull itself. Rarely is a suture visible on the true external surface of the skull, which precludes a direct comparison with the pattern of other pareiasaurs.

The palate and ventral surface of MNN-MOR72 is extremely damaged, being planed-off by erosion. Some bone and several sutures are evident in ventral view, although the majority of the palate is preserved only as impression. Substantial adhering matrix surrounds the occipital region and obscures this region's structure. Further preparation of the occiput is risky due to the thin skull roof bones in this region.

Figures 2, 3, and 4 show MNN-MOR72 with several of the 'skins' of bone in place. Because the external surface of these 'skins' is backed by an approximately even amount of matrix, we believe that the overall shape of *Bunostegos* is well portrayed. In the figures we have attempted to reconstruct the outline of the skull and project the placement of sutures onto its external surface. Caution should be used when comparing the sutural configuration of *Bunostegos* to that of other pareiasaurs because all of the sutures we illustrate are deep to some level (i.e., they are not on the true external surface of the bone).

Skull roof

Although its overall appearance is peculiar, *Bunostegos* is a pareiasaur based on its possession of the following diagnostic characters: anapsid cranium, single fused postparietal located on the skull roof, medially directed posterior choanae, and prefrontal-postfrontal sutural contact (Lee 1997a). Figures 2–4 demonstrate the important features of the genus, including three supranasal bosses, laterally elongated supraorbital bosses formed by the postfrontals, and additional bosses extending laterally from the supratemporals. The shape and distribution of these features is unique to *Bunostegos* and absent in all other pareiasaur genera.

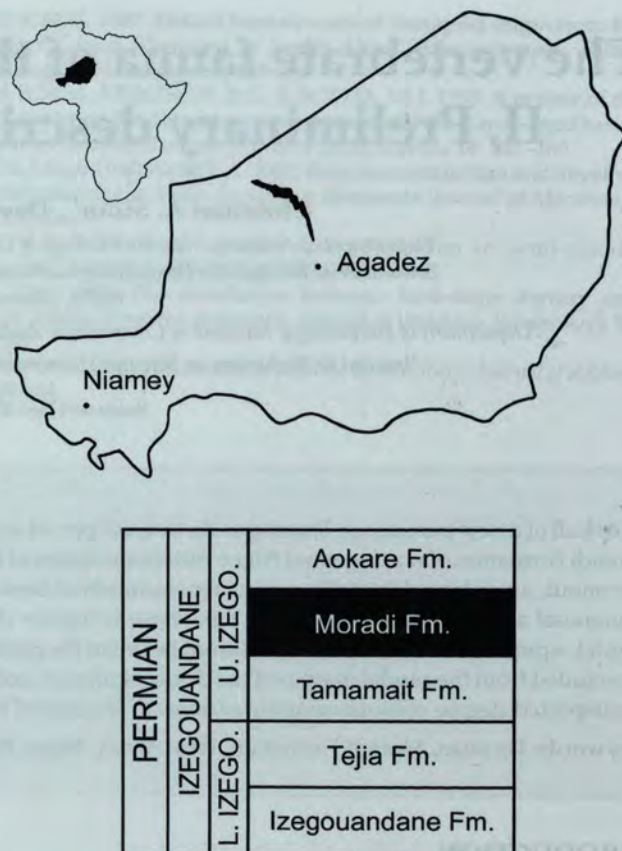


Figure 1. Geography and generalized Permian stratigraphy of the Republic of Niger. The position of Permian rocks is highlighted within the outline of Niger. Abbreviations: Fm. = Formation, Izego. = Izegouandane, L = Lower, U = Upper. Stratigraphic subdivisions based on Ministère des Mines et de l'Hydraulique, Direction des Mines et de la Géologie (1977).

Only the dorsal process of the premaxilla is preserved. Ventrally this element is so badly eroded that the tooth-bearing ramus of the premaxilla is completely absent. The nasal descends along the posterior margin of the premaxilla's dorsal process and may exclude the premaxilla from participating in the preserved anterior margin of the external naris. A similar condition was illustrated by Boonstra (1934: Pl. 2) for *Dolichopareia angusta* (now *Nochelesaurus angusta*; Lee 1997b). In anterior view, the pair of premaxillae form an inverted triangle that nearly reaches the base of a median boss.

The maxilla is typically a large, tooth-bearing element in pareiasaurs that makes up much of the lateral surface of the snout. In addition, it forms much of the posterior margin of the external naris. In *Bunostegos*, the external naris is incomplete and it is difficult to determine how much, if any, of the maxilla remains. This uncertainty is complicated by the poor delineation of the nasal and lachrymal bones.

Three hemispherical bosses are positioned at the rostral end of the skull roof: one boss is median and two are parasagittal. The median boss projects the furthest anteriorly and is slightly smaller than the other two swellings. In *Pareiasuchus nasicornis*, Lee *et al.* (1997) describe paired bosses above the external nares as separate ossifications sutured to the nasals. *Elginia mirabilis* also bears paired bosses above the external nares, although these are considered to be formed by the nasals (Spencer & Lee

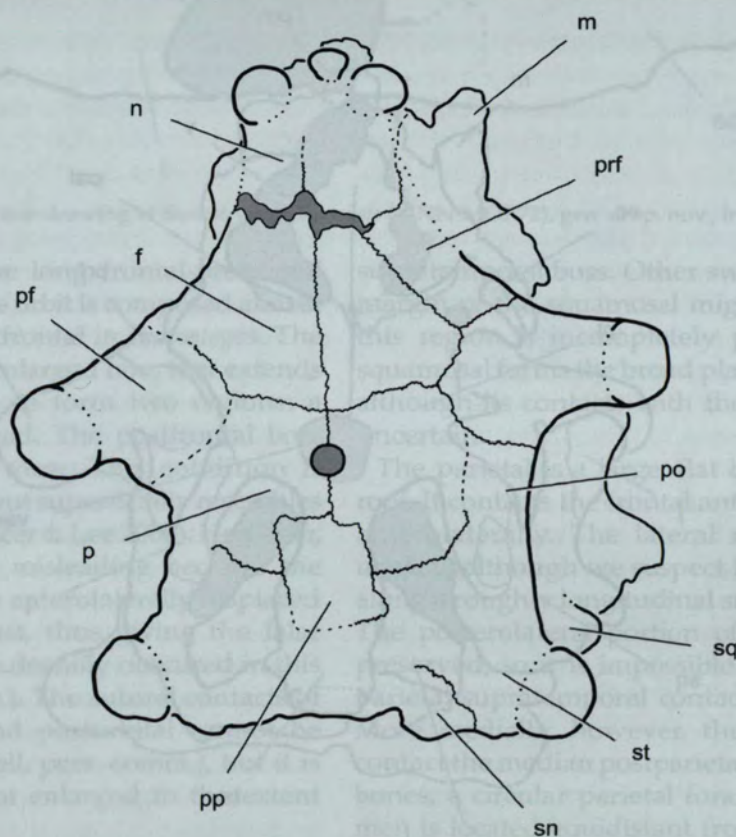


Figure 2. Stereophotographs and interpretive line-drawing of the skull of *Bunostegos akokanensis* (MNN-MOR72), gen. et sp. nov., in dorsal view.

2000; D. Maxwell, pers. comm.). We are unable to determine the precise location or osteological identity of the three bosses in *Bunostegos* because the relevant sutures are not visible.

The snout has been slightly flattened dorsoventrally and sheared to the left. This deformation has stretched the snout and widely separated the nasal from the frontal. The suture between these two elements can be seen as a transversely oriented gap, just anterior to the level of the orbit. On either side, the nasal bears a small, caudally directed tab at its posterolateral corner that slots into a corresponding socket on the frontal. A short contact between the nasal and prefrontal is visible on the right side. Only a small portion of the contact between the nasal

and lachrymal can be made out on the left side.

The anatomy of the prefrontal is more clearly exposed on the right side. On the skull roof, the prefrontal contacts the frontal along an anteromedially directed suture arising from the triple junction between the frontal, prefrontal, and postfrontal. The prefrontal's suture to the nasal is visible as a short contact, mostly located along the lateral surface of the snout. In dorsal view, the prefrontal-postfrontal contact is visible along the anterior margin of the supraorbital boss. Inside the orbit, the prefrontal can be seen to contact the lachrymal at the level of the orbit's midpoint.

The left lachrymal can be distinguished by virtue of its suture with the prefrontal and nasal, although its

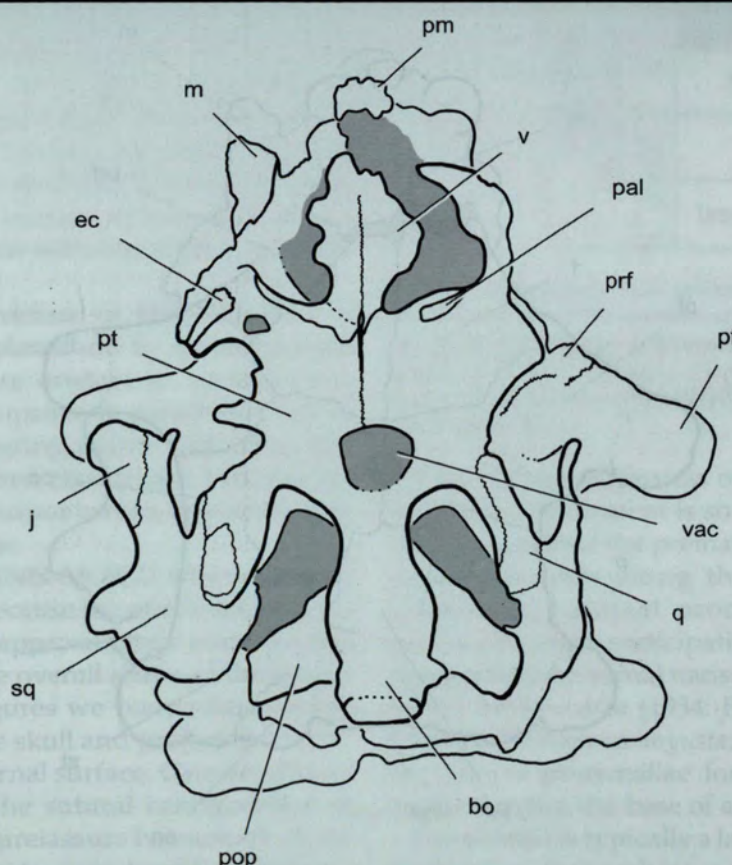
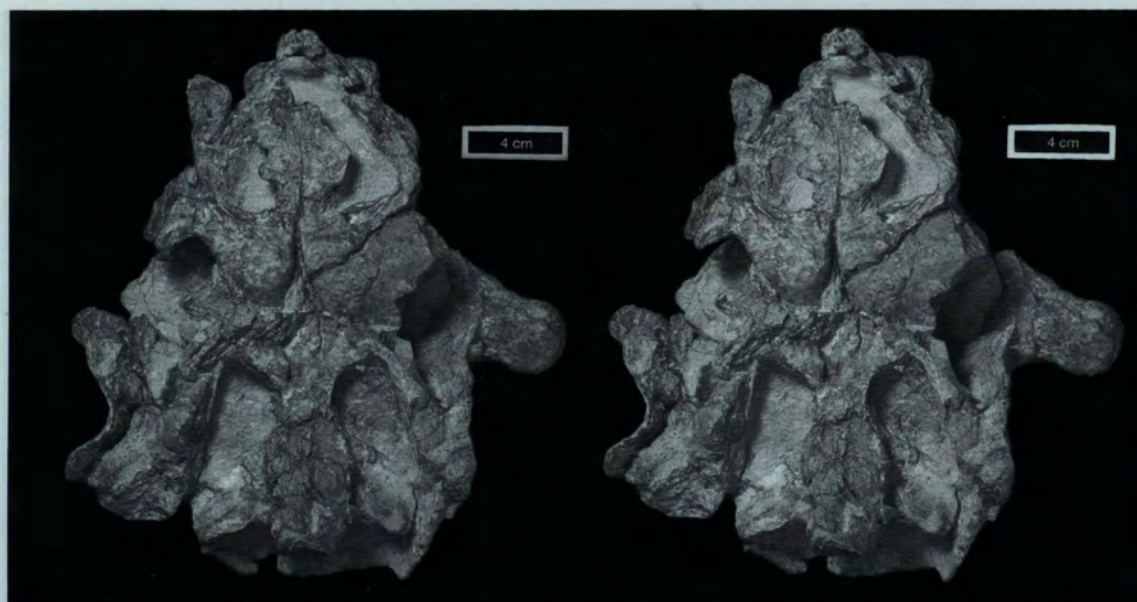


Figure 3. Stereophotographs and interpretive line-drawing of the skull of *Bunostegos akokanensis* (MNN-MOR72), gen. et sp. nov., in ventral view.

presumed ventral contact with the maxilla and jugal could not be determined. The lachrymal forms a portion of the orbital margin inferior to that of the prefrontal. This contact occurs approximately halfway up the left orbit's anterior border and then continues anteriorly and slightly upwards, where the nasal descends onto the lateral surface of the snout.

Owing to the degree of erosion, the suborbital portion of the jugal is absent on both sides of MNN-MOR72. However, on the right side, a well-defined suture with the postorbital is present on the inside of one of the 'skins' of bone and verifies that the jugal formed the inferior one-half of the orbit's posterior margin. Because the

relevant sutures are not visible, it is impossible to determine if the jugal is present anteroventral to the orbit.

As discussed above, the frontal's contact with the nasal is represented by a large, transverse gap on the dorsal surface of the snout. Further posteriorly, the frontal-parietal suture is also oriented roughly transversely, but it is located further back, in line with the posterior one-quarter of the orbit. The frontal-parietal contact bends slightly anteriorly as it progresses away from the sagittal plane, such that its full extent resembles a shallow 'U'. In dorsal view, the frontal-postfrontal contact is nearly as long as the frontal-prefrontal contact. Typically in pareiasaurs, the latter contact is the substantially longer of the two (Lee

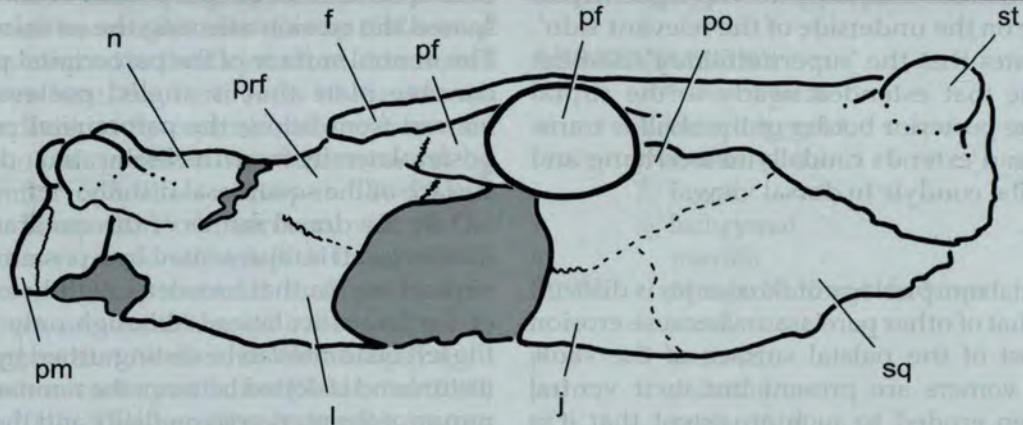


Figure 4. Photograph and interpretive line-drawing of *Bunostegos akokanensis* (MNN-MOR72), gen. et sp. nov., in lateral view. Scale bar = 4 cm.

1997: fig. 4). As a result of the long frontal-prefrontal contact, the dorsal margin of the orbit is composed almost exclusively of an enlarged postfrontal in *Bunostegos*. The postfrontal supports a greatly enlarged boss that extends laterally and expands distally to form two regions: a discrete neck and globular head. The postfrontal boss obscures the orbit in dorsal view. This condition is unknown in other pareiasaurs but superficially resembles reconstructions of *Elginia* (Spencer & Lee 2000). However, these reconstructions may be misleading because the dorsolateral skull roof has been anterolaterally displaced in the type specimen of *Elginia*, thus giving the false impression that the orbits were dorsally obscured in this taxon (D. Maxwell, pers. comm.). The sutural contacts of the prefrontal, postfrontal, and postorbital cannot be discerned in *Elginia* (D. Maxwell, pers. comm.), but it is clear that the postfrontal is not enlarged to the extent found in *Bunostegos*.

Anatomical information regarding the postorbital comes from both sides of the skull. In lateral view (Fig. 4), this element occupies roughly the upper half of the orbit's posterior border, sandwiched between the postfrontal, above, and the jugal, below. In dorsal view, the limits of the postorbital are more difficult to make out, although it presumably contacted the postfrontal, parietal, and supratemporal. On both sides, the dorsal portion of the jugal is preserved in articulation with the postorbital, but the remainder of the jugal has been lost due to the erosion of the cranium's ventral surface.

An internal suture is visible between the right supratemporal and right squamosal on the relevant 'skin' of bone. Although little detail can be made out, the position of this suture indicates that the squamosal supports a dorsolaterally projecting boss just ventral to the large

supratemporal boss. Other swellings along the posterior margin of the squamosal might have been present, but this region is incompletely preserved. Anteriorly, the squamosal forms the broad plate of bone behind the orbit, although its contacts with the postorbital and jugal are uncertain.

The parietal is a large, flat bone of the posterior skull roof. It contacts the frontal anteriorly and the postfrontal anterolaterally. The lateral margin of the parietal is unclear, although we suspect it contacted the postorbital along a roughly longitudinal suture, as indicated in Fig. 2. The posterolateral portion of the skull table is poorly preserved, so it is impossible to determine if the usual parietal-supratemporal contact is present in *Bunostegos*. More medially, however, the parietal can be seen to contact the median postparietal. Between the two parietal bones, a circular parietal foramen is present. This foramen is located equidistant from the frontal-parietal and parietal-postparietal contacts, which is approximately in line with the posterior margin of the orbit.

The postparietal is a median, rectangular element located on the skull roof. The anterior one-half of this element is enclosed within the parietals by a clearly defined suture. It is more difficult to determine the posterior extent of the postparietal. However, the remnants of a transversely oriented suture seem to indicate that the posterior border of the postparietal was located on the skull roof. That is, the postparietal was excluded from the caudal margin of the dorsal skull roof. Among pareiasaurs, this condition is observed only in *Elginia*, where it is due to the 'supernumerary' elements contacting each other on the midline (Lee 1997b; Spencer & Lee 2000). Enlarged 'supernumerary' elements are known in both *Elginia* and the 'Kupferschiefer pareiasaur' (referred

to *Parasuchus geinitzi* by Wild 1985). We suspect that a similar condition was present in *Bunostegos*, although a midline suture between the enlarged 'supernumerary' elements cannot be observed on either the skull roof or corresponding 'skin' of bone.

The supratemporal is poorly delimited on the skull roof. In the region where the supratemporal would be expected, a large boss projects laterally from the posterolateral skull roof. Similar to the supraorbital boss, the supratemporal boss has a distinct neck and terminates in a bulbous head. A portion of the medial boundary of the right supratemporal is visible on the underside of the relevant 'skin'. This suture indicates that the 'supernumerary' element was a broad bone that extended nearly to the supratemporal boss. The posterior border of the skull is transversely oriented and extends caudally to overhang and obscure the occipital condyle in dorsal view.

Palate

The ventral cranial morphology of *Bunostegos* is difficult to compare with that of other pareiasaurs because erosion has removed most of the palatal surface of the skull. Portions of both vomers are present but their ventral surfaces have been eroded to such an extent that it is impossible to discern the presence of vomerine teeth. Anteriorly, erosion has destroyed the contact between each vomer and its corresponding premaxilla. As in all pareiasaurs, the choanae are large, C-shaped openings that curve medially at their posterior margin.

At the posterior end of the choanae, a fragment of the palatine is preserved on both sides. The right palatine is more complete, and contacts either the maxilla or lachrymal deep within the choana.

An extremely fragmentary portion of the right ectopterygoid is present but little morphology is preserved (Fig. 3). Between the ectopterygoid and palatine, a remnant of the posterior palatal foramen may be present.

The palatal ramus of the pterygoid is preserved mostly as an impression of its internal (i.e. dorsal) surface. The right transverse flange of the pterygoid is partially preserved and an impression of the left transverse flange is also present. These may provide a good indicator of the lateral extent of the pterygoids and suggest that they failed to reach the cheek, as in other pareiasaurs. A small section of both pterygoids is present near the midline, and shows that these elements were sutured together until the interpterygoid vacuity. On the left side, the margin of this vacuity is reasonably well preserved and shows it to be relatively blunt anteriorly. In this respect, the interpterygoid vacuity of *Bunostegos* is most similar to that of *Deltavjatia* and *Bradysaurus*. A portion of the quadrate ramus of the pterygoid is present on both sides. These form the lateral aspect of the cranioquadrate space and are clearly sutured to their respective quadrates posterolaterally.

The ventral surface of the basisphenoid is highly eroded. In the region of the interpterygoid vacuity, remnants of the parasphenoid rostrum are present, but no detail can be made out. There is a distinct constriction of the basisphenoid posterior to the basicranial articulation. This condition is present in basal pareiasaurs such as

Bradysaurus and *Nochelesaurus* (Lee 1997a).

The position of the contact between the basioccipital and basisphenoid cannot be determined because of damage in this region. Further posteriorly, the basioccipital is represented by the occipital condyle, which is circular in posterior view and bears a deep notochordal pit. Contacts between the basioccipital and exoccipitals cannot be seen.

The paroccipital process of the opisthotic is relatively well preserved and visible primarily in ventral view. As a consequence of its deeper position within the skull, it was spared the erosion affecting the remainder of the palate. The ventral surface of the paroccipital process is a gently concave plate that is angled posteroventrally. When viewed from below, the paroccipital process is directed posterolaterally from the braincase and abuts the medial surface of the squamosal distally.

Only the dorsal ramus of the quadrate is preserved in *Bunostegos*. It is represented by a posterolaterally oriented vertical lamina that broadens slightly towards the region of the jaw articulation. Although only visible in section, the left quadrate can be distinguished by a change in bone texture and is slotted between the remnants of the quadrate ramus of the pterygoid medially and the squamosal laterally. If the orientation of the quadrate dorsal ramus reflects the position of the more ventral portions of this bone, it may indicate that the articular surface of the quadrate was located in a position nearly level with the anteroposterior midpoint of the basisphenoid. This configuration is atypical for pareiasaurs, where the quadrate rami are more transversely oriented and the jaw articulation is located at the level of the interpterygoid vacuity. Only in *Pareiasuchus nasicornis* is the jaw articulation located further posteriorly, just anterior to the basisphenoid-basioccipital suture (Lee *et al.* 1997).

DISCUSSION

Fauna of the Moradi Formation

The tetrapod fauna of the Moradi Formation now consists of two large-bodied, herbivorous reptiles: the pareiasaur *Bunostegos akokanensis*, and the multiple tooth-rowed captorhinid, *Moradisaurus*. The skull figured by Taquet (1976) either represents an additional species of pareiasaur from the Moradi fauna, or pertains to *Bunostegos*. A second pareiasaur occurring in the same beds would not be unexpected, given the fauna of the Karoo (Rubidge 1995; Lee 1997b).

The unnamed pareiasaur (Taquet 1976) is similar to *Bunostegos* in that its orbits are obscured in dorsal view by enlarged and laterally projecting bosses, although these do not appear to bear a distinct neck and spherical end. An additional similarity is that the region of the nasal bears an enlarged boss rostrally. However, as figured by Taquet (1976) the occipital condyle is visible in dorsal view, which suggest the absence of large supernumerary elements. The degree to which damage has influenced the overall shape of the figured skull is unclear. Overall, the smaller supraorbital bosses and the apparent shortening of the dorsal skull roof may indicate that Taquet's (1976) speci-

men is a different morphotype of *Bunostegos*, but this cannot be confirmed with certainty.

The Late Permian has been interpreted as a time of broad cosmopolitanism among terrestrial vertebrates (Olson 1962; Romer 1973). Faunal similarity, including the presence of shared genera in coeval South African, Indian, Zambian, and Russian rocks (Rubidge 1995; Ivachnenko *et al.* 1997; Ray 1999; Battail 2000), argues for relatively unrestricted dispersal among land-living tetrapods. It is surprising, then, to discover a West African fauna that fails to share genera with the stratigraphically thick and palaeontologically well known Beaufort Group (Sidor *et al.* 2003). Moreover, in contrast to the dicynodont-dominated faunas known elsewhere, the herbivores of the Moradi Formation are predominantly captorhinids, represented by *Moradisaurus*, and pareiasaurs, represented by *Bunostegos*. A similar condition occurs in the Upper Permian Argana Formation of Morocco, where the material identified as captorhinid by Jalil & Dutuit (1996) actually includes both captorhinid and pareiasaur remains (M. Lee, pers. comm.). Although based on preliminary data, we suggest that North and West Africa might have hosted an endemic tetrapod fauna (Sidor *et al.* 2003; see also Jalil 1999, 2001). This hypothesis requires testing by the further collection of vertebrate remains and the recognition of a plausible isolation mechanism for this section of Pangea.

Relationships of *Bunostegos*

Lee (1997a) presented the first cladistic analysis of pareiasaur interrelationships using data from both the cranial and postcranial skeletons. His analysis included 16 pareiasaur terminal taxa, which represented most of the described taxa at the time. The primary conclusions of this and the analysis of Lee (1995) were the paraphyly of pareiasaurs with respect to turtles and the recognition of several subclades within Pareiasauria. Lee's (1997a) detailed phylogenetic work has established a framework within which *Bunostegos* may be tentatively placed.

Bunostegos presents features of both primitive and derived pareiasaur taxa (Lee 1997a). For example, the shape of the interpterygoid vacuity is similar to *Deltavjatia* and *Bradysaurus*, both of which are stem pareiasaur taxa (Lee 1997a). *Elginia mirabilis*, a small anomalous pareiasaur from the Upper Permian of Scotland, shares two interesting characters with *Bunostegos*: postparietals that are excluded from the caudal border of the dorsal skull roof by enlarged 'supernumerary' elements, and enlarged squamosal and supratemporal bosses. *Bunostegos* may also resemble *Pareiasuchus nasicornis* from the Upper Permian of Zambia (Lee *et al.* 1997) if its anterior nasal bosses are discrete ossifications and its quadrate articular surfaces were displaced posteriorly. The ingroup relationships of the clade including both *Elginia* and *Pareiasuchus* ('Clade E' of Lee 1997a) are tenuous as they are presently supported by only a few characters. This diverse pareiasaur clade is the sister taxon to the clade to which turtles may belong. As the above comparisons attest, the phylogenetic affinities of *Bunostegos* are presently unresolved.

A new season of fieldwork was conducted in the Moradi Formation in March–April of 2003 (Sidor *et al.* 2003). Additional pareiasaur material was collected, including three partial skulls and substantial postcranial remains. We believe that most of this material will, upon preparation, be found to pertain to *Bunostegos*. This new material should shed much needed light on the detailed anatomy of this taxon and its phylogenetic relationships to other pareiasaurs. In addition, the identification of additional tetrapod taxa will provide data for the biogeographic endemism hypothesis proposed herein.

ABBREVIATIONS

bo	basioccipital
ec	ectopterygoid
f	frontal
j	jugal
l	lachrymal
m	maxilla
MNN	Musée National du Niger
n	nasal
p	parietal
pal	palatine
pf	postfrontal
pm	premaxilla
po	postorbital
pop	paroccipital process of opisthotic
pp	postparietal
prf	prefrontal
pt	pterygoid
q	quadrate
sn	'supernumerary element'
sq	squamosal
st	supratemporal
v	vomer
vac	interpterygoid vacuity

We thank P. Sereno for the opportunity to prospect the Moradi Formation in 2000, and the other team members (A. Beck, J. Conrad, E. Duneman, D. Duthiel, M. Hettwer, H. Larsson, G. Lyon, T. Lyman, R. Sadleir, and G. Wilson) for their interest in Permian vertebrates and dedication during the expedition. We are indebted to I. Kouada and the Government of Niger for permission to conduct fieldwork, E. Love for preparation of the *Bunostegos* holotype, and the David and Lucile Packard Foundation, the National Geographic Society, and the Pritzker Foundation for funding (to P. Sereno). Finally, we acknowledge R. Reisz, M. Lee, and B. Rubidge for their editorial contributions.

