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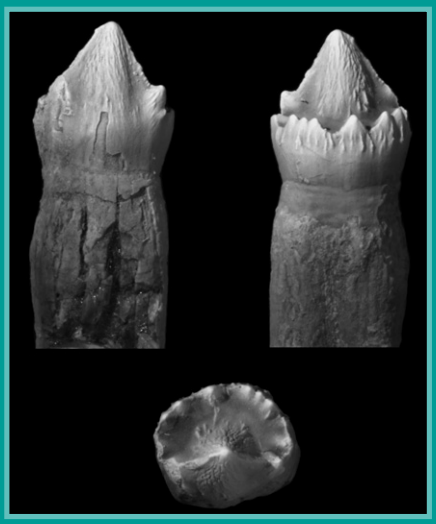
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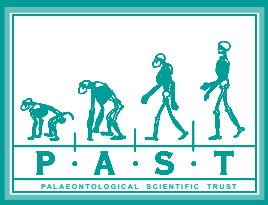
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CONTENTS

Articles

Kemp, T.S. — Phylogenetic interrelationships and pattern of evolution of the therapsids: testing for polytomy **1**

Nicolas, M. & Rubidge, B.S. — Assessing content and bias in South African Permo-Triassic Karoo tetrapod fossil collections **13**

Weide, D.M., Sidor, C.A., Angielczyk, K.D. & Smith, R.M.H. — A new record of *Procynosuchus delaharpeae* (Therapsida: Cynodontia) from the Upper Permian Usili Formation, Tanzania **21**

Fourie, H. & Rubidge, B.S. — The postcranial skeleton of the basal therocephalian *Glanosuchus macrops* (Scylacosauridae) and comparison of morphological and phylogenetic trends amongst the Theriodontia **27**

Govender, R. & Yates, A. — Dicynodont postcrania from the Triassic of Namibia and their implication for the systematics of Kannemeyeriiforme dicynodonts **41**

Geraads, D., Melillo, S. & Haile-Selassie, Y. — Middle Pliocene Bovidae from Hominid-bearing sites in the Woranso-Mille area, Afar region, Ethiopia **59**

Zipfel, B. & Berger, L.R. — Partial hominin tibia (StW 396) from Sterkfontein, South Africa **71**

Technical Note

Zipfel, B. & Berger, L.R. — New Cenozoic fossil- bearing site abbreviations for collections of the University of the Witwatersrand **77**

Abstracts

15th Biennial Meeting of the Palaeontological Society of Southern Africa

• **Reviewed Extended Abstracts**

Abdala, F., Martinelli, A.G., Bento Soares, M., de la Fuente, M. & Ribeiro, A.M. — South American Middle Triassic continental faunas with amniotes: biostratigraphy and correlation **83**

Atayman, S., Rubidge, B.S. & Abdala, F. — Taxonomic re-evaluation of tapinocephalid dinocephalians **88**

Backwell, L. & d'Errico, F. — Additional evidence of early hominid bone tools from South Africa. First attempt at exploring inter-site variability **91**

Bordy, E.M., Sztanó, O., Rubidge, B.S. & Bumby, A. — Tetrapod burrows in the southwestern main Karoo Basin (Lower Katberg Formation, Beaufort Group), South Africa **95**

Browning, C. — Nodular preservation of trilobite fossils from the Bokkeveld Group, Eastern Cape Province, South Africa **100**

Manegold, A. — The early fossil record of perching birds (Passeriformes) **103**

Mannion, P. D. — Review and analysis of African sauropodomorph dinosaur diversity **108**

Matthews, T., Marean, C. & Nilssen, P. — Micromammals from the Middle Stone Age (92–167 ka) at Cave PP13B, Pinnacle Point, south coast, South Africa **112**

Mostovski, M.B. — Brachyceran assemblages (Insecta: Diptera) as indicators of terrestrial palaeoenvironments in the Late Mesozoic **121**

Ovechkina, M.N., Watkeys, M. & Kretzinger, W. — Nannoplankton in the manganese deposits of the Mozambique Ridge and Mozambique Basin, southwestern Indian Ocean **126**

Ovechkina, M.N., Watkeys, M. & Mostovski, M.B. — Calcareous nannofossils from the stratotype section of the Upper Cretaceous Mzamba Formation, Eastern Cape, South Africa **129**

Rubidge, B. & Angielczyk, K. — Stratigraphic ranges of *Tapinocephalus* Assemblage Zone dicynodonts: implications for middle Permian continental biostratigraphy **134**

van Dijk, D.E. — Continental displacement: early lines of evidence that deserve attention **136**

• **Abstracts** **139**

• **Poster Abstracts** **190**

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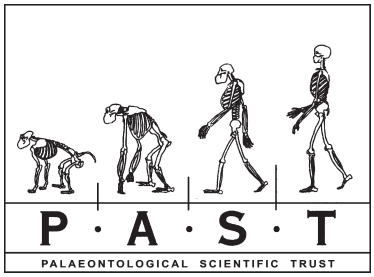
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Phylogenetic interrelationships and pattern of evolution of the therapsids: testing for polytomy

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There is little agreement on the interrelationships of the major therapsid subtaxa because none of the variously proposed sister-group relationships are supported by clearly defined, unambiguously distributed morphological characters. Rather than pursue a new cladistic analysis here, the hypothesis is explored that the lack of an agreed cladogram is because there was a polytomy at the base of the therapsid radiation that is not amenable to positive testing by conventional morphological cladistics, but that can be tested in four ways. The virtually simultaneous appearance of all the lineages except Cynodontia in the Middle Permian stratigraphic record supports the hypothesis. The palaeogeographic record, which shows a combination of taxa with first occurrences in different parts of Pangaea also supports it, though this is not strong evidence. The palaeoenvironmental record supports the polytomous hypothesis strongly by providing evidence of a coincidence between the start of the therapsid radiation and the appearance of a new suite of ecological opportunities for diversification within higher latitudes. Finally, a functional correlation analysis of the characters associated with feeding, and the reconstruction of lineages of functionally integrated organisms offers strong support by indicating that no two of the four respective lineages, Dinocephalia, Gorgonopsia, Anomodontia and Therocephalia, could have shared a functionally feasible common ancestral stage subsequent to a hypothetical ancestor at a biarmosuchian grade. The exception is Cynodontia and Therocephalia, which are inferred to have shared such a more recent common ancestral stage, and therefore to be sister-groups in the taxon Eutheriodonta.

Keywords: Therapsida, Permian tetrapods, Permian palaeoecology, correlated progression.

INTRODUCTION

The amniote clade Therapsida is highly significant in the history of terrestrial tetrapod life for two, no doubt interrelated reasons. One is that the anatomy indicates that from the very start therapsids were evolving the increased energy budgets and activity levels that were to culminate in the mammals, with the latter's huge potential for physiological and anatomical diversification. The second is that it was the nonmammalian therapsids that were primarily responsible for establishing what was to become the standard structure of fully terrestrial tetrapod communities – a fauna dominated by a very large preponderance of diverse amniote herbivore species. This structure was later repeated in essence by the dinosaur-dominated communities of the later Mesozoic, and by the mammalian-dominated communities of the Tertiary right up to the present day.

However, the details of the early radiation of the Therapsida are shrouded in obscurity. The earliest fossil record of several derived lineages occurs approximately simultaneously, and cladistic analysis has so far led only to a number of very weakly-supported and ambiguous interrelationships amongst these lineages. Indeed, the situation is remarkably comparable to the morphological analysis of placental mammal interrelationships. Here the taxon Placentalia on the one hand, and the individual constituent orders on the other, are very well-supported clades, but to a very large extent morphological characters proved unable satisfactorily to resolve the interrelationships between these orders. Only with the advent of sufficient molecular sequence data over the last decade did this resolution become possible, with the by now familiar but at the time utterly unexpected results (e.g. Kemp 2005; Springer *et al.* 2005). Thus the Therapsida are also of interest as a paradigm for how to interpret an evolutionary pattern of a taxon where morphological based cladistic analysis does not generate a well-supported set of sister-group relationships, but where molecular evidence is not available.

CURRENT VIEWS OF THE INTERRELATIONSHIPS OF THERAPSIDS

As reviewed most recently by Rubidge & Sidor (2001) and Kemp (2005), there are six widely recognized undisputed therapsid subtaxa, viz:

- *Biarmosuchia:* medium-sized carnivores retaining several sphenacodontid characters. No clear-cut shared derived characters so this may technically be a paraphyletic group, and certainly close in structure to the hypothetical therapsid ancestor.
- *Dinocephalia:* large to very large carnivores and herbivores but generally quite primitive. Characterized by a tendency to pachyostosis of the skull bones.
  Gorgonopsia: medium to large, highly specialized carnivores, characterized by very large canines and a jaw hinge and musculature capable of an extremely wide gape.
- *Anomodontia: s*mall to large, highly specialized herbivores, although including some quite primitive, basal forms. Apart from the latter, dentition largely or completely replaced by a horny beak, and extreme enlargement of the jaw muscles.
- *Therocephalia: s*mall to large-sized diverse carnivores, with a few specialized omnivores, and in the Triassic

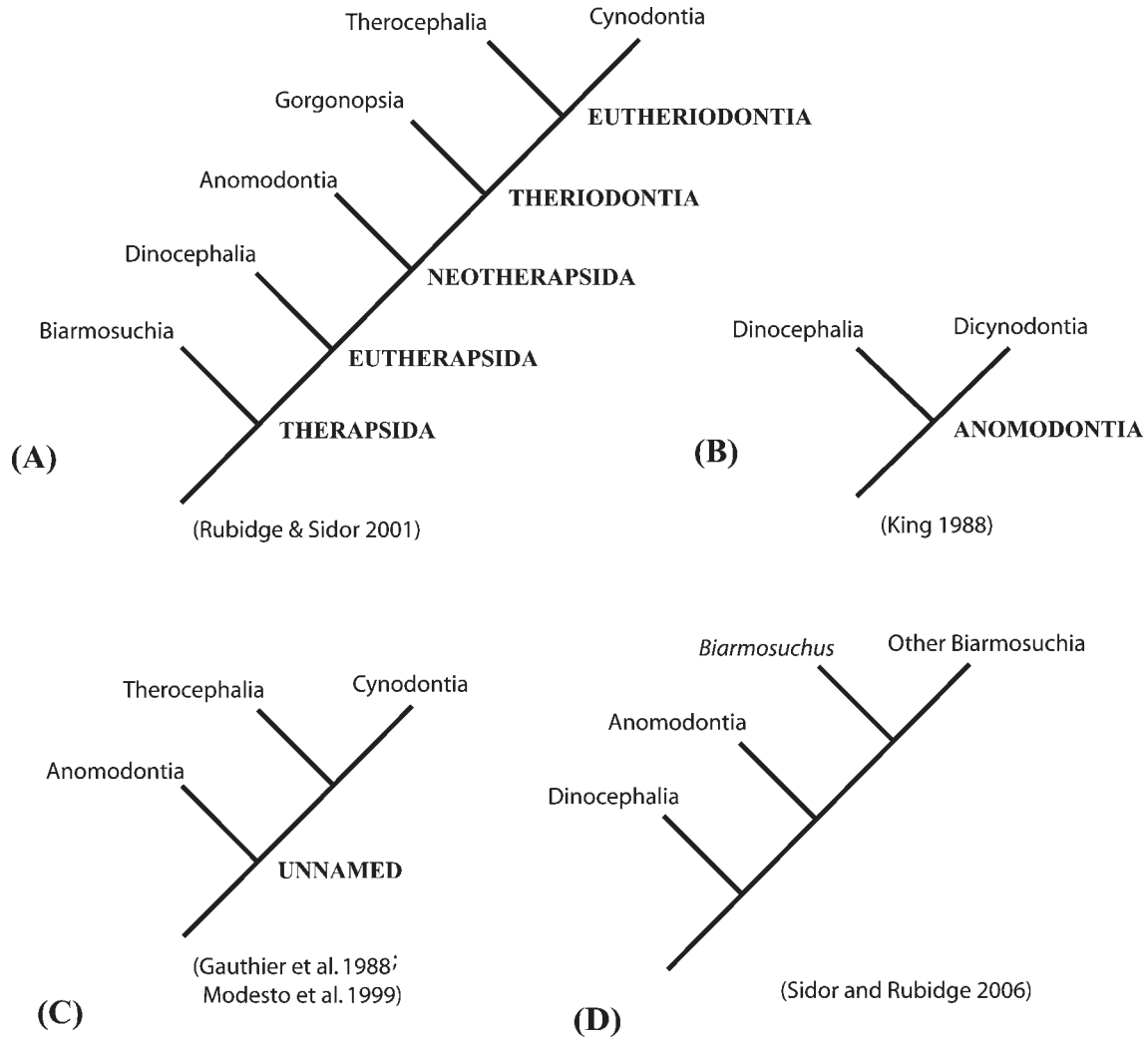


Figure 1. Current hypotheses of the interrelationships of major therapsid sub-taxa. See Table 1 for the characters used by respective authors to define the nodes.

one specialized herbivorous subgroup.

- *Cynodontia:* initially small to medium-sized carnivores, although a very diverse group in the Triassic. The most progressive taxon with many characters shared with mammals such as complex teeth, enlarged dentary and secondary palate.

The first of these subtaxa, Biarmosuchia, is recognized almost completely by a number of sphenacodontid-like plesiomorphic characters. One or two minor synapomorphies have been claimed for it (Hopson 1991; Sidor & Rubidge 2006), but the taxon may well be paraphyletic and include the ancestry of the rest of the therapsids. The rest of these therapsid subtaxa are well-supported clades.

There are also a few very poorly known forms from the Middle Permian of Russia, such as *Nikkasaurus, Microurania, Phthinosuchus* and *Niaftasuchus* (Ivakhnenko 2003; Kemp 2005). These are ignored here, although with better material they may well prove important. There is also a specimen that has been claimed to represent a very basal therapsid, *Tetraceratops,* which is represented by a single, poorly preserved specimen from the Lower Permian of North America. Laurin & Reisz (1996) described it as possessing certain therapsid features, but several authors have subsequently rejected this claim, and interpreted it as Romer & Price (1940) originally did as an aberrant pelycosaurian grade synapsid.

The most familiar cladogram of the major therapsid subtaxa (Fig. 1A) is that published in their review by Rubidge & Sidor (2001) and based mainly on the analysis and data set of Sidor & Hopson (1998). Although it is expressed as a fully resolved set of dichotomies, the number of characters supporting the major nodes is not only small or very small, but also the significance of many of these characters can be doubted on the grounds of their being either not unique to the taxon, probably non-independent, too vaguely defined for confidence that they are homologous, or based on a very small sample of species within the taxon (Table 1). Meanwhile, other authors have proposed different relationships, although on no more convincing grounds. King (1988) argued for a sister group relationship between the Dinocephalia and Anomodontia (Fig. 1B), to which combined taxon she applied the name 'Anomodontia' in a former usage. Cladistic analyses by Gauthier *et al.* (1988) and by Modesto *et al.* (1999) independently concluded that Anomodontia, is the sister group of Therocephalia plus Cynodontia (Fig. 1C). Recently Sidor & Rubidge (2006) published a cladistic analysis of several new and newly studied biarmosuchian grade therapsids, along with dinocephalians and basal anomodontians, but not including gorgonop-

Table 1. The putative synapomorphies for the proposed monophyletic groups in Fig. 1, extracted from the respective cited works, with comments on ambiguousness of distribution, impreciseness of the definition, or smallness of sample size as appropriate.

EUTHERAPSIDA – Fig. 1A. (all except Biarmosuchia)

Zygomatic arch bowed laterally. *No more so in the brithopodid dinocephalians (Orlov 1958) than in biarmosuchians (Sigogneau-Russell 1989; Ivakhnenko 1999) and not bowed but simply diverging slightly in therocephalians.*

No distinct ossified olecranon process of the ulna. *Prominent process in gorgonopsians (Colbert 1948) and present, if short, in cynodonts (Jenkins 1971).*

Only three phalanges in 5th pedal digit. *Extremely small sample of taxa available.*

NEOTHERAPSIDA – Fig. 1A. (Anomodontia, Gorgonopsia, Therocephalia and Cynodontia)

Ventrally expanded squamosal hiding most of quadrate in posterior view. *Difficult to accept as homologous because of the very different form and mode of attachment of the quadrate* in *gorgonopsians (Kemp 1969a), therocephalians (Kemp 1972b; van den Heever 1994) and anomodontians (King 1981).*

Epipterygoid broadly contacting underside of parietal. *Contact is narrow in gorgonopsians (Kemp 1969a), and anomodontians (King 1988). Ivakhnenko (2003, figs 6 and 9) figures an epipterygoid apparently very similar to that of gorgonopsians and anomodontians in both* Biarmosuchus *and the dinocephalian* Archaeosyodon.

Epiphyses on atlas vertebra. *An extremely small sample; Sigogneau-Russell (1989) states that the atlas of the biarmosuchian* Hipposaurus *is similar to that of gorgonopsians.*

Enlarged obturator foramen of pelvis. *An extremely small sample of biarmosuchians. In dicynodontians wide variation is reported, from minute to large (King 1988).*

THERIODONTIA – Fig. 1A. (Gorgonopsia, Therocephalia and Cynodontia)

Flat, low snout with dorsal surface of nasals horizontal.

Short internarial process. *Relatively long in the basal cynodont Procynosuchus (Kemp 1979), and short in pelycosaurs (Romer & Price 1940).*

Narrow temporal roof, equal or less than interorbital width. *Not the case in gorgonopsians generally (Sigogneau-Russell 1989).*

Greater flaring of zygomatic arch. *Not the case in therocephalians*.

Dentary with free-standing coronoid process. *The gorgonopsian coronoid process differs from those of therocephalians and cynodonts in its triangular rather than flat cross-sectional shape, indicating a different pattern of muscle attachments.*

Dentary with masseteric fossa. *Not present in gorgonopsians or therocephalians.*

Postdentary bones somewhat reduced in height. *Not absolutely in either gorgonopsians or therocephalians, but only relative to the increased height of the dentary due to the coronoid process.*

Humeral head slightly dorsal. *Very vague and just as true of some dicynodontians (King 1988).*

Deltopectoral crest more than 40% of humeral length. *Also in dicynodontians (King 1988)*.

Greater trochanter of femur still small but extends distal to head. *There is little manisfest difference in the greater trochanter of biarmosuchians and gorgonopsians (Sigogneau-Russell 1989).*

EUTHERIODONTA – Fig. 1A. (Therocephalia and Cynodontia)

Narrow intertemporal roof.

No contact between postorbital and squamosal on medial margin of temporal fossa. *Presumably correlated with previous character.*

Sagittal crest on parietal. *Also presumably correlated with the first character.*

Antero-posterior expansion of epipterygoid. *True, but only to a slight extent in most therocephalians.*

Loss of palatal teeth. *Also in anomodontians.*

Postero-ventral part of dentary thickened and angular in trough.

Fenestra between dentary, surangular and angular.

UNNAMED TAXON – Fig. 1C. (Anomodontia, Therocephalia and Cynodontia)

Frontal margins with lappet entering orbital margin. *Virtually identical in most other therapsids, such as brithopian dinocephalians (Orlov 1958) and gorgonopsians, but not true of even basal cynodontians.*

Postfrontal small. *Still substantial in early therocephalians (van den Heever 1994) and the basal anomodontians* Otsheria *(Chudinov 1960) and* Patranomodon (Rubidge & Hopson 1996).

Postorbital region of skull longer than preorbital region. *Not true of more basal therocephalians, and lengths about equal in basal cynodonts.*

Palatine with separate palatal and choanal rami. *Difficult to distinguish from the gorgonopsian condition (Kemp 1969a; Sigogneau-Russell 1989)*

Mandibular fenestra present. *Different construction in anomodontians (King 1988) compared to therocephalians (Kemp 1972b), for example in the former the dentary extends above and below it, but only above it in the latter.*

Palatine teeth absent.

Teeth on transverse process of pterygoid absent.

Tabular separated from opisthotic by squamosal. *Not the case in basal cynodonts.*

Odontoid fused to axis in adult.

Second intercentrum fused to axis in adult. *Probably functionally correlated with the previous character.*

Atlas neural arch separated from atlas intercentrum. *Doubtful as they function together as a ring (Kemp 1969b).*

Clavicles narrow medially. *They broaden medially in at least the therocephalian* Regisaurus *(Kemp 1986; Fourie & Rubidge 2007) and the basal cynodontian* Procynosuchus *(Kemp 1980)*

Humeral head articular surface bulbous and inflected. *No more so in some therocephalians (Kemp 1986; Fourie & Rubidge 2007) than in gorgonopsians (Kemp 1982).*

Ilium more than twice height of acetabulum. *Not in therocephalians (Kemp 1986).*

Continued on p. 4

Table 1 (*continued*)

Obturator foramen between pubis and ilium, rather than in pubis alone. *Condition unclear in gorgonopsians (Sigogneau-Russell 1989).*

Femoral head oblong and spherical (rather than elongate, subspherical, or protuberant). *Very vague and hard to exclude gorgonopsians or even biarmosuchians (Sigogneau-Russell 1989).*

ANOMODONTIA *sensu* King (1988) – Fig. 1B. (Dinocephalia and Anomodontia *s.s.*)

Loss of coronoid bones.

Non-terminal nostrils and long posterior spur of premaxillae. *Also in biarmosuchians (Sigogneau-Russell 1989; Ivakhnenko 1999) and the basal cynodontian* Procynosuchus (*Kemp 1979).*

Grooved or troughed palatal exposure of vomers. *Difficult to see a significant difference between biarmosuchians and dinocephalians, and complicated by the evolution of a secondary palate in anomodontians.*

Reduction or loss of internal trochanter of femur.

sians, therocephalians or cynodonts (Fig. 1D). Their strict consensus tree of nine equally parsimonious trees included a fourfold polytomy of, respectively, Dinocephalia, Anomodontia, the genus *Biarmosuchus* alone, and the other biarmosuchians. A majority rule consensus of the nine trees generated Dinocephalia as the most basal and Anomodontia and Biarmosuchia as sister groups.

It is, of course, possible that a new cladistic analysis with more thoughtful selection of characters would produce a more strongly supported set of resolved interrelationships. However, in the absence of radical new material, and in the light of the universal problem of how objectively to recognize unit morphological characters, this is unlikely, and is not attempted here. Rather, it is the purpose of this paper to propose that the failure to discover a well-supported and fully resolved tree of therapsid interrelationships lies in the inability of cladistic methodology to deal with a situation where the real evolutionary pattern may have been a virtually simultaneously polytomous splitting of several lineages from the ancestor. In such a case, alternative, non-cladistic tests for true polytomy need to be considered.

TESTING FOR POLYTOMY

It must be accepted as a matter of evolutionary biology that in principle a polytomous split of several lineages from a low taxonomic level can occur. At the extreme the multiple lineages would all arise directly from a single ancestral species, although more plausibly perhaps they would arise from different respective species sharing the typical morphological disparity of a single genus, or from different genera sharing the typical disparity of a taxonomic family. As has always been understood, such a situation creates difficulties in principle for cladistic analysis (e.g. Maddison 1989). If there are no characters defining successive nodes on the tree, cladistic methodology is required to attribute this to a failure to find them, not to their absence. Put another way, for cladistics the null hypothesis is unresolved polytomy and therefore polytomy cannot itself be a testable hypothesis, but only an expression of ignorance of enough characters (e.g. Maddison 1989; Walsh *et al.* 1999). Hence the response to such a situation is to continue the search for defining characters, and in the meanwhile accept provisionally the best supported tree, however weak and unconvincing the support is.

Several molecular systematists (Walsh *et al.* 1999; Poe & Chubb 2004; Whitfield & Lockhart 2007) have addressed the problem of resolving the interrelationships amongst lineages of modern taxa that appear to have arisen by an 'explosive', polytomous radiation. The issue is that the external branches (major subtaxa) of the tree are much longer (i.e. greater molecular differences between them) than the internal branches (the inferred initial diversifications at the base of the tree), to the extent that the molecular evidence lacks the resolving power to distinguish between a succession of finely spaced dichotomies (a 'soft polytomy') on the one hand (Fig. 2B) and a single polytomous split (a 'hard polytomy') on the other (Fig. 2A).

The molecular situation described is clearly analogous to the morphological problem of therapsid interrelationships, and the same terminology is appropriate: therapsids exhibit a soft polytomy in that the morphology can reveal the major subtaxa, but cannot satisfactorily resolve a complete set of dichotomous nodes between them, and therefore cannot discriminate between soft and hard polytomies. In the case of molecular sequence based systematics, there are a number of possible statistical tests of the likelihood that a soft polytomy actually is a hard or true polytomy, because of the ease of recognizing a very large number of objectively definable 'unit' characters (i.e. nucleotides). In the case of a soft polytomy that is based solely on the morphology of fossils, other positive tests for hard polytomy need to be considered, of which there are four kinds.

The stratigraphy test

A polytomy implies a virtually simultaneous origin of the separate lineages. If the stratigraphic sequence covering the time of the event has both adequate temporal resolution, and a dense enough fossil record it can offer support for the polytomy hypothesis.

The relative dating of the first appearance of the major therapsid subtaxa has been reviewed most recently by Lucas (2006), Kemp (2006a) and Abdala *et al.* (2008) (Fig. 3). They are currently known from Middle Permian deposits of three areas: the lower part of the Beaufort Group of South Africa, the cis-Uralian region of Russia, and a sparse fauna from the Xidagou Formation of Dashankou, China. There are disagreements about the dating of Middle Permian continental localities relative to the standard, marine-based sequence (Rubidge 1995; Izart *et al.* 2003; Lucas 2004; Tverdokhlebov *et al.* 2005), but from the nature of the fossil faunas, two aspects of the temporal

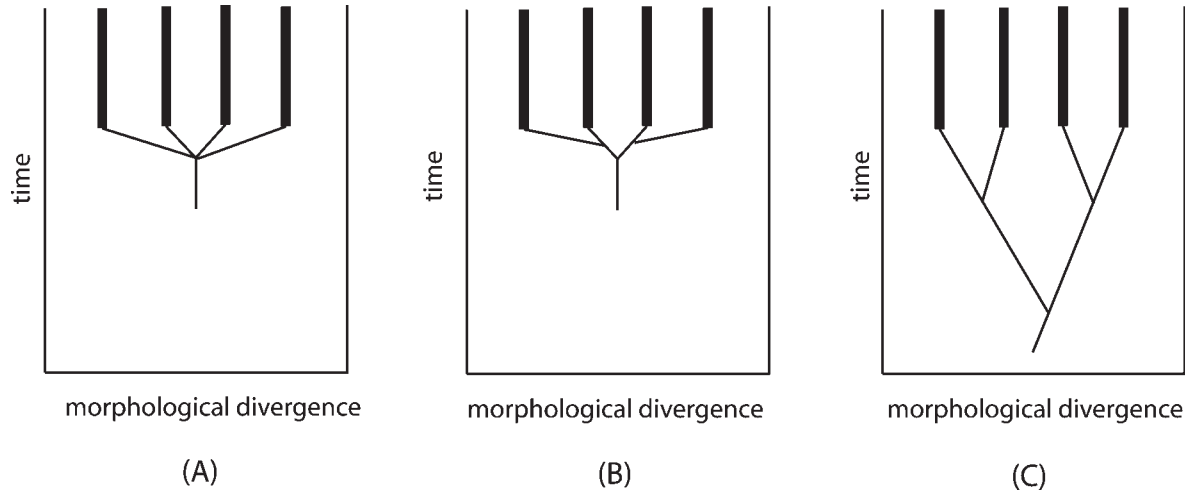


Figure 2. Possible patterns of evolution; thick lines represent the fossil record, thin lines the true phylogenetic lineages. **A**, A 'hard' or true polytomy. **B**, A 'soft' polytomy in which the internal branches are too short to be resolvable by morphological characters. **C,** A sequence of dichotomies with long ghost lineages.

pattern of occurrence of early therapsids are generally agreed upon. First, the three formations that have so far yielded early, Guadalupian-aged therapsids are closely spaced in time. Abdala *et al.* (2008) believe that the South African *Eodicynodon* Assemblage-Zone is around the Roadian-Wordian boundary, and that both the Russian Ocher Assemblage and the Chinese Xidagou Formation fauna are Roadian, and so slightly older. The actual therapsids currently known from this time include all the major subtaxa except one. The Cynodontia did not appear until some 6–7 million years later, in the Late Permian Tatarian of Russia and the approximately contemporaneous *Tropidostoma* Assemblage Zone of South Africa (Botha-Brink & Abdala 2008). Second, it is believed that there is a significant hiatus between the last occurrence of the North American pelycosaurs and these earliest therapsids. It has been termed 'Olson's Gap' by Lucas (2004), after E.C. Olson who first proposed its existence (Olson 1962), and is perhaps about five million years in length.

There is also a general belief that a very considerable therapsid ghost lineage of about 35 million years must have existed, from the first appearance of therapsids in the Middle Permian right back to the first appearance of their presumed sister-group, the sphenacodontid pelycosaurs in the Late Carboniferous (Abdala *et al.* 2008). However, as Kemp (2006a) has pointed out, on the currently available evidence the possibility cannot be ruled out that Sphenacodontidae is paraphyletic, and that Therapsida is the sister-group of a much later, Early Permian member of that taxon. If this is so, then at the minimum the ghost lineage need be scarcely any longer than that of the the five million years of Olson's Gap. The temporal pattern of first appearances of fossil therapsids is completely compatible with a simultaneous splitting of an ancestral therapsid into all the major subtaxa except Cynodontia in Roadian times. This support for the polytomy hypothesis must nevertheless be treated with some caution because of the existence of Olson's Gap, and because of the impossibility on the basis of presently known characters of knowing the precise relationships of Therapsida to the sphenacodontian pelycosaurs, and therefore how long the therapsid ghost lineage really is.

The palaeobiogeography test

A second implication of polytomy is that all the lineages first appeared in the same geographical region. The fossil record of a radiation could in principle be compatible with such a pattern. Alternatively, it could suggest a pattern of separate regions of origin for different combinations of taxa, implying a succession of dichotomies.

The earliest therapsid fossils occurring in the three regions of mid-Permian Pangaea do not show a clear taxonomic differentiation between the areas. Four of the lineages occur together in South Africa, Dinocephalia, Anomodontia, Gorgonopsia and Therocephalia (Rubidge 1995). In Russia there are three, Biarmosuchia, Dinocephalia and Anomodontia (Ivakhnenko 2003), and in China only two, Biarmosuchia and Dinocephalia (Li & Cheng 1996; Li *et al.* 1997). Thus the palaeogeographic pattern tends to support a polytomy rather than pointing to possible vicariant or dispersal events separating successive dichotomies. However, the very small number of localities, and the paucity of fossils within them renders the pattern too weak to be regarded as particularly significant.

The palaeoenvironmental test

A polytomous divergence of several lineages virtually simultaneously is a realistic possibility, and such an event can be presumed to have a potentially discoverable cause. Explanations of explosive radiations have long been sought, in terms of such concepts as key innovations (Hunter 1998) and ecological opportunities (Kemp 2007b). For example, it is suggested that the Cambrian explosion is related to increase in oxygen levels (e.g. Marshall 2006), and that the Tertiary radiation of placental mammals was facilitated by the removal of competitive exclusion by dinosaurs (e.g. Kemp 2005). A hypothesis of polytomy may in principle be supported by evidence of the sudden origin in the ancestral taxon of a novel biological potential, or evidence of the coincidental origin of a series of new ecological opportunities.

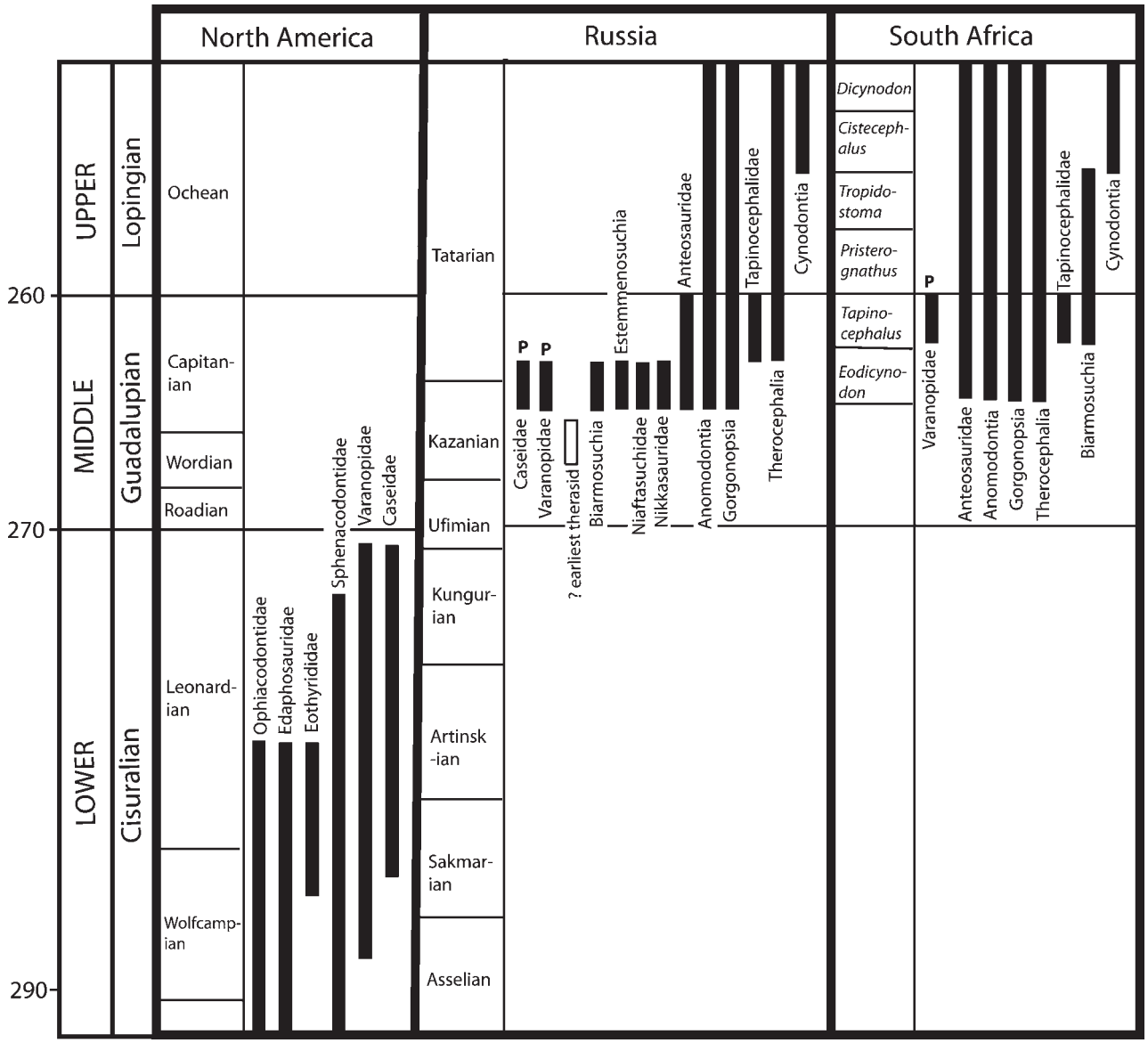


Figure 3. Stratigraphic occurrences of synapsid taxa indicating the virtually simultaneous first appearance of the major therapsid subtaxa in the Middle Permian. The earliest Dinocephalia are indicated by Anteosauridae. **P** indicates pelycosaurian taxa surviving into the Middle Permian. The open box labelled '?earliest therapsid' refers to some extremely poorly preserved fragments from the Copper Sandstones of Russia that have been dubiously claimed to be therapsid limb bones (see Kemp 2006a). The exact stratigraphic correlation between these three regions and also the Xidagou Formation of China, which is not shown, are not yet agreed (see Izart *et al.* 2003; Rubidge 2005; Lucas 2006; Abdala *et al.* 2008). Reproduced with slight modifications from Kemp (2006a).

In the case of the Therapsida, Kemp (2006a) proposed an explicit palaeoenvironmental model for both the origin of basal therapsids, and for their divergence in the Middle Permian into a series of subtaxa (Fig. 4). To summarize briefly, the evidence that was adduced for the model is in part functional interpretation of therapsids as tetrapods with higher energy budgets, and greater internal thermoregulatory and chemoregulatory abilities (Kemp 2007b). This supposedly allowed them to remain continuously active in highly seasonal environments, notably the Summerwet Biome that occupied the tropical zones of Early Permian Pangaea (Rees *et al.* 2002). The second line of evidence is a shift in the palaeoclimatic zones at the start of the Middle Permian. Hitherto, extensive desert zones had isolated the tropical regions from the temperate regions in both hemispheres, but at this time the Summerwet Biome appears to have expanded northwards and southwards along the eastern edge of Pangaea (Rees *et al.* 2002) . For the first time it became possible for therapsids to disperse from tropical into temperate regions. According to the model, this new ecological opportunity for a taxon already adapted for fluctuating, seasonal conditions resulted in the explosive radiation of the group. Rapidly and simultaneously several lineages diverged into a series of new niches – large and small body sizes, carnivores, herbivores and omnivores.

Thus the hard polytomy hypothesis of the interrelationships of therapsids is corroborated by this evidence of a plausible environmental cause occurring coincidentally in time and place with the fossil record of the radiation.

The functional systems test

However plausible an evolutionary scenario can be built on the basis of stratigraphic, biogeographical and palaeoenvironmental evidence, any hypothesis of phylogenetic relationships of organisms must be supported

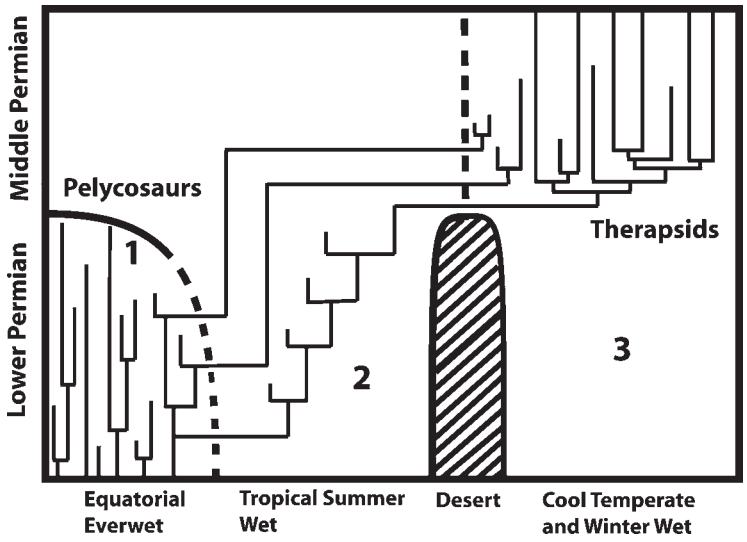


Figure 4. Model of the origin of Therapsida. **Phase 1**: radiation of pelycosaur-grade synapsids in an Everwet biome existing in the equatorial regions of Lower Permian Pangaea. **Phase 2**: evolution of adaptations for remaining active throughout the seasonal fluctuations in the Tropical Summerwet biome, leading to basal therapsids. **Phase 3**: retraction of the mid-latitudal desert zones along the eastern margin of Pangaea opened new dispersal routes to the northerly and southerly temperate biomes, within which therapsids rapidly radiated into a variety of new taxa. Reproduced from Kemp (2006a), which should be consulted for details.

primarily by the analysis of characters. The impasse between the realistic possibility of polytomous branching having occurred on the one hand, and the logical inability of standard cladistic methodology to provide a positive test for it on the other has been pointed out. There is, however, an alternative way of treating characters that in principle at least could detect a polytomy.

Cladistic analysis of morphological characters assumes that the organism can be atomized into a set of objectively recognizable discrete, independent, and initially equally weighted characters. The most parsimonious distribution of these characters amongst the organisms being analysed is then taken to indicate the best estimate of relationships – the best supported tree. However, all these assumptions are to a degree unrealistic, because of course organisms are actually integrated wholes in which the parts are structurally and/or functionally integrated, and they act together to produce the biological attributes of the phenotype (e.g. Dullemeijer 1974; Schwenk 2001). Where large amounts of character data give strongly supported relationships, there is no reason not to accept the most parsimonious tree as a good estimate. However, when there is poor support for any one tree, and little or no agreement amongst different authors concerning which is the best supported tree, then the probability that characters are being over-interpreted is high.

An alternative to the atomistic model of cladistic methodology is the much more realistic correlated progression model (Kemp 2006b, 2007a,b). Here it is assumed that characters are indeed functionally interdependent on one another within an integrated organism. They evolve in loose correlation with one another, and the probability of a change in one particular character depends on what changes have already occurred in others. Meanwhile the coordinated changes amongst the characters always maintain a fully integrated, well-functioning organism.

Applying the correlated progression model as a test for polytomy requires an understanding of the functional interrelationships between the known characters of a derived phenotype. Once this is achieved, a more primitive hypothetical stage can be reconstructed, in which the individual parts are more plesiomorphic but between which the functional relationships are maintained. For example, there must always be correlation between the size and orientation of the inferred site of origin and site of insertion of a muscle; between the form of the dentition and the mandibular mobility permitted by the shape of the jaw articulation; between the inferred action of the forelimb and the action of the hindlimb; between body size and various allometrically related structures, and so on. By performing such an analysis several times, a hypothetical sequence of successively more plesiomorphic, ancestor-like stages can be reconstructed all the way back to the inferred ancestral state of the whole lineage. The third step is to compare this sequence of reconstructed historical stages for one lineage with those of other lineages, in order to see if there is a possible coincidence of structure and function at any point. Absence of such coalescence implies that the two lineages evolved independently from the common ancestor of the whole taxon, even if in a cladistic analysis there are certain isolated characters in common. And if several lineages lack coalescence with any others, then a hypothesis of polytomy is corroborated.

The most comprehensively studied functional aspect of therapsids is the feeding mechanism, which involves numerous integrated structures. The architecture of the jaw musculature is related to the size and shape of the temporal fenestrae, the posterior palate, and such structural features as a coronoid eminence, a discrete coronoid process of the dentary, fossae on the angular and dentary bones, ridges on the reflected lamina of the angular, and the form of the retroarticular process of the articular. Also integrated with the jaw muscle forces and directions are dental features such as interdigitating incisors, large, reduced or absent canines, reduced or elaborated post-

canines, and inferred keratinous beaks. The jaw articulation may vary in form and degree of robustness for stress resistance, and in design for size of gape, and often propalinal movements of the mandible. The nature of the attachment of the quadrate to the squamosal is surprisingly variable amongst therapsids, which reflects the vectors of the stresses generated by the jaw muscles, and mobility in some groups. There are also various structural elements of the skull associated with stress resistance, such as the epipterygoid and parocciptal process.

Much less is currently understood about the mechanics of the postcranial skeleton and locomotory system of therapsids, so although in principle this part of the phenotype could equally well be incorporated into a correlated functional analysis, for the present purpose attention is restricted to the skull and jaws.

The ancestral state (Fig. 5A)

The Russian biarmosuchian *Biarmosuchus* (Chudinov 1960; Ivakhnenko 1999) combines therapsid characters with sphenacodontid characters, and has few if any significant autapomorphies (Hopson 1991; Rubidge & Sidor 2001; Sidor & Rubidge 2006). It is therefore a good model for an ancestral therapsid-stage from which the remaining major taxa evolved. The long, convex preorbital region, relatively small temporal fenestra, modest coronoid eminence of the mandible, and well-developed postcanine dentition are all comparable to features of the sphenacodontid pelycosaurs. The more striking of the many detailed differences from the sphenacodontid are the much larger upper canine tooth, a degree of dorso-ventral expansion of the temporal fenestra, enlargement of the reflected lamina of the angular, and an anterior rotation of the occiput. Kemp (2005) attempted a simple reconstruction of the jaw musculature, concluding that the adductor mandibuli consisted mainly of a single muscle mass originating on the medial and posterior edges of the temporal fenestra, and no doubt from an aponeurotic sheet of connective tissue across it (Barghusen 1976b). It inserted in primitive sphenacodontid fashion along the dorsal and medial parts of the coronoid region of the jaw, and had not invaded the lateral surface of the jaw at all. The incisor teeth may have interdigitated, although this is not certain. The jaw articulation was a simple, roller-like hinge between the quadrate and articular bones. No attention has yet been paid to the mechanical structure of the skull, but it seems likely from the estimated muscle sizes that the stresses generated by the biting action were small compared to most of the more derived therapsids. Stress transmission between skull and mandible was probably adequately accommodated by the relatively firm attachment of the large quadrate to the squamosal, and by the generally robust intertemporal and occipital regions of the skull.