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Barendskraal, a diverse amniote locality from the *Lystrosaurus* Assemblage Zone, Early Triassic of South Africa

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A diverse amniote fauna has been recovered from Lower Triassic *Lystrosaurus* Assemblage Zone exposures on the farm Barendskraal, near Middelburg in Eastern Cape Province, South Africa. The fauna includes the dicynodont therapsid *Lystrosaurus* sp., the therocephalian therapsids *Tetracyonodon darti*, *Moschorhinus kitchingi* and *Erciolacerta parva*, the archosauromorph reptiles *Proterosuchus fergusi* and *Prolacerta broomi*, and the procolophonoid reptiles *Owenetta kitchingorum*, *Sauropareion anoplus* and *Saurodectes rogersorum*. The locality is remarkable in that although it is fossil-rich, *Lystrosaurus* fossils do not appear to be as abundant as elsewhere in this assemblage zone, and the diversity of taxa at Barendskraal (at least nine species) is surpassed only by that of the famous Harrismith Commonage locality in the northeastern Free State province (at least 13 species). However, the fauna at Harrismith Commonage is typical of most other *Lystrosaurus* biozone localities in being dominated numerically by *Lystrosaurus*. Study of the tetrapod taxa from Barendskraal is providing new insights into procolophonoid phylogeny and survivorship across the Permo-Triassic boundary, as well as the stratigraphic ranges of various taxa in the Lower Triassic deposits of the Karoo Basin.

Keywords: Amniota, Barendskraal, Karoo, Lower Triassic, *Lystrosaurus* Assemblage Zone.

INTRODUCTION

In 1935, a South African Museum field crew led by the late L.D. Boonstra recovered a small collection of Karoo fossils from the farm Barendskraal (an annexe of the original farm Klip Fonteyn 234), approximately 11 km south of Middelburg in Eastern Cape Province, South Africa. This collection consisted mainly of material belonging to the dicynodont therapsid *Lystrosaurus* and the archosauromorph reptile '*Chasmatosaurus*' (= *Proterosuchus*), along with a small, bone-bearing nodule labelled 'amphibian'. That nodule later proved to contain the partial skeleton of a new procolophonoid parareptile, *Sauropareion anoplus* (Modesto *et al.* 2001). In his compilation of tetrapod species distribution in the Karoo, Kitching (1977) listed four species from Barendskraal, namely *Proterosuchus vanhoepeni* (= *P. fergusi*) and three species of *Lystrosaurus*, both index genera for the *Lystrosaurus* Assemblage Zone (Groenewald & Kitching 1995). Successive expeditions to Barendskraal in 2001 and 2002 by the authors, prompted by the description of *S. anoplus*, resulted in the recovery of additional procolophonoid material, which proved to be part of a diverse amniote fauna (Damiani *et al.* 2002) that we report fully in this paper.

The *Lystrosaurus* Assemblage Zone is part of the succession of eight biostratigraphic assemblage zones that comprise the Upper Permian–Middle Triassic Beaufort Group of the Karoo Basin, South Africa (Rubidge *et al.* 1995), a sequence that is generally accepted as the standard for non-marine Permian and Triassic time (Lucas 1998). The

Lystrosaurus biozone is the type fauna for the Lootsbergian Land Vertebrate Faunachron of Early Triassic age (Lucas 1998), and records the recovery of terrestrial vertebrate faunas following the end-Permian extinction event, the largest such event in Earth history (Erwin *et al.* 2002). Note, however, that the genus *Lystrosaurus* has also been documented in uppermost Permian strata (Smith 1995; Smith & Ward 2001), so that the biozone does not encompass the full stratigraphic range of the genus *Lystrosaurus*. The tetrapod fauna of the *Lystrosaurus* biozone is dominated numerically by the dicynodont therapsid *Lystrosaurus*, which comprises some 95% of its known fossils (Groenewald & Kitching 1995); the remaining fauna consists of dicynodont, cynodont, and therocephalian therapsids, procolophonoid and diapsid reptiles, and temnospondyl amphibians (Groenewald & Kitching 1995).

The fauna recovered to date from Barendskraal, surveyed below, contains typical elements of the *Lystrosaurus* Assemblage Zone but is remarkable for the diversity of amniote taxa, which includes three newly described procolophonoid species (Modesto *et al.* 2001, 2003; Reisz & Scott 2002). In addition, material of *Lystrosaurus* is relatively scarce, in contrast to most other *Lystrosaurus* biozone localities where *Lystrosaurus* is the dominant fossil taxon recovered (Kitching 1977; Groenewald & Kitching 1995). No temnospondyl amphibian material has yet been recovered, despite intensive collecting efforts.

All material recovered during the 2001 and 2002 field seasons is deposited in the Bernard Price Institute for

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Palaeontological Research, Johannesburg (abbreviated 'BP'). Other institutional abbreviations used in the text are as follows: RC, Rubidge Collection, Wellwood, Graaff-Reinet; SAM, South African Museum, Cape Town.

GEOLOGICAL SETTING

General

In the south of the main Karoo Basin the *Lystrosaurus* Assemblage Zone, as currently recognized by the South African Committee for Stratigraphy (SACS 1980), includes the uppermost member of the Balfour Formation (Palingkloof Member), the Katberg Formation, and the lower third of the Burgersdorp Formation (Groenewald & Kitching 1995). However, in the north of the basin the entire Burgersdorp Formation contains a fauna assignable to the lower part of the *Cynognathus* Assemblage Zone (Welman *et al.* 1991; Hancox *et al.* 1995), and Neveling (2002) has restricted the *Lystrosaurus* biozone to the Palingkloof Member and Katberg Formation only.

The Palingkloof Member is a thin, predominantly argillaceous unit characterized by red and maroon mudstones and subordinate, light olive to light grey sandstones (SACS 1980; Hiller & Stavrakis 1984; Smith 1995). The Palingkloof strata broadly represent high-sinuosity channel and floodplain deposits that accumulated under semi-arid climatic conditions (Smith 1995; Groenewald 1996). The overlying Katberg Formation is a predominantly arenaceous unit that consists of stacked, tabular sheets of fine to medium-grained sandstones, with subordinate red and greenish-grey mudstones (SACS 1980; Smith 1995; Groenewald 1996). Deposition of this unit is thought to have occurred within a low sinuosity, braided river system under dry climatic conditions (Hiller & Stavrakis 1984; Smith 1995; Groenewald 1996; Ward *et al.* 2000; Neveling 2002). The rapid change in fluvial style from sinuous channel (Palingkloof) to braidplain (Katberg) deposits has previously been attributed to the combined effects of source area uplift and increasing aridity (Hiller & Stavrakis 1984; Smith 1995). More recently, this transition was attributed to a rapid and basin-wide die-off of floodplain vegetation, leading to increased sediment loads and a weakening of channel banks, and consequently the development of braided channels (Ward *et al.* 2000).

The main bone-bearing exposures on Barendskraal occur on the slopes of a small, isolated hill (referred to locally as a 'koppie') known as 'Maanhaar', and on a nearby larger koppie known as 'Agterkamp'. The strata of the Palingkloof Member and overlying Katberg Formation are exposed on both koppies, and a description of these units at Barendskraal is provided below. All of the fossils discovered come from the finer mudstone/siltstone facies, representing overbank or abandoned channel deposits. Loose, reddish-brown calcareous nodules containing indeterminate and relatively large postcranial bones, probably those of *Lystrosaurus*, also occur throughout the sequence. Figure 1 shows a stratigraphic section of the sequence at the Maanhaar locality. Note that, for convenience, the stratigraphic distribution of fossils on

both Maanhaar and Agterkamp are plotted together on this section.

Palingkloof exposures at Barendskraal

The Palingkloof exposures on Maanhaar consist of greyish-red and greyish-brown mudstones and siltstones, with subordinate, thin (<1.5 m) tabular sandstones. The sandstones are of two types. The first consists of fine to very fine-grained, laterally extensive, 1–1.5-m-thick units that are bounded by erosive bases and grade upwards into massive silt- and mudstones. The presence of basal erosional scours, intra-formational pebbles, horizontal stratification with primary current lineation, and isolated trough cross-stratification, are indicative of deposition in the upper part of the lower flow-regime. However, deposition under lower flow-regime conditions during waning flow is also evident through the presence of ripple cross-stratification and the gradual fining-upwards into siltstones. Based on their erosive bases, tabular geometry, and evidence for rapid, but fluctuating, flow, these sandstones are interpreted as broad, shallow, unconfined channels, similar to the sheetflow sandstones proposed for this interval by Smith (1995) and Ward *et al.* (2000). The second sandstone type is more numerous, thinner (20–600 mm), and tends to pinch out laterally. It contains a larger siltstone component, and is usually massive in nature, although ripple cross-stratification also occurs. These sandstones have abrupt bases, often drape underlying topography, and are interpreted as the distal extremities of crevasse splays.

The mudstones and siltstones of the Palingkloof Member on Maanhaar outcrop as units 2–12 m thick, although they can usually be subdivided into smaller packages based on internal architecture, grain size, and the occurrence of incipient pedogenic horizons. The massive mudstones at the base of the section consist of stacked, thin (<25 mm), interbedded layers of siltstone and mudstone. Higher up in the Palingkloof Member, the siltstone packages are thicker (30–300 mm), and separated by thin, mudstone veneers. As a rule, weathering processes obliterate any original sedimentary structure in the fines. Silt particles predominate, but rare, fining-upward and coarsening-upward trends have also been documented in the mudrocks. Rare incipient pedogenic horizons are characterized by calcareous nodules of various sizes. These nodules occur sporadically throughout the sequence, but in places they amalgamate to form laterally continuous horizons. Subvertical, siltstone-filled *Taenidium* invertebrate burrow casts occur abundantly in both the mudstones and sandstones, as documented within Palingkloof exposures elsewhere in the basin (Smith 1995; Smith & Ward 2001).

The Palingkloof strata exposed on the koppie Agterkamp display the same general sequence as on Maanhaar, except for the absence of thicker (0.5–1.5 m), laterally extensive sandstones. The sequence consists almost exclusively of massive siltstones and mudstones, although they display some vague, tabular internal architecture. In general, the Agterkamp exposures appear to represent a lower energy depositional setting compared to the sequence exposed on Maanhaar.

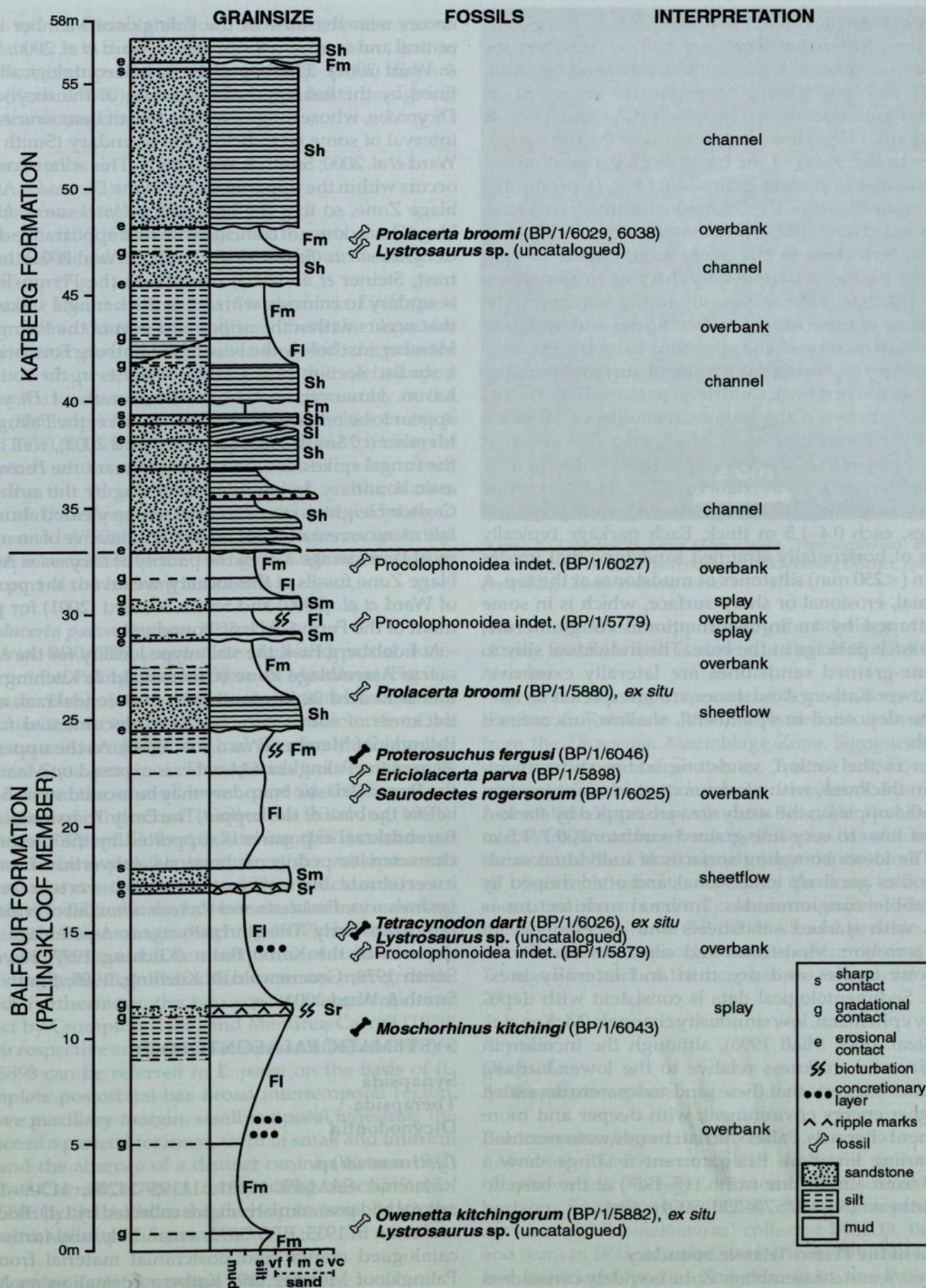


Figure 1. Stratigraphic section of the koppie 'Maanhaar', farm Barendskraal, Eastern Cape Province, South Africa. Strata of the lower part of the Early Triassic *Lystrosaurus* Assemblage Zone are exposed. For the sake of simplicity, fossil occurrences on Agterkamp are also plotted here. Fossil occurrences on Maanhaar are denoted by open bone symbols, whereas those on Agterkamp are denoted by closed (black) symbols. Facies codes (after Miall 2000): Fl, finely laminated sand, silt and mud (interbedded); Fm, massive fines (mudstone, siltstone); Sh, horizontally laminated sandstone; Sl, low-angle cross-bedded sandstone; Sm, massive sandstone; Sr, ripple cross-laminated sandstone.

Katberg exposures at Barendskraal

Earlier workers considered the contact between the mudstone-dominated Palingkloof Member and the sandstone-dominated Katberg Formation to represent an erosional unconformity (Hotton 1967; Anderson & Cruickshank 1978). However, outcrops of the Palingkloof Member in the south of the basin display a gradual upwards increase in average grain size (cf. Fig. 1), prompting some workers to define the Palingkloof-Katberg contact as gradational (Smith 1995; Groenewald 1996; Ward *et al.* 2000). Nevertheless, in the study area, thicker (>4 m) sandstone packages, bounded by sharp or erosional contacts at the base, appear abruptly in the sequence. The appearance of these sandstones coincides with a significant upward increase in the sandstone to mudstone ratio. We consider the horizontal, erosional surface bounding the base of the first thick sandstone package (Fig. 1) to be the contact between the Balfour (Palingkloof Member) and Katberg formations. In the study area, this surface is laterally extensive and serves as a correlatable marker horizon. The contact is overlain by a 7-m-thick sandstone sequence consisting of several stacked, fining-upward packages, each 0.4–1.5 m thick. Each package typically consists of horizontally stratified sandstone that grades into thin (<250 mm) siltstones or mudstones at the top. A horizontal, erosional or sharp surface, which is in some cases draped by an intra-formational conglomerate, bounds each package at the base. The individual silty to very fine-grained sandstones are laterally extensive. These lower Katberg sandstones are interpreted as having been deposited in ephemeral, shallow, unconfined channels.

Higher in the section, sandstone bodies show an increase in thickness, with a concomitant increase in grain size. Both koppies in the study area are capped by stacked sheets of fine- to very fine-grained sandstone, 0.7–1.5 m thick. The lower bounding surfaces of individual sandstone bodies are sharp to erosional, and often draped by mud-pebble conglomerates. Internal architecture is simple, with stacked sandsheets and no evidence of lateral accretion. Mudstones and siltstones overlie the sandstone bodies and are thin and laterally inextensive. Sedimentological data is consistent with deposition by ephemeral, low sinuosity channels (McKee *et al.* 1967; Stear 1985; Miall 1996), although the increase in grain size and thickness relative to the lower Katberg sandstones suggests that these sandstones were deposited in a higher energy environment, with deeper and more permanent channels. Palaeocurrent trends were recorded from parting lineation. Palaeocurrent readings show a change from almost due north (15–195°) at the base, to east-northeast (50–230°; 70–250°) at the top.

Position of the Permo-Triassic boundary

The *Lystrosaurus* Assemblage Zone is widely considered to be Early Triassic in age (e.g. Lucas 1998), although the position of the Permo-Triassic boundary has been the subject of some debate (see review in Hancox 2000). Currently, the boundary is drawn at the base of a distinctively laminated mudrock horizon, some 3–5 m thick, that

occurs near the base of the Palingkloof Member in the central and southern Karoo Basin (Ward *et al.* 2000; Smith & Ward 2001). The boundary is palaeontologically defined by the last appearance datum of the dicynodont *Dicynodon*, whose range overlaps that of *Lystrosaurus* in an interval of some 40 m below the boundary (Smith 1995; Ward *et al.* 2000; Smith & Ward 2001). This zone of overlap occurs within the uppermost part of the *Dicynodon* Assemblage Zone, so that the base of the *Lystrosaurus* Assemblage Zone does not coincide with first appearance datum of *Lystrosaurus* (Smith 1995; Smith & Ward 2001). In contrast, Steiner *et al.* (2003) considered the Permo-Triassic boundary to coincide with a 1 m thick fungal spike zone that occurs within the uppermost part of the Palingkloof Member, just below the base of the Katberg Formation, in a studied section near Carlton Heights in the southern Karoo. However, in that section, fossils of *Dicynodon* appear to be restricted to the lower part of the Palingkloof Member (cf. Smith 1995; Smith & Ward 2001), well below the fungal spike zone considered to mark the Permo-Triassic boundary. In addition, collecting by the authors at Carlton Heights in the 2002 field season yielded abundant *Lystrosaurus* remains, but no fossils indicative of an uppermost Permian age. Given the paucity of *Dicynodon* Assemblage Zone fossils at this locality, we favour the proposal of Ward *et al.* (2000) and Smith & Ward (2001) for placement of the Permo-Triassic boundary.

At Lootsberg Pass, the stratotype locality for the *Lystrosaurus* Assemblage Zone (Groenewald & Kitching 1995) that is located 20 km southwest of Barendskraal, a total thickness of some 35 m has been documented for the Palingkloof Member (Ward *et al.* 2000). As the uppermost 30 m of the Palingkloof Member is exposed on Maanhaar, the Permo-Triassic boundary may be located some 5–10 m below the base of the koppie. The Early Triassic age of the Barendskraal exposures is supported by the presence of characteristic pedogenic horizons, subvertical *Taenidium* invertebrate burrow casts, and the vertebrate taxa *Lystrosaurus*, *Prolacerta* and *Proterosuchus*, all of which are typical of Early Triassic *Lystrosaurus* Assemblage Zone deposits of the Karoo Basin (Kitching 1977; Keyser & Smith 1979; Groenewald & Kitching, 1995; Smith 1995; Smith & Ward 2001).

SYSTEMATIC PALAEONTOLOGY

Synapsida Therapsida Dicynodontia

Lystrosaurus sp.

Material. SAM-PK-11191, 11195–11206, 11209–11210, cranial and postcranial remains collected by L.D. Boonstra and team in 1935; BP/1/5893, a mandible; and further uncatalogued cranial and postcranial material from the Palingkloof Member and Katberg Formation on Maanhaar and Agterkamp (Fig. 1).

Remarks. Kitching (1977) listed three species of *Lystrosaurus* from Barendskraal, namely *L. declivis*, *L. murrayi* and *L. oviceps*, presumably through inspection of the South African Museum material (which is listed as '*Lystro-*

saurus sp.' in their catalogue). However, as the genus *Lystrosaurus* is in dire need of taxonomic revision, and as distortion is so prevalent amongst large Karoo dicynodonts (Renaut 2000), we do not feel confident in assigning *Lystrosaurus* material to species level.

Therocephalia

***Moschorhinus kitchingi* Broom, 1920**

Material. BP/1/6043, a large skull with associated postcranial elements, from the Palingkloof Member on Agterkamp (Fig. 1).

Remarks. The moschorhinid *Moschorhinus kitchingi* is known from a number of localities in both the *Dicynodon* and *Lystrosaurus* assemblage zones, and, with the possible exception of species of *Lystrosaurus*, is the sole tetrapod species that crosses the Permo-Triassic boundary in the Karoo (Kitching 1977; Smith 1995). Nevertheless, Smith & Ward (2001) did not report any specimens of *M. kitchingi* in their study of the stratigraphic ranges of vertebrate taxa spanning the Permo-Triassic boundary in the Karoo. Fossils of *M. kitchingi* are relatively rare, and according to Groenewald & Kitching (1995), the species range in the Triassic is restricted to the Palingkloof Member and the lower part of the Katberg Formation.

***Eriolacerta parva* Watson, 1931, Fig. 2**

Material. BP/1/5898, a complete skull and partial skeleton, from the Palingkloof Member on Maanhaar (Fig. 1).

Remarks. The holotype of the scaloposaurid *Eriolacerta parva* consists of a small skull and partial skeleton from the *Lystrosaurus* Assemblage Zone at Harrismith Commonage, Free State province. This species has also been reported from the coeval lower part of the Fremouw Formation of Antarctica (Colbert & Kitching 1981). Kitching (1977) and Colbert & Kitching (1981) considered *E. parva* to be a possible juvenile of the scaloposaurid *Scaloposaurus constrictus* (Owen 1876), which occurs at a number of localities in the *Lystrosaurus* biozone, including Harrismith Commonage (Kitching 1977). However, the skulls of *E. parva* and *S. constrictus* are of a similar size, which suggests that their differences are not growth-related. Furthermore, the two species were considered distinct by Crompton (1955) and Mendrez-Carroll (1979) in their respective analyses of scaloposaurid relationships. BP/1/5898 can be referred to *E. parva* on the basis of its incomplete postorbital bar, broad intertemporal region, concave maxillary margin, small temporal fenestrae, the absence of a parietal foramen, teeth of small and uniform size, and the absence of a distinct canine (Watson 1931; Mendrez-Carroll 1979). A forthcoming description of BP/1/5898 by the authors should help to consolidate the taxonomic validity of *E. parva*.

***Tetracynodon darti* Sigogneau, 1963, Fig. 3**

Material. BP/1/6026, an incomplete but articulated skull and postcranial skeleton, from the Palingkloof Member on Agterkamp (Fig. 1). Although found as surface float, BP/1/6026 had most likely weathered from a low rock ledge some 1–2 m above the point where the specimen

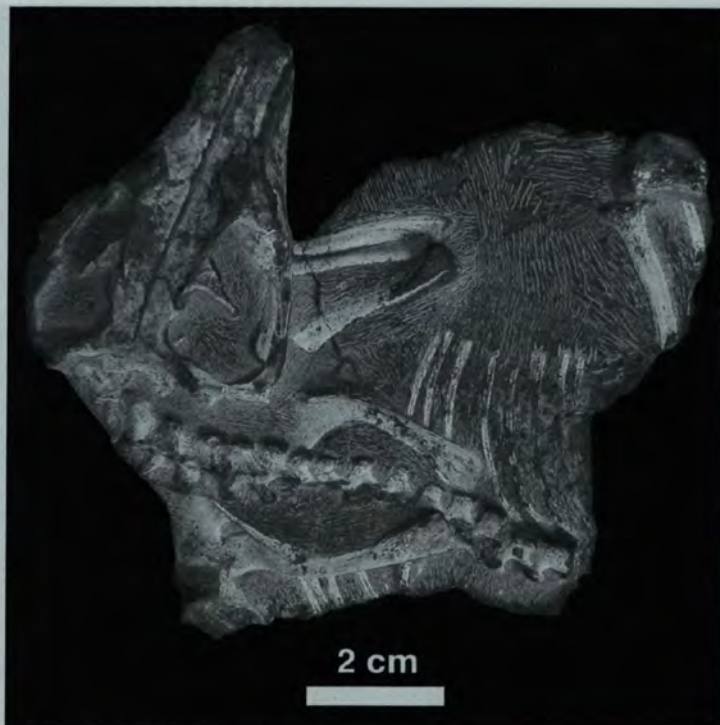


Figure 2. *Eriolacerta parva* (Therapsida, Therocephalia), BP/1/5898, referred specimen from Barendskraal (Middelburg District; *Lystrosaurus* Assemblage Zone) in dorsal view.

was found. This is supported by the lithology of the enclosing matrix which is closest to that of the Palingkloof Member.

Remarks. The type species of *Tetracynodon*, *T. tenuis* (Broom & Robinson 1948), is based on a small skull from the *Dicynodon* Assemblage Zone. Sigogneau (1963) described a new, larger species, *T. darti*, based on a skull and associated postcranial elements from *Lystrosaurus* Assemblage Zone deposits near Bergville, KwaZulu-Natal. BP/1/6026 can be referred to *T. darti* as it is of a comparable size and has a skull morphology identical to *T. darti* in all observable aspects, especially the long and narrow snout and correspondingly slender mandible. The exceptional preservation of BP/1/6026 should provide insight into the otherwise poorly known postcranial anatomy of *Tetracynodon* and of therocephalians in general (Fourie 2001).

Reptilia

Diapsida

Archosauromorpha

***Proterosuchus fergusi* Broom, 1903**

Material. RC 59, a complete skull, the holotype of '*Elaphrosuchus rubidgei*' (Broom 1946), of unknown horizon; SAM-PK-11207–11208, cranial and postcranial remains of '*Chasmatosaurus*' collected by L.D. Boonstra and team in 1935, of unknown horizon; BP/1/6046, a skull and associated partial skeleton, from the Palingkloof Member on Agterkamp (Fig. 1).

Remarks. Kitching (1977) lists *Proterosuchus 'vanhoepeni'* as the senior synonym for the proterosuchid species from the Karoo. However, '*Chasmatosaurus vanhoepeni*' and '*Elaphrosuchus rubidgei*' are now considered subjective



Figure 3. *Tetracyonodon darti* (Therapsida, Therocephalia), BP/1/6026, referred specimen from Barendskraal (Middelburg District; *Lystrosaurus* Assemblage Zone) in (A) dorsal and (B) ventral views.

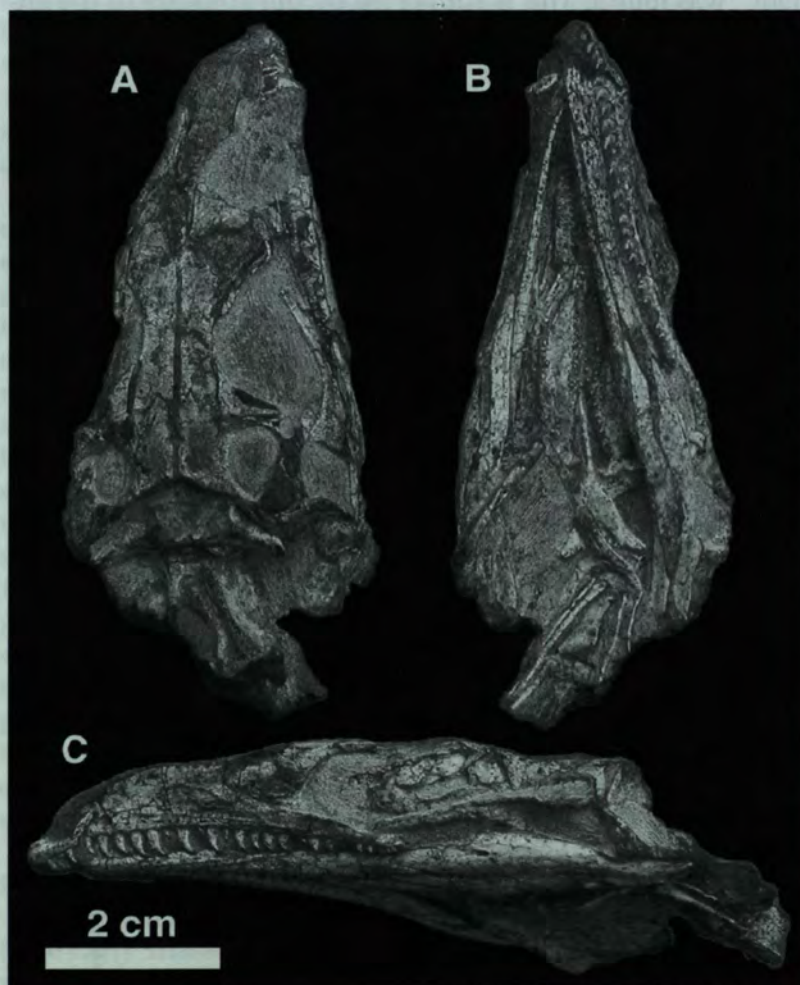


Figure 4. *Prolacerta broomi* (Reptilia, Archosauromorpha), BP/1/5880, referred specimen from Barendskraal (Middelburg District; *Lystrosaurus* Assemblage Zone) in (A) dorsal, (B) ventral and (C) left lateral views.

junior synonyms of *Proterosuchus fergusi* (Welman 1998). Although the taxonomy of the South African proterosuchids has now been clarified (Welman 1998; Welman & Flemming 1993), a detailed redescription of the anatomy of *P. fergusi* is needed, especially in light of the continuing debate with regard to archosauromorph phylogeny.

Prolacerta broomi Parrington, 1935, Fig. 4

Material. BP/1/5880, a complete skull, from the Palingkloof Member on Maanhaar but found as surface float (Fig. 1); BP/1/6029 and BP/1/6038, partial skulls and associated postcranial elements, from the Katberg Formation on Maanhaar (Fig. 1).

Remarks. Like its larger archosauriform relative *Proterosuchus fergusi*, the small archosauromorph *Prolacerta broomi* requires a detailed reappraisal. Gow's (1975) study added much detail to our understanding of the anatomy of *P. broomi*, in particular his description of a complete skeleton (BP/1/2675), but his description of the skull is inaccurate in a number of respects. The skull is the subject of a forthcoming reappraisal by S.P. Modesto & H-D. Sues.

Parareptilia Procolophonoidea

Sauropareion anoplus Modesto *et al.*, 2001, Fig. 5

Material. SAM-PK-11192 (holotype), a skull and associated postcranial elements, of unknown horizon. A number of additional, unprepared procolophonoid specimens (BP/1/5779, 5879, 6027),

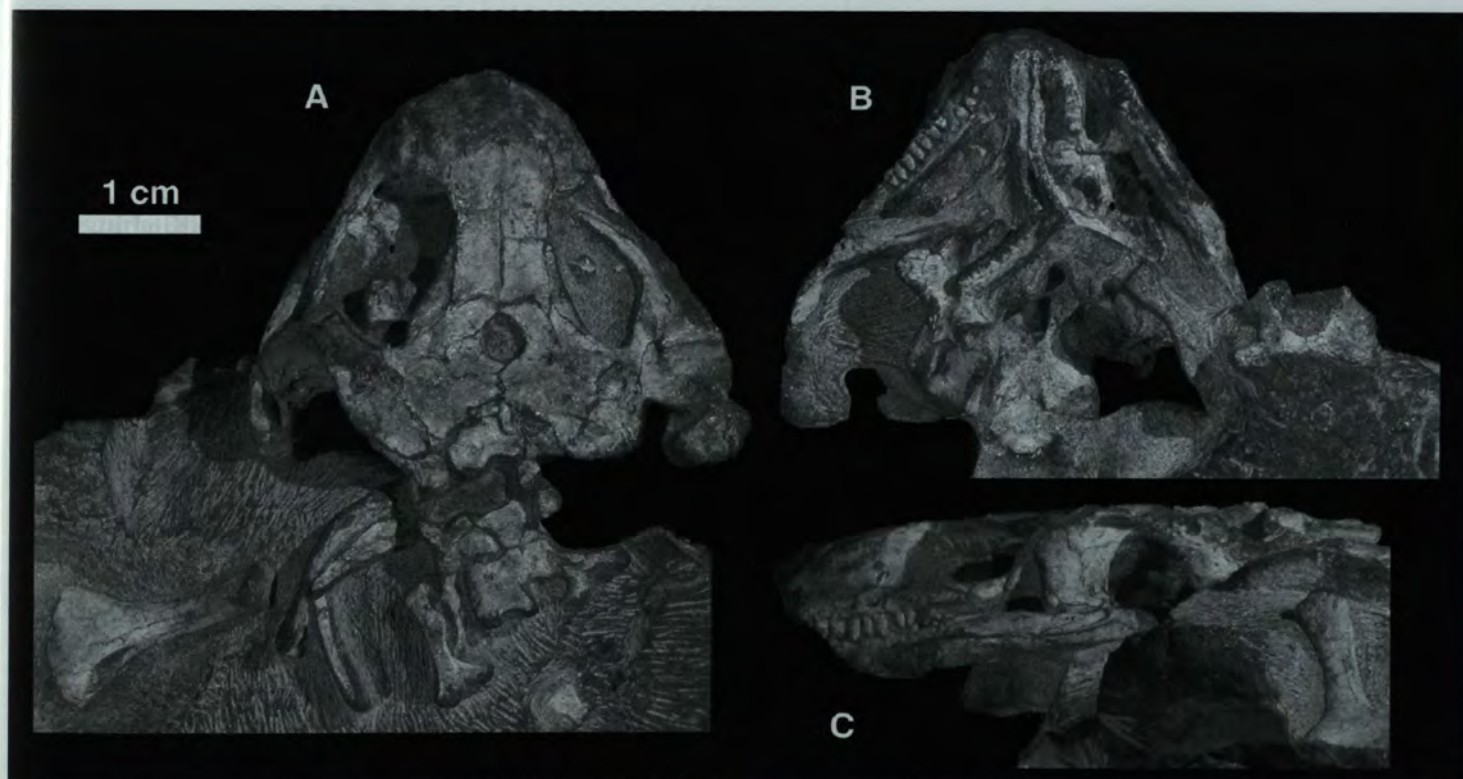


Figure 5. *Sauropareion anoplus* (Reptilia, Procolophonoidea), SAM-PK-11192, holotype specimen from Barendskraal (Middelburg District; *Lystrosaurus* Assemblage Zone) in (A) dorsal, (B) ventral and (C) left lateral views.

represented by cranial and postcranial remains, were collected from the Palingkloof Member on Maanhaar (Fig. 1). Preliminary observation suggests that they are basal procolophonoids probably referable to established taxa from Barendskraal, but full preparation of these specimens is still pending.

Remarks. Phylogenetic analysis identifies *Sauropareion anoplus* as the sister-taxon of the Procolophonidae. Thus, it is more derived than the owenettid taxa from the same strata, *Owenetta kitchingorum* and *Saurodectes rogersorum* (Modesto *et al.* 2001, 2003). Stratigraphic calibration of procolophonoid phylogeny is suggestive of ghost lineages (*sensu* Norell 1992) extending back into the Permian for all three procolophonoid taxa from Barendskraal (Modesto *et al.* 2003). We may therefore expect to discover these species in the uppermost Permian strata of the Karoo.

***Owenetta kitchingorum* Reisz & Scott, 2002, Fig. 6**

Material. BP/1/5882, the anterior half of a skull and associated postcranial elements, from the Palingkloof Member on Maanhaar, but found as surface float (Fig. 1).

Remarks. BP/1/5882 is a small procolophonoid that can be referred to *O. kitchingorum* (Owenettidae) because it possesses the autapomorphy of a midline contact between the prefrontals that separates the nasals from the frontals (Reisz & Scott 2002). All previously known specimens of *O. kitchingorum* (listed by Reisz & Scott 2002) were recovered from the *Lystrosaurus* Assemblage Zone on the farm Tweefontein, Bethulie District, Free State province. Note, however, that one of the specimens referred by Reisz & Scott (2002) to *O. kitchingorum*, BP/1/4196, is actually a crushed, partial *Prolacerta* skull (Gow 1975; Damiani,

pers. obs.). Two other specimens are known that may be referable to *O. kitchingorum*. The first is represented by a crushed skull and partial skeleton uncovered during recent preparation of an undescribed galesaurid cynodont (RC 845) from the farm Fairydale, Bethulie District (Damiani pers. obs.). The second is based on the supposed early lizard *Colubrifer campi* (Carroll 1982), questionably



Figure 6. *Owenetta kitchingorum* (Reptilia, Procolophonoidea), BP/1/5882, referred specimen from Barendskraal (Middelburg District; *Lystrosaurus* Assemblage Zone) in dorsal view.



Figure 7. *Saurodectes rogersorum* (Reptilia, Procolophonoidea), BP/1/6025, holotype specimen from Barendskraal (Middelburg District; *Lystrosaurus* Assemblage Zone) in (A) dorsal and (B) left lateral views.

from the *Lystrosaurus* Assemblage Zone at Thaba N'chu, Free State Province. The holotype of this taxon was recently reinterpreted as a specimen of *Owenetta*, although a specific determination was not possible because of poor preservation (Evans 2001). If the horizon is correct, attribution to *O. kitchingorum* seems likely. For the moment, BP/1/5882 remains the only undoubted specimen of *O. kitchingorum* collected outside of the Bethulie District.

Saurodectes rogersorum Modesto *et al.*, 2003, Fig. 7

Material. BP/1/6025 (holotype), a partial skull with associated postcranial elements, from the Palingkloof Member on Maanhaar (Fig. 1). BP/1/6044, 6045 and 6047 are small, unprepared procolophonoids represented by partially articulated cranial and postcranial remains that were collected from the same excavation point as BP/1/6025. They may be referable to *S. rogersorum* but require additional preparation.

Remarks. *Saurodectes rogersorum* is a procolophonoid referable to the Owenettidae, and is most closely related to *Owenetta rubidgei* and *Barasaurus besairei* from the Upper Permian of South Africa and Madagascar, respectively (Modesto *et al.* 2003). This suggests that the genus *Owenetta*, currently with two nominal species, may be polyphyletic.

DISCUSSION

Intensive collecting over two field seasons on Barendskraal has resulted in the recovery of nine tetrapod species from this locality. With few exceptions, this count far exceeds the norm of two to three species found at most other *Lystrosaurus* Assemblage Zone localities, where *Lystrosaurus* is by far the dominant taxon (Kitching 1968, 1977). In addition, the four tetrapod genera that cross the Permo-Triassic boundary in the Karoo (Rubidge *et al.* 1995), namely *Lystrosaurus*, *Moschorhinus*, *Tetracynodon* and *Owenetta*, are present at Barendskraal. Note that for the present discussion we do not distinguish among the various species of *Lystrosaurus* because of taxonomic uncertainty. According to Kitching (1977), only the famous collecting grounds of Harrismith Commonage in the northeastern Free State have yielded a more diverse fauna, with at least 13 species. However, that count includes three cynodonts (*Galesaurus planiceps*, *Platycraniellus elegans*, *Thrinaxodon liorhinus*) and two temnospondyls (*Lydekkerina huxleyi*, *Broomulus dutoiti*; see Shishkin *et al.* 1996), two groups not currently recorded from Barendskraal. Given the relative abundance of cynodonts (particularly *Thrinaxodon*) and temnospondyls (particularly *Lydekkerina*) at Harrismith and other *Lystrosaurus* biozone localities, their absence at Barendskraal may indicate that these animals were not living in the depositional area, or that there was a bias against their preservation.

It is noteworthy that Harrismith Commonage has been intensively prospected by both local and foreign researchers for over 75 years. In contrast, most other *Lystrosaurus* biozone localities, including Barendskraal, have, to our knowledge, received relatively little attention. This suggests that the high species counts at Harrismith and Barendskraal may represent a collection bias. Although most of the Barendskraal fauna belongs to established taxa, it contains two new procolophonoid species, *Sauropareion anoplus* and *Saurodectes rogersorum*, that shed light on the diversity and survivorship of procolophonoid reptiles in post-extinction, earliest Triassic time (Modesto *et al.* 2001, 2003). Clearly, there remains the potential for future discovery of new taxa from Barendskraal and other relatively unexplored localities in the *Lystrosaurus* biozone.

Our work at Barendskraal also sheds light on the stratigraphic distribution of some taxa within the *Lystrosaurus* Assemblage Zone. First, our documentation of *Lystrosaurus* in the Palingkloof Member (Fig. 1) corroborates the findings of Smith (1995) and Smith & Ward (2001), who first confirmed the occurrence of *Lystrosaurus* below the Katberg Formation (*cf.* Hotton 1967; Keyser & Smith 1979; Groenewald & Kitching 1995). Second, previous authors have suggested that *Prolacerta broomi* was present only in the upper Katberg Formation or the middle-upper part of the *Lystrosaurus* biozone (Kitching 1977; Groenewald & Kitching 1995). However, *Prolacerta* has been documented by Kitching (1977) on the farms Tweefontein and Fairydale in the Bethulie District, Free State province, where it co-occurs with *Owenetta* (Reisz & Scott 2002; this paper). At these localities, the strata exposed is the Paling-

kloof Member and lower part of the Katberg Formation, hence the lower part of the *Lystrosaurus* Assemblage Zone (Ward *et al.* 2000, and field observations by the authors). Thus, the occurrence of *Prolacerta* at these localities, combined with our field observations at Tweefontein and Fairydale, suggests a much earlier appearance in the *Lystrosaurus* biozone for this reptile. The presence of *Prolacerta* in the Palingkloof Member at Barendskraal (Fig. 1) confirms that the stratigraphic range of *Prolacerta* extends from the Palingkloof Member to the middle or upper horizons of the Katberg Formation. Third, the stratigraphic occurrence of the therocephalian *Eriolacerta parva* in the *Lystrosaurus* Assemblage Zone was tentatively identified as being within the Katberg Formation (Groenewald & Kitching 1995). The Barendskraal specimen of *E. parva* (Fig. 1) indicates a more extensive stratigraphic range for this therocephalian, one approximately equal to that now identified for *Prolacerta*, which builds on the former, single occurrence at the type locality of Harrismith Commonage.

It is interesting to note that the Palingkloof exposures at Barendskraal have yielded three genera of basal procolophonoids, but no remains of the well-known and otherwise relatively abundant procolophonid *Procolophon*. The lowest stratigraphic occurrence of *Procolophon* is at present speculative because of insufficient data, although it has apparently been documented from localities (e.g. Fairydale, Bethulie District) in which strata of both the Palingkloof Member and Katberg Formation are exposed (Kitching 1977; Smith & Ward 2001). Nevertheless, fossils of *Procolophon* appear to be rare in the lower part of the *Lystrosaurus* Assemblage Zone, but increase in abundance toward the upper reaches of the biozone (Keyser & Smith 1979; Neveling 2002). On the other hand, there is no evidence for the occurrence of the basal procolophonoid *Owenetta* in the upper part of the *Lystrosaurus* biozone (contra Rubidge *et al.* 1995 and Smith 1995), whereas its presence in the lower part of the biozone, as postulated by Kitching (1977), is now firmly established by its occurrence in the Palingkloof Member at Barendskraal (Fig. 1).

Based on available evidence, including our data from Barendskraal, it appears that *Owenetta* and other basal procolophonoids are restricted to the Palingkloof Member, and that *Procolophon* is the only procolophonoid that is present in the Katberg Formation. It is tempting to conclude that *Procolophon* succeeded *Owenetta*, *Sauropareion* and *Saurodectes* during *Lystrosaurus* Assemblage Zone 'time'. However, the possible occurrence of *Procolophon* in the Palingkloof Member (Smith & Ward 2001), and its co-occurrence with *Owenetta* on the farm Fairydale in Bethulie (Kitching 1977; this paper), suggests that *Procolophon* may have been partially contemporaneous with its more basal procolophonoid relatives. As the transition from the Palingkloof Member to the Katberg Formation marks a major, basin-wide change in fluvial conditions (Ward *et al.* 2000), the presence of *Procolophon* but not its more basal procolophonoid relatives in the Katberg Formation may be interpreted in two ways. The first is a result of different selective pressures imposed by the two fluvial regimes, allowing some procolophonids

such as *Procolophon* to survive, whereas more basal procolophonoids perished. Alternatively, the preservation of some procolophonoid reptiles in the *Lystrosaurus* Assemblage Zone is facies-specific. At present, there is insufficient evidence for either hypothesis, and more intensive collecting efforts in the *Lystrosaurus* biozone are needed to investigate both this issue and the related problem of terrestrial vertebrate extinctions around the Permo-Triassic boundary.

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A definite prosauropod dinosaur from the Lower Elliot Formation (Norian: Upper Triassic) of South Africa

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A new sauropodomorph dinosaur specimen is described and identified as a prosauropod. It is tentatively placed as the sister taxon of *Riojasaurus incertus* from Argentina. The systematic position of all commonly accepted sauropodomorph dinosaurs from the Lower Elliot Formation of South Africa is reviewed and it is found that none can be positively identified as prosauropod. *Euskelosaurus browni* is a *nomen dubium* based on material that cannot be identified further than Sauropodomorpha. *Blikanasaurus cromptoni* and *Antetonitrus ingenipes* are basal sauropods. *Melanorosaurus readi* is probably another basal sauropod but opinion remains divided. *Plateosaurus cullingworthi* presents conflicting character data and at present is classified as Sauropodomorpha *incertae sedis*. Consequently the specimen described here represents the only prosauropod specimen currently recognized in the Lower Elliot Formation of South Africa.

Keywords: Triassic, Lower Elliot Formation, South Africa, Sauropodomorpha, Prosauropoda.

INTRODUCTION

Prosauropod dinosaurs in the broad sense, that is any basal sauropodomorph that is not a member of the derived, columnar-limbed sauropod clade (i.e. *Vulcanodon* + *Eusauropoda*), have long been known from the Lower Elliot Formation (Upper Triassic, Karoo Supergroup) of South Africa. Indeed, the unit contains a moderate diversity of such dinosaurs, with three taxa, *Euskelosaurus browni*, *Melanorosaurus readi* and *Blikanasaurus cromptoni*, commonly being accepted as valid (e.g. Galton 1990). Another taxon, *Antetonitrus ingenipes*, has recently been added to the list but this was explicitly described as a basal sauropod, rather than a prosauropod (Yates & Kitching 2003). The previous three taxa are frequently referred to the Prosauropoda but recent phylogenetic work (Yates 2003, in press; Yates & Kitching 2003) suggests that none of them can be confidently placed in the Prosauropoda *sensu stricto* (i.e. the clade containing all sauropodomorphs that share a more recent common ancestor with *Plateosaurus* than with the sauropod *Saltasaurus*; Sereno 1998). The phylogenetic position of each of these taxa is briefly discussed below before the presence of true prosauropods in the Lower Elliot Formation is examined.

Euskelosaurus browni Huxley, 1866

Euskelosaurus browni is based on some fragmentary postcranial remains (BMNH R1625) of which a proximal right femur is most informative. It has been distinguished from *Melanorosaurus readi* on the basis of its sinuous femoral shaft, the placement of the lesser trochanter well away from the lateral margin of the femur in anterior view and the proximally placed fourth trochanter (Galton 1985). These are plesiomorphic features within Sauropodomorpha and there are at least two different taxa in the Lower Elliot Formation that display them. In addition, the holotype does not display any synapomorphies that would allow it to be identified as either prosauropod,

basal sauropod or basal sauropodomorph. Consequently the name should be discarded as a *nomen dubium*. The name *Plateosaurus cullingworthi* (Haughton, 1924) becomes the next available species name for the diagnostic material (SAM 3341–3356, 3602–3603, 3607–3609) that was referred to *Euskelosaurus browni* by Van Heerden (1979). This species was originally described as a new species of *Plateosaurus* but Huene (1932) erected the new genus *Plateosaurus* to accommodate it. *Plateosaurus cullingworthi* does not display any obvious, unique autapomorphies but can be diagnosed by an unusual combination of characters not found in any other sauropodomorph. These include: moderately large size (femur length of at least 545 mm); anterior dorsal neural spines with distal, lateral swellings; tall posterior dorsal neural spines reaching a height that is more than twice the length of their base; a relatively slender humerus where the width of the distal end is less than one third of the total length of the bone; a strongly sinuous deltopectoral crest that is only 42% of the length of the humerus; the postacetabular process of the ilium is square-ended; the ischial peduncle of the ilium has a posterior 'heel'; a femur that is sinuous in both lateral and anterior views; the fourth trochanter located entirely in the proximal half of the femur and placed centrally on the posterior surface of the femur, well away from the medial edge; the descending process of the distal tibia extends as far laterally as the anterolateral process. Unfortunately, the specimens of *P. cullingworthi* lack the critical anatomical regions that are rich in useful characters (e.g. the skull and manus). Consequently, it cannot be placed with any certainty in the Prosauropoda, Sauropoda, or in a position basal to these two. A cladistic analysis by the author (Yates 2003) has found weak support for this taxon (called '*Euskelosaurus*' in that analysis) as a basal sauropod, based largely on its tall dorsal neural spines (greater than 1.5 times the length of the base) and the reduced deltopectoral

crest of its humerus (less than 50% of the length of the humerus). However, its position became highly labile just one step away from the most-parsimonious tree. The distal end of the neural spine of the single known anterior (pectoral) dorsal vertebra possesses lateral swellings. This character was not included in the analysis of Yates (2003) but subsequent analyses by the author (Yates, in press; Yates & Kitching 2003) have interpreted this character state as a synapomorphy of the Prosauropoda. Thus further work may yet support the placement of this species within the Prosauropoda but at the moment the data are inconclusive and it should be classified as *Sauropodomorpha incertae sedis*.

***Melanorosaurus readi* Haughton, 1924**

This species was originally based on a composite collection of postcranial bones (SAM 3449, 3450), from which the femur (SAM 3450) is the most informative and it has been treated as the lectotype (Galton 1985; Van Heerden & Galton 1997), although this designation has not been formally proposed.

This species was also found to be a basal sauropod in the analysis by Yates (2003) and this has been strongly corroborated in subsequent analyses by the author (Yates, in press; Yates & Kitching 2003). Character states that support this position are the tall dorsal neural spines, dorsoventrally deep hyposphenes (equal to the diameter of the neural canal) on the dorsal vertebrae, the presence of four sacral vertebrae, a deep radial fossa on the ulna, and the failure of the descending process of the distal tibia to extend laterally to the craniolateral corner of the distal tibia. Only the last of these character states is actually visible in the syntype series, all of the others are gleaned from a set of referred specimens (two individuals both catalogued as NM R1551) (Van Heerden & Galton 1997). However, another recent analysis of early sauropodomorph relationships retains this taxon within the Prosauropoda (Galton & Upchurch, in press). This position is based on femoral character states that *Melanorosaurus readi* shares with the prosauropod *Riojasaurus incertus*. These include a straight femur in anterior view and a crest-like lesser trochanter that is shifted laterally. However, these characters are also present in basal sauropods such as *Antetonitrus ingenipes* and *Vulcanodon karibaensis* (Yates & Kitching 2003; Raath 1972; Cooper 1984). Thus, the identification of *Melanorosaurus readi* as a prosauropod is not compelling.

***Blikanasaurus cromptoni* Galton & Van Heerden, 1985**

This specimen is based solely on a left epipodium, tarsus and pes (SAM K403). No other specimens have been referred to it.

All recent cladistic analyses of early sauropodomorph relationships that have included *Blikanasaurus cromptoni* have found that it is a basal member of the Sauropoda (Yates 2003, in press; Yates & Kitching 2003; Galton & Upchurch, in press). Character states supporting this position include the smoothly rounded posteromedial margin of the astragalus in dorsal view, and a shortened third metatarsal (40% of the length of the tibia).

So are there any incontrovertible prosauropods in the

Lower Elliot Formation at all? A partial set of remains (BP/1/4953) from Hamelneuskop on the farm Nova Barletta, Clocolan district, Free State, cannot be referred to any of the taxa listed above and would appear to represent the first definite prosauropod remains to be recognized from the Lower Elliot Formation. The specimen was found in a horizon of large concretions near the top of the Lower Elliot Formation (Kitching & Raath 1984). It was initially identified as *Euskelosaurus* sp. (Kitching & Raath 1984) but at the time this name was simply used as a catch-all for large sauropodomorphs from the Lower Elliot Formation.

DESCRIPTION

An articulated series of ten dorsal vertebrae (probably the 3rd to the 12th dorsal vertebrae) and a right femur comprise the specimen. The quality of the preservation is not good. Indeed the first, second, and last vertebrae of this series are so distorted by explosive deformation that they yield no useful information. The positional identification of the vertebrae is based on the morphology of the first well-preserved vertebra (the third in the series) in comparison with the dorsal series of *Massospondylus carinatus* (pers. obs. of BP/1/5241), *Plateosaurus engelhardti* (Huene 1926) and *Riojasaurus incertus* (pers. obs. of PVL 3808). The third vertebra of BP/1/4953 possesses a neural spine that is cranio-caudally shorter and transversely broader than those following it and has strongly upturned transverse processes indicating that it derives from the anterior end of the dorsal column (dorsals 1–5 in *Plateosaurus engelhardti*; Huene 1926). The fourth vertebra of the series lacks these features, indicating that the first three vertebrae in BP/1/4953 represent dorsals 3–5.