Dinocephalia (Fig. 5B)

No comprehensive review of the jaw musculature of a dinocephalian has yet been undertaken, although Barghusen (1976a) and Kemp (1982) reconstructed the likely general features. The skull of *Titanophoneus* is presumed to have a structure close to that of the ancestral dinocephalian (Orlov 1958). The temporal fenestra has enlarged by dorso-ventral expansion compared to the ancestral therapsid condition, but there is no significant lateral or posterior expansion. The main distinction is an extension of the area of origin of adductor musculature onto a broadened lateral-facing surface of the intertemporal region. In this latter respect, the temporal fenestra of dinocephalians is entirely unlike that of gorgonopsians and the less specialized of the anomodontians. The form of the mandible indicates clearly that the insertion of this part of the adductor musculature had remained on the dorsal and medial parts of the lower jaw, much as in the ancestral stage, with no expansion onto the lateral jaw surface (Barghusen 1976a; Kemp 1982).

A reconstruction of the functional evolution of the ancestral dinocephalians from the ancestral therapsid condition consists only of the dorso-ventral expansion of the origin of the adductor muscles, which is entirely different from what occurred in any of the other main therapsid subtaxa. Indeed, none of the integrated jaw function features characteristic of any of the other taxa are found in dinocephalians. This absence of coalescence of derived functional organization supports the hypothesis of an independent evolutionary lineage for Dinocephalia.

Anomodontia (Fig. 5C)

The majority of anomodontians are the dicynodontians, which are the most modified of all therapsids, especially in terms of feeding function (Crompton & Hotton 1967; King 1981, 1988). The temporal fenestra is vastly increased in size by expansion both antero-posteriorly and, to varying extents, medially in different taxa. Furthermore, the posterior part of the skull has extended ventrally, which has the effect of lowering the position of the jaw articulation and so increasing the torque generated by the adductor musculature. It also creates another large area of origin for this musculature. Novel areas for insertion of the muscles on the lower jaw are also present. These are a broadened dorsal surface of the jaw, and shelves on the lateral surface of the dentary, often placed very far forwards (King 1988). The jaw articulation is modified to permit propalinic shifts, correlated with the evolution of a horny tooth beak. Of the dentition, at the most only upper, tusk like canines and a few very small postdentary teeth are present.

The functional evolution of anomodontians is better understood than that of other taxa because of a number of more basal anomodonts known from the Middle Permian of South Africa and Russia (King *et al.* 1989; Modesto *et al.* 1999; Reisz & Sues 2000). The cranial anatomy of *Patranomodon* (Rubidge & Hopson 1996), for example, illustrates a stage between the hypothetical ancestral therapsid and a basal dicynodontian such as *Eodicynodon* (Rubidge 1990). *Patranomodon* has retained a relatively long preorbital region, and its temporal fenestra is relatively small and little expanded medially. Incisor teeth are also retained. The lack of significant medial expansion of the temporal fenestra, or of any spread of the attachment of

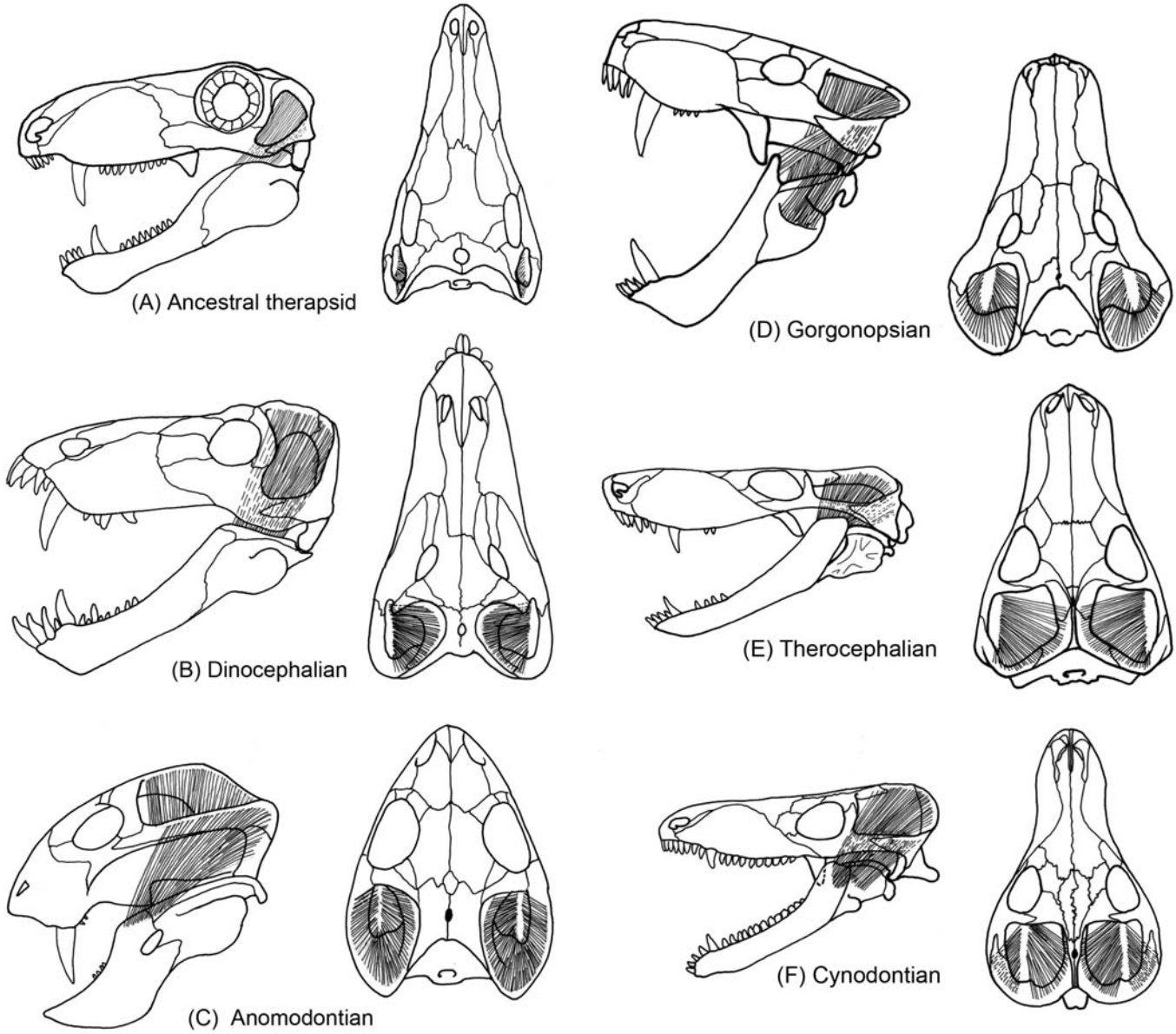


Figure 5. Reconstruction of the main adductor mandibuli musculature of the six major therapsid subtaxa. Outlines of skulls based on (**A**) *Biarmosuchus* (Ivakhnenko 1999); **B**, anteosaurid dinocephalian *Titanophoneus* (Orlov 1958); **C**, dicynodontian anomodontian *Eodicynodon* (Rubidge 1990); **D**, gorgonopsian *Arctognathus* (Kemp 1969a); **E**, therocephalian *Olivierosuchus* (Brink 1965); **F**, cynodontian *Procynosuchus* (Kemp 1979).

adductor musculature to a laterally-facing area of the edge of the intertemporal roof, but the presence already of the depression of the jaw articulation all indicate that functionally the anomodontian lineage could not have shared a common ancestry with either the dinocephalian or the therocephalian lineages, in which none of these features occur. Indeed, the reconstructed evolutionary trajectory from the ancestral anomodontian back to the hypothetical ancestral therapsid stage shows no sign of coalescence with that of any other taxon.

Gorgonopsia (Fig. 5D)

Kemp (1969) undertook a detailed analysis of the highly specialized jaw function system of gorgonopsians. The temporal fenestra was expanded posteriorly and laterally, but scarcely at all medially, and this is correlated with new areas of insertion on the lower jaw. There is a discrete coronoid process, which is obtusely triangular in cross-section, and part of the adductor musculature gained an insertion on the external face of the lower part. The lateral part of the adductor musculature expanded its area of origin onto the inside face of the broad, outwardly bowed zygomatic arch, and acquired a unique insertion onto a strong ridge occupying the reflected lamina of the angular. The part of the adductor musculature attached to the still narrow medial edge and the undersurface of the intertemporal roof corresponds to the ancestral temporalis musculature, and it still inserted on the medial side of the lower jaw.

This radical reorganization of the posterior and external parts of the adductor musculature is correlated with the ability of the lower jaw to open extremely widely, by more than 90°, and this was also reflected in a very specialized jaw articulation that permitted a wide gape while retaining a tight connection between the articular and quadrate (Parrington 1955). Finally, notwithstanding Laurin's (1998) claim that this was not the case, it is clear from well-preserved and fully prepared specimens that the

quadrate was moveably attached to the squamosal in such a way as to allow propalinal movement of the lower jaw (Kemp 1969a). The jaw could shift forwards to allow the upper and lower incisor teeth to interdigitate, and backwards to allow unencumbered energetic use of the huge opposing canines.

The various structures associated with gorgonopsian jaw action were integrated with one another within a functional system designed for highly active predation. Reconstruction of hypothetical evolutionary stages leading to the fully expressed gorgonopsian arrangement is constrained by the requirement that no one of the individual derived elements can be fully expressed in the absence of others, and in this case the correlations are especially apparent. Of particular relevance, the gorgonopsian coronoid process can only have evolved in correlation with a simultaneous posterior expansion of the temporal fenestra, since its function is to act as the insertion of that part of the adductor jaw musculature originating from the hind region of the fenestra (Kemp 1969a). This achieved an increased length of the musculature connecting them, which prevented undue restriction of the gape, and at the same time increased the torque applied to the lower jaw to increase the velocity of jaw-closing. A simultaneous expansion of the lateralmost part of the adductor mandibuli, was also necessary for generating a force adequate to operate the large canines.

Therocephalia (Fig. 5E)

The temporal fenestra was enlarged in a manner entirely unlike that of any of the previous groups. Medial expansion led to a narrowing of the intertemporal roof, but there is little development of the zygomatic arch. Kemp (1972b) interpreted the posteriormost root of the zygomatic arch as the area of origin of the homologue of the cynodontian and mammalian masseter muscle, although at this stage it did not extend anteriorly along the arch. The coronoid process is constructed differently from that of gorgonopsians, and is associated with medially and postero-medially directed musculature attached to the intertemporal region of the skull, rather than with posteriorly directed musculature as in gorgonopsians.

The jaw articulation (Kemp 1972b) is quite different from that of other groups, not allowing propaliny, but instead resisting a large postero-medially directed reaction from the temporalis and incipient masseter muscles.

The different arrangement of the adductor musculature between gorgonopsians and therocephalians implies independent modification from the hypothetical ancestral stage. The expansion of the temporal fenestra must have occurred independently in the two taxa because it is correlated with quite different parts of the adductor mandibuli muscle. Similar, the discrete coronoid process differs in form, and in the part of the musculature attached to it. The very different form of the jaw articulation reflects different reaction force regimes between the two. Therefore there is no sign of coalescence in the reconstructed morphological sequence between the hypothetical lineages leading to the therocephalians and the gorgonopsians, respectively.

Cynodontia (Fig. 5F)

Several authors have published reconstructions of the basal cynodontian jaw musculature (Barghusen 1968; Kemp 1979; Abdala & Damiani 2004). Most striking is the medial expansion of the temporal fenestrae creating a deep sagittal crest, and a simultaneous lateral expansion forming a bowed zygomatic arch. The latter was associated with a masseter muscle, which inserted into the lateral fossa of the broad coronoid process. According to Kemp (1979), in the basal cynodontian *Procynosuchus* this fossa was for the lateralmost part of the temporalis muscle and was only invaded by masseter muscle originating along the zygomatic arch in more derived forms. Abdala & Damiani (2004) differed in believing that the fossa was for the insertion of a true masseter muscle all along. However this does not greatly affect the reconstruction. The jaw articulation of the basal cynodontians is very similar to that of therocephalians, with the antero-laterally facing condyle of the quadrate designed to resist a postero-medially directed net reaction force applied by the articular. The epipterygoid of cynodontians is very broad, and together with the narrow intertemporal roof above and the basicranial axis below formed a box-girder, to strengthen the skull against the increased stresses arising from the enlarged adductor musculature (Kemp 1972a).

Thus the arrangement of the adductor musculature of the medial and posterior parts of the temporal fenestra of the basal cynodont *Procynosuchus* is very similar to that of therocephalians. The main difference between the two taxa lies in the absence of a muscle-bearing zygomatic arch and correlated invasion of the lateral surface of the mandible by adductor musculature in therocephalians. However, the coronoid process of both taxa is associated with a comparable medial expansion of the temporal fenestra. Therefore a functionally integrated common stage for the two lineages can be reconstructed, which is essentially therocephalian in nature. The recent description of an early and even more basal cynodontian *Charassognathus* (Botha *et al.* 2007) supports the hypothesis that the cynodontian and therocephalian lineages coalesce. Unlike *Procynosuchus,* it lacks an adductor fossa on the lateral surface of the coronoid process, but it does have a notch in the lower edge of the process that apparently represents an incipient invasion of the outer surface of the dentary from what would have been an essentially therocephalian-like arrangement of the musculature. The structure of the jaw articulation is very similar in therocephalians and *Procynosuchus,* and is correlated with the greater development of the medial and posterior parts of the adductor mandibuli. Even the expansion of the epipterygoid, to a modest degree in most therocephalians but more extensively in cynodonts and the therocephalian family Whaitsiidae, corroborates the essential similarity between the two of the integrated feeding system. Functional considerations therefore support a relationship between these two major therapsid subgroups.

Conclusion

Functional analysis of the skull and inferred mandibular musculature reveals that the integrated feeding system in

four of the five major derived therapsid subtaxa differed radically from one another. Each one evolved its own unique combination of characters from an hypothetical ancestral therapsid stage, approximately represented by the highly plesiomorphic *Biarmosuchus*. Furthermore, on reconstructing functionally integrated back-trajectories for the four, no two of them appear to have shared a common stage – to have coalesced – at any point subsequent to the common ancestor. This evidence corroborates the hypothesis that, at least at the level of morphological resolution available, there was a fourfold polytomy at the base of the therapsids, consisting of the dinocephalian, gorgonopsian, anomodontian and therocephalian lineages respectively.

By contrast, the Cynodontia possessed an integrated system that had several features also occurring in similar combination in the Therocephalia, and in this case evolutionary back-trajectories of the functional morphology of these two lineages appear to have coalesced at a common point subsequent to the biarmosuchian-grade ancestral stage. This supports the hypothesis that Therocephalia and Cynodontia are sister groups, constituting a monophyletic taxon Eutheriodonta.

These observations indicate that certain of the characters used in formal cladistic analyses to define various interrelationships cannot be regarded as homologous. A notable example is the presence of a coronoid process of the dentary used to support a monophyletetic Theriodontia, consisting of Gorgonopsia, Therocephalia and Cynodontia. It was concluded on functional grounds that this stucture must be convergent in the gorgonopsians and therocephalians because it is associated with different parts of the adductor musculature in the two. Another example is the character used to support a relationship between Anomodontia and Eutheriodontia (Fig. 2C), the increased postorbital length of the skull. Again this can hardly be regarded as a homologous character because it is associated with quite different ways of enlarging the temporal fenestra, and with different associated patterns of reorganization of the musculature, a conclusion confirmed by the discovery of the basal anomodontian *Patranomodon*.

CONCLUSIONS

The question posed in this essay is whether the weak support for, and extensive lack of agreement on a well-resolved phylogenetic tree of the major therapsid subtaxa is because of the failure yet to discover adequately known discriminating characters, or because there was a true polytomy in which several therapsid lineages diverged virtually simultaneously from a low-level ancestral therapsid taxon. The standard test for proposed phylogenetic relationships is formal cladistic analysis, but methodologically this is designed only to discover the best supported, fully dichotomous tree, however weak that support may be. Logically cladistics cannot be used positively to corroborate a hypothesis of therapsid polytomy. Four valid non-cladistic, non-tautological tests of polytomy are however available in principle, and when applied to the therapsid radiation three of them offer positive support for a fourfold polytomy from a biarmosuchian-like common ancestral taxon. The remaining one, the palaeobiogeographic test, is consistent with polytomy.

Of the three positive tests, it would be disingenuous to place too much weight on the stratigraphic relationships, but nevertheless this evidence offers very clear positive support for a fourfold polytomy. Only the Cynodontia appear in the fossil record significantly later and therefore, on this evidence, this taxon is a candidate for sharing a common ancestor with one of the other lineages.

The palaeoenvironmental evidence for polytomy is impressive, with the appearance in the fossil record of all the major lineages except Cynodontia coinciding with the appearance of a potential dispersal route to higher latitudes, north and south, areas of the globe that would suit well a group of tetrapods adapted to remain active throughout fluctuating seasonal conditions.

The most important test of polytomy is the functional correlation analysis of the morphology. In so far as this method of analysing morphology owes it origin to a much more realistic model of character evolution than that underpinning cladistics, it is potentially a more effective method for discovering true phylogenetic patterns including, critically, the power to detect polytomy. In the case of the therapsids, the correlated progression analysis unambiguously supports the hypothesis that four major lineages diverged independently from a biarmosuchian-grade ancestor. These are Dinocephalia, Gorgonopsia, Anomodontia and Therocephalia. Only one major subtaxon, Cynodontia, is inferred to have shared a common ancestor with another. Cynodontia and Therocephalia constitute the monophyletic taxon Eutheriodontia. All other proposed clades are rejected.

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Assessing content and bias in South African Permo-Triassic Karoo tetrapod fossil collections

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A standardized taxonomic database as well as a Geographical Information System (GIS) database of all fossil tetrapods collected from the Permo-Triassic Beaufort Group rocks of South Africa has been compiled from a number of South African museum catalogues. The data capture required rigorous evaluation of the accuracy of the original records and the degree of collecting bias. The outcome of this evaluation endorsed the accuracy of the two databases and showed no significant degree of collecting bias. This standardized database, now linked to a new GIS-based database, will be a valuable resource to scientists researching Permo-Triassic biodiversity and faunal distribution patterns.

Keywords: digitized data, fossil database, Beaufort Group.

INTRODUCTION

The rocks of the Beaufort Group (Adelaide and Tarkastad subgroups) of the Karoo Supergroup cover a large proportion of the surface of South Africa (Smith 1990) and comprise an approximately 3000 m thick sequence of predominantly sedimentary rocks which are internationally renowned for their wealth of tetrapod fossils. These fossil-bearing strata represent one of the most complete and best preserved palaeo-ecological records of pre-mammalian terrestrial vertebrates in the world (Keyser & Smith 1979) and are pivotal in evolutionary studies because during this period the stem lineages to both mammals and dinosaurs arose (Broom 1932; SACS 1980).

The absolute age of the Beaufort Group is not yet well constrained, with current dates based mainly on faunal correlations. The oldest stratigraphic units are considered Middle Permian (Kazanian) (Rubidge 1995a), and the uppermost strata as Middle Triassic (Anisian) (Ochev & Shishkin 1989; Hancox *et al.* 1995; Hancox & Rubidge 1996; Hancox 1998). Because of the extensive and largely unbroken temporal record of sediment deposition, coupled with the abundance of fossils, the succession is held by many to be the global biostratigraphic standard for the non-marine Permo-Triassic (e.g. Shishkin *et al.* 1995; Lucas 1998).

For more than a century large collections of vertebrate fossils from the Beaufort Group of South Africa have been amassed (Fig. 1) and although these are now housed in institutions around the world, by far the largest and most representative collections are in museums in South Africa. These are: Albany Museum, Grahamstown; Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; Council for Geoscience, Tshwane; Iziko South African Museum, Cape Town; National Museum, Bloemfontein; Rubidge Collection, Wellwood, Graaff-Reinet; and the Northern Flagship Institution (Transvaal Museum), Tshwane.

As part of a project to assess Permo-Triassic tetrapod biodiversity patterns and for use in biostratigraphy and basin modelling, the catalogues of these South African collections have been amalgamated onto a single standardized dataset (Beaufort Group database) as well as a Geographical Information System (GIS) of vertebrate fossil data for the Beaufort Group (Nicolas 2007). This is the first time that such datasets have been compiled for mid-Permian–mid-Triassic continental vertebrate faunas and the resource (Nicolas 2007) serves as a research tool providing standardized taxonomic, stratigraphic and locality data for all specimens.

Digital acquisition, integration and application of biological collections data is increasingly viewed as fundamental to biodiversity research (Beaman *et al.* 2004). In setting up the database the quality of fossil data from contributing collections had to be evaluated and categorized to determine the degree of compliance with digital information requirements. A summary of general spatial data quality standards (as required for optimum delivery of GIS-based data) is provided in Nicolas (2007). This assessment determined and evaluated the percentage of records that could potentially be used for spatial mapping. In addition records were analysed and categorized depending on their degree of taxonomic and locality resolution, a process which further refined the quality of the data eventually utilized in the spatial map of the Beaufort Group (Nicolas 2007). This evaluation was a necessary precursor for the establishment of the GIS fossil database. The above procedure has been adopted to ensure compliance with other international natural history collection database projects such as the Global Biodiversity Facility, the Biological Collection Access Service for Europe and the European Natural History Specimen Information Network.