All of the vertebrae have simple, hourglass-shaped centra with weakly defined pleural depressions. The neural arches are low (about equal to the height of the centrum), as are the neural spines. The anteroposterior length of the square-shaped neural spine of the 5th dorsal is short (half the total length of the vertebra). The transverse width of this neural spine is noticeably thicker than in the following vertebrae. In the following vertebrae (dorsals 6–8) the neural spine bases are much longer (three quarters of the total length of the vertebra) and almost twice as long as they are high. The posterior margin of these is strongly concave so that the caudodistal corner of the neural spine forms a triangular projection in lateral view. The neural arches are laminated as in most other saurischians (Wilson 1999) but these laminae resemble those of *Riojasaurus incertus* in being short, low and thick, especially those posterior to the 7th dorsal where they form such low ridges that the appellation 'lamina' is barely warranted. The 7th dorsal has a prezygodiapophyseal lamina but the vertebrae caudal to it do not (nomenclature of the laminae follows Wilson 1999). The paradiapophyseal lamina is present on all of the vertebrae that are well-preserved enough to retain their laminae except on the 12th dorsal where it is not present due to the proximity of the parapophysis to the diapophysis. The transverse processes are markedly short and thick. Those of the 5th dorsal are strongly upturned, whereas those

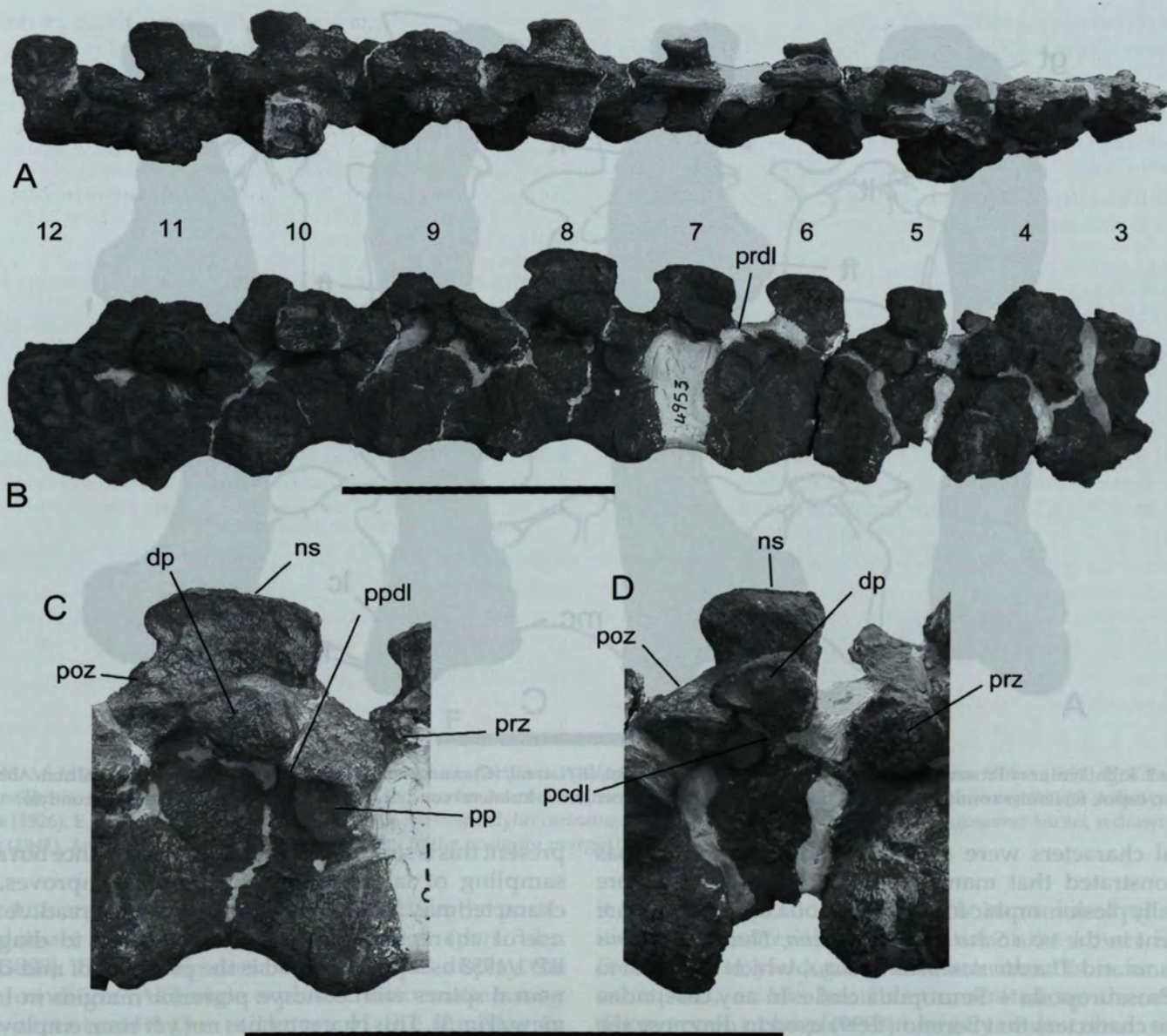


Figure 1. Articulated series of dorsal vertebrae of *Prosauropoda* indet. (BP/1/4953) in (A) dorsal and (B) right lateral views. C, 8th dorsal vertebra in right lateral view. D, 5th dorsal vertebra in right lateral view. Scale bars = 200 mm. Abbreviations: dp, diapophysis; ns, neural spine; pcdl, posterior centrodiapophyseal lamina; pp, parapophysis; ppdl, paradiapophyseal lamina; podl, postzygodiapophyseal lamina; poz, postzygapophysis; prdl, prezygodiapophyseal lamina; prz, prezygapophysis.

posterior to it are only slightly upturned.

The femur closely resembles that of *Plateosaurus engelhardti* from Trossingen and lacks any of the femoral specializations listed by Galton (1985) as diagnostic for 'Melanorosauridae'. The medial turning of the femoral head is not complete so that the long axis of the head lies at 45° to the transverse axis of the distal femur. The shaft is sigmoid in both lateral and anterior views. The antero-posterior diameter of the shaft is equal to the mediolateral diameter at the midlength of the femur. The lesser trochanter is a low, rounded ridge that is well removed from the lateral margin of the shaft in anterior view. The large fourth trochanter is placed entirely in the proximal half of the bone and is well removed from the medial margin of the shaft in caudal view. All of these features are found in more basal sauropodomorphs (e.g. *Thecodontosaurus antiquus* and *Efraasia minor*) and are primitive for *Prosauropoda*. Poor preservation makes it impossible to

determine if there was any sort of extensor depression on the anterior distal surface.

DISCUSSION

The presence of laminated dorsal vertebrae and the lack of ornithischian synapomorphies, such as a long, finger-like lesser trochanter and a 'hooked' fourth trochanter, clearly identify BP/1/4953 as a saurischian dinosaur. Amongst saurischians it can be clearly referred to the Sauropodomorpha by the proximodistally elongate lesser trochanter that is not separated from the shaft of the femur by a cleft, and by the absence of prezygodiapophyseal laminae from the mid dorsal vertebrae. Diagnosis of the *Prosauropoda* is somewhat problematic, with little agreement between workers over the content of the clade or its diagnostic characters. Sereno (1999) diagnosed *Prosauropoda* with a long list of mainly cranial and manual characters, although some cervical, pelvic and

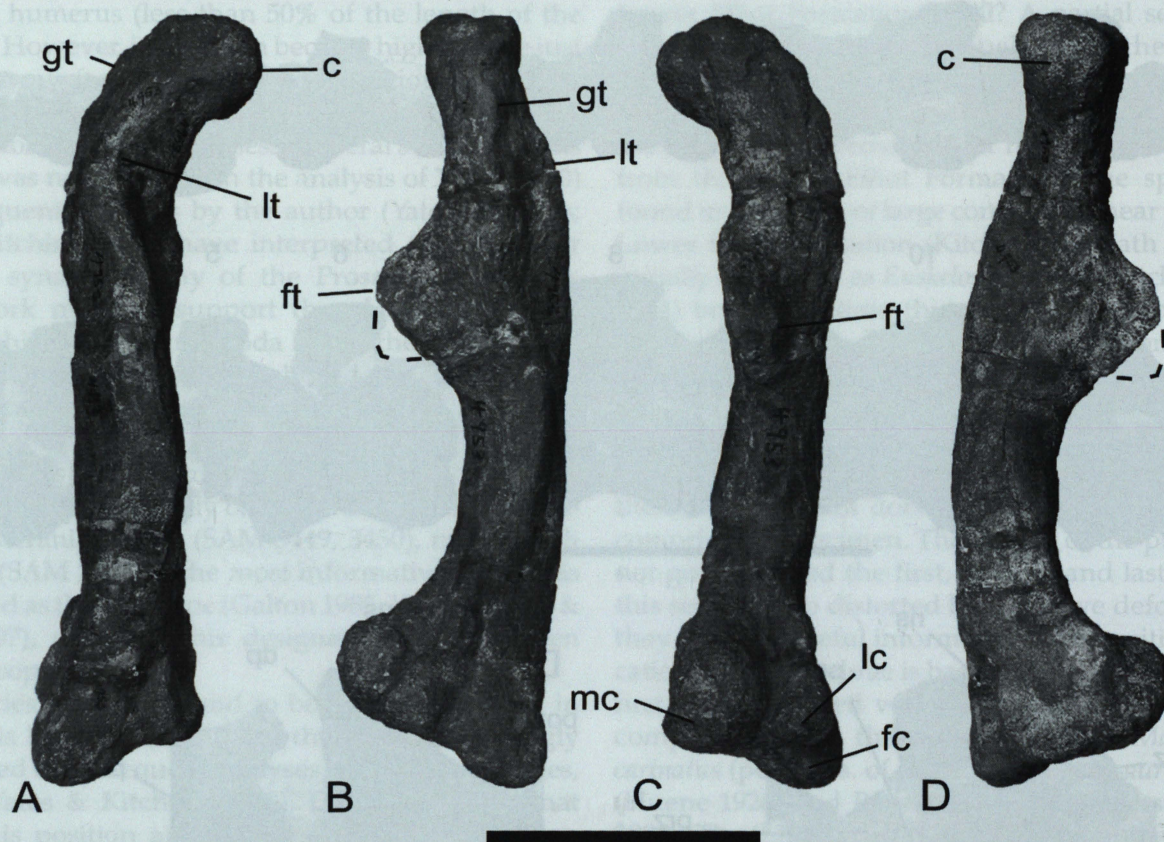


Figure 2. Right femur of *Prosauropoda* indet. (BP/1/4953) in (A) cranial, (B) lateral, (C) caudal and (D) medial views. Scale bar = 200 mm. Abbreviations: c, caput; fc, fibular condyle; ft, fourth trochanter; gt, greater trochanter; lc, lateral condyle; lt, lesser trochanter; mc, medial condyle.

pedal characters were also included. Yates (2003) has demonstrated that many of these character states are actually plesiomorphic for *Prosauropoda* because they are present in the taxa *Saturnalia tupiniquim*, *Thecodontosaurus antiquus* and *Thecodontosaurus caducus*, which are basal to the *Prosauropoda* + *Sauropoda* clade. In any case, none of the characters that Sereno (1999) used to diagnose the *Prosauropoda* can be determined in BP/1/4953. Of the character states used by Yates (in press) and Yates & Kitching (2003) to diagnose the *Prosauropoda*, only one could potentially be determined with the limited set of remains at hand. This is the presence of lateral swellings of the distal ends of the neural spines of the vertebrae in the pectoral region (dorsals 1–4 in *Riojasaurus incertus*; pers. obs. of PVL 3808). Unfortunately even this character cannot be determined with any certainty in BP/1/4953 because the neural spine of the presumed 3rd and 4th dorsals have been severely affected by explosive, pedogenic deformation. Nevertheless, the morphology of the 5th dorsal neural spine suggests that the derived condition was present in this specimen. In *Plateosaurus engelhardti* and *Riojasaurus incertus* the first vertebra following those with the lateral swellings is itself transversely expanded in comparison to all following vertebrae even though it lacks distinct swellings. Similarly, the neural spine of the 5th dorsal vertebra of BP/1/4953 is transversely expanded in comparison to those behind it, suggesting that the neural spines preceding it may have borne lateral expansions. It should also be noted that the derived condition for this character is also present in the theropod *Dilophosaurus wetherilli* (Welles 1984, fig. 13). At

present this is simply regarded as a convergence but as the sampling of larger, early saurischians improves, this character may be found to be more widespread. A more useful character state that can be used to diagnose BP/1/4953 as a *prosauropod* is the presence of mid-dorsal neural spines with concave posterior margins in lateral view (Fig. 3). This character has not yet been employed in cladistic analyses of sauropodomorph relationships but it can be seen to be well developed in *Riojasaurus incertus* (Bonaparte 1972, fig. 57a), in *Lufengosaurus huenei* (Young 1941, fig. 6), and to a lesser extent in *Plateosaurus engelhardti* (Huene 1926, plate 2, fig. 2). The condition is also present, but weakly developed, in *Massospondylus carinatus* (Galton 1976, fig. 4). In contrast, outgroups to *Prosauropoda*, or at least the clade *Riojasaurus* + *Plateosauria*, have neural spines with straight posterior margins and no projecting posterior distal corner. These include herrerasaurids (e.g. *Herrerasaurus ischigualastensis*; Novas 1994, fig. 1), theropods (e.g. *Dilophosaurus wetherilli*; Welles 1984, figs 14 & 15), sauropods (e.g. *Kotasaurus yamanpalliensis*; Yadagiri 2001, fig. 4g) and *Efraasia minor* (pers. obs. of SMNS 12354).

Further evidence supporting the position of BP/1/4953 can be gleaned from a derived character that the specimen shares with *Riojasaurus incertus*, suggesting that these two taxa might have a sister-group relationship within *Prosauropoda*. *Riojasaurus incertus* is remarkable amongst sauropodomorphs in having poorly developed lamination of the neural arches of the dorsal vertebrae, especially those from the middle and posterior end of the series. Instead of forming tall, thin webs of bone, the laminae of

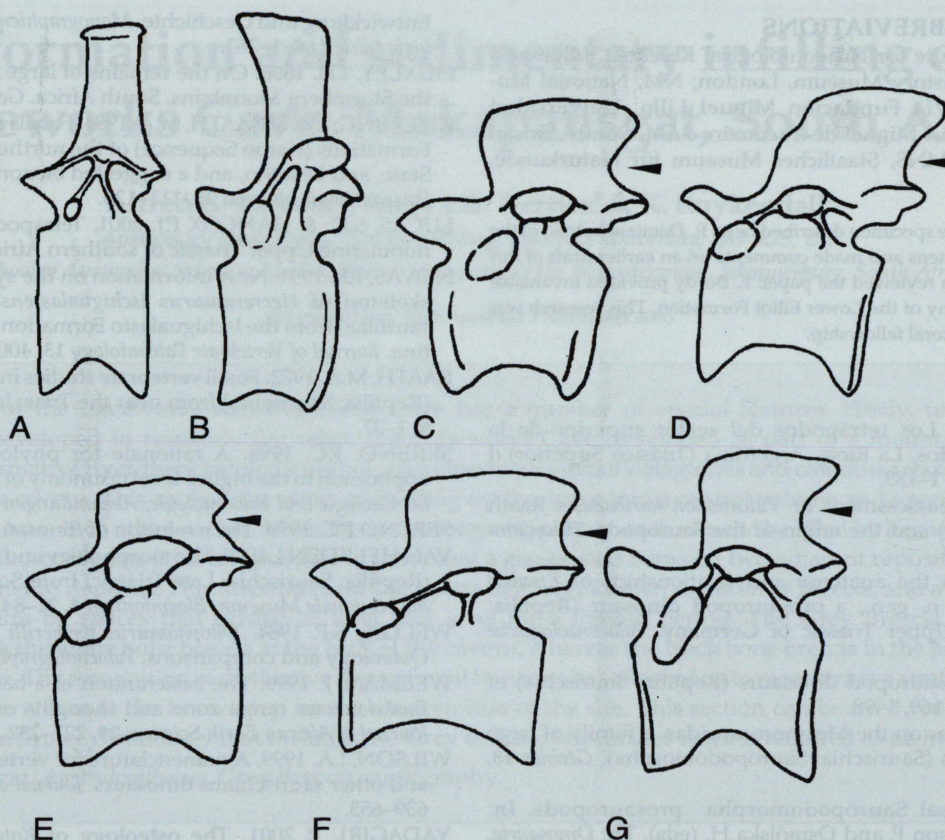


Figure 3. Middle to posterior dorsal vertebrae of various saurischians. **A**, *Herrerasaurus ischigualastensis*, redrawn from Novas (1994). **B**, *Kotasaurus yamanpalliensis*, redrawn from Yadagiri (2001). **C**, *Riojasaurus incertus*, redrawn from Bonaparte (1972). **D**, *Plateosaurus engelhardti*, redrawn from Huene (1926). **E**, *Prosauropoda* indet. (BP/1/4953). **F**, *Massospondylus carinatus*, redrawn from Galton (1976). **G**, *Lufengosaurus huenei*, redrawn from Young (1941). Arrows indicate the derived concavity in the posterior margin of the neural spine of prosauropods.

R. incertus are low, short, thick ridges which in the posterior dorsals are as wide as they are high (pers. obs. PVL 3808). The middle dorsals of BP/1/4953 display the same condition. Although explosive deformation may have accentuated the thickness of the laminae in BP/1/4953 it does not explain their lack of height and the character is accepted as having a biological rather than diagenetic origin.

The low neural spines of BP/1/4953 (where the height is less than length of the base) distinguish this specimen from *Plateosaurus cullingworthi*. In the latter taxon the middle and posterior neural spines are at least twice as high as they are long at the base (Van Heerden, 1979, pl. 9–12). The same character distinguishes BP/1/4953 from *Melanorosaurus readi* and *Antetonitrus ingenipes*, but these taxa can also be distinguished from BP/1/4953 on the basis of femoral morphology. In the latter taxa the femur is straight in cranial view, the lesser trochanter is crest-like and has shifted towards the lateral margin of the shaft, and the fourth trochanter straddles the boundary between the proximal and distal halves of the bone. BP/1/4953, on the other hand, retains the primitive condition for these characters with a sinuous femoral shaft in cranial view, a low, ridge-like lesser trochanter that is placed well away from the lateral margin of the shaft, and a fourth trochanter that is placed entirely in the proximal half of the bone.

Although BP/1/4953 is clearly distinct from the named, valid sauropodomorph taxa of the Lower Elliott Formation,

it is not prudent to create a new name based on such incomplete material. The potential of the Lower Elliott Formation to yield good dinosaur remains is far from exhausted, as has been demonstrated by the recent discovery of a complete, but largely undescribed, sauropodomorph skull and skeleton (NM R3314; Welman 1999). The erection of new names based on low-quality types will only lead to taxonomic confusion in the future, as has been the case for dinosaurs from the Elliot Formation in the past.

The apparent close relationship between BP/1/4953 and *Riojasaurus incertus* from the Norian Los Colorados Formation of Argentina supports the hypothesis that the Lower Elliott Formation can be correlated with this unit (Lucas & Hancox 2001). *Antetonitrus ingenipes* from the Lower Elliott Formation is very similar to *Lessemsaurus sauropodoides* from the Los Colorados Formation. Both taxa are large and have tall neural arches and neural spines (general features widespread amongst sauropods) but also share the derived character of dorsal neural spines that expand transversely towards the distal end. An undescribed first metacarpal (almost certainly belonging to *Lessemsaurus sauropodoides*) from the Los Colorados Formation shares with *Antetonitrus ingenipes* the derived condition of being wider than it is long (pers. obs. of unregistered PVL material). Thus these taxa add further evidence of faunal similarity between the two formations and suggest that they are close to, if not actually coeval.

INSTITUTIONAL ABBREVIATIONS

BP, Bernard Price Institute for Palaeontological Research, Johannesburg; BMNH, Natural History Museum, London; NM, National Museum, Bloemfontein; PVL, Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán; SAM, South African Museum, Cape Town; SMNS, Staatliches Museum für Naturkunde, Stuttgart.

The late L. Huma collected the specimen described here. R. Damiani helped in the handling of the heavy specimens and made comments on an earlier draft of this work. P. Barrett and P. Galton reviewed the paper. E. Bordy provided invaluable discussions on the stratigraphy of the Lower Elliot Formation. This research was supported by a NRF postdoctoral fellowship.

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The formation and sedimentary infilling of the Limeworks Cave, Makapansgat, South Africa

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The remnant cavern of the Limeworks australopithecine site has a number of special features. Firstly, unlike Swartkrans and Sterkfontein, which developed in relatively flat relief, the Limeworks Cave developed as part of a mountain karst. Then upon abandonment by its formative river, there formed a unique, conjoined series of tall stalagmites and columns arranged in an irregular arc against the walls of the cavern. This arc had the effect of dividing up the space into a central volume and several lateral alcoves. The spaces were separated from each other, so that, when the cavern began to unroof, each came to be filled by its own surficial deposits or, in some cases, not at all. At only one level is it possible to show that a gap existed between two adjacent repositories so as to produce common, contemporaneous deposits. This turns out to be the hyena den layer known as the Grey Breccia, and a connection was made possible with the centre by spaces that existed at local roof level for a limited period. The Grey Breccia appears to be about contemporaneous with the white bone breccia at the back of the cavern, whereas the black bone breccia in the Main Quarry is slightly younger than these two. The recognition of distinctive depositional horizons has allowed us to reconstruct a stratigraphic section for all deposits from the known base to the known top on the western side of the site. This section can be used for magnetostratigraphic purposes to construct a firmer chronology that includes the Grey Breccia; but further work is required to tie in the eastern side.

Keywords: Makapansgat, *Australopithecus*, Grey Breccia, stratigraphy.

INTRODUCTION

The Limeworks Cave, Makapansgat, in the Northern Province, South Africa (Fig. 1), is well known for its finds of *Australopithecus africanus*. Currently the chronology of the site is believed to lie somewhere between at least 4 and 2 Ma. However, as the question of sequence stratigraphy is not settled this, in turn, has cast doubt on the chronology as determined by faunal correlation and by magnetostratigraphy (McFadden *et al.* 1979; White *et al.* 1981; Partridge and replies 1982; McFadden & Brock 1984) and, hence, the age of the bone breccia layers is uncertain. All workers now agree that, within the cavern, there were separate repositories rather than just one overarching sequence. An important task now, therefore, is to study the stratigraphy of these repositories to see whether, and how, they are linked. Part of the problem in understanding the deposits of the Limeworks is that the formation of the original cavern is not sufficiently well understood. So the first part of the paper presents simple, karstic, hydrogeological concepts of cave formation in order to explain the origin of the cavern before surface erosion and unroofing took place. Only then can the description of the deposits be presented with the interpretation of the phases of infilling and the processes that operated. Some of this work has been presented in Latham *et al.* (1999) and in Partridge (2000). As the work at Limeworks Cave is ongoing and forms part of a project to study afresh the magnetostratigraphy, this paper represents our current understanding of the configuration and origins of the Limeworks Cave deposits.

Note on nomenclature. For convenience, and where applicable, we refer to the main sedimentary layers on the west side by the Member names given by Partridge

(1979, 2000). We have also followed the advice of Maguire *et al.* (1980, 1985) in giving informal names to distinct repositories and to other specific areas. For reference, these names are marked on the plans and sections presented in this paper (Fig. 2 *et seq.*).

THE LIMESWORKS CAVE AS A FORMER RESURGENCE

An understanding of how the cave formed aids an understanding of its deposits. In this regard, the evidence and arguments that the Limeworks Cave was once part of a large river cave recapitulate parts of a paper on the nearby Cave of Hearths (Latham & Herries, *in press*).

Neither the Cave of Hearths – Historic Cave (CoH-HC) – complex nor the Limeworks Cave formed as a single isolated cavern under a watertable, as has sometimes been assumed. To begin with, watertables do not form in impermeable limestone or dolomite except where the rock body is highly fractured. Unlike more porous and permeable rocks such as sandstone, dolomite and limestone are too impermeable to allow groundwater to follow Darcy's law of diffuse flow except, possibly, in the very early stages of inception when the protoconduits are less than about 1 mm wide (Ewers 1982) or when the rock body is highly fractured. Laboratory experiments, modelling and field observations show that caves form in limestone by the integrated connection of one set of protoconduits that successfully competes over others (see Ford *et al.* 2000). The winning connective set of conduits is that which provides the least overall resistance to flow from source to resurgence. That set then enlarges rapidly over the alternatives until the whole of the flow is captured. The protoconduits form initially along bedding partings, cracks and faults so that the overall route from source to

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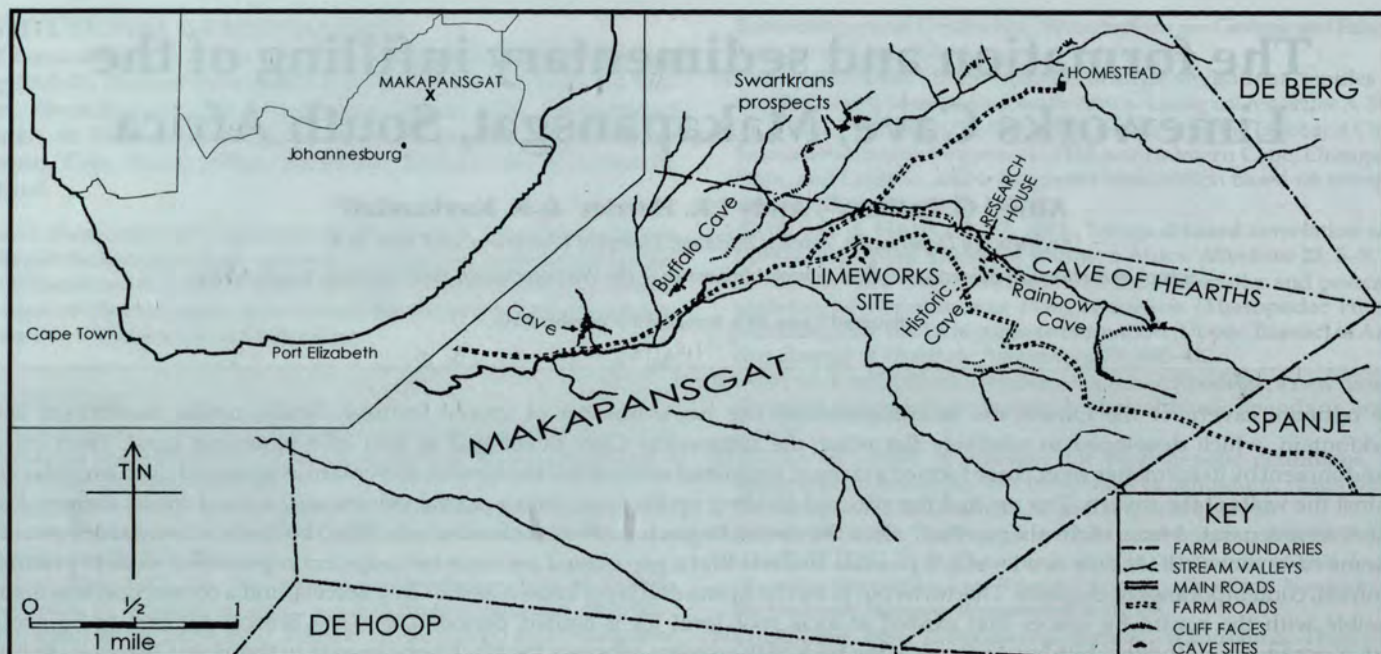


Figure 1. Location map of Makapansgat, the Cave of Hearths and related features (after Wells & Cooke 1957).

sink is seldom the shortest straight-line distance. Once sufficient flow has been established it is no longer possible for the maintenance of any continuous piezometric surface. For example, it is quite common, in karst worldwide, to find waterlogged passages lying above air-filled passages in the same cave system. It is therefore inappropriate to talk about a saturated zone since this term applies only to rock having connective porosity, that is, having permeability. Although it is not uncommon to find 'watertable' as a working concept in the literature, Jennings (1985) presents a list of observations to demonstrate why watertables only exist in limestones exceptionally. See also Bögli (1980) and various papers in Klimchouk *et al.* (2000).

In mountain karsts, such as at Makapan, the underground drainage creates just one set of connected passages. More complex systems occur when there are multiple inputs. Later incision of the valley provides an opportunity for the establishment of rerouting to a newer spring at a lower level and this results in the abandonment ('fossilization') of upper cave passages. (By contrast, those caves that are formed on the fault zone of the Swartkrans valley, such as Peppercorns, Ficus and Katzenjammer, demonstrate a hydrological behaviour more like that appropriate to the watertable scenario. The present-day water levels of these caves are connected and rise and fall together.)

In the case of Makapansgat, a large fault near the Red Cliffs (Fig. 3) has brought the host Malmani dolomite into contact with the stratigraphically lower Black Reef quartzite and this would have presented a zone of entry for water draining off the upper catchment. The Lime-works Cave must therefore have acted as the resurgence for the system, conducting water from this uplands catchment out to the Swartkrans valley. Fig. 3 shows this putative cave system overlain on the present lower valley (the Mwaridzi valley). It seems that, at some stage in the formation of the river cave, new passages developed to shift the system to the north leaving CoH-HC as an oxbow.

It is possible that streams occupying what is now the northern flank of the Mwaridzi valley, corresponding perhaps to the modern House, and Bee Rock, Gulleys, initiated this shift. The system thus developed a second, later outlet into the Swartkrans valley some 1 km to the north of the Lime-works resurgence. In the Mwaridzi section, the cave river was able to incise its bed until it reached the contact with the basal shale units and Black Reef quartzite. It is probable that downcutting was arrested in favour of undermining of the dolomite sides and, with help from surface dissolution, the roof eventually collapsed. Further flank erosion and dissolution of dolomite rubble over two to three million years resulted in the present canyon-like cross section. The modern Mwaridzi valley as far as the Red Cliffs thus occupies the position of the final river cave, and the Lime-works represents the bevelled remnant and infill of the earlier resurgence.

The possibility of an old connection to the Lime-works from the CoH-HC complex is discussed in Latham & Herries (in press).

The size and shape of the original cavern

Figure 2 shows the main features of the excavation and the position of the dolomite walls of the original cavern as outcrops. Prior to speleothem mining, the centre of the cavern was occupied by breccia and layered sediments and, to the sides, by huge masses of speleothem; most of the central breccia, referred to subsequently as the Central Debris Pile, was left intact. The cavern lies on the north-west flank of a low ridge sloping roughly east to west, and its deposits have been eroded away as part of the beveling of the surface from the ridge (Fig. 3). It can be assumed, fairly safely, that the present land surface in which the cavern lies has maintained approximately the same form for the last 3 to 4 millions of years. There does not appear to have been much catchment potential above the cavern for runoff to develop beyond the size of small

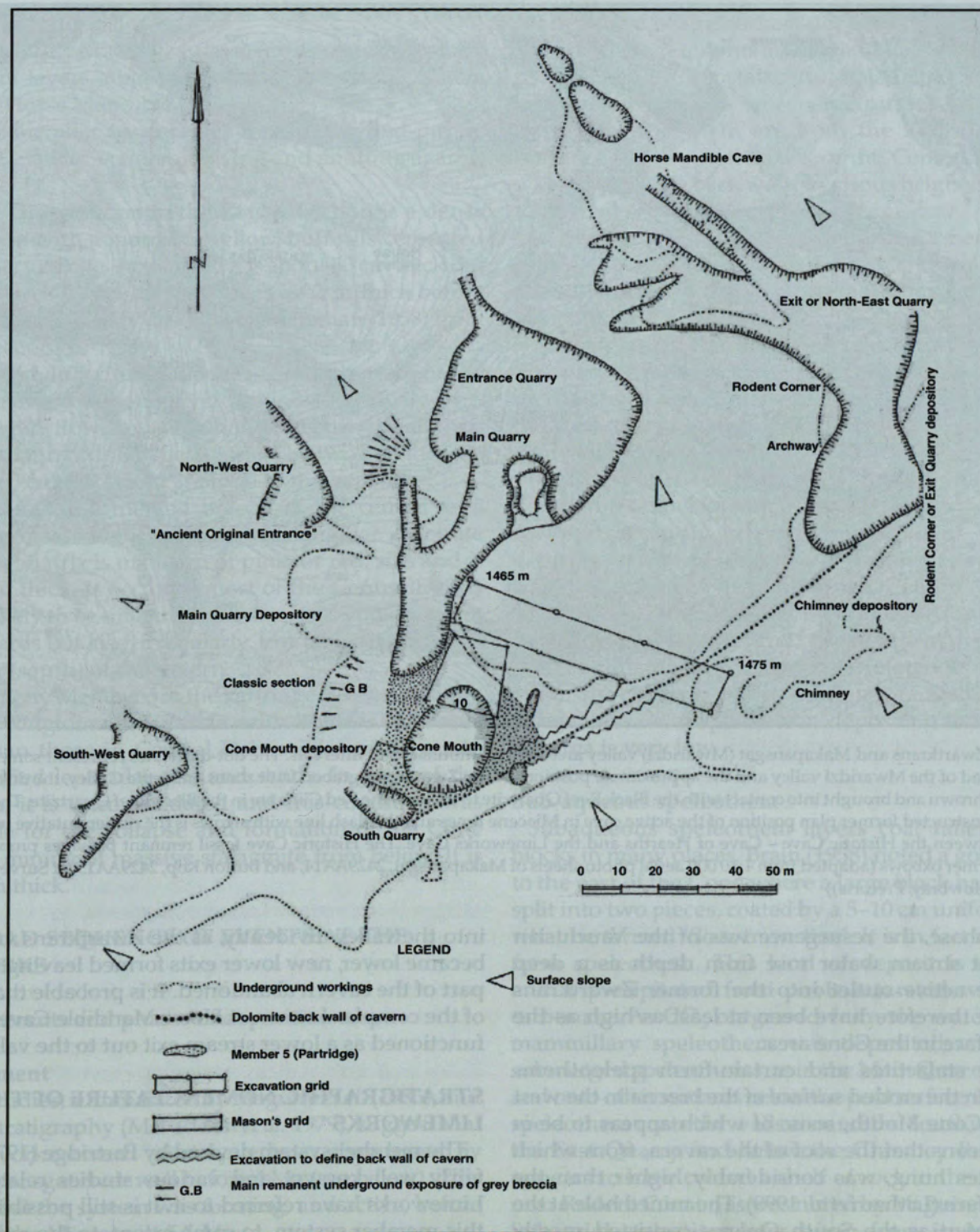


Figure 2. Map of the Limeworks site (after Maguire *et al.* 1980). The dotted area represents Member 4, the sediments winnowed from the Central Debris Pile and which were emplaced under an existing roof (see text).

streams and, consequently, there does not appear to have been any surface stream capture to, or from, any adjacent catchment. Thus, most of the erosion and later infill of the cavern was probably due to direct action of rainwater and surface runoff.

The configuration of the present floor of the cavern is discernible in places by the presence of large dolomite blocks that have fallen from the roof and, under the Central Debris Pile, by spot heights from bore cores drilled in 1993 (see Partridge 2000). It is not known what the configuration of the original floor was before block fall.

The Main Quarry and the Exit Quarry appear to have formed along faults and, judging by its straightness, this may also be true of the back wall of the cavern (Partridge 1975).

What was the form of the resurgence in its early active phase? Between the Cone and the Exit Quarry, the walls rise vertically some 20 m to the present surface and show no signs of having suffered significant rock breakdown. In other words, the rear walls most certainly reflect the last stages of solution of this part of the cavern when the emerging water filled it. This strongly suggests that, in its

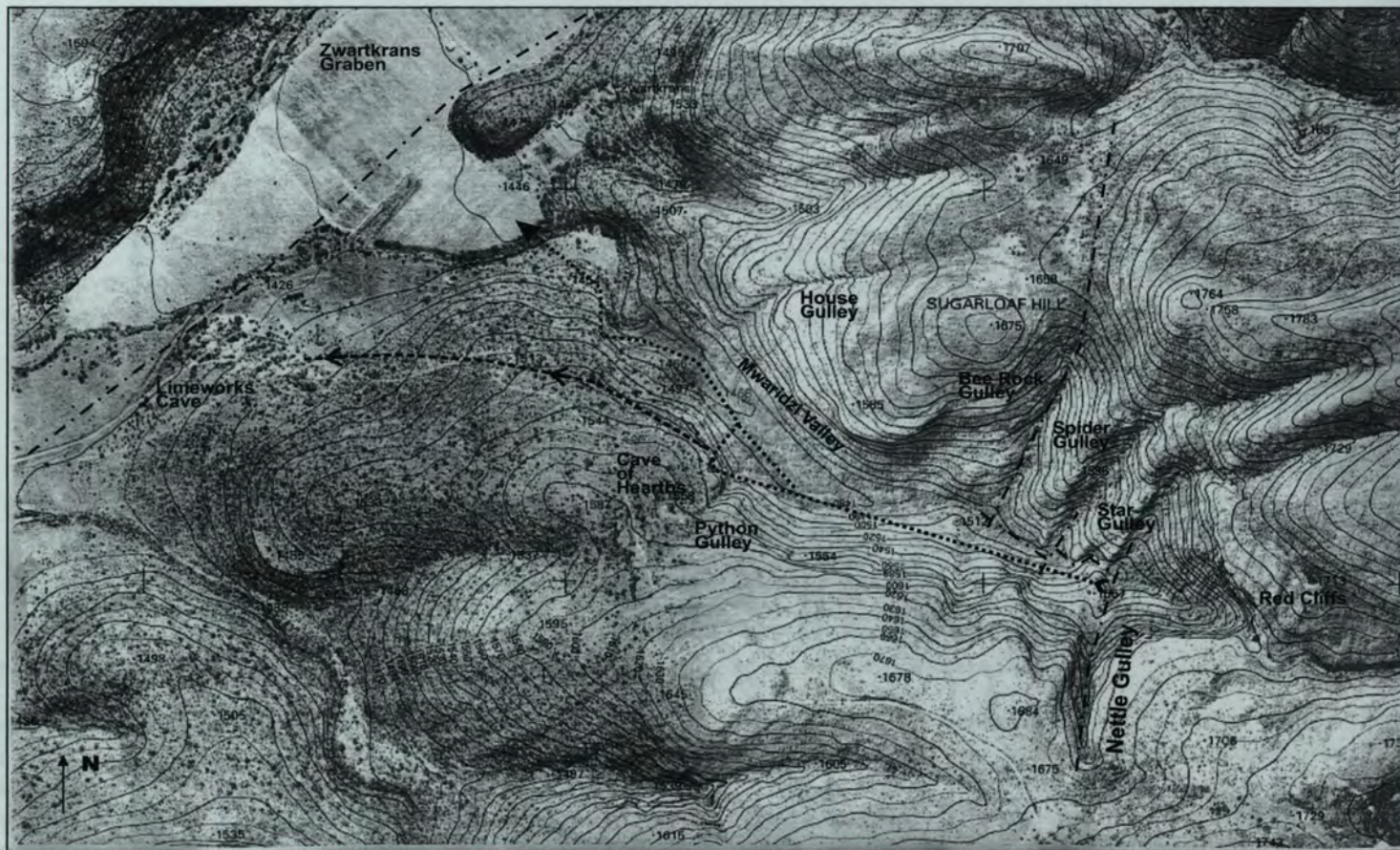


Figure 3. The Zwartkrans and Makapansgat (Mwaridzi) valley area, with contours at 5-m intervals. The dot-dash lines represent some of the main faults at the head of the Mwaridzi valley and the approximate positions of the Zwartkrans graben fault zones. In Nettle Gulley, the dolomite, to the west, is downthrown and brought into contact with the Black Reef Quartzite to the east; the Red Cliffs are in the Black Reef Quartzite. The dotted line marks the reconstructed former plan position of the active cave in Miocene times and the dash line with arrows is the earlier putative underground connection between the Historic Cave – Cave of Hearths and the Limeworks Cave. The Historic Cave fossil remnant passages probably occupy positions of former oxbows (adapted from 1:10 000 aerial photo sheets of Makapansgat, 2429AA14, and Button Kop, 2429AA15, of Surveys and Land Information, Mowbray, Pretoria))

formative phase, the resurgence was of the Vauclusian type in that stream water rose from depth as a deep spring. The active outlet into the former Zwartkrans valley must therefore have been at least as high as the present surface in the Cone area.

There are stalactites and curtain-form speleothems embedded in the eroded surface of the breccia in the west side of the Cone Mouth, some of which appear to be *in situ*. This means that the roof of the cavern, from which the stalactites hung, was considerably higher than the present surface (Latham *et al.* 1999). The mined hole at the surface known as the South Quarry consisted mostly of speleothem that must have hung down as a huge stalactite mass partly attached to the dolomite back wall. By projecting the curvature of some of the overhanging walls around the Cone area in section, we estimate that the original height of the cavern was some 20 m or more above the present surface in this area. The original Limeworks Cave would have approached in volume some of world's largest caverns of today (see Courbon *et al.* 1989 or Ford & Williams 1989).

On the western and northwest sides of the cave are two upward ascending exits, the one to the west being dubbed 'Original Ancient Entrance' (OAE). This entrance is artificially mined but outcrop traces show that it is part of a larger passage that probably acted as exit for stream water

into the valley. Evidently, as the Zwartkrans valley floor became lower, new lower exits formed leaving the upper part of the cavern abandoned. It is probable that the part of the complex known as Horse Mandible Cave also once functioned as a lower stream exit out to the valley.

STRATIGRAPHIC NOMENCLATURE OF THE LIMWORKS

The member system devised by Partridge (1979, 2000) is fairly well known, and various studies related to the Limeworks have referred to it. It is still possible to apply this member system, to some extent, to the repository of the west side of the Limeworks. The repositories on the east side such as the Exit Quarry Chimney repository or the Rodent Corner deposits cannot, however, be related with certainty to the deposits in the west side and cannot therefore be assigned with certainty to the member system. The deposits of the Central Debris Pile are certainly time transgressive.

Using the Member notation of Partridge (1979, 2000) the main western deposits are:

M1. Subaerial massive speleothem, now removed, originally in huge volumes up to 15 or even 30 metres wide in places, reaching 30 or more metres high. It was mined mainly from an irregular arc (Speleothem Arc) stretching from the Entrance Quarry out to the Exit

Quarry and beyond.

Unassigned. Mainly subaqueous, mammillary speleothem layers, ubiquitous to all parts of the system including Horse Mandible Cave.

M2. This member consists of 5 m of mostly red-purple silts in the Classic Section overlying and abutting against Member 1.

M3. The Grey Breccia in the Classic Section is a dense bone breccia with a matrix of yellow, buff silts cemented by secondary calcite. At the wall it is about 50 cm thick but in other places it had been as much as 2 m thick before mining. It is graphically described by Eitzman (1958) from his recollections of 1925.

Unassigned. In a dolomite overhang of the wall of the Classic Section, the bone layer is succeeded firstly by a compact white flowstone with holes (vugs) in it, and then by an undulating banded flowstone. The two together are about 40–60 cm thick, and are local to this section.

M4. This is the cemented breccia of the central area containing massive (>2 m) to small angular dolomite blocks. The matrix is made up of pink, or red, silts and is up to 20 m thick. It occupies most of the Central Debris Pile. It is likely to be time transgressive, and younging not only upwards but also, irregularly, from the front (north) to the rear (south) of the cavern.

M4 (Formerly Member 5 in the Partridge (1979) notation). This is a conglomerate-breccia with cobbles or clasts, smaller than those in Central Debris Pile, grading into finer stratified lenticular silts and sands. In parts of the Cone area, it is unconsolidated and this condition was responsible for the collapse and formation of the Cone following mining of massive stalagmite from below. It is up to 10 m thick.

THE BROAD SEQUENCE OF EVENTS AT THE LIMeworks

The main events and phases of deposition are:

Abandonment

Faunal studies, summarized by Maguire *et al.* (1985), and magnetostratigraphy (McFadden *et al.* 1979), suggest that the Limeworks cavern must have been abandoned by the Makapansgat river well before 4 Ma (see below). This suggests that the system was forming, and active, before the end of the Miocene at 5.1 Ma.

The fall of dolomite blocks

The oldest recognized deposits are large, fallen, dolomite blocks, and they are present in the Main Quarry, under the Central Debris Pile, around the back of the Cone on its east and west sides, in the Exit Quarry and outside the Original Ancient Entrance. There is, as yet, no evidence for the kind of basal, allochthonous sediments that might have originated from transport by the original river. For example, there do not appear to be any sedimentary coatings on fallen blocks or walls before the deposition of speleothem. We suggest that if such sediments are extant then they ought to contain a component of sand from the Black Reef Quartzite.

Main period of speleothem deposition

Speleothem remnants and their negative impressions in sediment show that stalactites, stalagmites, columns and massive flowstones were precipitated mainly as an irregular speleothem arc from the Main Quarry and Entrance Quarry to the back of the Cone Area, where it was joined to the back wall to various heights, and thence to the Exit Quarry.

In the Main Quarry these deposits formed two main spines or bosses reaching to the roof and walls, and each about 20 m wide (Fig. 5). The more northerly boss was deposited onto massive fallen blocks of dolomite. Brain (1958) suggested that, 'probably a structural weakness in that part of the roof caused first the blocks to fall – and then allowed large quantities of water to pass through the roof at that point, which on dripping to the floor, deposited the travertine. Similarly [elsewhere].'

In any event, the impression overall is one of fairly rapid deposition of speleothem that points, firstly, to a thinning roof and, secondly, to a fairly high rainfall. Voluminous deposits such as these are found mainly in tropical to sub-tropical karst areas such as Borneo, Central America and south China. The increase of temperature and especially humidity as a major control of speleothem deposition has been highlighted by Corbel (see references in Jennings 1985). By contrast, with an annual rainfall of 700 mm today, the rate of speleothem deposition in the caves of the area is very low.

Sub-aqueous speleothem

Subaqueous speleothem layers coat fallen dolomite blocks in many places. Brain (1958) noted a good example to the east of the Cone where a large block has fallen and split into two pieces, coated by a 5–10 cm uniform layer of what he termed 'floor travertine'. It is in fact mammillary form speleothem. This kind of deposit is subaqueous and it precipitated from pools saturated with calcium carbonate. As CO₂ outgassed from the water's surface, mammillary speleothem was deposited onto existing submerged speleothems, as in the Main Quarry west wall, and onto other surfaces below the pool surface. Mammillary speleothem coats the walls around the Southwest Alcove, the East Quarry and below the Chimney Repository. It appears to have coated a shelf of rock in the tunnel area near Rodent Corner, as was noted by Maguire *et al.* (1985). Subaerial stalactites later hung from it. Mammillary speleothems formed in the lower reaches of Horse Mandible Cave. Drill core samples extracted from the base of the Central Debris Pile also show that 'flowstone' (probably mammillary speleothem) was deposited inside the Arc (Partridge 2000).

At the base of the breccia on the east side of the Main Quarry some layers of subaerial speleothem of the central 'boss' cover the mammillary forms (Fig. 4). The question of which type preceded which cannot now be discerned in some areas because mining has removed much of the evidence, but these alternations in stratigraphic order strongly suggest that the carbonate-rich pools originated from a high rate of percolation from the surface that, in effect, fed both the subaerial, and subaqueous, speleo-



Figure 4. Photograph of eroded speleothem of the Main Quarry boss on the east side. The speleothem is a mammillary flowstone coating over a dolomite block that is in turn overlain by subaerial flowstone. The near wall of Central Debris Pile abuts against the inner truncation of the speleothem layers and shows that they were eroded before, or at the time, the fine sediments were emplaced. The fine sediments may represent a channel between the speleothem and the clast-dominated Central breccia.

thems more or less at the same time; the pools that formed from the high-flow seepage water fluctuated in level at various times.

There is also good evidence in the Main Quarry, Classic Section and Ancient Entrance to show that stalagmites and flowstones continued to form as later sediment entered the cave. This qualifies the strict, sequential two-stage M1A and M1B presented in Latham *et al.* (1999). There is evidence in the OAE that there were two phases of deposition of sub-aqueous speleothem, the first of which probably corresponds to the mammillary layers seen throughout the whole site.

Rodent Corner sediments

The Rodent Corner sediments in the Exit Quarry are so named for the red sediments containing the many rodent bones that appear to have resulted from owl roosts. These sediments and the underlying water-lain grits and sands, containing cave pearls, postdate mammillary speleothem; the sediments were laid down between stalactite curtains in the tunnel area (Maguire *et al.* 1985). It would probably be misleading to relate these sediments to the member system, which was constructed chiefly from repositories in the west side of the Limeworks. Among the rodent bones are those belonging to a rat, *Mystromys darti*, which is found in the Langebaanweg deposits and dated to between 7 and 4 Ma (Maguire *et al.* 1985).

Original Ancient Entrance sediments

Just inside the mined entrance, a short series of red-mud contaminated flowstones, which comes to resemble a mud-calcite breccia, lie at floor level and originate from outside the present OAE. As this series lies between two sub-aqueous layers, they are among the earliest deposits in the west side of the Limeworks. This unit is not assigned to the member system.

Collapse and infill of clastic sediments

Breccia Member 4 occupies the centre of the site and this phase represents cavern roof stoping and unroofing either together with, and certainly followed by, hillwash of red sediment and soil. The Central Debris Pile occupies the main part of the cavern and probably formed over a long period of time, beginning in the Miocene at the down valley, northern end, of the site. It is a fairly safe conjecture that the earliest clastic deposits of the Central Debris Pile were emplaced between the Entrance Quarry and the Exit Quarry and Horse Mandible Cave. This is because, from the slope of the bevelled surface, this is the most likely place for unroofing to have begun.

Sedimentation rate increases in the Original Ancient Entrance

In the OAE, the red silts of Member 2 include small dolomite blocks and bone fragments as a breccia but, by

the time the sediments wash into the Classic Section, they are free of large rock clasts. This period appears to represent retreat of the OAE cave brow.

Induration of breccia and other sediments

The surface of these deposits is now indurated except for vegetation root holes (known locally as makondos). When open to the rain and to surface runoff, the redistribution of carbonate from the dolomite debris has cemented the clasts and matrix into a hardened breccia. According to Brain (1958), samples of hardened breccia on the north side of the Cone contained about 95% carbonate cement. On the southwest side, dolomite overhangs may have prevented this kind of induration and so the deposits remained unconsolidated. An analogous situation obtains in the modern debris of the surrounding hill slopes. Debris consisting largely of dolomite clasts are indurated by carbonate cement whereas debris of non-carbonate rock are unconsolidated.

The eastern half of the roof of Horse Mandible Cave consists of hardened breccia with stalactites in several places. It seems that, at some stage in its history, loose breccia and sediment has been removed from underneath indurated breccia, allowing stalactites to form on the newly created roof. The existence of the competent breccia roof and of its stalactites thus doubly testifies to the induration process by carbonate cement.

Watertables or winnowing

The concept of fluctuating watertables has been invoked to explain deposition of the more horizontally bedded sediments in the Limeworks such as the rhythmities of Rodent Corner (Brain 1958; Rayner *et al.* 1993). This second usage of watertable concept was criticized by Latham *et al.* (1999) who showed that it was much more likely that such sediments resulted from the periodic inflow or winnowing of sediments. Repeated formations of mud cracks in the Original Ancient Entrance, in Member 2 of the Classic Section and at Rodent Corner elicit a picture of periodic flood events each followed by desiccation. It is tempting to think of each cycle as being seasonally driven.

THE SPELEOTHEM ARC: THE KEY TO THE REPOSITORIES

Because of its apparent continuity, the body of flowstones and stalagmites that constitute the Speleothem Arc caused several large alcoves at the sides and rear of the cavern to be isolated from each other and from the centre of the cavern. Visitors to the Limeworks walk chiefly where the purer speleothems existed prior to mining (Fig. 5). The width and height of the body of the Arc varied from a few metres to tens of metres and it was continuous all the way from the Entrance and Main Quarries round to the Cone and back out to the Exit Quarry. Eitzman (1958) stated that 60 000 tons of lime had been removed by 1937, which converts to about 180 000 m³. Owing to the irregularities of the present cavities it is difficult to make a precise estimate of the mined volume between the Entrance and Exit Quarries but a rough calculation puts it

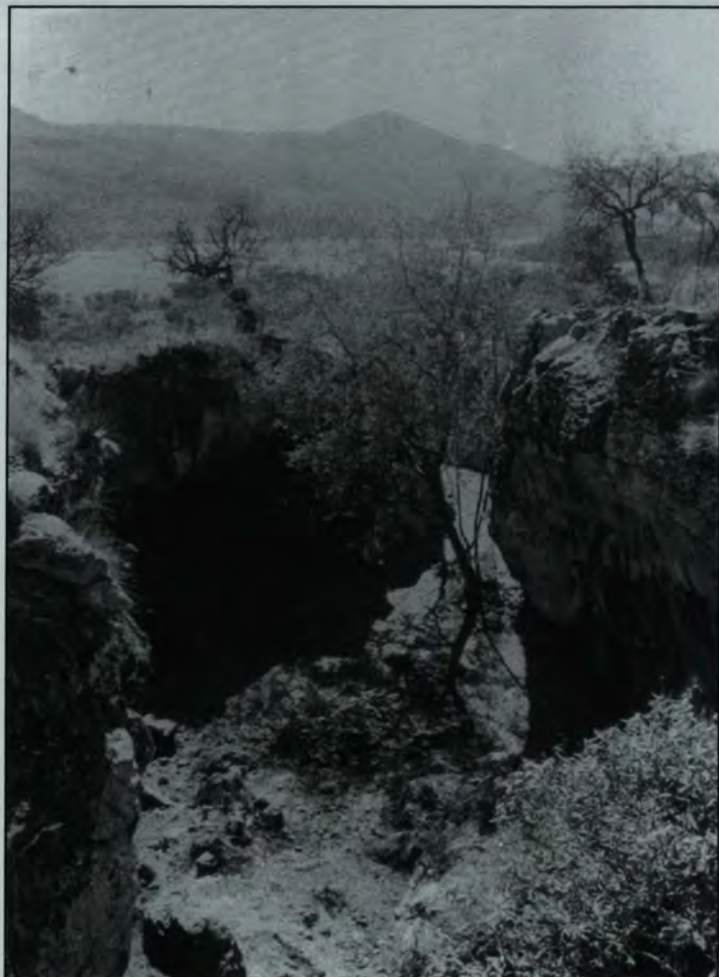


Figure 5. The Limeworks Main Quarry looking northeast. The dolomite roof and wall, to the left, contain the Classic Section (underneath, not visible) and the adjacent North and West alcoves. The central stalagmite boss, which was probably weathered before it was mined out, occupied the space. The wall to the right is the Central Debris Pile consisting of large dolomite blocks that came to lie against the (now mined) stalagmite. The negative imprint is in finer sediments that are probably channel fill deposits. Figure 4 was taken to the right behind the small tree in the foreground.

somewhere between 250 000 and 350 000 m³. Some of the material was dumped as unusable including breccia, sediment and impure calcite. Contacts and remnants show the speleothem mass was joined to the adjacent walls, overhangs and roof in many places. Brain (1958), Maguire *et al.* (1985) and others also noticed that remnants of massive flowstones near the Cone showed that they had suffered re-solution; flowstones were cracked, fallen away in blocks, and growth layers were truncated (Fig. 6). In fact, there are weathered remnants and weathered surfaces of speleothem in several places testifying to the likelihood that eroding streams had flowed past them or that they experienced direct rainfall. On the western side of the Cone Mouth there is a huge fallen block of speleothem that appears to have dropped off a nearby massive boss and both are now embedded in the finer sediments. Both remnants are now part of the cemented roof breccia left by the miners.

What this shows is that, before unroofing, the speleothem mass was even more voluminous than the amount the miners had access to. As the cavern eroded away,

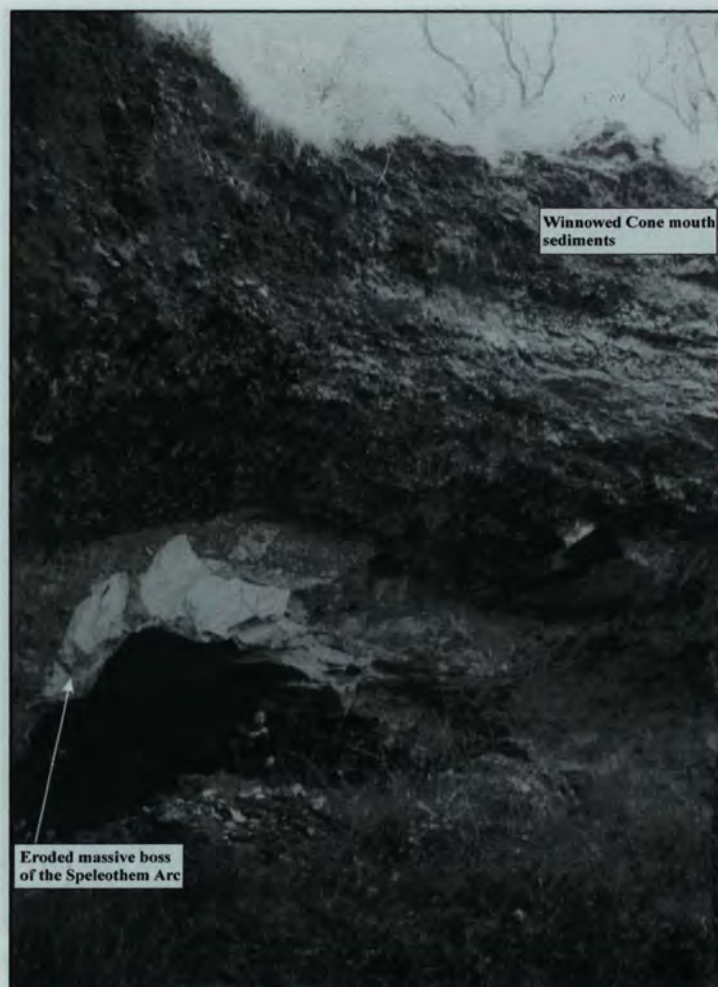


Figure 6. The southeast side of Cone Mouth taken from the collapsed Cone sediments. The dark space, behind the person, was originally occupied by massive flowstone speleothem, remnants of which are embedded in the breccia now acting as roof. This speleothem was truncated by weathering and had cracked apart before the emplacement of the breccia. Progressing from east to south (left to right), the breccia contains angular, subangular, subrounded and rounded cobbles in layers of gravel to silt, which suggest that streams swept underneath an extensive cave roof. Some parts of the sediments are calcited together whereas, to the south, the sediments are much less indurated.

some of the speleothem fell in and other parts of it were dissolved and eroded by water falling in from the slopes above. The important point to note is that it is this Speleothem Arc that later promoted separate repositories. That is, as the cavern unroofed upslope, the Arc acted as a barrier to prevent winnowed sediment from the Central Debris Pile from reaching some lateral alcoves, and alcoves were isolated from each other.