METHOD AND RESULTS

Primary analysis of original data from contributing collections

The original datasets provide 26 837 specimens that are theoretically usable for spatial mapping (Table 1). This figure is the sum of the original, unaltered records of each

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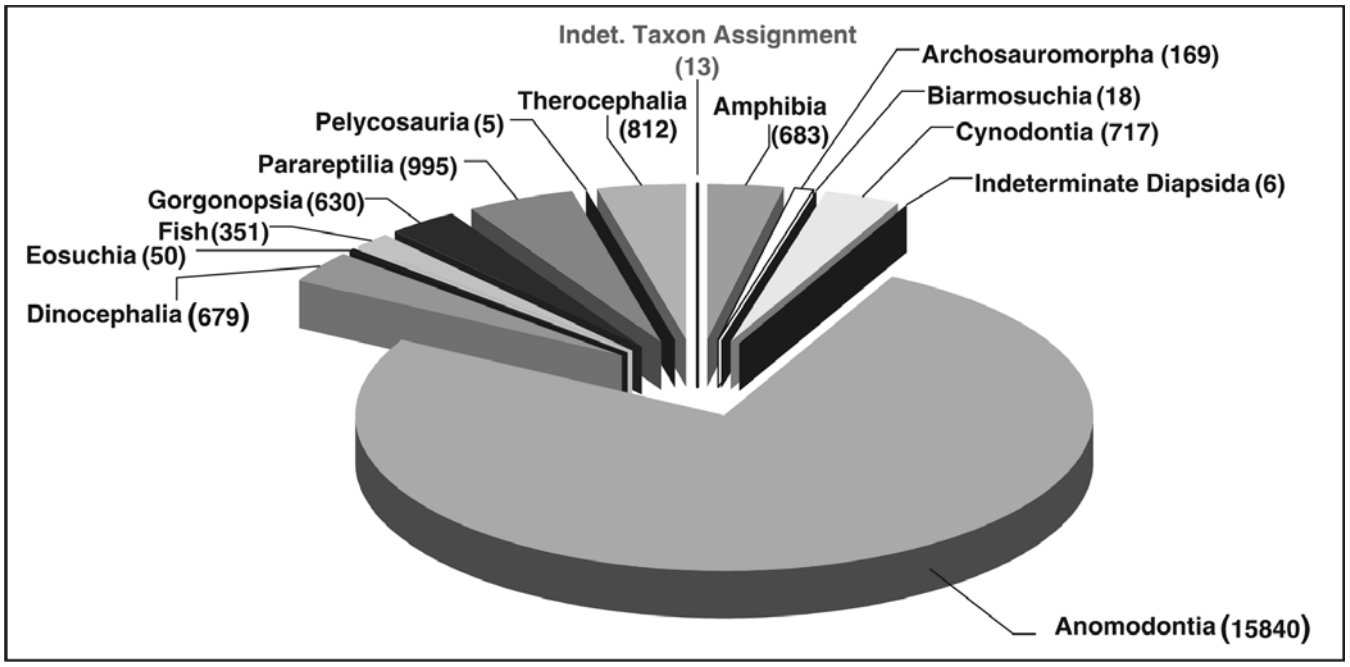


Figure 1. Relative numbers of fossils of taxa that have been recovered from the rocks of the Beaufort Group. Values in brackets reflect numbers of individuals. In the databases there are 13 taxon assignments for the Beaufort Group: Amphibia; Anomodontia; Archosauromorpha; Eosuchia, Biarmosuchia; Cynodontia; Diapsida; Dinocephalia; Fish; Gorgonopsia; Parareptilia; Pelycosauria and Therocephalia. Diapsida was subdivided into Archosauromorpha, Eosuchia and unidentified Diapsida for this study. The grouping of Diapsida is still retained to accommodate five errant specimens from the National Museum. In addition there is a final grouping of 13 fossils with unknown taxon assignment.

contributing museum. After careful investigation of the data from each museum catalogue, criteria for the elimination of unreliable data were established (Table 2). These included the removal of data pertaining to fossils not from the Beaufort Group, specimens that are not vertebrate, and records that had no identification and locality data. After this initial round of data elimination, the actual number of potentially useful vertebrate fossils from the Beaufort Group amounted to 20 968 (Table 1).

Primary analysis of the quality of Beaufort Group data

All recorded specimens from the Beaufort Group were categorized according to whether they had: locality data; no locality data; biozone data. This was necessary to assess the accuracy of locality information and is an exercise in quantifying the degree of compliance with digital information requirements. For this analysis no distinction was made for different methods of recording locality data (e.g. GPS coordinates or Farm Name data). However, such distinctions in locality data resolution were utilized in the establishment of the GIS database (Nicolas 2007). For accuracy it was necessary to update outdated biozone data in accordance with Rubidge (1995b), the currently accepted biozonation scheme of the Beaufort Group. The updating methodology (detailed in Nicolas (2007)) did not reconstruct biozone data for specimens with locality data. The majority of locality data from the contributing museum databases had written descriptions rather than geographic coordinates of localities. The difficulty in using these textual references to locate the provenance of specimens is problematic (Nicolas 2007) so it was decided to utilize the biozone assigned to each specimen in order to interpret biodiversity trends. The rationale for this action is that the portion of records with biozone data

Table 1. Useable data after initial elimination from original records. The original datasets from the seven contributing museum collections (Column 1) provide a *theoretical potential* of 26 837 (Column 2). The *theoretical potential* of 26 837 is the sum of the original, unaltered records of each contributing museum. Unreliable records were eliminated (see Table 2). After data elimination, the *actual potential of exploitable vertebrate specimens* in the Beaufort Group amounted to 20968 (Column 3). This table shows the number of records per museum collection remaining after elimination. These values are expressed as a percentage (column 4) of the records which can be utilized when compared to the original records.

Database	Total records	Record (after initial elimination)	% Potential viable data
Albany Museum	588	468	79.59
Bernard Price Institute	4780	4483	93.79
Council for Geoscience	7579	5322	70.22
National Museum	3520	3171	90.09
Rubidge Collection	854	850	99.53
Iziko South African Museum	6797	5424	79.80
Transvaal Museum	2719	1250	45.97
	Theoretical total	Potentially usable total	% Potential viable total
	26837	20968	78.13

would be capable of presenting broad biodiversity trends across and within the assemblage zones of the Beaufort Group. On completion of the GIS-initiative, all records will have been geo-referenced and so a fuller and more refined picture will result (Nicolas 2007).

Records with no locality and no biozone information cannot be used for either spatial mapping or biodiversity analysis. Those records with both biozone and locality data (with varying degrees of resolution) and those with only locality data may be used for spatial mapping. In so far as digital information is concerned, the optimum would be a 100% recording of fossil finds with locality information refined to thousandths of a degree, WGS datum coordinates. As it currently stands, 51% of the records from the Beaufort Group have locality information, but no biozone information; 44% have locality and biozone information; and 5% have neither locality nor biozone information.

Of the 9144 Beaufort Group specimens with biozone information, 57% (5193) are identified to genus level and the remaining 43% (3951) are unidentified (Fig. 2). The 9144 records with biozone information represent 44% of the total number of records for the Beaufort Group. This means that 25% of all records from the Beaufort Group are classified to genus level and have biozone information and 19% of records are unidentified, but have biozone information.

The unidentified specimens with biozone allocation (3951) (Fig. 2) were subdivided into their relative alliance to the eight biozones of the Beaufort Group. The *Eodicynodon* Assemblage Zone has 31 unidentified specimens, the *Tapinocephalus* Assemblage Zone has 140 unidentified specimens (1% of the total Beaufort Group population), the *Pristerognathus* Assemblage Zone lists five unidentified specimens, the *Tropoidostoma* Assemblage Zone lists 549 unidentified specimens (3% of the total Beaufort Group population), the *Cistecephalus* Assemblage Zone lists 2109 unidentified specimens (10% of the total Beaufort Group population), making it the biozone with the greatest amount of unidentified specimens, the *Dicynodon* Assemblage Zone lists 368 unidentified specimens (2% of the total Beaufort Group population), the *Lystrosaurus* Assemblage Zone lists 172 unidentified specimens (1% of the total Beaufort Group population) and the *Cynognathus* Assemblage Zone lists 259 unidentified specimens (1% of the total Beaufort Group population). The remaining 318 unidentified specimens that have biozone information are relegated to various transitional zones (Nicolas 2007).

Only 71% of all the 20 968 fossil vertebrates collected from the Beaufort Group have been identified to family, and of these only 5193 (25%) are identified to genus level and have biozone data. The *Eodicynodon* Assemblage Zone lists 51 specimens identified to genus level. The *Tapinocephalus* Assemblage Zone lists 183 specimens belonging to various genera (this comprises 1% of the total Beaufort Group vertebrate fossils), the *Pristerognathus* Assemblage Zone lists 34 specimens belonging to various genera, the *Tropidostoma* Assemblage Zone lists 361 specimens assigned to various genera (2% of the total Beaufort Group vertebrate fossils), the *Cistecephalus* Assemblage

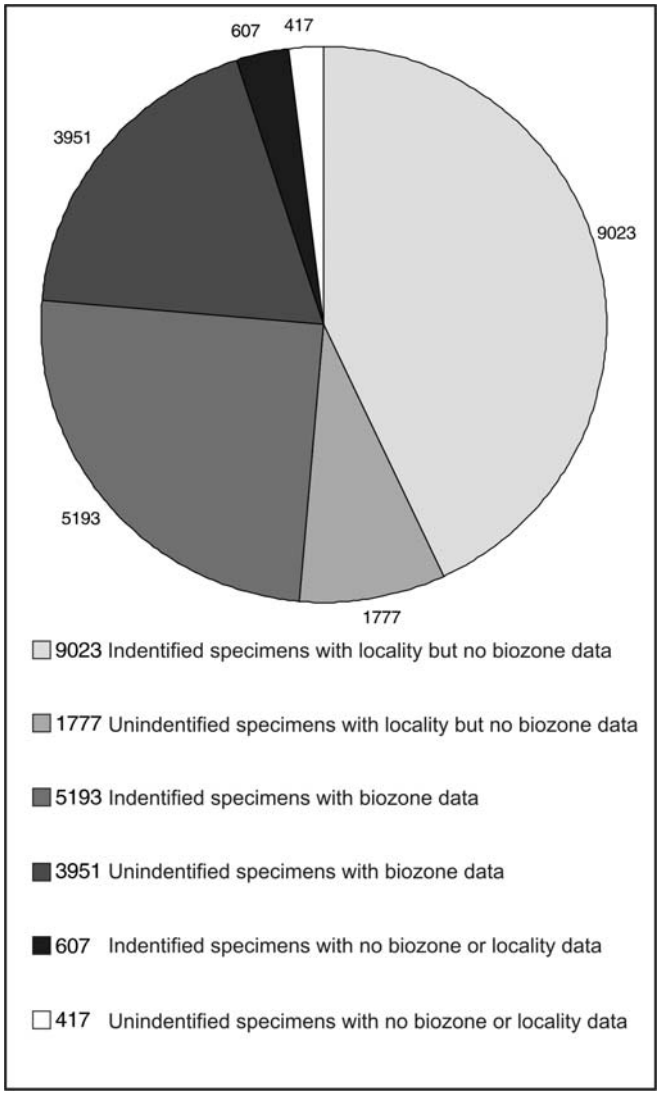


Figure 2. Analysis of Beaufort Group data, showing the subdivision of records into those identified to genus level or those as yet unidentified.

Zone lists 1037 specimens classified to various genera (5% of the total Beaufort Group vertebrate fossils), the *Dicynodon* Assemblage Zone lists 268 specimens belonging to various genera (1% of the total Beaufort Group vertebrate fossils), the *Lystrosaurus* Assemblage Zone lists 2559 specimens classified to various genera (12% of the total Beaufort Group vertebrate fossils), the highest count of identified specimens in the Beaufort Group, and the *Cynognathus* Assemblage Zone lists 562 specimens belonging to various genera (3% of the total Beaufort Group vertebrate fossils). The remaining 143 specimens identified to genus level are catalogued as being from various transition zones. The low numbers of specimens listed above are minimum values as only those records with assemblage zone data were utilized. There are 9023 specimens identified to genus level without a biozone allocated, but they do have locality data (Fig. 2). These will be allocated a biozone once the GIS database is completed.

Comparative analysis of contributing museum collections

A comparative analysis of different museum collections was performed by focusing on the specimen totals in each

Table 2. Elimination of non-viable data. After investigation of the content of each museum collection, criteria for the elimination of certain records were established. This table shows those records per museum collection requiring elimination. Bold font in column 2 refers to a specific datafield within a collection.

Collection name	Data Eliminated (Spreadsheet Rows)
Rubidge Collection	**Locality**: Unlisted farm locality & district information; Keetmanshoop; Lady Frere. Taxon: Mesosaurus; Sysphinctostoma
BPI Collection	**Biozone**: Equivalent of L. Cistecephalus Z. **Geology**: ?Stormberg; Equivalent of Beaufort. **District/Country**: Ficksburg (FS); Namaqualand (NC); Fouriesberg (FS); Clocolan (FS); Ceres (WC); Worcester (WC); Calvinia (NC); Prieska (NC); Marquard; Ladybrand; Ladygrey; Zambia. **Genus**: Tritylodon; Amniota; Dinosauria; Plants; Taxon Indet.; Squamata? ?Diapsida; Reptilia; Indet.; Tetrapoda; Trace Fossil; Worm Burrows; Indet. Amniote; Indet. Dinosaur; Indet. Reptile; Indet. Tetrapod Burrow Cast; Unidentified Bone in Lag. **Locality**: Unlisted Locality Information; Locality Unknown; Various Localities.
National Museum Collection	**Taxon**: Unidentified Taxon & Current Identification; Aetonyx; Saurischia; Dinosauria; Anchisaurus; Baroqueosuchus; ?; Basutodon (Large Thecodont); Bothriolepis; Invertebrata; Conchostracans; Elpistostege; Euskelosaurus; Roccosaurus; Fabrosaurus; Footprints (Bradysaurus?); Unlisted Information; Gryponyx; Herrerasaurus; Holopthychius; Hout; Footprint (Ichnitis); Massospondylus; Melanosaurus; Mesosaurus; Orthosuchus; Mollusca (Palecypoda); Pedeticosaurus; Plant; Rauisuchid; Reptile; Riojasaurus (Prosaurosushia); Saurischia; Scaumenacia; Sysphinctostoma; Thecodontosaurus; Tritylodon; Unidentified; Unknown; Various; Worms; Dinosauria; Invertebrata; Lacertilia; Ornithischia. **Country/Locality**: Unlisted district/farm; Unlisted province; Quebec (Canada); Barkley East; Bethlehem; Clarens; Golden Gate; Clocolan; Elliot; Essex (England); Ficksburg; Fouriesburg; Gumtree; Herschel; Hopetown; Jamestown; Lady Frere; Ladybrand; Leribe; Marquard; Mafeteng; Maseru; Rosendal; Slabberts; Zastron; Wes Duitsland (Holzmaden). **Geology**: Non-applicable Biozone; Elliot; Clarens; Molteno; Ecca; Stormberg; Waterford; Whitehill. Zone: Euskelosaurus; Massospondylus; Trityledon Acme Zone
Iziko South African Museum Collection	**Geology/Age/Biozone**: Ecca; Stormberg; Dwyka; Witteberg; Carboniferous; Bokkeveld; Devonian; Late Jurassic; Early Cretaceous; Cretaceous; Eocene; Middle Pennsylvanian; Upper Dwyka; Sakemena; Adolphspoort; Blue Lias; Carbondale; Elliot; Great Oolite; Green River Shale; Greensand; Irati; Kirkwood; Kupferschiefer; Lower Chalk; Lower Elliot; Lower Greensand; Lower Sakemena; Rio Bonito; Serra Alba; Whitehill; Early Triassic; Earliest Triassic; Early Carboniferous; Early Devonian; Early Jurassic; Early Permian; Jurassic; Kimmeridgian; Late Cretaceous; Late Jurassic/Early Cretaceous; Late Triassic; Lower Devonian; Lower Permian; Middle Devonian; Oligocene; *Euskelosaurus*; Reptile Beds. **Country**: Scotland; USA; Tanzania; Madagascar; Zambia; Namaqualand; Angola; Australia; Brazil; England; France; Germany; Great Britain; Ireland; Lebanon; Lesotho; Malawi; Mozambique; Namibia; North America; Wales; Zimbabwe; Unlisted locality (district/farm). **Province**: Caithness; Cambridge; Dumfries; Illinois; Mocamedes; New South Wales; Parana. District: Barkley East; Boputhatswana; Calvinia; Britstown; Ceres; Clocolan; Carnarvon; Dorset; Elliot; Fouriesburg; Hay; Herbert; Herschel; Hopetown; Kirkwood; Jansenville; Lady Grey; Ladybrand; Luangwa; Maclear; Mafeteng; Messina; Mokerong; Not Known; Outshoorn; Port Elizabeth; Port Shepstone; Prieska; Swellendam; Ranohira; Quacha's Nek; Quthing; Sebungwe; Uitenhage; Underberg; Utrecht; Will County; Williston; Wodehouse; Worcester. **Genus**: Beetle; Mammal; Osteolepis; Acanthodes; Acanthodian; Acanthopterygid; *Acrodus*; *Adroichthys*; *Aestuarichthys*; *Aetonyx*; *Astrodon*; Camarasauridae; *Opisthias*; *Pleurocoelus*; *Algoasaurus*; *Alopias*; *Anaethalion*; Anchisaurid; *Anoxypristis*; Anura; Arthrodire; *Asteracanthus*. **Class/Subclass**: Aves; Insect; Insecta; Mammalia; Placodermi; Vertebrata incertae sedis; Holocephali; Lepospondyli; Neornithes; Prototheria; Testundinata; Theria; Insectifora; Antiarchi; Anura; Arthrodira; Batoidea; Chelonia; Crocodylia; Cyprinodontiformes; Ellimmichthyformes; Elopiformes; Gadiformes; Galeomorpha; Ichthyopterygia; Lepisosteiformes; Mesosauria; Ornithischia; Sauropodamorpha; Lebias; Diplomystus; Elopoidei; Dastilbe; Anaethalion; Palaeomolva; Lamna; Carcharodon; Squalicorax; Isurus; Alopias; Heterodontus; Campylodon; Communis; Leptolepiformes; Pachycormiformes; Paleospondyliformes; Pelecaniformes; Perciformes; Salmoniformes; Saurischia; Triconodonta
Council for Geoscience Collection	**Genus**: Indet.(No identification listed); Anura; Anomodontia; Lower Jaw; Nodules; Padda; Stromatolite; Therapsida; Theriodont; Vertebrata; Indet. Anomodontida. **Locality**: Unlisted locality information
Albany Museum Collection	Plants, Unlisted Acc. No., **Geology**: Buntsandstein, Lower Triassic; Elgin Sandstone; Gravel Banks; Cave Sandstone; Red Beds; Elliot Formation; Dwyka; Kirkwood Formation; Uitenhage Group (Kirkwood Formation); Upper Dwyka Shales; Shale. **Country and Locality**: England (Shale); Lyas (Switzerland). **District**: Barkley East; Scotland; Farm Rietfontein; Barkley Pass; Lyme Regis, England; Bolotive; Bunter Landstein, Switzerland; Farm Glencoe (Barkley East); Ibid.; Kirkwood Cliffs, Sunday's River; Lady Frere, Glen Gray; Mafeteng District, Lesotho; Moirosi's Mount, Lesotho; N. Luangwa Valley, N. Malawi; Near Alice; Penhoek, Stormberg; Riechen, Switzerland; Skietnek, Kirkwood Village; Thaba-Chau (Tsueu, Chu, Cho); Unknown. **Taxon**: Unknown; Small Reptile; Unidentified; Massopondylus; Chelonia; Unidentified; Sauropod Dinosaur; Dinosaur Prosauropod; Anomodont; Fossil Wood – Podocarpus; Dinosaur-like Styracosaurus; Hortalotarsus; Large Prosauropod? *Euskelosaurus*; *Mesosaurus*; Saurischia – Prosauropod Dinosaur; Saurischia (perhaps *Plateosaurus*); Saurischia (Dinosaur); Saurischia (Euskelosaurus); Small Reptile; Thecodontia – Pseudosuchian; Therapsid; Therapsid – Unidentified; Theropod – *Nqebasaurus*; Unidentified; Unidentified Small Reptile; Unidentified Small Dinosaur; Unknown; Unlisted Taxon Information
Transvaal Museum Collection	**Genus**: Unidentified; Undescribed Anomodont; Bivalve Shells; Boks 140; *Aristosaurus*; *Eozostrodon*; Fossil Bone with Matrix; Fossil Reptile; *Gangomopteris* (a plant); *Gigantoscelus*; Large Anomodont; Large Mammal; *Massopondylus*; Reptile; Small Anomodont; Therapsid?; Theriodontia?; Theropoda; Unident.; Unlisted Genera. **Biozone**: Cave Sandstone; Red Beds; Rhaetic (Late Triassic). Locality: Tunnels; 'Tunnels' Donga; Senekal; Jame's Donga; Provenance Unknown; St. Fort (Setsoanastad) Bethelehem District; Witjies Hoek; Milius Donga; Unlisted locality information; Letjiesbosch; Klipbank; Karoo Site; Arcadia Donga; Commander Jone's House; Apparently East of Fossil Valley; 'Diamond Diggings'. **Province**: Unlisted locality information. **Country**: Unlisted locality information; England

Table 3. Total numbers of specimens per collection.

Museum collection	Total number of specimens	Unidentified specimens	Total number of identified specimens
Albany Museum	468	44	424
Bernard Price Institute	4 483	2 470	2 013
Council for Geoscience	5 322	58	5 264
National Museum	3 171	987	2 184
Rubidge Collection	850	509	341
Iziko South African Museum	5 424	1 629	3 795
Transvaal Museum	1 250	448	802
Totals	20 968	6 145	14 823

collection and the diversity of genera in each collection. This exercise identified the collections which curate the largest sample of any particular taxon and will thus facilitate future research. In addition it has highlighted problems in the fossil record and where future collecting should be undertaken. We have found that the content of the different collections is dependent on: geographic position of the museum; research focus of past and present palaeontologists employed by the museum; and diligence of the palaeontologists to pursue fieldwork. Because of these variables the numbers of specimens and taxonomic diversity of the individual collections varies greatly.

Specimen totals in each collection

The total number of specimens within each of the collections is recorded in Table 3. This total includes both unidentified specimens as well as specimens identified to genus level. Any record that had no taxonomic classification (e.g. 'Unknown' or 'Unidentified' or 'Indet.') or the taxonomic classification was too broad (e.g. 'Parareptile' or 'Synapsid') was relegated to the category 'Unidentified Specimens'. Because of the very large number of records spread between the seven contributing collections, it was considered beyond the scope of the project to verify each entry from each museum for correct identification. However, because of the accessibility of the BPI Palaeontology, the classification in the amphibian and anomodont categories were updated, verified and recorded in the synthesized records of the Bernard Price Institute for Palaeontological Research (Nicolas 2007). The remaining taxa were updated in so far as current taxonomy allowed. Flaws in the contributing datasets became apparent after completion of the standardization and 'clean-up' procedures (Nicolas 2007: appendix F). The contents of this Appendix F will be used as part of the data-cleaning component in Phase 1 of the GIS-initiative (Nicolas 2007) and will fast-track the taxonomic updating of all the museum collection records.

Diversity of genera in each collection

Iziko South African Museum has the greatest diversity of genera (163), followed by the Bernard Price Institute (124), the National Museum (88), the Rubidge Collection (85), the Transvaal Museum (73), the Council for Geoscience (63) and the Albany Museum (56) (Table 4)

Table 4. Diversity of genera within each collection. This table lists the diversity of genera within each collection, in order of decreasing diversity.