Given the importance of the Speleothem Arc to understanding the Limeworks repositories, we now focus attention on the Central Debris Pile and the areas around the Original Ancient Entrance, the Classic Section and the Cone. The reasons are that; (1), the areas include three bone breccia horizons, one of which is the Grey Breccia, Member 3, (2) several of the layers can be correlated across the western side of the site and, (3), together they encompass layers from the lowest, earliest, phase to the topmost, on the western side, and thus provide the greatest potential for magnetostratigraphy. Rodent Corner and the Exit Quarry Repositories have been discussed by Turner

(1980), Maguire *et al.* (1985) and Pocock (1985, 1987) and will not be discussed further.

THE CENTRAL BRECCIAS AND SEDIMENTS: MEMBERS 4 AND 5

Clearances of vegetation on the surface of the Central Debris Pile show that the area between the Main Quarry, the Exit Quarry and the Cone Mouth is dominated by large blocks of dolomite, typically up to 3 m on a side, some up to 20 m (Partridge 2000), often in contact with each other, between which is a matrix of fine sediment containing much smaller clasts and occasionally pieces of speleothem. This clast-supported breccia, Member 4, stretches to the Main Quarry, over to the Exit Quarry and is evident at the surface to within 3–5 m of the edge of the Cone Mouth. By contrast, the sediments around the Cone Mouth down at the base consist of matrix-supported breccia, conglomerates and stratified, lenticular, gravels grading into sands (Partridge 1979). The sediments grade from cobble layers to massive, dark-red, sandy-mud, layers toward the back of the cavern and against the dolomite wall (Fig. 6).

Partridge (2000) represented the interior breccia as matrix-supported material falling onto a central point and rolling away from it. As the large blocks are in contact with each other, however, the breccia must be clast-supported. This suggests that, at that time, roof-fall was occurring faster than the inwash of surficial material and that the finer sediments were being winnowed out from the block clasts. In the base of the cavern on the north side of the Cone, it is observed that the matrix-supported debris, with its partly rounded quartzite cobbles and pebbles, actually extends under the Central Debris area more than 10 m away from the base of the Cone. The dolomite blocks appear to lap onto the conglomerates and winnowed sediments. Such a configuration points strongly to the likelihood that the dolomite blocks represent progressive stoping and unroofing in an uphill direction (Fig. 7).

Where stoping of the roof preceded actual unroofing to daylight, the dolomite blocks preceded the finer matrix sediments that later came to lie within the pile. Once most of the roof had been removed and blockfall ceased almost entirely, the deposits came to be dominated by reworked surficial deposits. The finer sediments of the Cone that were deposited to the sides of the breccia represent the winnowing of the breccia matrix.

These events are additionally supported by the following observations:

1. Under the hanging calcified sediments to the west of the Cone there is a water-worn remnant of massive speleothem against which lies the underside of about 10-m long arcuate deposit of sediment that is U-shaped, 0.5–1 m deep, and up to about 1–2 m wide (Fig. 8). This feature contains negatives of mud cracks and clearly operated for some time as a substantial channel. There is no clear indication of the direction of flow but it was probably away from the back of the Cone and toward the Main Quarry.
2. Though not so clear, there is the underside of another channel, going away from the Cone on the north side

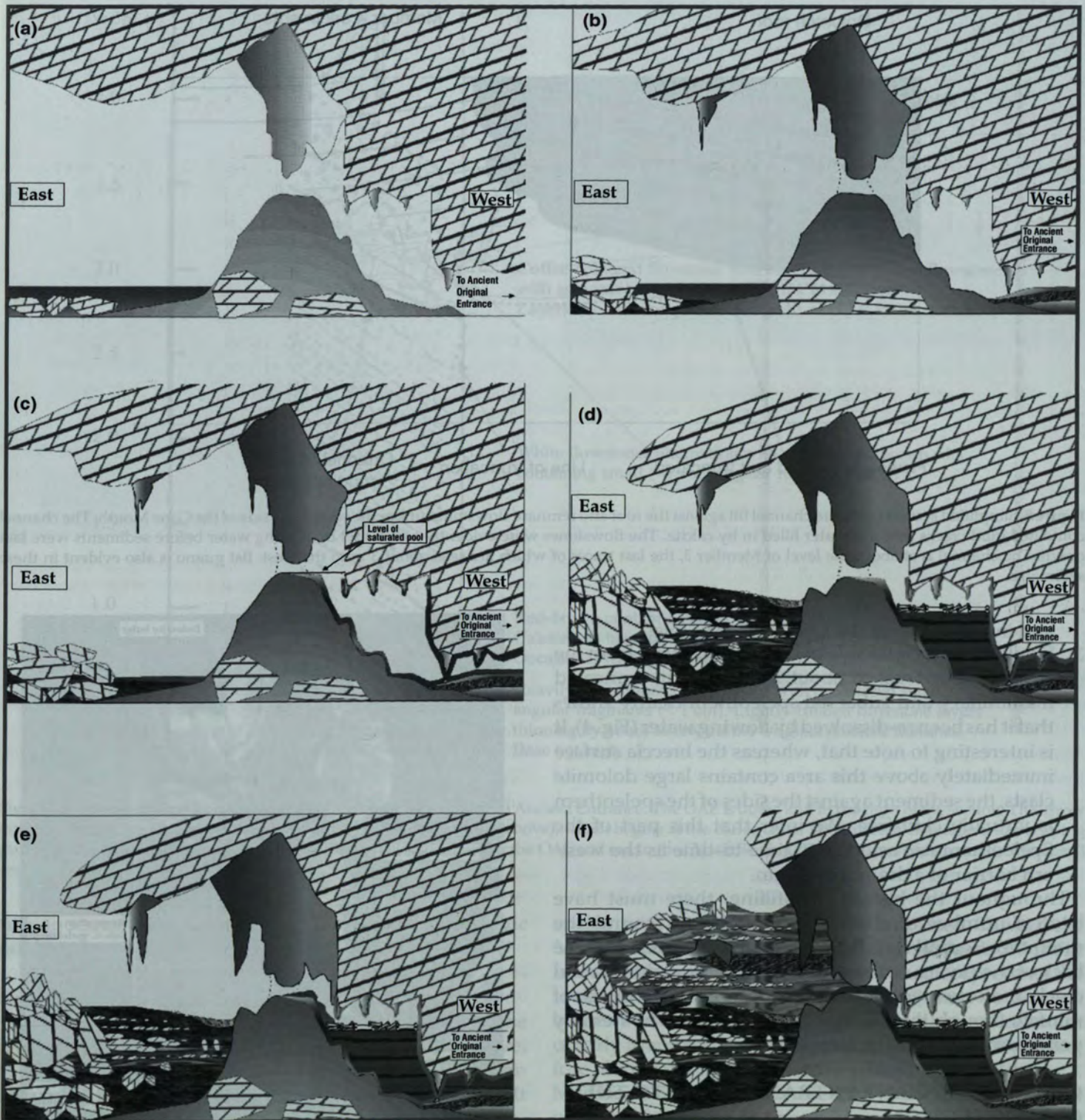


Figure 7. Interpretative diagrams to illustrate the main stages of deposition and erosion of the western side of the Limeworks site. (a), begins with blockfall and deposition of massive speleothem to form the speleothem arc. Between the Cone (East) and the lateral Classic Section (West) there is a gap that is not 'plugged' until after M3 times. (b), shows the start of unroofing to the southeast and the beginning of the build-up of the Central Debris Pile, M4. Carbonate-saturated pools allow coatings of sub-aqueous speleothem; subaerial deposition of speleothem continues to be deposited. On the western side of the Speleothem Arc, sediments wash in from the direction of the OAE. (c), in addition to carbonate-saturated pools in the Central Debris Pile, a pool develops between the OAE and the Classic Section. Mammillary speleothem is deposited on all surfaces. Initially it is pure but becomes increasingly contaminated with fine mud leading to a mud calcite breccia and a second sub-aqueous layer. (d), Sediment of M2 times is deposited from OAE to the Classic Section. Animals are able to enter from OAE to den near the Main Quarry. Eventually deposition ceases as the low dolomite roof in the OAE area obstructs sediment ingress to the Classic Section. The Central Debris Pile continues to grow, and run-off winnows the sediments to the Cone area; channels form round the inside of the Speleothem Arc. Deposition at the rear of the cavern reaches a level where animals can gain access to the Classic Section. Bone breccias are created in the Classic Section (M3) and at the rear of the Cone together with more phases of flowstone. (e), speleothem deposition and then sediment seals the gap between Central Debris Pile and the Classic Section. The roof continues to retreat with the destruction of some of the massive speleothem stalactites and columns. (f), in the Cone Area, winnowed fluvial sediments continue to build up to higher than the present day surface. Lateral alcoves at the rear of the cavern and part of the Classic Section remain unfilled.

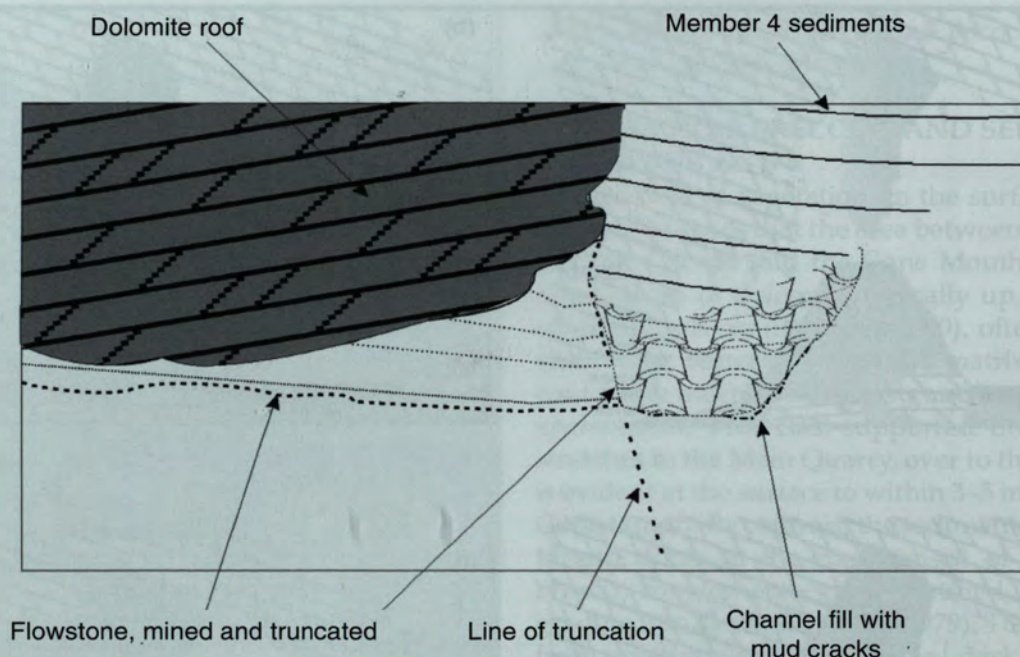


Figure 8. Simplified section of stream channel fill against the roof and remnant flowstones under the southwest side of the Cone Mouth. The channel contained mud cracks that were later filled in by calcite. The flowstones were evidently weathered by flowing water before sediments were laid down. The channel is at about the level of Member 3, the last traces of which are seen about 3 m to the west. Bat guano is also evident in these sediments.

and into the base of the Central Debris Pile.

3. Similarly, in the east side of the Main Quarry, from the present floor level to about 2 m above it, truncated mammillary and subaerial speleothem clearly shows that it has been re-dissolved by flowing water (Fig. 4). It is interesting to note that, whereas the breccia surface immediately above this area contains large dolomite clasts, the sediment against the sides of the speleothem is virtually clast-free. We infer that this part of the Speleothem Arc acted from time-to-time as the western barrier of a drainage system.

Throughout the history of infilling, there must have been a number of channels through and round the mounting Central Debris Pile to drain the water from the back of the cavern out to the valley. The presence of mud cracks indicates periods of desiccation between periods of rainfall, though that in itself cannot tell us whether any periodicity was daily or seasonal.

ORIGINAL ANCIENT ENTRANCE (OAE) TO THE CLASSIC SECTION

The section most likely to provide a long magnetostratigraphic record is the area from the OAE to the Classic Section and the Cone Mouth. Hence the stratigraphy of these sections is now dealt with in more detail.

Partway through the OAE deposits, a well-defined 4–8 cm thick subaqueous layer of mammillary speleothem formed on all available surfaces from the OAE to the Classic Section reaching as high as the roof above the Grey Breccia. Fine red-brown silts, grading laterally into a mud-calcite breccia, followed this mammillary layer. Then followed another sub-aqueous layer though not reaching quite as high as the first. These two sub-aqueous layers negate the normal superposition principle and lead to locally inverted stratigraphy. But otherwise, both

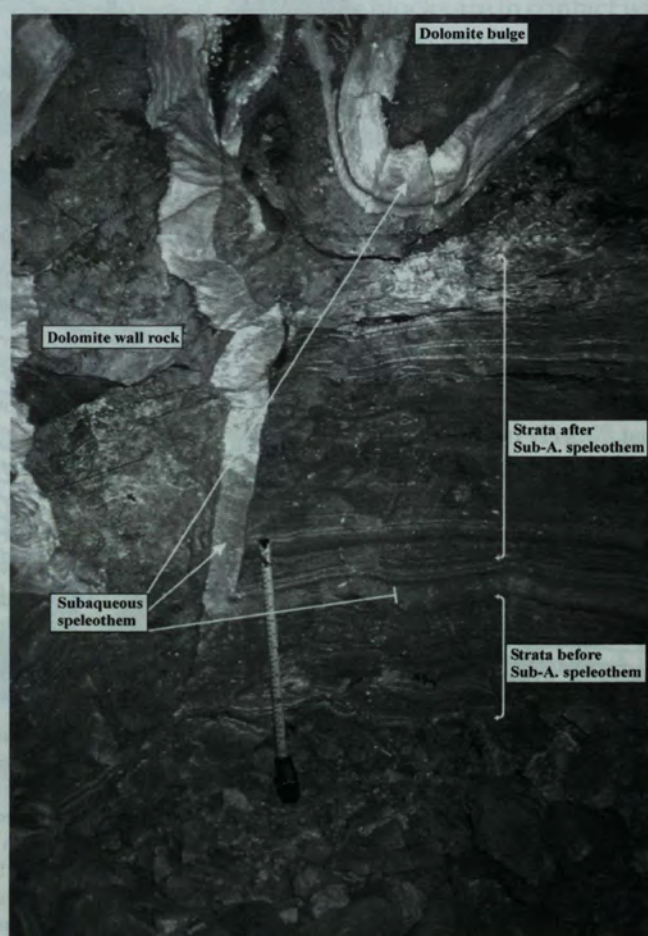


Figure 9. The early layering inside the mined Original Ancient Entrance. The visible sequence is 20–30 cm of fine calcite-indurated sediments intercalated with flowstones. A 6–10 cm thick mammillary layer covered these sediments, wall and roof to be followed by increasingly mud-contaminated speleothem. This was followed by a calcite-raft breccia in mud. The mammillary layer is ubiquitous to the whole area from the OAE, to the North Alcove as far as the Main Quarry, and to the top of the Classic Section reaching higher than Member 3.

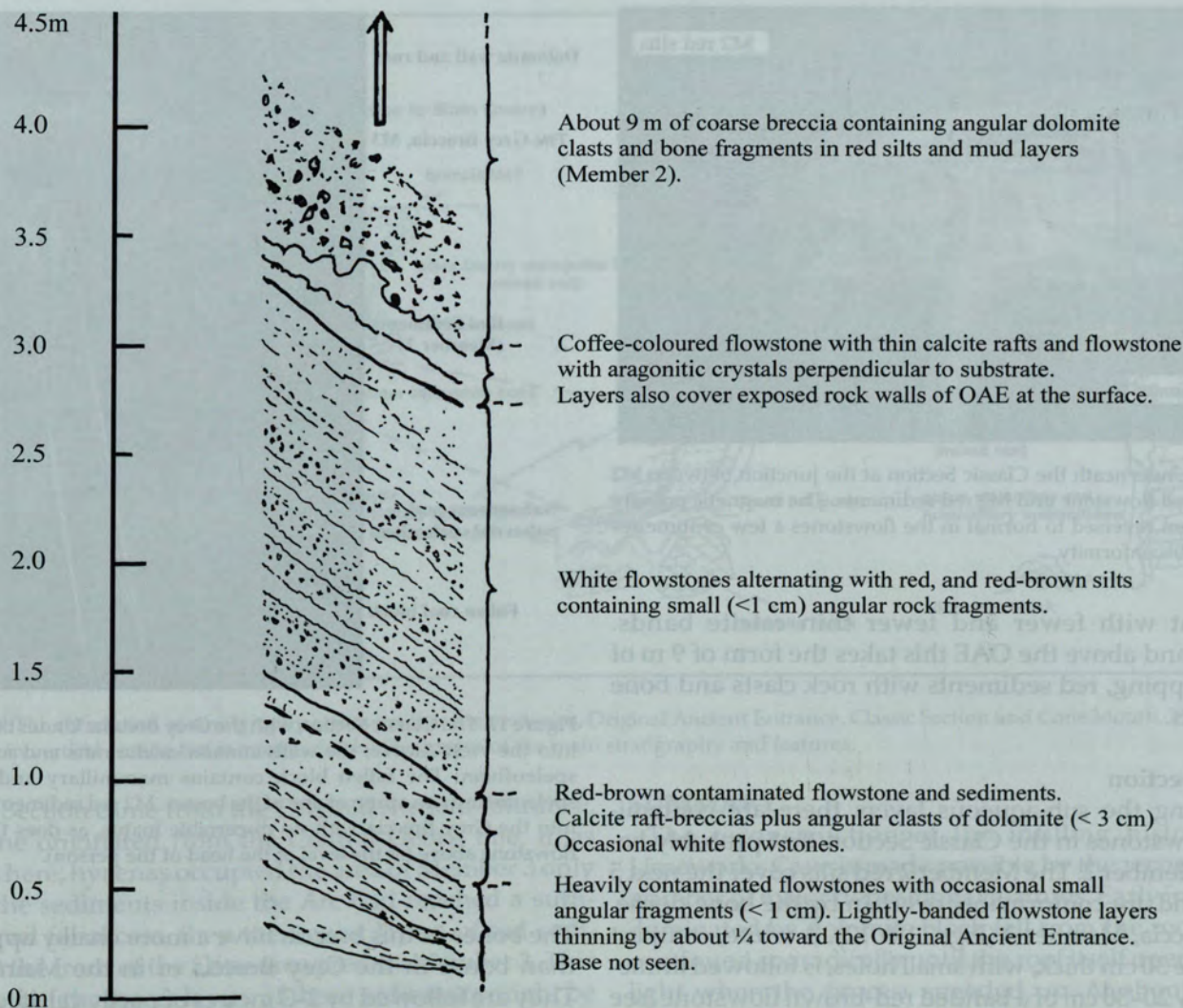


Figure 10. The stratigraphy on a section 8 to 15 m outside the Original Ancient Entrance. The OAE is down and to the right of the section. The arrow points to the top surface of bevelled (eroded) Member 2 (about 3 m above), which begins at the coffee layer. The coffee speleothem and overlying purer flows are the equivalents of the mammillary speleothem under the OAE and out to the Classic Section. There are bone fragments in Member 2 immediately overlying the coffee layers.

sub-aqueous layers make useful chronostratigraphic markers for all of this area (Fig. 9).

North Sequence

A clear sedimentary sequence can be recognized in the section from outside the OAE, up under the North Alcove, to the black bone breccia in the overhang of the Main Quarry northwest wall and to the Classic Section. It begins in the North Alcove with a large 3 m high stalagmite boss. About 40 cm of contaminated flowstones, which originated from the OAE, abut against the boss. Outside the OAE, all sediments dip down into the opening itself at about 30° (Fig. 10). The impure flowstones are followed by the sub-aqueous layers, which have coated all existing surfaces including the roof and walls above Grey Breccia Member 3. In the alcoves the mammillary speleothem grades into calcite-raft clasts in fine mud. This very distinctive and unusual mud and calcite breccia deserves a separate treatment and will be discussed elsewhere.

It is clear that most of the mass of the two speleothem bosses in the Main Quarry and the smaller boss under the North Alcove had already formed before the mammillary

speleothem and raft-calcites were emplaced. Toward the Main Quarry, the steeply dipping surfaces of more massive Member 1 flowstone shows that it represents the lower shoulder or apron of the Main Quarry stalagmitic bosses. Flows continued to form during the emplacement of early Member 2 sediments and, stratigraphically, therefore, these later flows have to be placed within Member 2. Member 1 also made a more-or-less continuous contact with the dolomite overhang of the cavern, resulting in the isolation of the alcoves from the Central Debris Pile.

In the Main Quarry, the manganese-blackened long bones and other remains occur on top of the shoulder of later flows from the Main Quarry boss. They appear to have resulted from a period of animal denning partway through the deposition of Member 2, the denning animals having gained access via the OAE. Most importantly, from its higher altitude (by several metres), and its higher stratigraphic position, this bone breccia would appear to postdate the Grey Breccia.

In the depositional basin inside the OAE, the red silts, which constitute most of Member 2, progressively contaminate the subaerial flowstone layers of Member 1 or alternate with it. Finally, red sediment becomes rapidly



Figure 11. Underneath the Classic Section at the junction between M2 contaminated flowstone and M2 red sediments. The magnetic polarity changes from reversed to normal in the flowstones a few centimetres below the disconformity.

dominant with fewer and fewer thin calcite bands. Outside and above the OAE this takes the form of 9 m of 20–40° dipping, red sediments with rock clasts and bone fragments.

Classic Section

Following the sub-aqueous layers there are contaminated flowstones in the Classic Section that probably belong to Member 2. The Member 2 red silts cover the next 5 metres and are conformably overlain by the bone dense, Grey Breccia, Member 3 (Figs 11 & 12). A white, compact flowstone 30 cm thick, with small holes, is followed immediately by 20–30 cm of a banded red-brown flowstone (see also Plate 3.1 of Maguire *et al.* 1985). Out in the roof and toward the Cone, the bone breccia lies between partly rotted stalactites that were earlier coated in mammillary speleothem (see also Figs 3 and 4 of Maguire *et al.* 1980). The remains of stalagmite contacts with the wall at the end of the Classic Section clearly show that the massive, subaerial central flows of the stalagmite boss were close to sealing off the Classic Section space, leaving a gap of about 1 metre between it and the roof. If, as seems most likely, the hypothesis of hyaena denning is used to explain the presence of bones in the Grey Breccia, then this gap demonstrates how it would have been possible for these animals to gain access from the direction of the Cone at a time when this part of the cavern was not yet filled.

THE SEDIMENTS OF THE CONE MOUTH

The miners removed a large speleothem boss joined to the south, rear, wall of the Cone Mouth and this eventually resulted in the collapse of the overlying, winnowed sediments, now the Cone, only part of which had been indurated. The weathered surfaces of extant speleothem and contact relationships show that these sediments were laid down against the rear wall from a height that is just above the level of Grey Breccia. Unlike the Grey Breccia, however, these Cone sediments were deposited inside the Speleothem Arc. The section thus begins with speleothem attached to the lower dolomite wall, up through about a metre of white bone breccia and some fossil guano deposits.

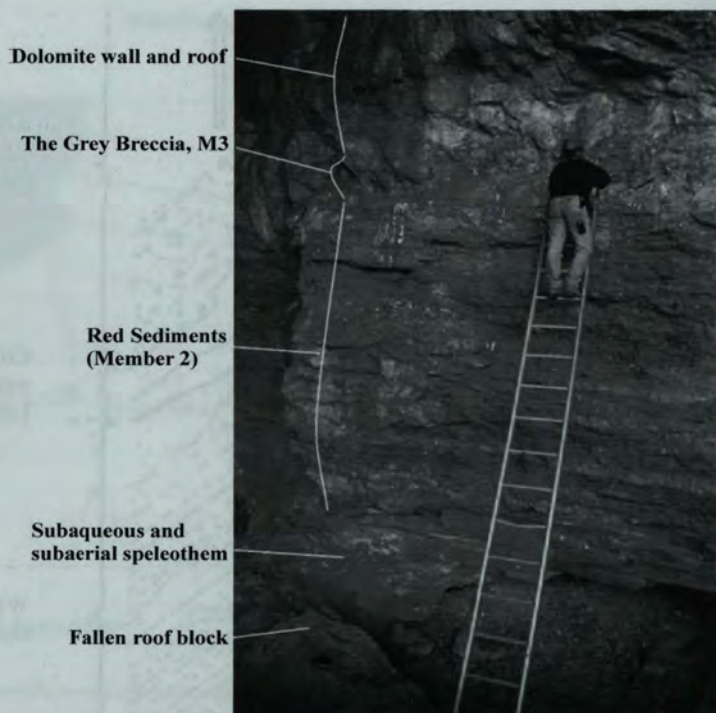


Figure 12. The Classic Section with the Grey Breccia. Under the base and into the West Alcove, the walls contain calcite rafts and mammillary speleothem. The fallen block contains mammillary and subaerial speleothem as an apron of one of the bosses. M2 red sediments continue into the Grey Breccia with no discernible hiatus, as does the banded flowstone above (at the level of the head of the person).

The bones in this breccia have a more chalky appearance than bones in the Grey Breccia or in the Main Quarry. They are followed by 2–3 metres of partly calcited breccia, and then 15m of silts up to the present surface.

The bone breccia on the rear wall is at about the same height as the Grey Breccia. It is unfortunate that much of the intervening sediment at roof level between the Grey Breccia and the Cone bone breccia has been removed. The Grey Breccia can, however, be traced about two thirds of the way from the Classic Section to the rear wall, and so it is not unreasonable to suppose that these two bone breccias resulted from hyaena denning at about the same time. There thus seems little doubt that a connection existed for a while between Grey Breccia and the Cone area and that stratigraphic continuity, perhaps with some overlap, exists between the Classic Section and the Cone Mouth section.

THE RECONSTRUCTION OF REPOSITORY SEQUENCES: DISCUSSION

Apart from the presence of sub-aqueous speleothem, the principal of superposition and younging upwards allows us to reconstruct a stratigraphic order for each of the repositories (Fig. 13), and affords a basis for correlation between sections.