Museum collection	Diversity of genera
Iziko South African Museum	163
Bernard Price Institute	124
National Museum	88
Rubidge Collection	85
Transvaal Museum	73
Council for Geoscience	63
Albany Museum	56

Extent of collecting bias of fossils from the Beaufort Group

Once the amalgamated Beaufort Group dataset and the foundation GIS database of fossils from the Beaufort Group were established, it was essential to determine the 'validity' of the collection for biodiversity analyses by calculating the degree of collecting bias (this bias being the over-representation of fossils from a particular locality, biozone or of a specific taxon). The foundation GIS database was utilized only to determine the extent of collecting bias within the Beaufort Group (Karoo Supergroup) of South Africa caused by the specialist interest of a field collector/palaeontologist currently or in the past and is currently undergoing further refinement, with the end result that it will be an invaluable research tool. The methods and processes involved in setting up the foundation GIS-database are explained in Nicolas (2007).

Using geo-spatial data in the form of Neighbourhood and Gap Analysis to determine collecting bias

To test the reliability of the Beaufort Group data for analytical purposes it was necessary to determine 'evenness' in the geographic distribution of fossil localities in the Beaufort Group. If the distribution of fossil localities were found to be highly localized or biased to specific regions, this would impact negatively on the accuracy and significance of any current or future distribution or biodiversity study. Accordingly a 'Gap and Neighbourhood' Analysis was undertaken to determine if there was any geographic bias in the museum records.

Arcview 3.2 program with its spatial analysis extension were used to create a distance surface. The distance was calculated between the locations of all the specimen points. A contrast stretch was applied to the resultant surface to improve the visualization of the surface

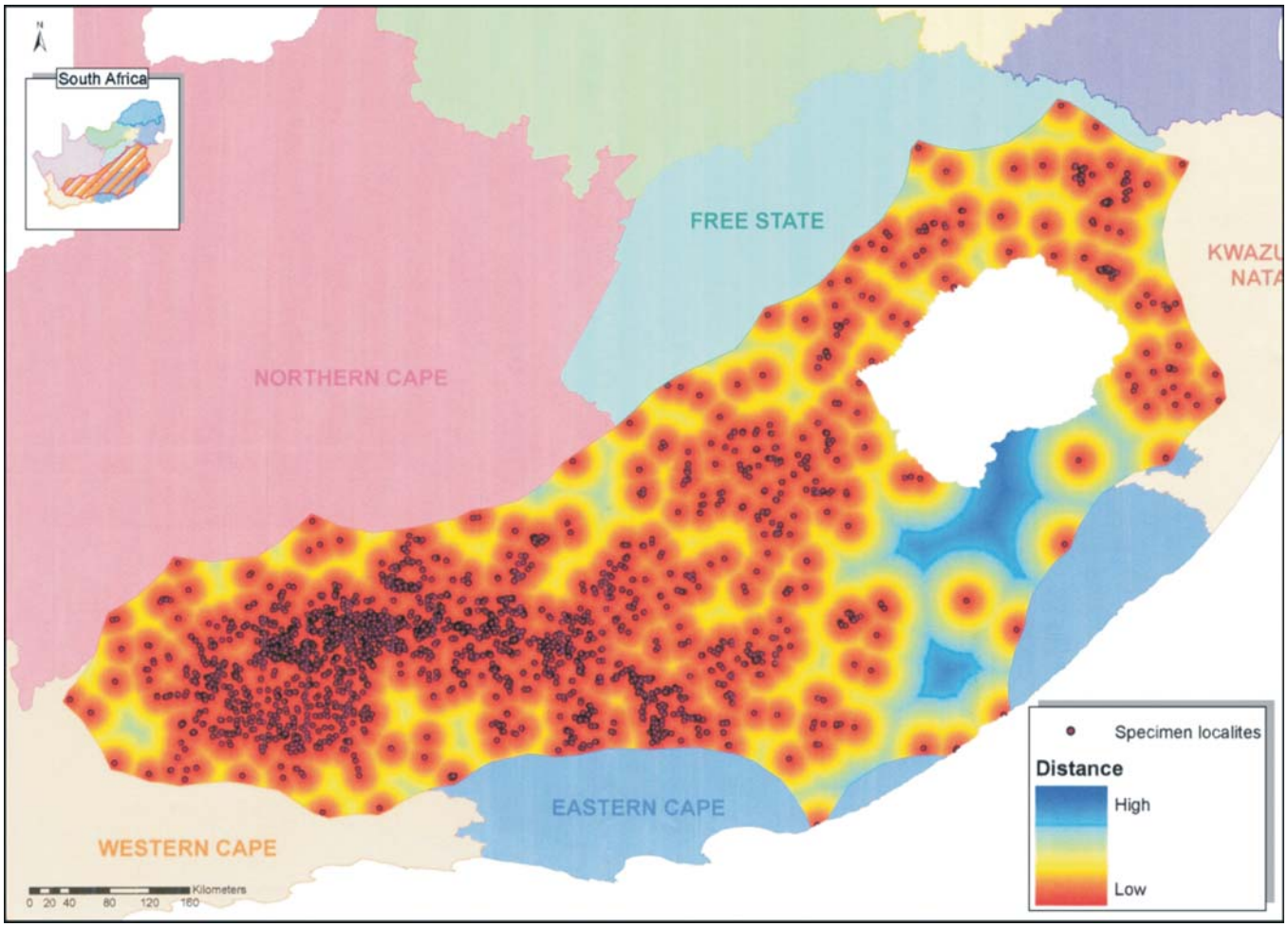


Figure 3. Gap analysis of tetrapod fossil localities in the Beaufort Group of South Africa.

(Cooper & Netterberg 2004). The surface was derived for an area larger than the extent of the Beaufort Group, and then masked to the extent of the sampling to remove edge effects.

Figure 3 indicates the sampling distribution of fossils in the Beaufort Group. Several factors could account for a lack of sampling in certain areas. These include absence of outcrop; lack of prospecting; or paucity of fossils. Blue shading indicates a substantial distance between fossil collecting sites, while a red–orange spatial pattern indicates a relative closeness of fossil sites to each other. The overwhelming dominance of orange–red (Fig. 3) indicates that the majority of fossil localities are in close proximity to each other with an *even* distribution and points to a lack of sampling bias. This implies that the sampling of the Karoo fossil fauna as represented by the fossils in the collections will provide an accurate interpretation of the reality of faunal distribution patterns and ecological representation for the Beaufort Group.

Once the equality of the distribution of fossil finds across the Beaufort Group was established, Neighbourhood Analysis Technique was applied to determine where the highest density of specimens was located (Fig. 4). The Neighbourhood Statistic used was the sum of all the points, with a circle neighbourhood within an 8-km radius (Cooper & Netterberg 2004). This was used to provide an indication of the number of specimens from a given locality. The resultant surface was 'smoothed out' to improve visual representation of the analysis (Cooper & Netterberg 2004).

The incidence of dark red shading represents those localities which have the highest density of specimens (Fig. 4). The obvious horizontal line of red/orange dots in Figure 4 highlights that it is most certainly a collecting bias caused by the superior vertical exposures of fossil bearing strata in the Sneeuberg and Neuweveld mountain ranges along the Great Escarpment. The strata most exposed in the escarpment belong to the *Tropidostoma, Cistecephalus* and *Dicynodon* biozones. Figures 3 & 4 clearly show the geographic collecting bias along the Great Escarpment. This means that these biozones may have been over-collected compared to other biozones.

As indicated by the yellow shading in Fig. 4 most fossil sites yield an average of 1–60 specimens. Localized bias on the yield of fossils at specific sites is the result of differing resolutions of locality information (i.e. GPS, Farm Name, and District) and well as the result of superior exposures. Localized biases become inconsequential when viewed across the scale of the entire Beaufort Group because the finer details of locality data specifics are blurred in the light of the larger low resolution picture of the Beaufort Group. We are satisfied that the concentration of collecting in the Great Escarpment is the result of superior and extensive exposures of clean rock faces and that the Gap and Neighbourhood analyses generally reflect a lack of collecting bias as regards individual taxonomic specializa-

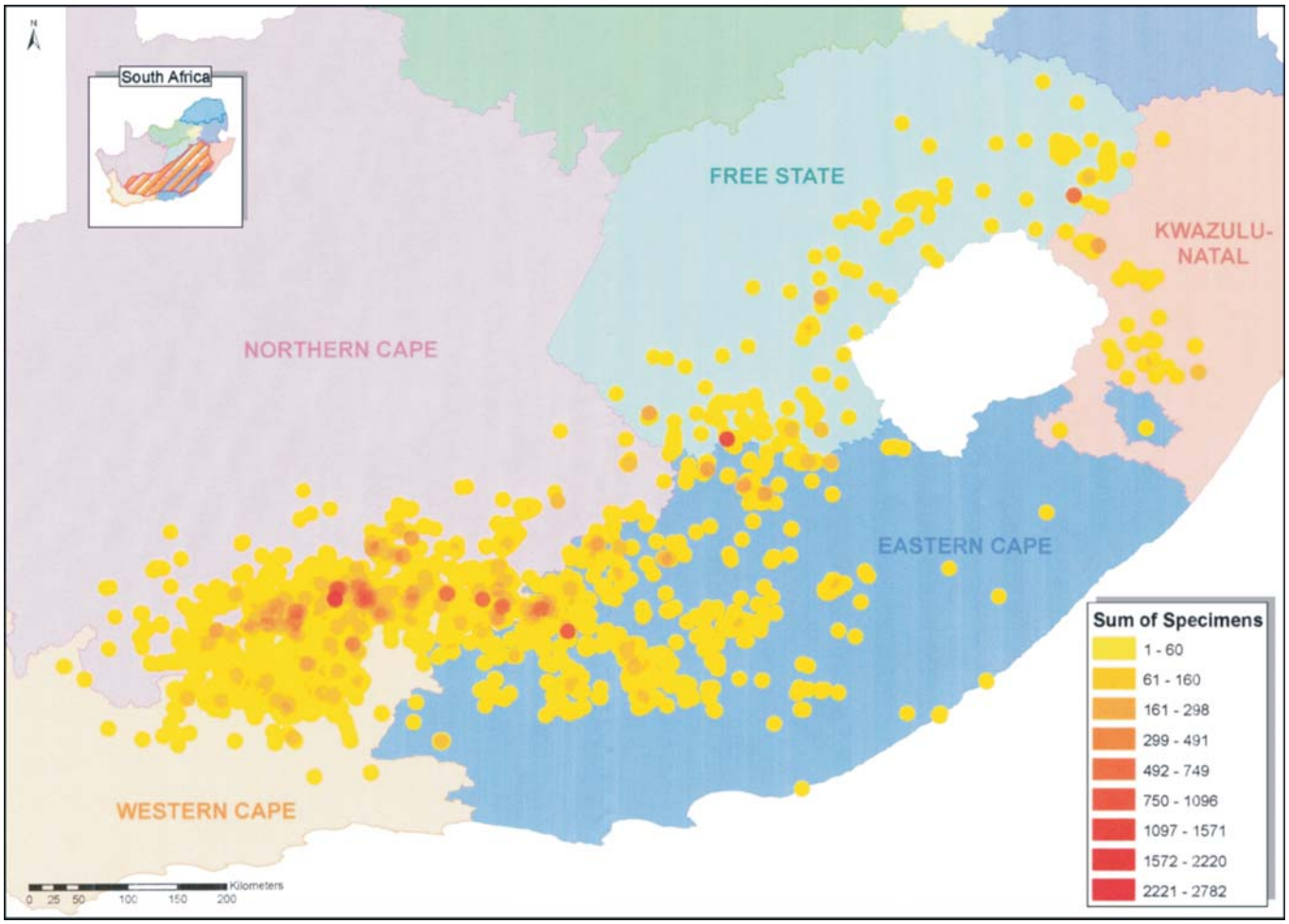


Figure 4. Neighbourhood analysis of fossil finds in the Beaufort Group of South Africa.

tions, or localized over-representation. Such a resultant allows researchers to confidently analyse the faunal distribution assemblage as well as biodiversity patterns of the Beaufort Group (Karoo Supergroup) of South Africa.

CONCLUSION

For the first time an amalgamated, standardized database (Beaufort Group database) as well as a GIS database incorporating all tetrapod fossils from the rocks of the Beaufort Group has been established. They are stored on a dedicated computer at the Bernard Price Institute for Palaeontological Research and are available to scientists to be utilized as a research tool. As the Beaufort Group succession preserves the most complete record of Middle Permian to Middle Triassic continental tetrapod biodiversity, this database is of great importance for an understanding of biodiversity changes and for biostratigraphic input to basin modelling over this extended period.

The databases reflect the diversity of tetrapod genera and the collections where they are curated, including numbers of specimens of each genus and their respective locality and/or biozone data. This unique dataset provides accurate numbers of specimens of the various taxa which have been collected. In addition the database will facilitate future taxonomic research as it is now possible for researchers to identify museums which curate the largest sample of any particular taxon. Finally, future researchers can be assured of the reliability of their results pertaining to biodiversity within the Beaufort Group because we have found no taxonomic bias due to selective collecting of particular taxa by specialist palaeontologists.

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A new record of *Procynosuchus delaharpeae* (Therapsida: Cynodontia) from the Upper Permian Usili Formation, Tanzania

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Procynosuchus, the best-known Permian cynodont, has a remarkably broad geographic range, with records stretching from southern Africa to Europe. Fossils of *Procynosuchus* are most common in the Upper Permian *Dicynodon* Assemblage Zone of South Africa, but also occur in coeval East African rocks. Currently, there is one documented occurrence from the Madumabisa Mudstone Formation of Zambia, and two specimens from the Usili (=Kawinga) Formation of Tanzania. The Tanzanian specimens include a poorly preserved, incomplete skull and a partial cranium originally attributed to *Parathrinaxodon proops.* The latter is now considered a subjective junior synonym of *Procynosuchus delaharpeae.* Here we report on a new specimen collected in 2007 near the base of Kingori Mountain in Tanzania. It preserves the postorbital region of the skull and the posterior portions of both lower jaws, each containing several intact teeth. A well-preserved postcanine tooth exhibits the dental hallmarks of *Procynosuchus* and permits unambiguous referral to this taxon. Recent fieldwork corroborates previous suggestions that the Usili tetrapod fauna includes representatives of the *Tropidostoma, Cistecephalus* and *Dicynodon* assemblage zones of South Africa. Moreover, the presence of several endemic Usili taxa (e.g. *Katumbia, Kawingasaurus, Peltobatrachus*), suggests that a straightforward correlation between the Usili tetrapod fauna and a particular assemblage zone from the Beaufort Group may not be possible.

Keywords: *Procynosuchus,* Cynodontia, Permian, Tanzania, Usili Formation, Songea Group, Ruhuhu Basin.

INTRODUCTION

Cynodonts were the last major group of therapsids to diversify in the Permian, first appearing in the *Tropidostoma* Assemblage Zone of South Africa (Botha *et al.* 2007; Botha & Abdala 2008). They underwent a second radiation in the Triassic, diversifying into a wider range of body sizes and, presumably, ecological niches (Rubidge & Sidor 2001; Kemp 2005). With Mammalia as its extant subclade, Cynodontia is key for understanding the timing of the acquisition of numerous mammalian features, such as multicusped postcanines, a bony secondary palate, wide zygomatic arches, and a masseter muscle (Hopson & Barghusen 1986; Abdala & Damiani 2004; Sidor & Smith 2004).

Procynosuchus has been considered the first cynodont to attain a global distribution (Sues & Boy 1988; Abdala & Allinson 2005). The genus is well represented in the Beaufort Group of South Africa, especially in the *Dicynodon* Assemblage Zone, but less so elsewhere. In Germany, isolated postcanine teeth referred to *Procynosuchus* sp. have been recovered from the fissure-fill deposits within the lower Zechstein (Sues & Boy 1988; Sues & Munk 1996). Kemp (1979, 1980) described a nearly complete skeleton collected from the Madumabisa Mudstone Formation of Zambia. Finally, two specimens have been recorded from Tanzania: a fragmentary skull described by von Huene (1950) and a specimen that Parrington (1936) originally attributed to *Parathrinaxodon proops* (Gay & Cruickshank 1999; Abdala & Allinson 2005). Von Huene's specimen preserves the snout, but neither the braincase nor postorbital regions of the skull. Parrington's fossil is more complete, but lacks the zygomatic arches and the dorsal and posterior portions of the braincase. Neither Tanzanian specimen preserves the lower jaw.

Here we report on *Procynosuchus* material recently collected from the Upper Permian of Tanzania. Its identification lends further support to Abdala & Allinson's (2005) conclusion that *Procynosuchus* was widespread in southern Gondwana near the end of the Permian, and that only a single cynodont genus was present in the Usili (=Kawinga) Formation.

GEOLOGICAL SETTING

The main Karoo Basin of South Africa is a retro-arc foreland sag basin first formed in the Late Carboniferous in response to compressional thrusting and crustal loading along the subducting southern margin of Gondwana (Johnson *et al.* 1996). The basin was fairly continuously infilled with terrestrial sediments until the Early Jurassic, after which the tectonic regime switched to one of extension as eastern Gondwana began to break up. At the time of the infilling of the Karoo Basin, the crust to the north was subjected to several extensional phases punctuated by quiescence, forming a series of pull-apart rifts, grabens and half grabens filled with locally derived terrestrial sediments. Today, these small fault-bounded basins occur in a roughly NE/SW trending corridor extending from the coast of Kenya through Tanzania, Malawi and Zambia, and terminating in Zimbabwe. The best and most complete

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exposures of Karoo-aged strata in these fault bounded basins are located in the Ruhuhu Basin, which is situated in southern Tanzania (Stockley & Oates 1931; Stockley 1932; Kreuser 1990; Kaaya 1992; Wopfner 2002; Catuneanu *et al.* 2005).

Within the Ruhuhu Basin, the rocks of the Songea Group range in age from Late Carboniferous to Middle Triassic and have been divided into six formations and one informally recognized unit (viz. Idusi, Mchuchuma, Mbuyura, Mhukuru, Ruhuhu and Usili formations and the informal Manda Beds, Wopfner 2002; Fig. 1). The Usili Formation (formerly K6 or Kawinga Formation) is considered Late Permian in age (Parrington 1936; Wopfner & Kreuser 1986; Wopfner 2002) and comprises alluvial fan conglomerates at the base followed by playa lake deposits of green and red mudrocks with interbedded fluvial siliciclastics (Wopfner & Markwort 1991).

The Usili Formation has been correlated with the Balfour and/or Teekloof formations of the South African Beaufort Group (Adelaide Subgroup) on the basis of their shared tetrapod fauna (Gay & Cruickshank 1999; Wopfner 2002; Catuneanu *et al.* 2005). In particular, dicynodonts such as *Dicynodon, Dicynodontoides* (formerly *Kingoria*; see Angielczyk *et al.*, in press), *Oudenodon* and *Rhachiocephalus* suggest a broad temporal correspondence between the Ruhuhu Basin and the upper parts of the Karoo Permian sequence (Angielczyk 2007; Angielczyk *et al.*, in press).

MATERIALS AND METHODS

The present specimen, NMT RB3, was collected in the Usili Formation near the base of Kingori Mountain in June, 2007. It was partially prepared at the South African Museum, with final cleaning at the Burke Museum of Natural History. Comparative data for *Procynosuchus* was based mainly on Parrington (1936), Broom (1938), Kemp (1979) and Abdala & Allinson (2005), with supplementary data from von Huene (1950) and Kemp (2005).

SYSTEMATIC PALAEONTOLOGY

Synapsida Osborn, 1903
Therapsida Broom, 1905
Cynodontia Owen, 1861

Procynosuchus delaharpeae Broom, 1937

Holotype. RC 5, well-preserved cranium missing the temporal arches and anterior portion of the premaxilla.

Diagnosis. Cynodont with shallow fossa positioned high on lateral surface of coronoid process, multicusped lingual cingulum on lower postcanines and absence of labial cingulum, interpterygoid vacuity relatively broad (modified from Kemp 1979).

Referred specimen. NMT RB3, which consists of the postorbital portion of skull, posterior portions of both mandibles, and an isolated postcanine tooth.

Locality. Usili Formation, Songea Group, Ruhuhu Basin. Present specimen collected near the base of Kingori Mountain, Songea District, Tanzania at the following coordinates: 10°14.293'S, 35°3.591'E. This is in the general vicinity of Stockley's (1932) locality B19 and Nowack's (1937) Kingori Mountain localities, although both have proven difficult to relocate precisely.

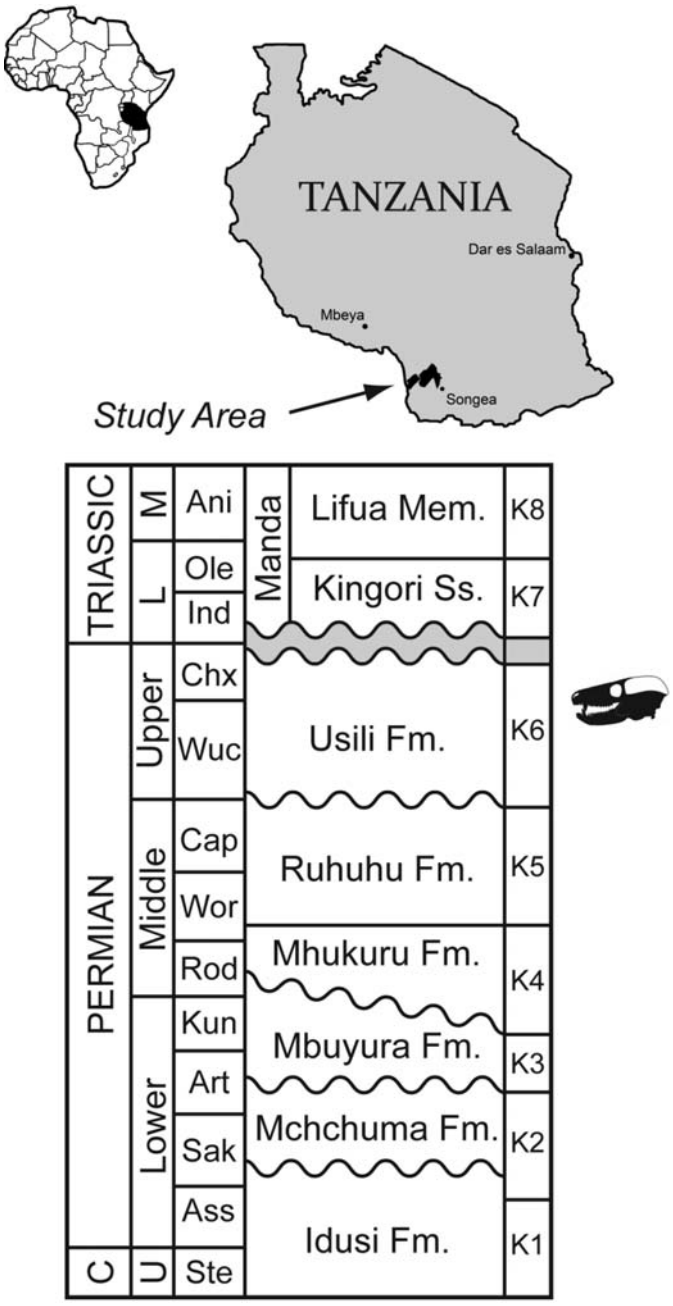


Figure 1. Generalized geology and geography of the Songea Group (Ruhuhu Basin). Correlations between lithostratigraphy and marine stages based on Wopfner (2002). Skull icon (modified from Hopson, 1994) denotes approximate stratigraphic position of *Procynosuchus*.

DESCRIPTION

General preservation

The partial cranium consists of the intertemporal region, the caudal part of the left zygomatic arch, and much of the braincase and occiput. Posterior sections of both lower jaws are also preserved, with both dentaries retaining postcanine teeth. In addition, a beautifully preserved postcanine was found suspended in matrix next to the parietal foramen.

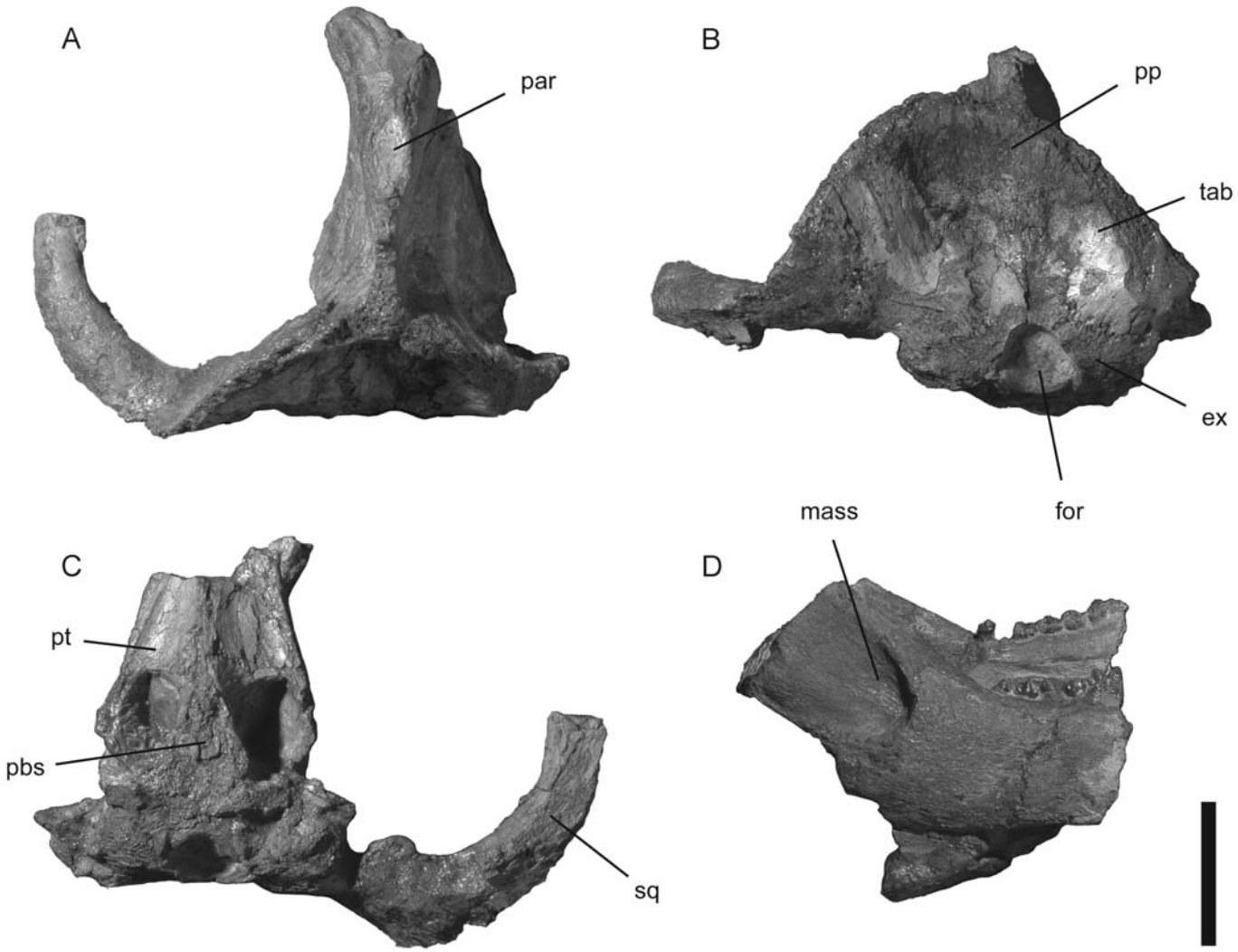


Figure 2. Partial skull of *Procynosuchus delaharpeae* (NMT RB3) in (**A**) dorsal, (**B**) occipital and (**C**) ventral views. Posterior portions of lower jaws of the same specimen in right lateral view (**D**). Scale bar = 2 cm.

Temporal region

Despite its fragmentary nature, the specimen retains the broad outlines of a cynodont temporal region in dorsal view, with a narrow sagittal crest between enlarged temporal fenestrae (Fig. 2A). An oval parietal foramen is incorporated into the sagittal crest, and is about twice as long as it is wide. Part of the temporal ramus of the left postorbital is preserved overlying the corresponding parietal. A midline suture between the parietals is impossible to discern, which, along with the specimen's large size, suggests that the fossil pertains to a mature individual. Comparison with complete skulls of *Procynosuchus* suggests a skull length of approximately 140 mm for NMT RB3.

The confluence of the sagittal and lamboidal crests is eroded dorsally, but more laterally the parietal-squamosal suture is visible on the left side and conforms to the arrangement shown in Kemp (1979, fig. 3). The posterior half of the left zygomatic arch is present. It is formed primarily by the squamosal, but a small wedge of the jugal remains attached to its medial surface. The ventral margin of the squamosal is weathered and incomplete.

Beneath the parietal, the medial wall of the temporal fenestra is formed by the descending lamina of the parietal, as well as by the expanded epipterygoid characteristic of cynodonts (Hopson & Barghusen 1986; Sidor & Smith 2004). The latter element is trapezoidal in outline, with its free anterior edge inclined anterodorsally and its more vertical, posterior margin sutured to the prootic. The venous channel is well developed on both sides, but is positioned relatively lower than depicted by Kemp (1979: fig. 16).

Basicranium

In ventral view, the braincase and posterior portion of the palate are present (Fig. 2C). The basicranial rami of the pterygoids are separated from one another by a very narrow interpterygoid vacuity. As noted by Kemp (1979), the retention of an interpterygoid vacuity is characteristic of *Procynosuchus* among cynodonts, although the relatively large opening present in the specimen that he described (TSK34) suggests that it belongs to a juvenile individual (Abdala & Allinson 2007; see also van Heerden 1972). Immediately anterior to the vacuity, the medial borders of the pterygoids are pinched together into a midline crest.

The cultriform process of the parasphenoid is visible for a short distance between the basipterygoid processes, before it disappears above the pterygoids. Further posteriorly, the ventral surface of the parabasisphenoid complex is quite eroded, such that internal carotid foramina are not

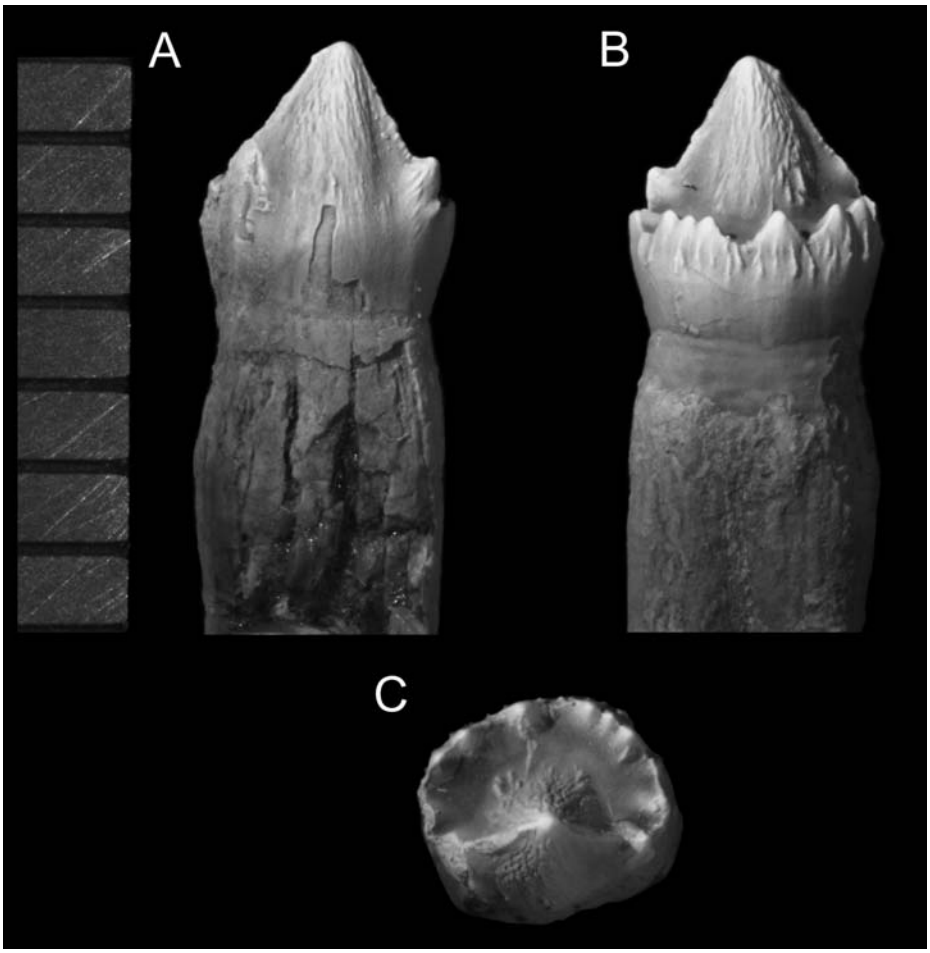


Figure 3. Isolated lower postcanine tooth of *Procynosuchus delaharpeae* (NMT RB3) in (**A**) labial, (**B**) lingual, and (**C**) occlusal views. Scale bar divisions in mm.

apparent. Additionally, both the external surface of the basioccipital as well as the entirety of the occipital condyles is missing. On the left side, the rugose lateral margin of the fenestra ovalis is preserved, along with part of the lateral process of the prootic.

Occiput

The occiput is nearly vertical and well preserved (Fig. 2B). The tabulars and supraoccipital form the bulk of the occipital surface and together create a large concave surface for the attachment of cervical muscles. Erosion has reduced the total height of the occiput, but the postparietal is still clearly visible above the supraoccipital. The upper margin of the foramen magnum is well preserved and formed by the supraoccipital. The dorsolateral margins of the foramen magnum are formed by the exoccipitals, but ventrally the occipital condyles are eroded away, leaving the eroded basioccipital on the ventral midline. Lateral to the foramen magnum, a suture separating the exoccipital and paroccipital process of the opisthotic is not discernible. The dorsal rim of the left post-temporal fenestra is intact and formed by the tabular.

Mandibles

The posterior portions of both mandibles were found closely associated, but displaced and positioned within the left temporal fenestra. As prepared, there are a few millimeters of matrix between the right and left rami, making identification of postdentary bones such as splenial and articular difficult. However, next to the ventral face of the left mandibular ramus is a thin sheet of bone attached to the matrix. We interpret this element as the left splenial, or possibly angular, that has slipped ventrally.

The lateral surface of both dentaries is completely exposed. On the right side (Fig. 2D), a conspicuous masseteric fossa is located relatively high on the coronoid process of the dentary, as is typical for *P. delaharpeae* and *Dvinia prima* (Tatarinov 1968: fig. 5; Kemp 1979: fig. 6). The horizontal rami of both dentaries are broken approximately halfway along their length.

Dentition

The right dentary retains five intact postcanines (Fig. 2D) whereas the left retains six. Each postcanine conforms to the general dental pattern of *Procynosuchus,* with a dominant cusp flanked by anterior and posterior accessory cusps, and bordered lingually by a well-developed cingulum studded with fine cuspules (Kemp 1979). In occlusal view, the lingual cingulum gives the postcanines an oval section (i.e., longer mesio-distally than labio-lingually). A labial cingulum is absent. The penultimate tooth position on the left dentary is represented by an edentulous gap.

An isolated postcanine tooth was found suspended in matrix next to the sagittal crest. This tooth is nearly pristine

(Fig. 3), and although its original position cannot be determined with confidence, the presence of eight lingual cingulum cuspules suggests that it came from the posterior portion of the tooth row. For descriptive purposes, we consider this tooth to belong to the lower jaw, although the upper and lower postcanines of *Procynosuchus* generally are very similar. If this position is accepted, the anterior accessory cusp is broken. Beyond this, however, the crown lacks visible wear, and thus was likely newly erupted.

Fine crenulations are visible on the lingual aspect of the main cusp as well as below the lingual cuspules. Similar crenulations are visible on the labial face of the principle cusp, but these are somewhat more muted. Interestingly, the crenulations were hardly visible before the specimen was smoked with magnesium for photography. Kemp (1979) makes no mention of enamel crenulations in his description, and we are unaware of this feature's recognition in the literature.

The crown is separated from its single, long root by a slight narrowing at the cervix. As preserved, the root forms approximately two-thirds of the total height of the tooth.

DISCUSSION

All of the available craniodental evidence indicates that NMT RB3 pertains to the well-known Permian cynodont *Procynosuchus.* For example, the lower postcanine teeth exhibit a dominant main cusp flanked by small anterior and posterior accessory cusps as well as a denticulated lingual cingulum (Kemp 1979). Likewise, the relatively small masseteric fossa, which does not reach the ventral edge of the dentary, corroborates its referral to *Procynosuchus,* although *Dvinia* also retains this feature (Tatarinov 1968).

NMT RB3 confirms the presence of *Procynosuchus* in the upper half of the Usili Formation. Unfortunately, because the specimen was found *ex situ,* we cannot place its occurrence more precisely. However, the specimen was found in close proximity to several partial gorgonopsian skulls, as well as a short-faced, tusked dicynodont likely referable to '*Dicynodon*', and a snout of the therocephalian *Theriognathus.* As noted by Angielczyk *et al.* (2008), our field observations have failed to find evidence for more than one tetrapod assemblage within the Usili Formation (contra von Huene 1950). The dicynodont component of the fauna is particularly uniform throughout the thickness of the formation, given our field observations and locality information available for specimens in museum collections.

Gay & Cruickshank (1997), Abdala & Allinson (2005) and Angielczyk (2007) all made note of the interesting mix of widespread [e.g. *Endothiodon, Kingoria* (now *Dicynodontoides*; Angielczyk *et al.,* in press), *Oudenodon*] and endemic (e.g. *Kawingasaurus, Katumbia, Peltobatrachus*) taxa recovered from the Usili Formation. The Usili fauna is also remarkable in its apparent lack of several genera commonly found in the Beaufort Group of South Africa (e.g. *Diictodon, Emydops*). One potential factor affecting faunal composition could be the influence of basin subsidence rates (e.g. retroarc sag basin in the Karoo versus fault-bounded rift in the Ruhuhu). The sedimentary facies of the Usili Formation show that initially high-energy alluvial fans prograded from the bounding fault scarps, depositing tongues of reworked conglomeratic sand into the margins of a deep stratified axial lake (see Wopfner 2002).

Later, as subsidence slowed, the alluvial fans amalgamated to form a fairly continuous alluvial plain with meandering channels and expansive floodplains dotted with shallow playa lakes. Under semi-arid climatic conditions, these floodplains likely supported perennial vegetation, including glossopterid trees, shrubs and ferns. The tetrapod fossils occur in two main taphonomic modes: concentrated pockets of disarticulated and broken elements in the basal conglomerates, and as isolated, more complete skeletons within the floodplain fines. The conglomerates contain numerous stromatolitic carbonate nodules that have clearly been eroded from the underlying Ruhuhu mudstones during a hiatus in sedimentation. It is likely that the bone concentrations were also generated at the same time as the conglomerates and as such they represent a much larger time interval than the overlying mudrock-hosted skeletons. However, despite this likely difference in time-averaging, there is no significant difference in the faunal composition of the two types of bone occurrence. Regardless of its basis, the Usili tetrapod fauna is unique and straightforward correlation with a particular assemblage zone of the Beaufort Group may not be possible.

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ABBREVIATIONS

Institutional

NMT	National Museum of Tanzania, Dar es Salaam
RC	Rubidge Collection, Graaff-Reinet
TSK	Collection of Thomas Kemp, currently housed in the Oxford University Museum of Natural History

Stratigraphic

Ani	Anisian
Art	Artinskian
Ass	Asselian
C	Carboniferous
Cap	Capitanian
Chx	Changhsingian
Fm	Formation
Ind	Induan
Kun	Kungurian
L	Lower
M	Middle
Mem	Member
Ole	Olenekian
Rod	Roadian
Sak	Sakmarian
Ss	Sandstone
Ste	Stephanian
Wor	Wordian
Wuc	Wuchiapingian

Anatomical

ex	Exoccipital
for	Foramen magnum
mass	Masseteric fossa
par	Parietal foramen
pbs	Parabasisphenoid
pp	Postparietal
pt	Pterygoid
sq	Squamosal
tab	Tabular

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The postcranial skeleton of the basal therocephalian *Glanosuchus macrops* (Scylacosauridae) and comparison of morphological and phylogenetic trends amongst the Theriodontia

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The postcranial morphology of the early scylacosaurid therocephalian *Glanosuchus macrops* from the *Pristerognathus* Assemblage Zone of the Beaufort Group is described and compared with that of later therocephalians. This database is used as a basis to identify postcranial differences between therocephalians, gorgonopsians and cynodonts in an attempt to increase understanding of the postcranial anatomy of theriodont therapsids. It is demonstrated that some postcranial elements can be used to identify particular theriodont groups. The T-shaped interclavicle, absence of ossified sternum, humerus without shaft area, and large pubic foramen are characteristics of therocephalians from the *Tapinocephalus* Assemblage Zone of the Beaufort Group of South Africa.

Keywords: Therocephalia, *Glanosuchus,* therapsid postcranium, Theriodontia.

INTRODUCTION

The rocks of the Karoo Supergoup are internationally acclaimed for their richness and diversity of fossil therapsids of Mid Permian to Early Jurassic age. Despite being one of the six important therapsid clades, the Therocephalia has received relatively little recent research attention, apart from the basal forms (Abdala *et al.* 2008; van den Heever 1994). Therocephalians have a wide geographic distribution, being known from southern and eastern Africa (Keyser & Brink 1979; Boonstra 1935; Drysdall & Kitching 1963; Boonstra 1969; Kitching 1977), China (Li & Cheng 1995), Russia (Tatarinov 1974), eastern Europe (Golubev 2000), and Antarctica (Colbert & Kitching 1981) and together with dicynodonts, have the longest stratigraphic range of any therapsid clade.

As relatively little work has been done on the postcranial anatomy of basal therocephalians this description of a recently discovered skeleton of a scylacosaurid is of importance in our understanding of the development and functioning of early therapsid postcranial morphology. Broom (1936) superficially described the incomplete skeleton of *Pristerognathus baini* (now *Glanosuchus*) (van den Heever 1994) and Boonstra (1964) described the girdles and limbs of the Lycosauria and the Scylacosauria. Cys (1967) described the postcranium of *Cynariognathus platyrhinus.* Ray *et al.* (2004), as part of a groundbreaking comparative study of bone microstucture of selected therocephalian, gorgonopsian and cynodont genera, described the bone histology of *Pristerognathus.* Our study is the first description of both the axial and appendicular skeleton of a scylacosaurid therocephalian and provides a comparison with postcranial elements of other theriodont nonmammalian therapsids.

MATERIAL

The specimen of *Glanosuchus macrops* (SAM-PK K 7809) which forms the basis of this study was found in 1989 by Roger Smith on the farm La de Da, Beaufort West, which is situated in the *Pristerognathus* Assemblage Zone (Lower Teekloof Formation) of the Beaufort Group. Mechanical preparation, carried out by Annelise Crean at the Iziko South African Museum, exposed the dorsal side of the curled-up skeleton (Fig. 1). In comparison with other therocephalian postcrania from the lower Beaufort, which are generally poorly and incompletely preserved (van den Heever 1994), this articulated specimen is uniquely well preserved and fairly complete.

Basal Therocephalia comprises two clades, Scylacosauridae and Lycosuchidae, which are both characterized by the presence of serrated teeth, three lower incisors, large canines, narrow unfused vomer and a well-developed postfrontal. *Glanosuchus* is identified on cranial features as a large scylacosaurid with dental formula I5+1, C1, Pc5; first five incisors large but sixth inconstant and when present very small; canine large and strong; postcanines moderately to weakly developed; skull large (maximum length 315–321); preorbital hollow fairly shallow, not sharply demarcated and really not more than a groove stretching from the orbit in the direction of the canine; septomaxilla and septomaxillary foramen well developed; snout broader than high, slightly narrowed between orbit and canines; orbits well in posterior half of skull; mandibular symphyses formed solely by dentaries with weak, unankylosed sloping mentum; epipterygoid only slightly widened; sagittal crest of parietals only moderately high but fairly sharp (van den Heever 1994).