In contrast to the Classic Section where the M2 red sediments are followed by the M3 bone breccia, the area at the back of the Cone shows that the white bone breccia precedes the Cone sediments. Whereas the Classic Section was on the outside of the Arc, the back of the Cone was on its inside. And whereas Member 2 sediments in the

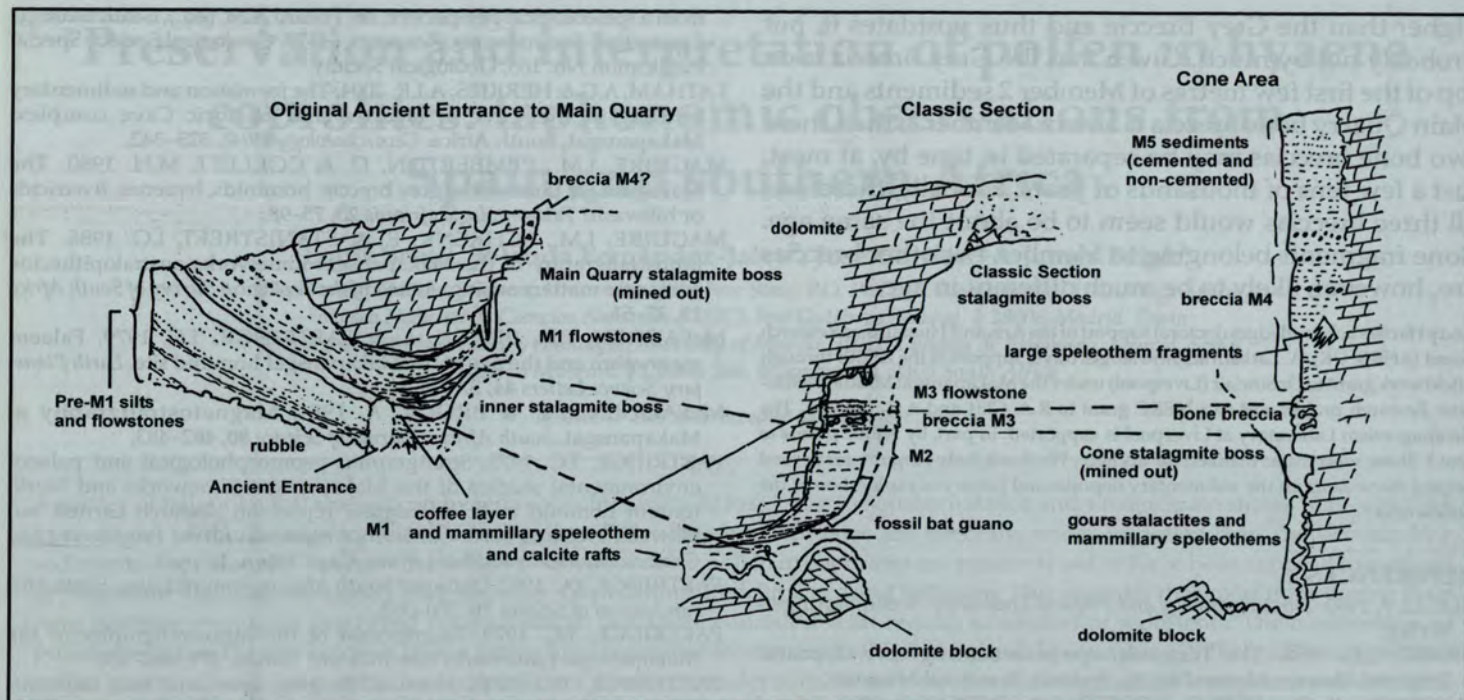


Figure 13. The correlation of stratigraphy across the three repositories, Original Ancient Entrance, Classic Section and Cone Mouth. The diagram is not exact in vertical section but is intended to be illustrative of the main stratigraphy and features.

Classic Section came from the Original Ancient Entrance, the Cone originated from the Central Debris Pile. If, as argued here, hyaenas occupied the area of Member 3 only when the sediments inside the Arc had reached a sufficient level for access, then the lowest layers of red sediment at the front of the Cone area predate Member 3. This implies that the lower layers of these sediments might be roughly contemporaneous with Member 2 and that all sediment above the Cone Mouth bone breccia postdates Member 3.

The clastic sediments are continuous to the top of the Cone Mouth without hiatus so that, in effect, the sequence from the rear, base of the Cone represents the history of sediment deposition for the Limeworks from M3 times onwards. No hiatuses or erosional features have been detected in the Cone clastic sediments.

As magnetostratigraphy at Limeworks Cave requires a sampling of both chemical and clastic sediments, the question of relative rates of deposition is obviously important. In some speleothems, the visible sediment banding is probably due to seasonal flooding and they often show that contamination increased with time. The observation that Member 2 red sediment is partly calcified and has calcite horizons, and that Member 3 is overlain by flowstones, shows that speleothem deposition did not cease in this area. However, in all areas to the west of the Main Quarry, clastic sedimentation eventually out-competed speleothem deposition. It is therefore probable that when unroofing was underway, the deposition of winnowed sediments was faster than the precipitation rate in most places. It is important to note possible relative rates of deposition in this regard because any magnetostratigraphic record will be stretched and compressed in various places and magnetic reversal chronos and subchronos of differing duration could be wrongly identified.

SUMMARY

The reconstruction of the infilling history of the Limeworks Cave is made possible by the recognition of a number of major depositional features. Early infilling was dominated by dolomite block fall from the roof, and this continued sporadically until the roof itself opened to daylight when the process speeded up. At about the same time, massive subaerial speleothem in the form of stalactites, stalagmites and flowstones were deposited mainly around the outside of the cavern. The huge masses of speleothem are probably good evidence that, during Member 1 times, the area enjoyed a climate that was significantly more humid than that of today. In time, speleothem formed a more-or-less continuous arc that became joined to walls and roof in several places so as to isolate various alcoves from each other and from the centre of the cavern. The result was that when erosion began to remove the roof, these alcoves were either filled by sediment from directions other than the centre or were not filled at all. The Classic Section was filled by sediment coming from the Original Ancient Entrance. The Cone, on the inside of the Speleothem Arc, was filled firstly by the winnowing of matrix sediments from the Central Debris Pile, and then by the reworking of colluvium falling from the surface as the cave brow continued to retreat upslope.

Thickening bands of contamination in flowstones indicate increasing sedimentation with time so that in many places clastic sediments came to replace the precipitated flowstones. This means that any attempt at magnetostratigraphic dating based on the sequence will have to take these relative rates of deposition into account.

The white bone breccia at the rear of the Cone is at about the same level as Grey Breccia. In the repository that includes the Classic Section and the Main Quarry, the bone breccia in the Main Quarry is stratigraphically

higher than the Grey Breccia and thus postdates it, but probably not by much. Given that the Grey Breccia is on top of the first few metres of Member 2 sediments and the Main Quarry bone breccia is also in Member 2, then these two bone breccias may be separated in time by, at most, just a few tens of thousands of years. Faunally, therefore, all three breccias would seem to be about the same age. Bone fragments belonging to Member 4 or other breccias are, however, likely to be much different in age.

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Preservation and interpretation of pollen in hyaena coprolites: taphonomic observations from Spain and southern Africa

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A survey of palynological research on hyaena coprolites from 10 fossil sites in southern Africa and 4 from Spain shows that coprolites from 10 out of the 14 sites contained fossil pollen. Pollen-bearing coprolites are generally richer in pollen than the surrounding sediments. Provisionally it seems that the sites with poor or no pollen in coprolites are relatively old or have been exposed to wet and dry moisture fluctuations, namely Makapansgat, Gran Dolina, Redcliff Cave and Erfkroon. This suggests that conditions during their long histories eventually destroyed pollen through oxidation associated with regular saturation of sediments. The composition of pollen spectra and preservation of pollen grains from coprolites is compared with that in fresh hyaena dung. SEM studies suggest that pollen grains in fresh dung and in fossil coprolites if preserved under suitable cave conditions, are generally well preserved with little damage. The damage traits require further systematic investigation in order to assess their taphonomic significance but selective destruction of pollen through ingestion, if any, seems to be light. Of particular interest to palaeoenvironmental studies is the observation that pollen assemblages preserved in hyaena dung are likely to provide relatively unbiased characterizations of vegetation representative of the wide surroundings in which the hyaenas were active. This implies that where pollen was relatively well-preserved in coprolites, it can provide palaeoenvironmental information extending beyond the immediate environs of the site in which they were found. Any possible bias introduced through behaviour-related pollen trapping is, however, difficult to exclude.

Keywords: palynology, hyaena coprolites, taphonomy, South Africa, Spain.

INTRODUCTION

Some hyaena coprolites contain rich pollen spectra, e.g. those from Equus Cave, South Africa and Las Ventanas Cave in Spain (Scott 1987; Carrión *et al.* 2001). In arid areas where pollen traps such as lakes and swamps do not occur, coprolite palynology can serve as an alternative to conventional pollen analysis (Scott 2000) although high resolution cannot be expected. When pollen is preserved

in hyaena coprolites in caves, preservation often seems to be better there than in the associated sediment. Hyaena scats are durable (Bearder 1977) and probably insulate organic matter, including sporopollenin, more effectively from local oxidizing environments. Several questions arise when pollen from hyaena coprolites are considered as an indicator of palaeoenvironments. In this paper we assess the quality of preservation of pollen grains and their surfaces as well as pollen-assemblage composition in hyaena coprolites from sites in South Africa and Spain

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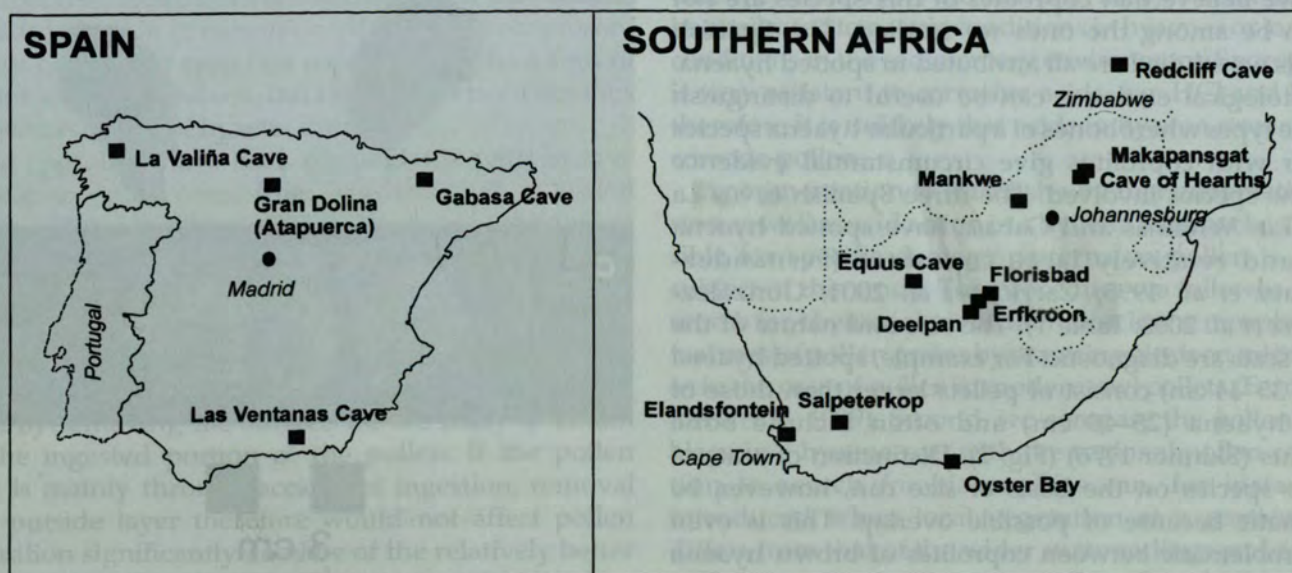


Figure 1. Locations of southern African and Spanish hyaena coprolite sites referred to in the text.

Table 1. Sites in southern Africa and Spain where palynology of hyaena coprolites was attempted.

Region	Site	Reference
Southern Africa	Equus Cave	Scott 1987
	Florissbad	Van Zinderen Bakker 1989; Scott & Brink 1992
	Deelpa	Scott 1987; Scott & Klein 1981; Scott & Brink 1987
	Makapansgat	Scott 1995
	Oyster Bay	Carrión <i>et al.</i> 2000
	Erfkroon	Churchill <i>et al.</i> 2000
	Cave of Hearths	L. Scott, unpubl. data
	Redcliff Cave	R.G. Klein and L. Scott, unpubl.
	Elandsfontein	Van Zinderen Bakker in Singer & Wymer 1968, and notes
	Salpeter Kop	G. Avery & L. Scott, in prep.
Spain	Ventanas Cave	Carrión <i>et al.</i> 2001
	La Valiña	Fernández-Rodríguez <i>et al.</i> 1995
	Gabasa Cave	González-Sampériz <i>et al.</i> 2003
	Gran Dolina	This paper

(Fig. 1). We look for signs of digestion and anomalies in the composition of pollen assemblages and for signs of selective pollen trapping. The investigation involved comparisons of modern and fossil spectra in hyaena dung and those from natural pollen rain in surface soils of the wider surroundings of a scat site. This paper briefly reviews previous studies on hyaena coprolite palynology and is a provisional assessment of its value in palaeoenvironmental studies.

TAPHONOMIC CONSIDERATIONS

An important question is how well pollen spectra in hyaena coprolites are preserved and how well they represent contemporary vegetation. Selective trapping of pollen in coprolites of different hyaena species can be due to behavioural differences. Unfortunately, coprolites cannot always be linked conclusively to particular hyaena species. We believe that, except for the older deposits of Makapansgat (Maguire *et al.* 1980), pollen-bearing coprolites and fresh hyaena dung investigated in this study are derived mainly from brown hyaena (*Parahyaena brunnea*) and spotted hyaena (*Crocuta crocuta*) (Table 1). Since the striped hyaena (*Hyaena hyaena*) occurs in the Middle East, India and North Africa but not southern Africa, we believe that coprolites of this species are not likely to be among the ones we studied. The Spanish materials we studied are all attributed to spotted hyaena. Palaeontological evidence can be useful to distinguish coprolite types where bones of a particular hyaena species together with coprolites give circumstantial evidence about the species involved. The three Spanish caves La Valiña, Las Ventanas and Gabasa have spotted hyaena bones and relatively large coprolites (Fernández-Rodríguez *et al.* 1995; Carrión *et al.* 2001; González-Sampériz *et al.* 2003; Table 1). The size and nature of the hyaena scats are diagnostic. For example, spotted hyaena scats (c. 35–44 cm) consist of pellets larger than those of brown hyaena (25–40 cm) and often include bone fragments (Skinner 1976) (Fig. 2). Distinction of scats of the two species on the basis of size can, however, be problematic because of possible overlap. This is even more problematic between coprolites of brown hyaena and the closely related striped hyaena.

Although spotted hyaenas may sometimes leave bones

at open feeding sites (Dart & Craig 1959), they are also known to accumulate bones in caves and burrows (Kruuk 1972; Bearder 1977; Sutcliffe 1969, 1970). Although they include some fruits and seeds in their diet, brown and striped hyaenas often accumulate large numbers of bones in dens where their young are raised (Skinner 1976; Skinner *et al.* 1980; Skinner & van Aarde 1980; Siegfried 1984; Mills 1989).

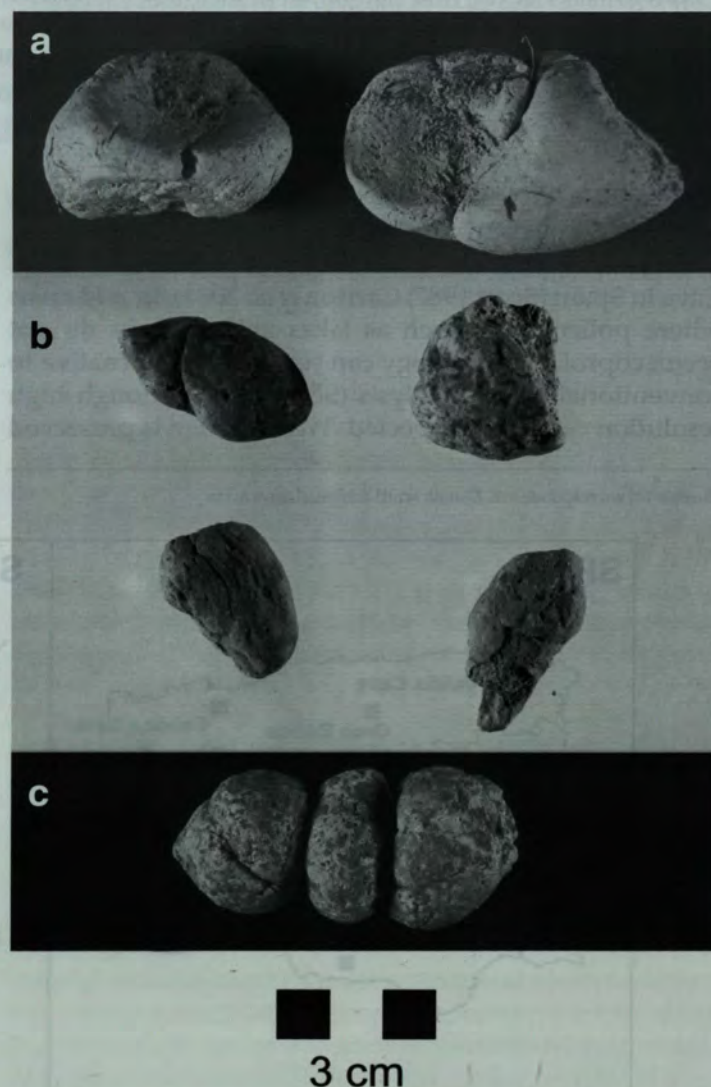


Figure 2. a, Fresh *Crocuta* dung from Laetoli; b, *P. brunnea* dung from Equus Cave; c, coprolite from Gran Dolina TD6, Atapuerca, Spain.

Table 2. Productivity and age of hyaena coprolites used in palynological analysis (for references see Table 1).

Site	Site type	Type of hyaena	Age or culture	Productive coprolites
Deelpan	Burrow	<i>P. brunnea</i>	~100–200 yr	5/5
Salpeter Kop	Cave	<i>P. brunnea</i>	100 yr	3/3
Equus	Cave	<i>P. brunnea</i>	Up to 27 ka	39/50
Las Ventanas	Cave	<i>C. crocuta</i>	~9.5–10.7 ka	10/25
Gabasa	Cave	<i>C. crocuta</i>	c. 40–50	8/12
La Valiña	Cave	<i>C. crocuta</i>	c. 35 ka	4/8
Oyster Bay	Burrow	<i>P. brunnea</i>	~70 Ka?	9/12
Florisbad	Spring	<i>C. crocuta</i>	> 250 ka	6/6
Erfkroon	Burrow	Unidentified	MSA	0/4
Redcliff	Cave	<i>C. crocuta</i> ?	MSA	0/1
Cave of Hearths	Cave	<i>C. crocuta</i>	ESA	1/5
Elandsfontein	Surface	<i>P. brunnea</i> ?	ESA (Midle Pleistocene)	14/?
Gran Dolina	Cave	<i>C. crocuta</i>	~780 ka	0/2
Makapansgat	Cave	<i>H. hyaena makapani</i>	2.6 million yr	0/23

The relative importance of different pollen sources cannot be easily determined in individual coprolites. It is important to know how pollen is trapped and what part of the assemblage was ingested accidentally or through feeding. The sources might include dust that settles on food before ingestion, dust that settles on dung after defecation, flowers in hyaena diets, or pollen contained in drinking water. All these possibilities probably occur and could potentially result in a biased pollen composition. Spotted hyaenas do not consume the rumen contents of herbivorous prey (Smithers 1983: 361) while rumen and viscera seem to be the least popular parts eaten by brown hyaenas (Bowland *et al.*, no date). A bias in pollen composition from this source therefore seems possible but probably not typical.

Previous studies suggest that hyaena coprolites in general are not markedly biased compared with the regional pollen rain (Scott 1987; Carrión *et al.* 2001). This suggests that much of the pollen in hyaena dung is accidentally ingested. For instance, leaves ingested by hyaenas are good pollen traps and reflect local vegetation both in terms of species composition and relative cover (Gutiérrez *et al.* 1998), but ingestion of pollen-rich flowers may cause a bias in composition. Massive over-representation of one pollen type in a coprolite may be a sign of ingestion of whole anthers, but this has not been obvious in previous studies of hyaena dung.

When coprolites have been consolidated with fixative glue, e.g. in some cases from Makapansgat, it sealed modern pollen contaminants from the time of excavation in cracks (Scott 1995). It is therefore essential first to remove the coprolite surface before extracting pollen. Cleaning in the laboratory before sample preparation may remove fossil pollen clinging to the original surfaces which might differ slightly in composition from ingested pollen. By removing the surface we are likely to obtain only the ingested portion of the pollen. If the pollen source is mainly through accidental ingestion, removal of the outside layer therefore would not affect pollen composition significantly. In view of the relatively better preservation evident in coprolites compared to the surrounding sediment matrices (Scott 1987; Carrión *et al.*

2001), it is likely that the surfaces of faeces would experience more unfavourable conditions for pollen preservation than interior parts. Therefore the loss of surface would not affect composition greatly.

Apart from individual pollen grains, other coprolite inclusions can provide information about hyaena behaviour, e.g. insect remains, parasites, fungi, hair and plant remains. The Las Ventanas Cave hyaena coprolite preparations showed algal zygospores possibly derived from drinking water (Carrión *et al.* 2001).

The amount of pollen in hyaena coprolites varies from nil to extremely rich (290 000 grains per gram) (Carrión *et al.* 2001). Primary factors such as seasonal pollen scarcity might affect numbers. Since it is unlikely that no pollen would be present, secondary factors such as selective preservation through gastric action or sediment conditions may play a role. Where pollen is consistently absent in several coprolites from the same site, unfavourable conditions for preservation over the long term are probably the cause. Good as well as poor fossil pollen preservation, including exine thinning, has been reported in coprolites from sites such as Equus Cave and Oyster Bay (Table 2) (Scott 1987; Carrión *et al.* 2000). This could either be attributed to gastric conditions in hyaenas or long-term conditions in the sedimentary environment. Sporopollenin is very resistant to corrosive acids, e.g. HCl and HF, and therefore it is unlikely that acids in hyaena stomachs will corrode pollen.

Experimentation to establish whether enzymatic corrosion as well as acid action in a hyaena's stomach is responsible for specific damage patterns on pollen is not the subject of this study. The procedure we follow is, first, to search for obvious signs of alteration in the morphological features of pollen grains by scanning electron microscopy, as in the case of pollen in modern owl pellets (Fernández-Jalvo *et al.* 1999). Second, we compare the pollen assemblage in a hyaena scat with the regional pollen composition to search for biases. Bias can, for instance, be introduced when local vegetation at a particular site differs from that of the wider surroundings and coprolite pollen spectra appear to generally reflect the latter (Scott 1987; Scott & Brink 1992). This suggests that pollen is

collected largely during hyaena movements away from dens. Furthermore, small dung pellets that are often recorded at dens may be those of young hyaenas. Since they do not venture far from their dens they may be more likely to represent the immediate surroundings. However, their food is brought in from wider surroundings and this would introduce a regional component. In addition, any atmospheric pollen rain, such as can be expected in coprolites, will represent a regional component.

PREVIOUS WORK

At least 10 hyaena sites in South Africa and four in Spain (Fig. 1) have been subjected to palynological examination of coprolites (Tables 1 & 2). Hyaena coprolites have also been studied in other regions such as Israel, Sicily, France and Britain (Sutcliffe 1969, 1970; Horwitz & Goldberg 1989; Larkin *et al.* 2000; M. Weinstein-Evron, J.A. López Sáez & A. Cinzia, pers. comm.) but published pollen records for these areas were not available to us. Information regarding the nature and age of sites containing coprolite and pollen yields are shown in Table 2. Five examples of hyaena coprolite palynology are discussed below.

Deelpan

Hyaena coprolites and bone accumulations were discovered in in-fillings of a hyaena burrow in Late Holocene lunette dunes on the eastern edge of Deelpan, a playa lake (Scott & Klein 1983). The rich bone assemblage indicates a brown hyaena den. The pollen assemblages were compared with surface pollen samples from the surroundings of Deelpan (Scott 1987; Scott & Brink 1992). The high proportion of grass pollen in the coprolites differed from the local pan spectra, suggesting that the hyaenas preferred the distant grassy surroundings of the pan using the burrow only for shelter and breeding. Although the bones from the den were thought to be Late Holocene, previously unpublished radiocarbon dating showed that they were surprisingly young (Scott & Brink 1992). The dates on bone collagen (120 ± 45 yr BP, Pta-6348; 150 ± 20 yr BP, Pta-6346) show that the den represents the period immediately before or during the first arrival of Boer settlers in the region. The fossil bones together with the coprolites are of interest because they give evidence of the environment in the western Free State just before farming disturbance and the introduction of cattle and sheep that largely replaced the original fauna.

Equus Cave

A rich accumulation of Late Pleistocene and Holocene bones and brown hyaena coprolites was collected from Equus Cave (Scott 1987; Klein *et al.* 1991). Compared with pollen in the surrounding sediment matrix, pollen spectra from the coprolites represent an open grassy environment. This suggests that the hyaena coprolites contained more pollen from the wider environment than from the slopes around the cave, which are naturally likely to have been more wooded than open areas (Scott 1987). The coprolite pollen yield is also richer than that recovered from the sediment matrix. The pollen sequence demonstrates a transition from cool Late Pleistocene

vegetation with grass and small shrubs to the warmer environment of the Holocene containing more woody shrubs.

Oyster Bay

Several coprolites were discovered in a soil horizon on an open-air coastal site at Oyster Bay (Carrión *et al.* 2000). The size of the pellets suggests but do not prove that they relate to brown hyaenas. The soil possibly represents deflated remains of hyaena burrows and also contains vertebrate remains conforming to other early Last Glacial assemblages. Except for recently exposed specimens, the bones in the original soil did not show wind abrasion and therefore no signs of reworking. The association of these finds with Howieson's Poort-type artefacts is not clear but these possibly represent a surface broadly contemporaneous with the faunal burrows. The pollen contents of the coprolites, however, suggest an environment different from that along the present coast, indicating conditions typical of higher altitudes and therefore cooler conditions with the coastline not as near as at present. Sediments associated with coprolites were not tested for pollen but they appeared to be typically unproductive sands, while the original sedimentary context and burrow structure was probably lost.

Florisbad

Middle Pleistocene hyaena coprolites associated with a rich faunal assemblage and Middle Stone Age artefacts from spring sediments at Florisbad spring were attributed to spotted rather than brown hyaenas on the basis of size, the presence of bone fragments and taphonomical associations (van Zinderen Bakker 1989; Scott & Brink 1992). The grass-dominated pollen from the coprolites compared with the spring sequence that includes local pan halophytes (Chenopodiaceae) and spring sedges, suggests hyaena activity in the grassy surroundings of the spring and saltpan. The grass pollen represents one of the moist grassy phases in the sequence that shows strong variations between grass, sedge, Asteraceae and Chenopodiaceae (van Zinderen Bakker 1989; Scott & Brink 1992).

Las Ventanas

Thousands of coprolites and abundant bone remains of spotted hyaena (*Crocota crocota*) were found in association with bones of their prey in Las Ventanas Cave in Spain (Fig. 1). Coprolites were dated to between c. 9500 and 10 500 yr BP (Carrión *et al.* 2001). Despite the lack of pollen in some coprolites, ten of them showed good pollen preservation and diversity and concentrations of up to approximately 290 000 pollen grains per gram. The surrounding sediments were barren of pollen (Carrión *et al.* 2001). The coprolite pollen record is similar to that from Late Glacial sediments in an adjacent archaeological cave site and other regional pollen records.

MATERIALS AND METHODS

The pollen from two coprolites in Las Ventanas Cave and pollen from three modern brown hyaena pellets from Mankwe (Fig. 1), were studied by scanning electron

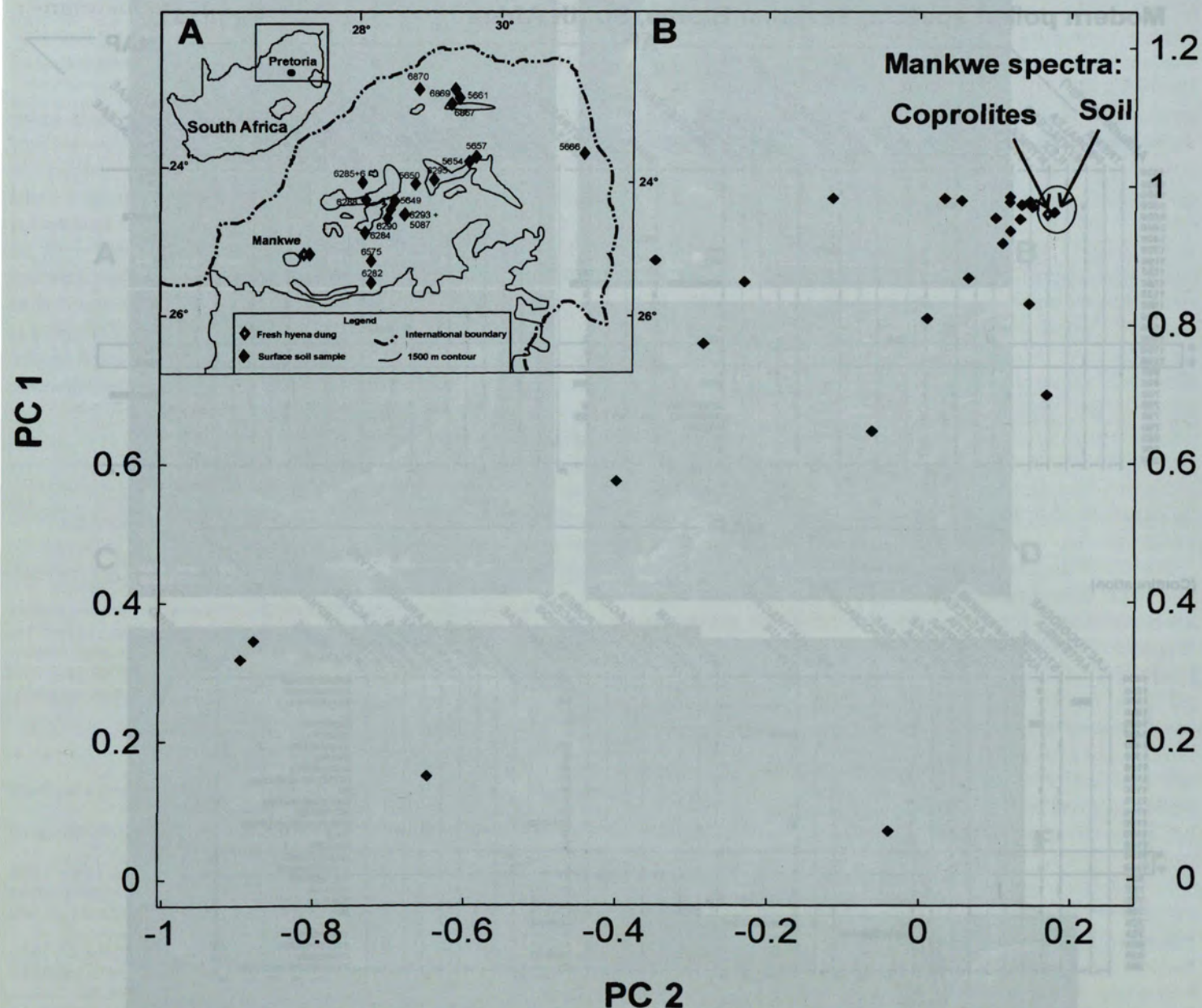


Figure 3. A, localities of surface pollen samples from Bushveld region and hyaena coprolites from Mankwe; B, PCA of dung and surface pollen spectra from bushveld region.

microscopy. Pollen types in the latter were counted under a light microscope. The samples from Mankwe (Fig. 1) and of five modern spotted hyaena dung samples from Laetoli (Serengeti, Tanzania) were processed for light microscopy. Since coprolites are destroyed during chemical extraction of pollen, we first tested fragments from two coprolites of the Grand Dolina site (Atapuerca, Spain). When they proved to be sterile we saved the better specimens for other purposes because it was likely that they also do not contain pollen (Fig. 2).

Before extraction of pollen from the coprolites and dung, pellets were thoroughly cleaned to remove their outer layers. The samples were then crushed and immersed in 10% HCl, followed by 40% HF treatment to break up coprolite matrices to release pollen. The samples then underwent mineral separation using $ZnCl_2$ solution with a specific gravity of 2. Pollen concentrations were determined according to the method of Stockmarr (1971).

Pollen residues were mounted on stubs for SEM investigation, while some were mounted in glycerine jelly for light microscopy.

A modern pollen spectrum from local soil was obtained for comparison with the Mankwe dung material. These spectra were also compared with previously published modern spectra of surface soils from the wider savanna and grassland region (Scott 1982) (Fig. 3A). In order to look for differences between hyaena dung and soil pollen assemblages the total data set was subjected to principal components analysis (PCA).

RESULTS

Together with pollen, numerous other items, including plant fibres, fungal spores, microscopic charcoal, insect remains and unidentified objects were recorded. The minute spherical bodies (c. $2\ \mu m$) found in abundance in owl pellet preparations that might represent pigment

Modern pollen spectra, Savanna Biome, South Africa



Figure 4. Comparison of modern pollen spectra from Mankwe dung (*) and soil (+) compared with soil pollen spectra from savanna and grassland samples in South Africa (Scott 1982). The dung spectrum was derived from counts on three pellets.

bodies from prey hairs (Fenández-Jalvo *et al.* 1999, unpubl. data) were not found in the hyaena dung. The resistant, transparent covering of owl pellet pollen, which is invisible under a light microscope, was also not found in hyaena coprolites. Relatively high pollen concentrations, ranging between 1300 and 93 000 grains per gram (Table 3) were recorded for modern dung pellets from Mankwe and Laetoli, respectively. No pollen could be found in the Early Pleistocene coprolite fragments from Gran Dolina, Atapuerca. Modern coprolite pollen assemblages in the hyaena dung from Mankwe are presented in Fig. 4 together with previously published surface pollen spectra (Scott 1982). It appears that the dung spectra show variability that places them within the range of surface pollen spectra. These results of PCA suggest that the coprolite pollen spectra conform well to the surface pollen data from the region, falling within the general cluster, albeit in a slightly peripheral position (Fig. 3B). This position cannot be considered to indicate a significant difference in

view of the slightly out-lying geographical position of the Mankwe samples compared with other localities. Further, the Mankwe coprolite and soil-surface spectra show great similarity to each other and compared with pollen data from regional soils, suggest that coprolites give a good reflection of the regional pollen rain. The pollen grains in fresh spotted hyaena dung from Laetoli were not subjected to SEM investigation. Examination under a light

Table 3. Pollen concentrations in modern brown and spotted hyaena dung pellets from Mankwe and Laetoli.

Site and hyaena species	Pollen grains per gram
Mankwe, <i>P. brunnea</i>	30837
Mankwe, <i>P. brunnea</i>	48986
Mankwe, <i>P. brunnea</i>	8163
Laetoli, <i>C. crocuta</i>	1273
Laetoli, <i>C. crocuta</i>	1827
Laetoli, <i>C. crocuta</i>	92759
Laetoli, <i>C. crocuta</i>	4107

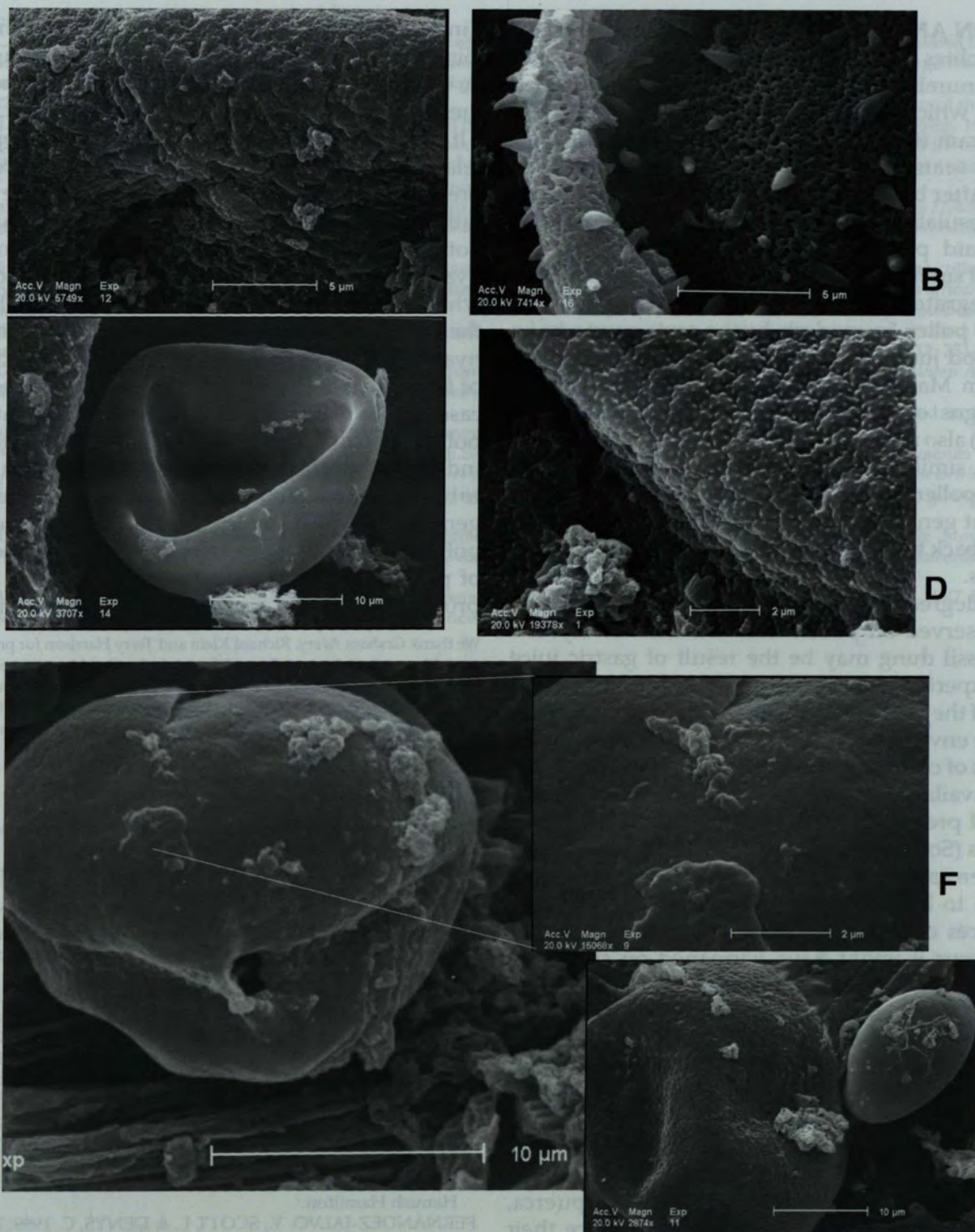


Figure 5. Palynomorphs (pollen and other microscopic objects) from fresh *Parahyaena brunnea* dung from Mankwe that show light signs of corrosion. A, an apparently corroded (flaked) surface of an unidentified pollen type. B, unidentified pollen with spine-covered surface showing an irregular reticulate pattern that might be a sign of corrosion. C, smooth structure, probably of fungal or algal origin, showing minute cracks. D, grass pollen grain surface showing generally good preservation except for a small area of pitting. E, a smooth colpate pollen grain (unidentified), showing a crack, a small cover patch and other minute loose debris (lines indicate area enlarged in F). F, detail of E. It is uncertain whether the cover patch (in E and F) is the remains of an outer layer, a swelling, or a foreign object. G, a grass pollen grain with well preserved surface, an unidentified elliptical structure (fungal spore?) showing narrow linear ridges, and loose debris.

microscope revealed their preservation to be excellent. The SEM results for modern brown hyaena coprolites from both Mankwe (Fig. 5 D,G) and spotted hyaena coprolites from 10 000-year-old sediments in Las Ventanas Cave (not illustrated) show generally well preserved pollen grains, although signs of limited damage can be seen. Some cases of fracturing are noticed on unidentified structures (probably fungal remains) from the scats

(Fig. 5C) but we restricted our observations mainly to grains that could be identified as pollen. At least 15 of the more than 20 pollen grains in Mankwe scats and Las Ventanas Cave coprolites showed no signs of corrosion or damage, although some of the Las Ventanas specimens were severely folded or partly obscured by fine debris from the coprolite, rendering it difficult to assess the damage.

DISCUSSION AND CONCLUSIONS

Since coprolites in caves and burrows in some cases contain high numbers of pollen, e.g. those in Las Ventanas Cave, Spain, which yielded between 20 000 and 290 000 grains per gram (Carrión *et al.* 2001), it seems that high numbers in scats can be retained under favourable conditions. After being subjected to acid gastric environments, encapsulation of pollen in hyaena faecal material appears to aid preservation by affording protection against direct sunlight and moisture fluctuations until the scats disintegrate or are buried and preserved. The condition of pollen in modern hyena scats seems to be generally good judging from the preservation of pollen surfaces from Mankwe and of Laetoli, which show no abnormal signs of corrosion. Van Zinderen Bakker & Müller (1987) also made no mention of any such corrosion on pollen in similar dung from the Namib Desert. The condition of pollen grains in Las Ventanas Cave coprolites indicates that generally good preservation of pollen can be expected back to at least 10 000 years despite folding of pollen grains.

The small degree of fracturing and surface flaking that has been observed on pollen from the modern hyaena scats and fossil dung may be the result of gastric juice digestion. Experimental work on damage traits is needed to establish if they exceed the degree of natural damage of pollen in the environment. As yet no published statistical observations of corrosion and fracturing of natural pollen spectra are available for comparison. Exine thinning that we observed previously in Equus Cave and Oyster Bay pollen grains (Scott 1987; Carrión *et al.* 2000) may or may not have been caused by gastric action. Outer surfaces of pollen seem to be unaffected but we did not examine inside surfaces of pollen by SEM. If gastric thinning of exine did occur it might have happened on the inner (endexine) layer due to differential resistance, but as yet there is no evidence for this. An alternative explanation for exine destruction or thinning could, however, be long-term post depositional deterioration due to local conditions in sediments. It seems more likely to find pollen in relatively young fossils (Table 2). In contrast with the good pollen yields from 10 000-year-old coprolites from sites such as Las Ventanas Cave, no pollen has been recorded in coprolites from Gran Dolina, Atapuerca, which have been preserved *c.* 780 000 years since their burial (Parés & Pérez-Gonzalez 1999). Pollen is also missing from the 2.6-million-year-old coprolite-rich layer at Makapansgat (Scott 1995). The lack of pollen in coprolites from these older sites and the exposed site Erfkroon (Table 2) (Churchill *et al.* 2000) may be due to unfavourable local events such as moisture saturation and accompanying oxidation episodes in surrounding sediments at specific times during their long histories. On the other hand, the Middle Pleistocene pollen in coprolites from the Florisbad spring, which are possibly more than 200 000 years old (Scott & Brink 1992) is well preserved when viewed under a light microscope. This good preservation is probably due to reducing conditions in the spring deposits that also preserved rich pollen in the surrounding sediments. Pollen grains were extracted by van

Zinderen Bakker from coprolites from Elandsfontein (Singer & Wymer 1968) that are of last glacial age but may be 400 000 years old. Unfortunately, there is no record of their exact provenance (G. Avery, pers. comm.).

It can be concluded that 1) although age appears to be related to the survival of pollen grains in coprolites, their preservation under reducing or moisture-free conditions rather than oxidizing conditions appears to improve their potential for long-term preservation. 2) Pollen spectra in hyaena dung are representative of the whole area in which hyaenas move around and not only that around the hyaena habitation site. 3) It must be kept in mind that hyaena behaviour, e.g. dietary preferences like ingestion of flowers, or consumption of viscera as proposed in the case of Las Ventanas Cave coprolites, might influence pollen spectra (Carrión *et al.* 2001). 4) Variability between individual coprolite pollen spectra and pollen rain needs to be investigated thoroughly to identify such effects. 5) In general, however, on account of good preservation of pollen in coprolites, and the apparently random pattern of palynomorph trapping, hyaena dung can potentially provide a good reflection of regional palaeoenvironments.

We thank Graham Avery, Richard Klein and Terry Harrison for providing hyaena coprolites or fresh hyaena dung. Support in South Africa was received from the National Research Foundation (GUN 2053236) and in Spain from projects MCYT-DGI(BTE 2000-1309), PI-17/00739/FS/01, BOS 2000-0149 and REN 2003-02499-GL. Graham Avery's critical comments on the manuscript are greatly appreciated, and those of an anonymous reviewer.

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Dicynodonts were a diverse group of herbivorous, non-mammalian therapsids ('mammal-like reptiles'), which flourished during the Permian and Triassic periods. Dicynodont fossils have been recorded from every continent and an enormous number of genera and species have been named, many of which are ill-diagnosed or based on poorly preserved material (King 1988). Not surprisingly the taxonomy and phylogenetic inter-relationships of dicynodonts remains contentious (e.g. Angielczyk 2001; Hanchi *et al.* 2003).

During the course of a redescription of the well-known African dicynodont *Kannemeyria simodiplatus* (Reinart 2000), the first author encountered an incongruity in the taxonomy of two other dicynodont species, *Rechinsaurus cristatidens* and *Kannemeyria cristatidens*, which are outlined in this note.

Institutional abbreviations used in the text are as follows: BP, Bernard Price Institute for Palaeontological Research, Johannesburg; ISI, Indian Statistical Institute, Calcutta; R, Geological Survey of Namibia, Windhoek.

TAXONOMY

Ray-Chowdhury (1970) described the partial skull (BP R37) of a large dicynodont from the Middle Triassic Yerrapalli Formation of India, which he assigned to a new genus and species, *Rechinsaurus cristatidens*. Later in the same year Crozier (1970) published a brief description of two dicynodonts from the 'lower freshwater horizon' of the Middle Triassic Ntawere Formation of Zambia, referring one of these specimens, BP/13638, to *Rechinsaurus cristatidens*. Ray-Chowdhury (1974) accepted this taxonomic referral with some reservation.

In their seminal review of Triassic dicynodont systematics, Keyser & Cruickshank (1979) re-examined BP/13638 from Zambia, as well as R37, a specimen from the Middle Triassic Omungande Formation of Namibia which had

been assigned to *Rechinsaurus cristatidens* by Keyser (1974). Keyser & Cruickshank (1979) recognized that BP/13638 and R37 were in fact conspecific with *Kannemeyria*, but a different species from *Kannemeyria simodiplatus*. Consequently, Keyser & Cruickshank (1979) accepted that BP/13638 was conspecific with the Indian *Rechinsaurus cristatidens* Ray-Chowdhury, argued that *Rechinsaurus* was a junior synonym of *Kannemeyria*. This recognized the new combination *Kannemeyria cristatidens* (Ray-Chowdhury) for the Indian and Zambian dicynodonts. Note, however, that this synonymy was based entirely on an analysis of the characters present in the African specimens that had been referred to *Rechinsaurus cristatidens*, rather than on the holotype described by Ray-Chowdhury (1970).

The synonymy of *Rechinsaurus* with *Kannemeyria* was implicitly accepted by Cooper (1980), Cui & Li (1983) and Cruickshank (1986). However, Bandyopadhyay (1985) showed that the holotype of *Rechinsaurus cristatidens* was clearly morphologically distinct from the African *Kannemeyria simodiplatus*, and that there were no grounds for synonymy. Although much of her argument (Bandyopadhyay 1985, 1989) was based on skull morphology, a feature that Reinart (2000) has shown to be unreliable, she did also draw attention to a number of characters that can be used to distinguish between *Rechinsaurus* and *Kannemeyria*. Distinguishing characters of *Rechinsaurus* include the large ventrally projecting caniniform process, the flattened palatal surface of the secondary palate, a larger lacrimal than in *Kannemeyria* that precludes prefrontal-maxilla contact, the probable presence of an ectopreygoid and (in referred specimens) the extension forward of the zygomatic process of the squamosal. Thus, in her review of the Dicynodontia, King (1988: 119), following Bandyopadhyay (1985), states 'It is clear then, that the genus *Rechinsaurus* should stand with its one original species, *R. cristatidens*'. In a publication King (1988) retained the name *Rechinsaurus cristatidens*.

A taxonomic note concerning a dicynodont (Synapsida: Anomodontia) from the Middle Triassic of East Africa

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The complicated histories of the Indian dicynodont *Rechnisaurus* and the East African dicynodont *Kannemeyeria cristarhynchus* has led to the incorrect use of the name '*cristarhynchus*' for the latter taxon. This paper therefore proposes a new species name and diagnosis.

Keywords: Triassic, therapsid, *Kannemeyeria*.

INTRODUCTION

Dicynodonts were a diverse clade of herbivorous, non-mammalian therapsids ('mammal-like reptiles'), which flourished during the Permian and Triassic periods. Dicynodont fossils have been recorded from every continent and an enormous number of genera and species have been named, many of which are ill-diagnosed or based on poorly preserved material (King 1988). Not surprisingly, the taxonomy and phylogenetic inter-relationships of dicynodonts remains contentious (e.g. Angielczyk 2001; Hancox *et al.* 2000).

During the course of a redescription of the well-known African dicynodont *Kannemeyeria simocephalus* (Renaut 2000), the first author encountered an incongruity in the taxonomy of two other dicynodont species, *Rechnisaurus cristarhynchus* and *Kannemeyeria cristarhynchus*, which we outline in this note.

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TAXONOMY

Roy-Chowdhury (1970) described the partial skull (ISI R37) of a large dicynodont from the Middle Triassic Yerrapalli Formation of India, which he assigned to a new genus and species, *Rechnisaurus cristarhynchus*. Later in the same year, Crozier (1970) published a brief description of two dicynodonts from the 'lower fossiliferous horizon' of the Middle Triassic N'tawere Formation of Zambia, referring one of these specimens, BP/1/3638, to *Rechnisaurus cristarhynchus* Roy-Chowdhury. Keyser (1974) accepted this taxonomic referral with some reservation.

In their seminal review of Triassic dicynodont systematics, Keyser & Cruickshank (1979) re-examined BP/1/3638 from Zambia, as well as R313, a specimen from the Middle Triassic Omingonde Formation of Namibia which had

previously been referred to *Kannemeyeria simocephalus* by Keyser (1973). Keyser & Cruickshank (1979) recognized that BP/1/3638 and R313 were in fact congeneric with *Kannemeyeria*, but a different species from *Kannemeyeria simocephalus*. Consequently, Keyser & Cruickshank (1979), accepting that BP/1/3638 was conspecific with the Indian *Rechnisaurus cristarhynchus* Roy-Chowdhury, argued that *Rechnisaurus* was a junior synonym of *Kannemeyeria*. This recognized the new combination *Kannemeyeria cristarhynchus* (Roy-Chowdhury) for the Indian and Zambian dicynodonts. Note, however, that this synonymy was based entirely on an analysis of the characters present in the African specimens that had been referred to *Rechnisaurus cristarhynchus*, rather than on the holotype described by Roy-Chowdhury (1970).

The synonymy of *Rechnisaurus* with *Kannemeyeria* was implicitly accepted by Cooper (1980), Cox & Li (1983) and Cruickshank (1986). However, Bandyopadhyay (1985) showed that the holotype of *Rechnisaurus cristarhynchus* was clearly morphologically distinct from the African *Kannemeyeria simocephalus*, and that there were no grounds for synonymy. Although much of her argument (Bandyopadhyay 1985, 1989) was based on snout morphology, a feature that Renaut (2000) has shown to be unreliable, she did also draw attention to a number of characters that can be used to distinguish between *Rechnisaurus* and *Kannemeyeria*. Distinguishing characters of *Rechnisaurus* include the large ventrally projecting caniniform process, the flattened palatal surface of the secondary palate, a larger lacrimal than in *Kannemeyeria* that precludes prefrontal maxilla contact, the probable presence of an ectopterygoid and (in referred specimens) the massive forward extension of the zygomatic process of the squamosal. Thus, in her review of the Dicynodontia, King (1988: 110), following Bandyopadhyay (1985), states: 'It is clear then, that the genus *Rechnisaurus* should stand, with its one original species, *R. cristarhynchus*'. Inexplicably, King (1988) retained the name *Kannemeyeria crista-*

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rhynchus Roy-Chowdhury for the Zambian (BP/1/3638) and Namibian (R313) dicynodonts, while maintaining the Indian *Rechnisaurus cristarhynchus* Roy-Chowdhury as a separate taxon.

This taxonomy was subsequently accepted by Bandyopadhyay (1989) and continues to be in use (e.g. Lucas 1998; Renaut & Hancox 2001). Clearly, however, the use of the name '*cristarhynchus*' as applied to the Zambian and Namibian specimens of *Kannemeyeria* violates Article 49 of the International Code of Zoological Nomenclature (ICZN 2000), which states the following (relevant names included by us in square brackets): 'A previously established species-group name [*Rechnisaurus cristarhynchus* Roy-Chowdhury] wrongly used to denote a species-group taxon because of misidentification [*Kannemeyeria cristarhynchus* (BP/1/3638, R313)] cannot be used for that taxon [*Kannemeyeria*] even if it and the taxon to which the name correctly applies [*Rechnisaurus*] are in, or are later assigned to, different genera'.

No other names have been applied to the Zambian and Namibian dicynodonts referred to *Kannemeyeria* '*cristarhynchus*'. Accordingly, we propose a new species name here, along with a new diagnosis of BP/1/3638 (Renaut 2000), which we designate as the holotype. A full re-description of BP/1/3638 and R313 will be the subject of a forthcoming publication.

Kannemeyeria lophorhinus sp. nov.

Rechnisaurus cristarhynchus (Roy-Chowdhury) Crozier 1970

Kannemeyeria simocephalus (Weithofer) Keyser 1973

Kannemeyeria cristarhynchus (Roy-Chowdhury) Keyser & Cruickshank 1979

Holotype. BP/1/3638, a partial skull and complete mandible (Crozier 1970; Renaut 2000).

Type locality and horizon. Locality 16, approximately one kilometre north of Sitwe in the Upper Luangwa Valley, Zambia; 'lower fossiliferous horizon' of the N'tawere Formation, Middle Triassic (Kitching 1963).

Etymology. A combination of *lophos* Greek for 'crested', and *rhinos* Greek for 'snout', referring to the well-developed median dorsal mid-nasal ridge that extends from the premaxilla onto the frontal.

Diagnosis. Distinguished from *Kannemeyeria simocephalus* by the following characters: skull more robust; total skull width equals total skull length; greater lateral and ventral development of caniniform process; snout deeper and wider; well-developed median dorsal ridge flanked by marked grooves; larger preparietal; zygomatic arches bowed slightly laterally; short, stubby parietal extensions of frontal onto parietal crest; broader intertemporal region; shorter temporal fenestrae; shorter secondary palate; pterygoid complex same length as, or longer than, secondary palate; reduced pterygoid process of maxilla; larger ventral median palatal ridge; wider median,

ventral parabasisphenoid sulcus; lacks pterygoid fossa; squamosal forms planar occiput; wide basioccipital notch, with tubera extending ventrolaterally; large, expanded quadratojugal foramen; lateral dentary shelf of mandible developed into marked ledge; posterior edge of reflected lamina nearly contacts ventral surface of retroarticular process.

Referred specimen. R313, a near-complete skull, from the northern slope of Mount Etjo on the farm Etjo Nord, Otjiwarongo District, Namibia; Omingonde Formation, Middle Triassic (Keyser 1973).

We thank the Geological Survey of Namibia, Windhoek, for allowing us to examine R313. We extend our gratitude to Drs Sean Modesto and Michael Maisch for the constructive criticism of an earlier version of the manuscript. The National Research Foundation and University Research Committee of the University of the Witwatersrand are thanked for financial support.

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CROMPTON, A.W. 1962. On the dentition and tooth replacement in two bauriamorph reptiles. *Annals of the South African Museum* 46(9), 231–255.

HOPSON, J.A. & BARGHUSEN, H.R. 1986. An analysis of therapsid relationships. In: Hotton, N., MacLean, P.D., Roth, J.J. & Roth, E.C. (eds), *The Ecology and Biology of Mammal-like Reptiles*, 159–168. Washington, Smithsonian Institution Press.

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