POSTCRANIAL DESCRIPTION

Only the left side of the skull of SAM-PK K 7809 is exposed and the left forelimb, including the articulated manus, is well preserved close to the cranium (Fig. 1). The right forelimb is beneath the body and has not been prepared. Most of the dorsal view of the pectoral girdle is obscured by thoracic vertebrae and ribs, allowing description of only parts of the clavicles. Well-preserved and

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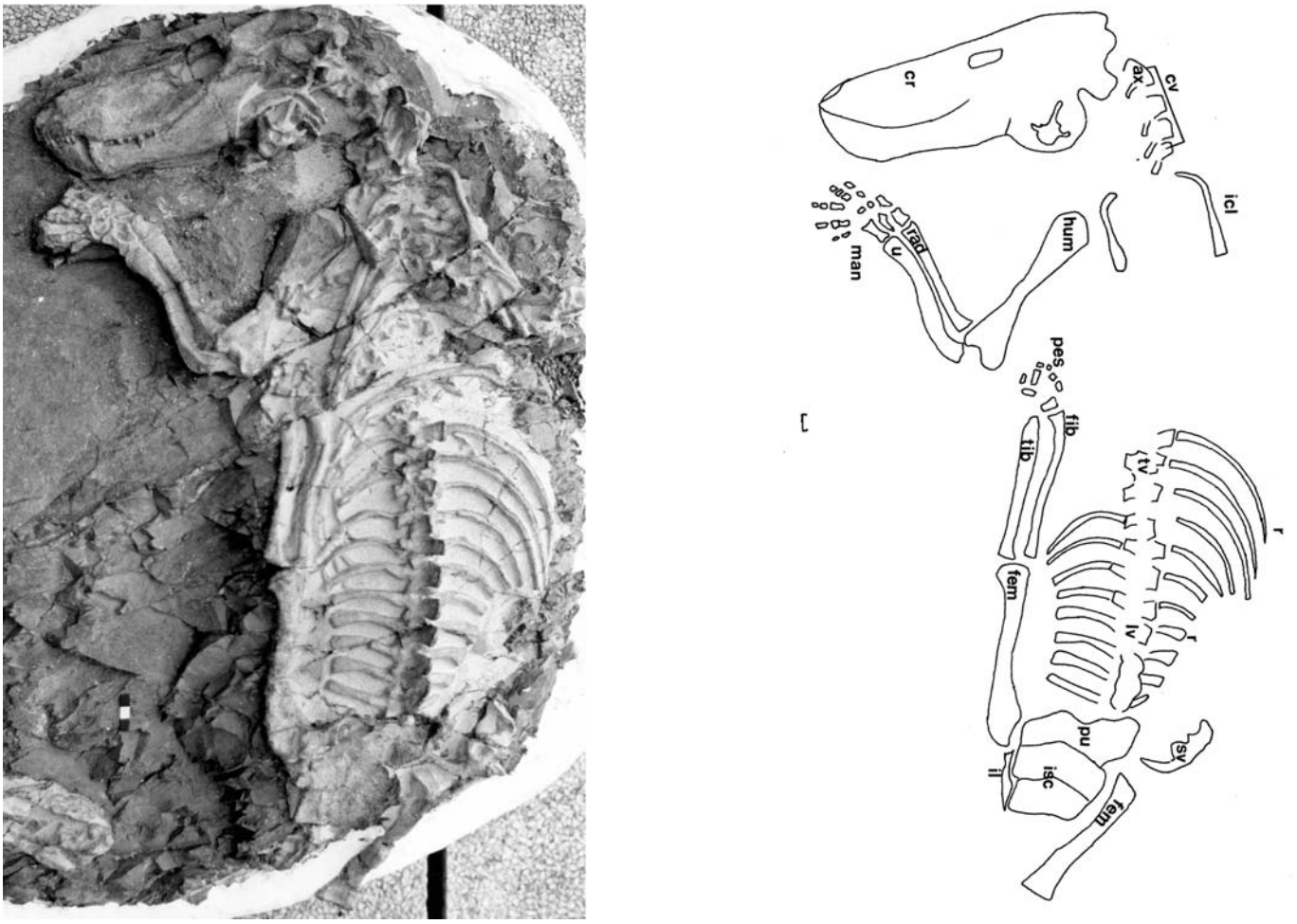


Figure 1. Dorsal view of *Glanosuchus macrops* (SAM-PK K 7809) to illustrate the position in which the postcranial elements are preserved (scale 10 mm) and photograph of dorsal view of *Glanosuchus macrops* (SAM-PK K 7809) to show morphological detail (scale 10 mm).

fully articulated dorsal vertebrae are present behind the clavicles, making it possible to differentiate between thoracic and lumbar vertebrae and their respective ribs. In the sacral region only one sacral vertebra and one pair of ribs are visible. Of the pelvic girdle, both the pubes and ischia, and only the left ilium are preserved. The right hind limb lacks the tibia, fibula and pes, while the left hind limb is well preserved with the exception of the pes which is crushed. Only a few of the caudal vertebrae are preserved.

Vertebrae

The vertebral column, which is almost completely articulated, allows a vertebral count of at least forty-one vertebrae (Fig. 2). This figure includes 28 presacrals, one sacral, four caudals and eight unidentifiable vertebrae. Presacrals are divided into cervical, thoracic and lumbar vertebrae and are easy to distinguish on morphological grounds (Fourie 2001). Of these, six cervicals are preserved; the first five vertebrae (including the atlas and axis) are in articulation and the posterior cervical was disarticulated and displaced prior to fossilization. At least 22 dorsal vertebrae (sixteen thoracic, six lumbar) are preserved with attached ribs.

Very little of the proatlas can be described as only a very small portion of the right neural arch of this vertebra is visible in dorsal view as a rectangular piece of bone. The atlas neural arch is wider laterally than medially with a convex dorsal surface. The axis is preserved in articulation with the remaining three or four cervicals and has the same morphology as described for *Cynariognathus* (Cys 1967), a baurioid (Kemp 1986), and *Regisaurus* (Fourie & Rubidge 2007). The longitudinally expanded axial neural spine, when viewed from above, is thin dorsally, almost sharp and slopes gently anteroventrally making it higher posteriorly than anteriorly (Fig. 2A). Of all the cervical vertebrae, the neural spine of the axis has the greatest anteroposterior expansion and is widest at its most dorsal extremity. The postzygapophysis, which protrudes posteriorly beyond the centrum, is disc-like with slightly rounded dorsal, posterior and posterolateral areas. Anteroventral to the postzygapophysis the long, rectangular transverse process slopes slightly ventrally. The prezygapophysis is positioned anterior to the transverse process and extends anteriorly beyond the centrum. In lateral view the centrum is hourglass-shaped and in anterior view it is amphicoelus.

Apart from the atlas and axis there are 3–4 additional cervical vertebrae which have narrower rectangular neural spines and a triangular dorsal surface with the apex pointing anteriorly. The morphology of the rest of the vertebra is similar to that of the axis. As in other therocephalians (Fourie & Rubidge 2007), cervical vertebrae are easily distinguished from those of the thoracic-lumbar

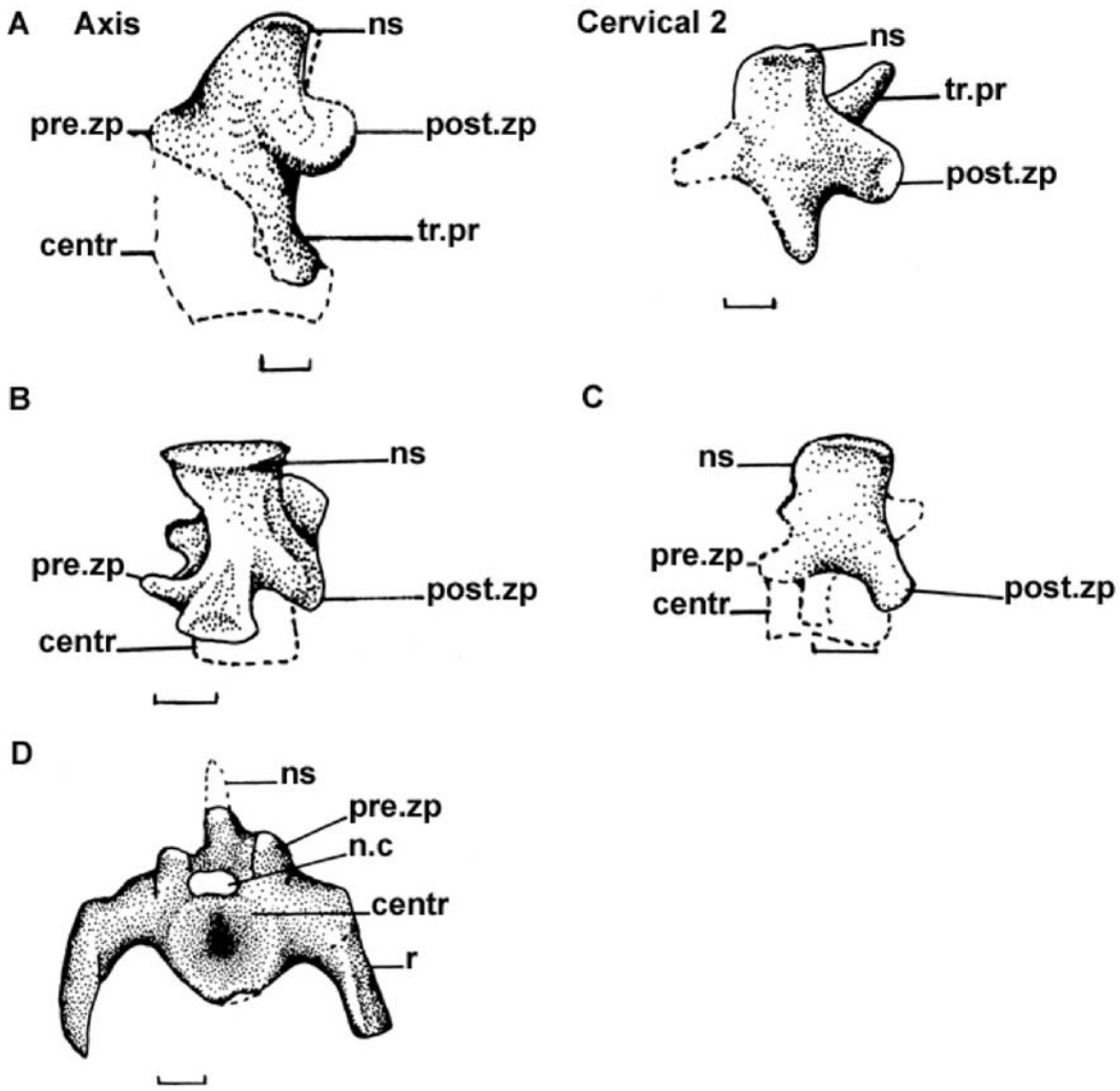


Figure 2. Vertebrae of *Glanosuchus macrops* (SAM/K 7809); **A**, axis and cervical C2 (lateral view); **B**, thoracic T13 (lateral view); **C**, lumbar L2 (lateral view); **D**, sacral (anterior view) (scale 10 mm).

region in that the cervicals are more massive.

Sixteen thoracic vertebrae are present in SAM-PK K 7809 and each has the same general morphology as the cervical and lumbar vertebrae (Fig. 2B) described for *Glanosuchus* and *Cynariognathus* (Cys 1967). In comparison with the thoracic vertebrae, in lateral view the lumbar neural spines (Fig. 2C) are shorter and broader, with that of the first lumbar being the broadest. In addition, lumbar vertebrae are easily recognized by their short and broad posteroventrally sloping transverse processes and shorter ribs which are fused to the transverse process and have no connection with the sternum.

Only one sacral vertebra is preserved and is exposed in anterior view (Fig. 2D). The amphicoelus centrum is large, concave towards the centre and round with a circular neural canal. A slight longitudinal elongated depression is present between the centrum and the base of the neural canal. The terminally rounded prezygapophysis, situated dorsolateral of the neural canal, slopes posteroventrally towards the transverse process. The transverse process is large and rounded dorsally.

The caudal series is incomplete, but the presence of four vertebrae indicates that the number in life was in excess of this. The first caudal vertebra is large, has prominent transverse processes, and appears to have the same morphology as that of other therocephalian genera (Fourie & Rubidge 2007). The short neural spine slopes down towards the almost square transverse process which is short, thick and rounded dorsally.

Ribs

Most of the ribs of SAM-PK K 7809 are preserved semi-articulated with their corresponding vertebrae (Fig. 3). The only preserved cervical rib was displaced prior to fossilization and is visible only in posterior view. This rib is short, slender and slightly curved with a double head. The tuberculum is thicker than the capitulum which is longer and thinner and has a short groove extending midway down the posterior side of the shaft as far as the distal end. The shaft portion of the rib is anteroposteriorly flattened with both dorsal and ventral edges rounded.

The anteriormost thoracic ribs are disarticulated and are preserved in the pectoral region, while five posterior thoracic ribs are preserved in articulation and are not fused to their corresponding vertebrae. Ribs in the thoracic region are long with double-heads, the capitulum

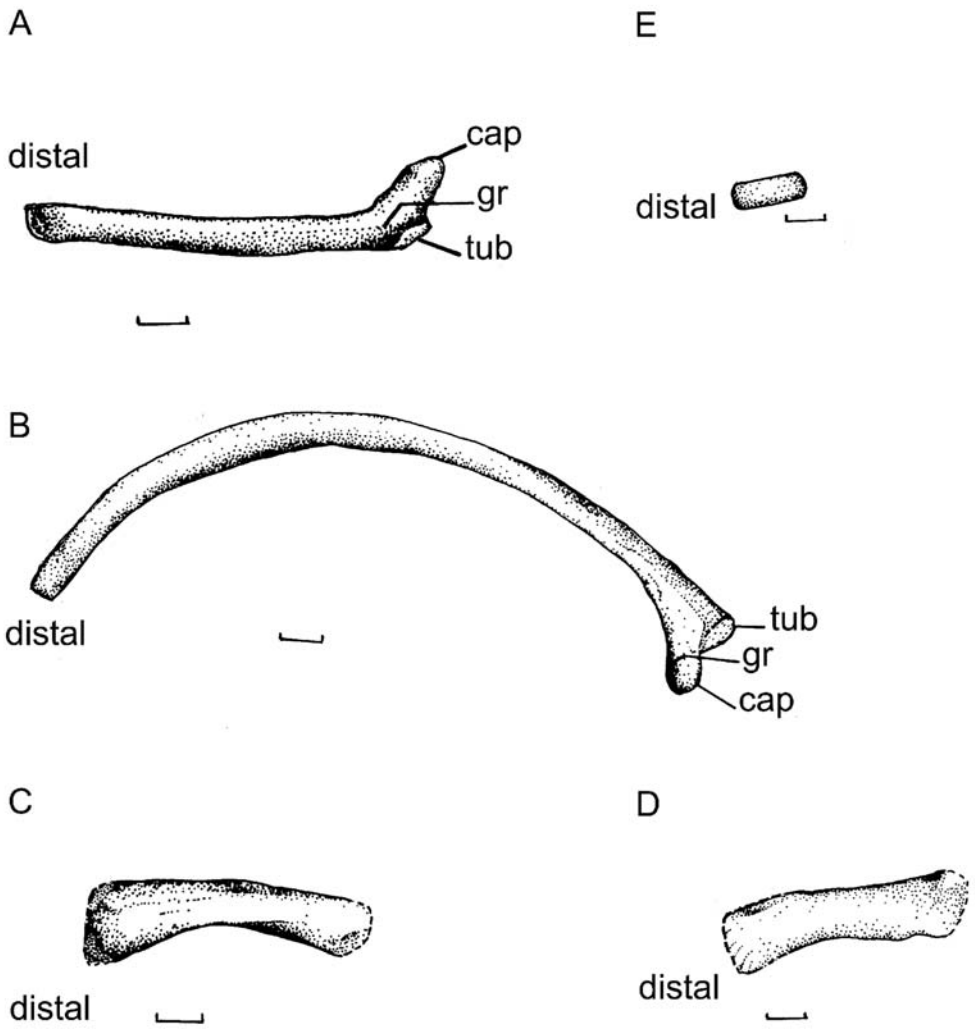


Figure 3. Ribs of *Glanosuchus macrops* (SAM-PK K7809); **A**, cervical (posterior view); **B**, thoracic (posterior view); **C**, lumbar (posterior view); **D**, sacral (anterior view); **E**, caudal (posterior view) (scale 10 mm).

being longer than the small rounded tuberculum. The middle thoracic rib (±14) is the longest, posteriorly they become progressively shorter towards the lumbar region (Fig. 1). Thoracic ribs (Fig. 3B) are similar in morphology to cervical ribs, but the shaft region curves ventrally for only one-third of its length, and the rest of the shaft is almost straight.

Six single-headed, short flat and straight lumbar ribs (Fig. 2B) are fused to the transverse processes of their respective vertebrae. These ribs become progressively shorter and straighter posteriorly and have rounded dorsal and concave ventral surfaces.

Only one pair of laterally expanded and single-headed sacral ribs is preserved (Fig. 3D). These are fused to the sacral vertebrae and have both proximal and distal ends enlarged to give the ribs a dorsoventrally flattened hourglass shape. In other Therocephalia there are normally three to four pairs of sacral ribs (Fourie & Rubidge 2007) and we presume the same would be true for *Glanosuchus.*

Four caudal vertebrae are present, each having a short rib which is fused to the transverse process. The ribs are single-headed, rectangular, short, and have rounded dorsal and ventral surfaces (Fig. 3E). The anteriormost caudal rib is the longest, and the remaining ribs become progressively shorter posteriorly.

Pectoral girdle

The scapula of scylacosaurids is a broadly fan-shaped bone which is slightly medially curved to follow the shape of the thorax. A prominent glenoid cavity has a dorsal scapular facet which faces dorso-laterally and slightly posteriorly, while the coracoid forms the ventral margin (Boonstra 1964).

The clavicle of *Glanosuchus* (Fig. 4A) has the same morphology as that described for *Lycosuchus (Zinnosaurus)* (Boonstra 1964) and is a long, thin and curved bone with expanded ends. Proximolaterally the bone surface is convex and narrows towards the middle of the almost circular shaft. It points upward past the anterior end of the procoracoid and lower part of the scapula to meet the anterior edge of the scapular blade. Only fragmentary sections of the procoracoid and interclavicle are preserved, and are positioned between displaced thoracic vertebrae. For all scylacosaurids the coracoidal plate rests on the upper face of the interclavicle and comprises a large procoracoid and a smaller posterior coracoid which curve gently inwards towards the mid-line. The procoracoid takes no part in the formation of the glenoid cavity. The foramen procoracoideus is present in the procoracoid only. Ventrally the spatulate end of each clavicle curves below around the anterior end of the interclavicle to fit into an

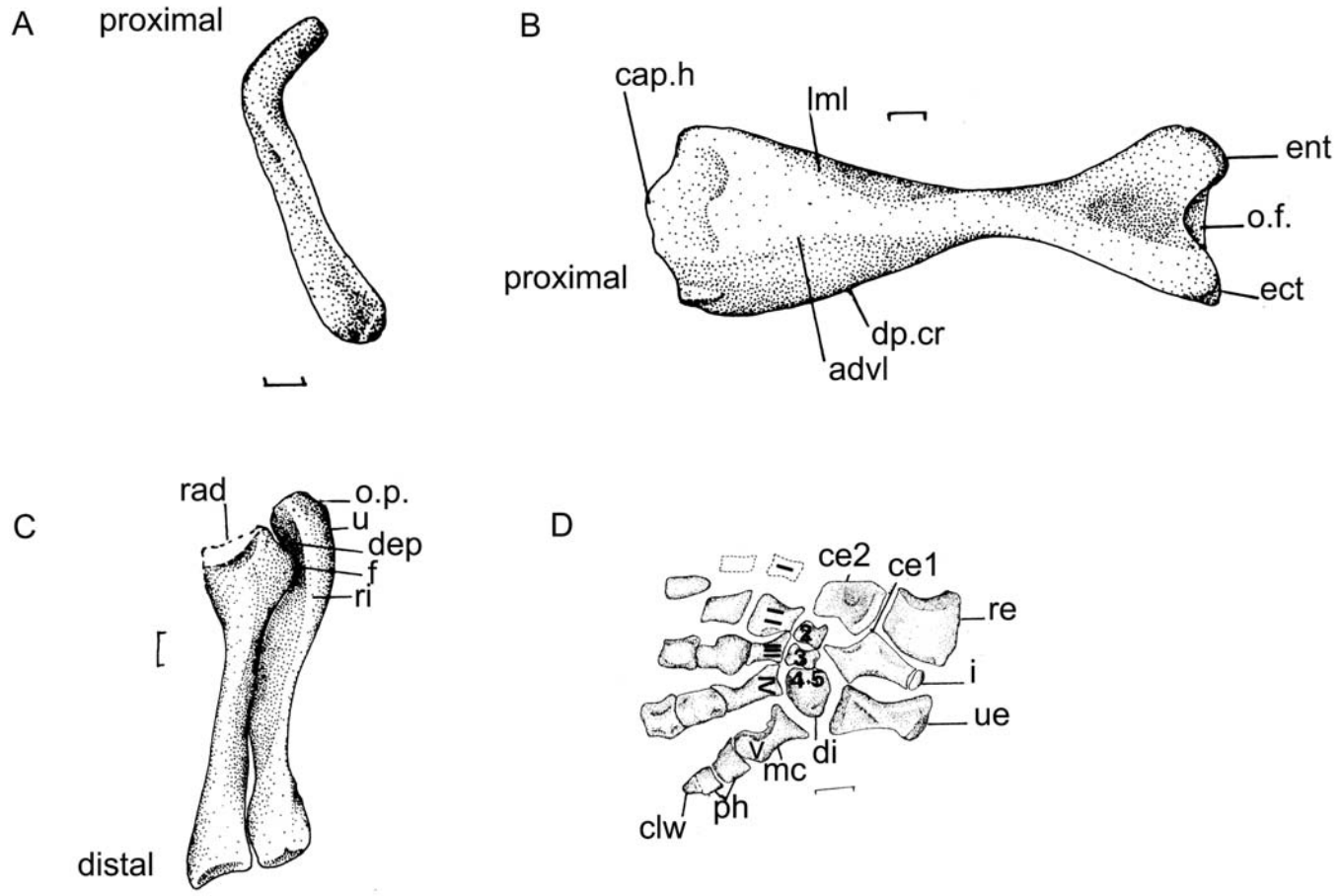


Figure 4. Left clavicle and forelimb of *Glanosuchus macrops* (SAM-PK K 7809); **A**, clavicle (anterior view); **B**, humerus (anterior view); **C**, radius and ulna (anterior view); **D**, manus (dorsal view) (scale 10 mm).

oval hollow on the under face of this bone. The interclavicle is a long bone with the anterior end rounded, and curving slightly upwards. The sternum is not preserved and is considered to have been cartilaginous (Boonstra 1964). It presumably lay above the posterior end of the interclavicle and extended to the coracoids.

Postcranial morphological trends through time in the pectoral girdle of Therocephalia have been discussed by Fourie & Rubidge (2007). It is recognized that suites of postcranial characters can be used to identify specific genera. For example, *Regisaurus* is identified by a slender scapula with a low ridge and shallow depression; procoracoid foramen in procoracoid; interclavicle short and broad; and ossified sternum. *Lycosuchus* has a broad scapula with a low ridge lacking a depression next to it; procoracoid foramen in procoracoid; interclavicle T-shaped; and lack of an ossified sternum (Table 1). An obvious morphological trend through time in the therocephalian pectoral girdle is the position of the procoracoid foramen. This is entirely enclosed within the procoracoid in *Lycosuchus* (Boonstra 1964), *Cynariognathus* (Cys 1967), *Mirotenthes* (Attridge 1956), *Ictidosuchus* (Broom 1901), *Regisaurus* (Kemp 1978); is present on the procoracoid-coracoid suture in *Ericiolacerta* (Watson 1931), *Tetracynodon* (Sigogneau 1963), baurioid (Kemp 1986), *Macroscelesaurus* (Haughton 1918); and on the procoracoid-scapula suture in *Bauria* (Watson 1931). The sternum is unknown in the basal scylacosaurid and lycosuchid therocephalians and has been considered to have been cartilaginous (Boonstra 1964), but more derived therocephalians such as *Regisaurus* and *Olivierisuchus* (Fourie 2001) have an ossified sternum.

Forelimb

The left humerus (Fig. 4B) is preserved in articulation with the ulna and radius and is fifteen centimetres long. It is robust, lacking a well-defined shaft. A dorsoventrally expanded deltopectoral crest is positioned proximally, followed more distally by a short shaft area and the double condyle at the distal end. The articulation surface of the caput humerus (Fig. 4B, cap.h) with the scapulocoracoid is thin and curved. The anterior surface of the deltopectoral crest is characterized by three regions or processes edged by the lateromedial line (Fig. 4B, lml) and the anterior dorsoventral line (Fig. 4B, advl) (*sensu* Boonstra 1964) which are slightly raised linear surfaces of bone. As is the case in all scylacosaurids the bicipital fossa is deep (Boonstra 1964) and well-developed capitellum and radial condyles are present. The morphology of the *Glanosuchus* bicipital fossa differs from that of *Lycosuchus* (SAM-PK K 12185) where the proximal extremity of the fossa has a gentle curve in *Glanosuchus,* but in *Lycosuchus* it slopes steeply towards the ventral side of the shaft. Small rounded entepicondylar and ectepicondylar foramina are present as in all scylacosaurids (Boonstra 1964). On the dorso-distal surface, the trochlear fossa is shallow with a small distal lip which prevented the olecranon from dislocating.

Table 1. Comparison of postcranial characters in different therocephalian genera.

Genus	***Glanosuchus***	***Lycosuchus***	***Mirotenthes***	***Theriognathus***	***Regisaurus***	***Bauria***
Biozone	*Tapinocephalus*	*Tapinocephalus*	*Cistecephalus*	*Dicynodon*	*Lystrosaurus*	*Cynognathus*
Vertebra						
Cervical	5–6		7	>5	6	?
Thoracic	>16		?	14–16	17	>2
Lumbar	6		?	6–7	5	>2
Sacral	>1		3–4	4	3–4	?
Caudal	>4		14	>3	>4	?
Presacral	27–28		>7	>25	28	27
Scapula	?	Broad	Slender	Slender	Broad	Broad
Ridge	?	Low	Low	?	Low	Prominent
Depression	?	Absent	Absent	?	Shallow	Deep
Pc/Cc foramen	?	Absent	Absent	?	Absent	?
Pc/Sc foramen	?	Absent	Absent	?	Absent	?
Pc foramen	?	Present	Present	?	Present	?
Interclavicle	T-shaped	T-shaped	?	Short/broad	Short/broad	?
Sternum (ossified)	Absent	Absent	?	?	Present	?
Humerus						
Entepicondylar foramen	?	Present	Absent	?	Present	Present
Ectepicondylar Foramen	?	Present	?	?	Absent	Present
Humerus shaft	Short	Short	Long	Long	Long	Long
Manus						
Mc IV longest	Yes	No	Yes	?	Yes	Yes
Pelvis						
Obturator foramen	Absent	?	?	Large	Large	Large
Pubic foramen	Large	?	?	Absent	Absent	Absent
Pes						
Os calcis	?	?	Absent	?	Present	Present

The sigmoid curved ulna is long and thin (Fig. 4C). Proximally it is greatly expanded and extends dorsally into a short thickened olecranon with a rugose surface. The sigmoid face of the articulatory area for the reception of the humerus is shallow with a well-developed medial coronoid process. On its dorsal side, the ulna is concave to receive the head of the radius in a marked depression. The ulna has an anterior ridge which extends from the proximal extremity down the middle of the anterior surface to the lateral surface of the shaft and fades away about three quarters of the distance down the shaft. On the medial side of this ridge is a slight depression (Fig. 4C, dep). The distal articulation facet with the ulnare is slightly ovoid.

The radius is an elongate, straight and lateromedially flattened bone which is situated medial to the ulna. The proximal extremity is expanded and concave medially to provide an articulation facet for the humerus while the distal end receives the radiale in a shallow oval depression.

Manus

Only the dorsal side of the manus (Fig. 4D) has been prepared. All the elements of the wrist are preserved, except for the pisiforme. The ulnare (Fig. 4D, ue) is longer and more slender than the radiale (Fig. 4D, re) and is hour-glass-shaped. Proximally the ulnare contacts the ulna along most of the length of the distal end of the ulna in a slightly convex contact area of the ulna such that the proximal head of the ulnare is smaller than the ulnar condyle.

Proximally the dorsal surface of the ulnare is flat and has a slight ridge on the medial side which extends only half way down the length of the bone. At the distal extremity the ulnare is slightly concave with a flat dorsal surface. Both proximal and distal articulating facets are ridged towards the dorsal side. The ulnare contacts the intermedium proximomedially, centrale 1 (medially) in a concave facet of the ulnare, and the fused distals four and five distally.

The radiale, which is the largest element in the wrist of *Glanosuchus,* is roughly quadrangular. It is twice as wide as long and has a convex dorsal surface for the proximal articulation with the radius. It is in contact with the intermedium posteromedially, centrale 1 anteromedially and centrale 2 distally and is dorsally rounded and not depressed as is the situation in *Regisaurus* (Fourie & Rubidge 2007). Centrale 1 has a medial concave facet to accommodate the rounded contact surface of the radiale.

The intermedium, which also has a rounded dorsal surface, is a small oval elongate bone situated between the ulnare, radiale, and centrale 1 which in turn has a concave articulation facet for the intermedium.

Centrale 1 is a broadly L-shaped bone situated between the ulnare laterally, intermedium proximally, radiale proximomedially, distals 3, 4 and 5 distolaterally, and distal 2 and centrale 2 distomedially. Proximally it is thin and long to fit between the ulnare and radiale. Centrale 1 widens distolaterally so that it is widest in the middle of the bone which is in contact with centrale 2. The dorsal surface of centrale 1 is rounded with slight depressions on either side. Centrale 2, one of the larger wrist bones, is roughly rectangular with rounded sides. It has contact with the radiale proximally, centrale 1 medially and distal 2 distomedially. The dorsal surface is slightly depressed.

Distals 2 and 3 which have rounded dorsal surfaces, are

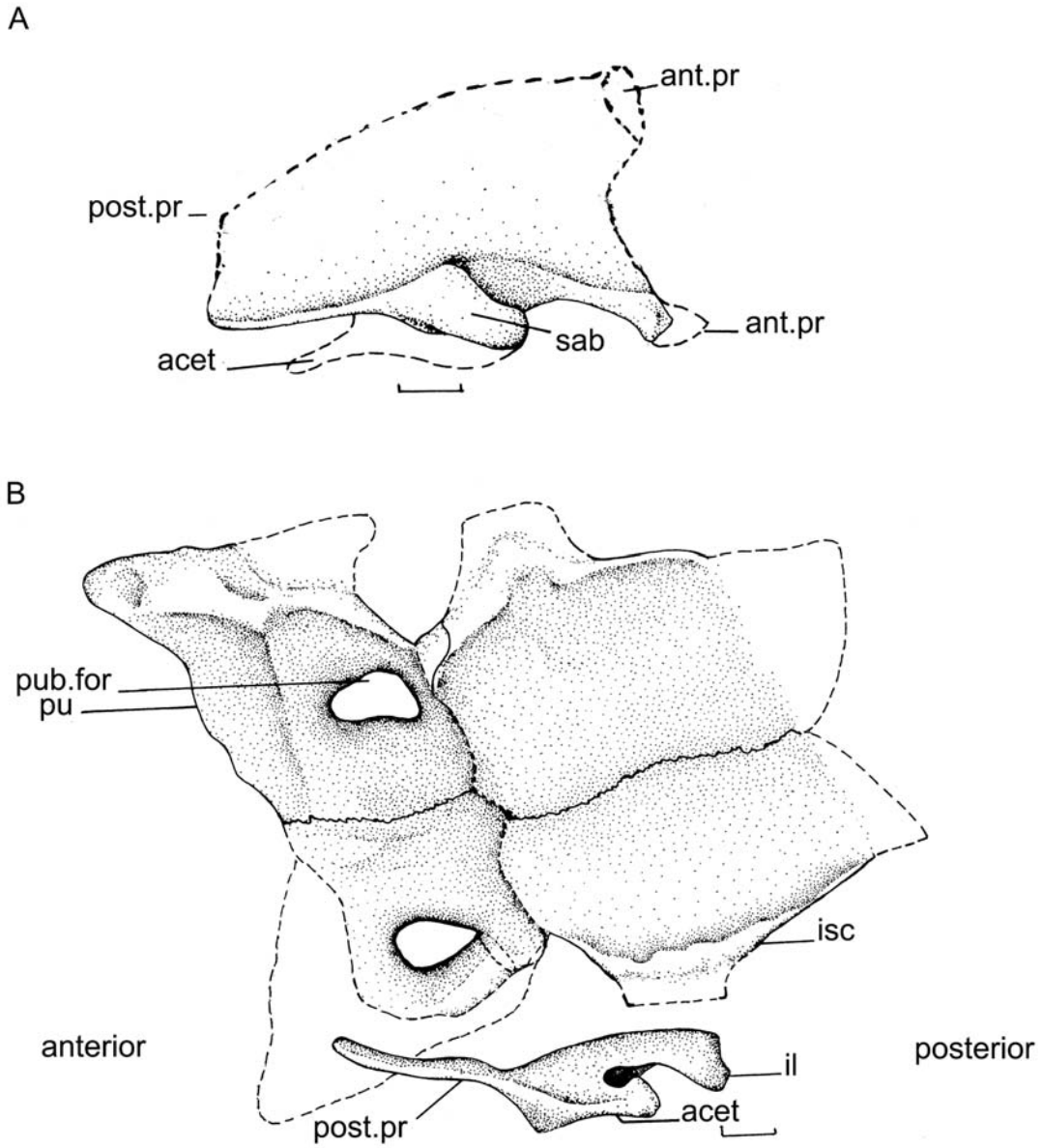


Figure 5. Pelvis of *Glanosuchus macrops* (SAM-PK K 7809); **A**, ilium (lateral view); **B**, pubis, ischium and ilium (dorsal view) (scale 10 mm).

almost square in outline, are slightly constricted towards the middle and have rounded ends. Distal 2 contacts centrale 2 proximally and metacarpal II on the distal side. Distal 3 contacts centrale 1 proximally, distal 2 medially, fused distals 4 and 5 laterally, and metacarpal III on the distal side. Distal bones 4 and 5 are fused to a single bean-shaped element which is situated lateral to distal 3 and the ulnare proximally, and metacarpal IV and V, distally.

Metacarpal I is not preserved and metacarpals II, III, IV and V, which are hourglass-shaped, are preserved in contact with their corresponding phalanges. Metacarpals II and III are short and wide, wider distally than proximally. Metacarpal IV is the longest in *Glanosuchus,* but not in *Lycosuchus* (Boonstra 1964). Metacarpal V is the second longest and the thinnest of all the metacarpals.

Phalanges are almost square with slightly narrower mid-sections and double condyles at each end. The terminal phalanges are missing except for digit 5 which has a triangular claw which is rounded at the apex and blunt on the opposite side.

Pelvic girdle

The pelvic girdle of SAM-PK K 7809 has been dorsoventrally compressed and is badly distorted so that the original shape and orientation cannot easily be determined. The left ilium is exposed in lateral view. The iliac blade is large, flat in lateral view, and has two anterior processes and one large posterior process as in all other Therocephalia (Fig. 5A; Fourie 2001). The ilium narrows towards the ventrolaterally situated acetabulum which is large, shallow, almost circular in outline and faces laterally. Mediolaterally the ilium has attachment sites for the sacral ribs. The lateral surface of the blade is flat, slopes ventrally, but increases in width towards the region of the strong supra-acetabular buttress. Above the buttress, to the back of the ilium blade, is the posterior process which is bigger and more robust than the slimmer anterior processes. One anterior process is situated high up on the blade and the other is lower down. A supra-acetabular notch is situated behind the supra-acetabular buttress.

In anterior view the roughly rectangular pubis is concave and slopes medially to meet its counterpart in a straight

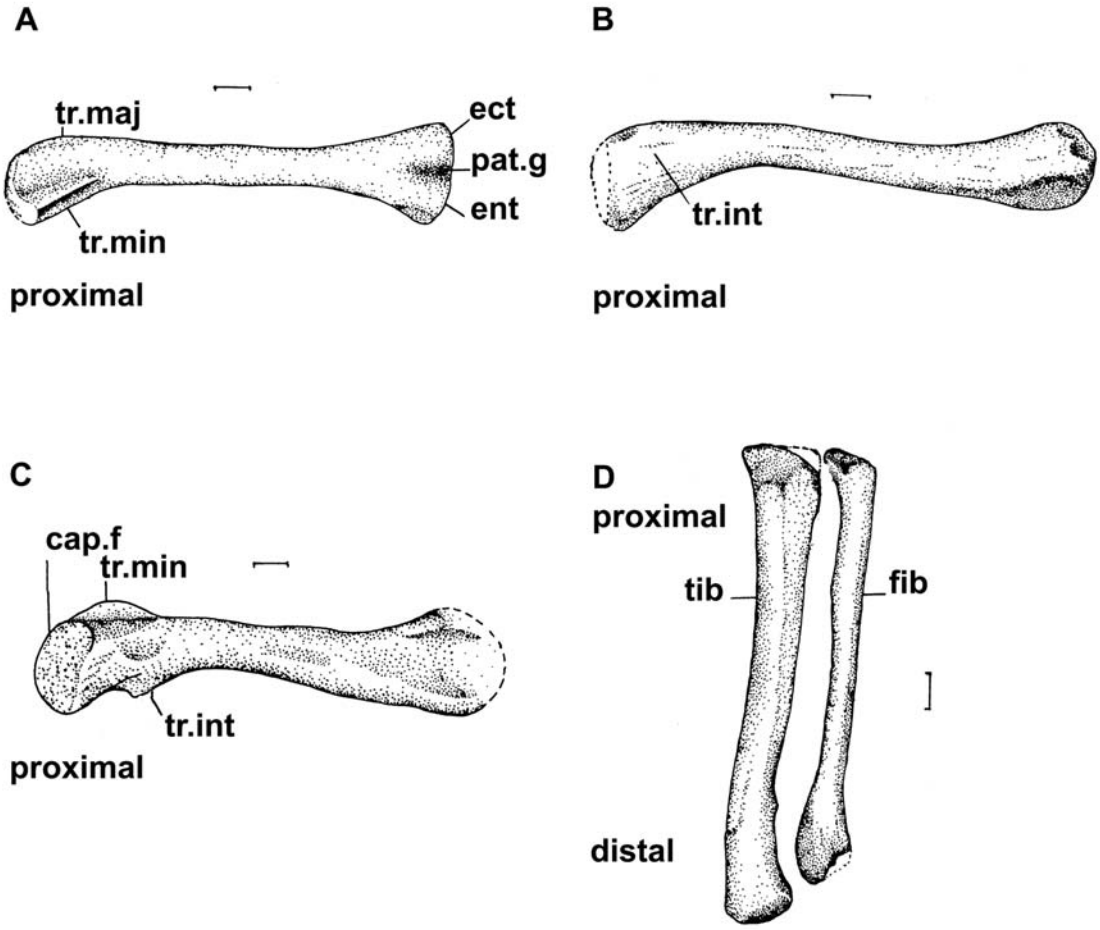


Figure 6. Hindlimb of *Glanosuchus macrops* (SAM-PK K 7809); **A**, left femur (dorsal view); **B**, right femur (ventral view); **C**, right femur (posterior view); **D**, left tibia and fibula (anterior view) (scale 10 mm).

midline symphysis. At its posterior end the pubis curves medially and forms a deep, rounded area for a short contact with the ischium. Laterally the pubis is concave with a rounded anterior edge and a posterior acetabular portion. The contribution of the pubis to the acetabulum is oval and small. The large pubic foramen described for scylacosaurids (Boonstra 1964), and present in *Glanosuchus,* is not present in any other Therocephalia.

Only the anterior portion of the blade-like ischium is preserved with the left side of the girdle being displaced over the more ventrally situated right side (Fig. 5B).

Hind limb

Both femora are preserved (Fig. 6A–C), with the left one complete and the right femur lacking a small part of the shaft. The femur is long and more massive than that of other therocephalians, with a gentle sigmoid curve. It has a flattened proximal end which is expanded anteroposteriorly, and a slightly expanded double condyle at the distal end. A large trochanter minor (anterodorsal), small trochanter major (posterodorsal), and trochanter internus (ventral) are all present on the proximal head. At the proximal extremity the caput femoris (Fig. 6, cap.f) curves medially. Rounded ente- and ectepicondyles, with a shallow ventral triangular patella groove between them (Fig. 6, pat.gr), are present on the distal end of the bone.

The left tibia and fibula (Fig. 6D) are preserved in articulation with the femur as long, straight bones. The tibia, the major weight-supporting element of the lower leg, is more robust and longer than the fibula. Its proximal end is flattened anteroposteriorly and expanded lateromedially, while the slightly expanded distal facet for the articulation of the astragalus is concave and oval. The fibula is a straight, slender bone with slightly expanded proximal and distal ends. On the medial surface is a small proximal tuberosity, and a proximal facet for the tibia and a terminal oval facet for the femur. The shaft, which has a medial groove, thins towards its mid-section and broadens distally to form an elongated oval articulation facet with the proximal end of the calcaneum.

The left pes is not well preserved and only the astragalus, calcaneum, one centrale, distal 1 and fused distal 4 and 5 are recognizable. The almost rectangular calcaneum is larger than the astragalus with two distinct ridges, one near the distal end of the fibula and the other on the outside edge, with a deep depression between them. It abuts against the astragalus medially and fused distal 4 and 5 posteriorly. A tuber calcis is lacking on the calcaneum of *Glanosuchus,* lycosuchids and other scylacosaurids (Boonstra 1964).

The astragalus articulates with the tibia (dorsally) and centrale (posteriorly). This bone is robust and roughly ovoid, it has a slightly indented area for the articulation with the tibia. A shallow median depression and calcano-astragular foramen are present. The centrale, which has

been displaced, is a prominent square bone. Rounded distal 1 is displaced and fused distals 4 and 5 is rectangular. Distals 2 and 3 are not preserved.

Only metatarsals IV and V and three phalanges are present but are poorly preserved. Triangular unguals are present.

DISCUSSION

Therocephalians and dicynodonts bear the unique distinction in that they are the only therapsid clades to be represented in all the biozones of the Beaufort Group (Rubidge 1995). They survived the Permo-Triassic extinction event, and were represented for a period of at least 65 million years (Rubidge 2005; Sidor 2000). Research on the postcrania of a number of therocephalian genera from different biozones eg. *Bauria* (King 1996; Fourie 2001), baurioid (Kemp 1986), *Regisaurus* (Fourie & Rubidge 2007; Kemp 1978), *Aneugomphius* (Brink 1958), *Ictidosuchoides* (Broom 1938), *Mirotenthes* (Attridge 1956), *Tetracynodon* (Sigogneau 1963), *Silpholestes* (Broom 1948), *Cynariognathus* (Cys 1967), *Lycosuchus* (Boonstra 1964) and *Glanosuchus* (this study) offers the opportunity to compare the postcranium of different therocephalian genera, determine postcranial morphological differences between the genera, and assess postcranial evolutionary trends over the extended time that therocephalians were present. In addition, because the postcrania of therapsids are relatively poorly known, our study has enabled comparison of various postcranial elements of different theriodont taxa and provided information to taxonomically identify isolated theriodont postcranial elements. This has biostratigraphic application in areas where fossils are not plentiful.

The general postcranial morphology of therocephalians is consistent amongst the different genera, but there are important generic differences which are highlighted here. Enhanced understanding of postcranial morphological variation amongst different therocephalian genera has further enabled broad scale comparison between postcranial elements of therocephalians, cynodonts and gorgonopsians as far as they are currently known.

Vertebrae

The axis in all therocephalians has a robust construction and the laterally wide neural spine is a distinctive feature, as in gorgonopsians (Sigogneau 1970; van Rooyen 1990) but not in cynodonts where axial morphology is similar to that of the remaining cervical series (Jenkins 1971). In all therocephalians a slight increase in width of the neural spine of the last cervical vertebra marks the end of that series, whereas in gorgonopsians it is the upward shifting of the parapophyseal facet, and the change of the zygapophyseal articulation from a horizontal plane to one of 45° (Boonstra 1934). In cynodonts it is the abrupt change in zygapophyseal orientation from 45° to 55° and the tallest neural spine (Jenkins 1971) which are the only definite markers separating cervical (seventh) from thoracic (eighth) vertebrae.

Intercentra are present between the first seven vertebrae in the therocephalian genus *Ordosia* (Lianhai 1979), but they are absent in all other therocephalian genera. They are absent in all postcervical vertebrae of cynodonts and therocephalians (Jenkins 1971), but are present between the cervical and anteriormost thoracic vertebrae in the gorgonopsian *Lycaenops* (Colbert 1948).

Thoracic vertebrae of all therocephalians have their transverse processes positioned further ventrally and posterolaterally than those of the preceding cervical vertebrae. In gorgonopsians the width across the zygapophyses in the dorsal vertebrae abruptly decreases at the transition from the cervical to the dorsal vertebrae; the diapophysial processes increase in length and are more horizontally directed, so that the facet is at a higher level than in the cervicals; the parapophysial facets shift higher up on to the centrum (Boonstra 1934). Cynodont thoracic vertebrae differ from the cervical vertebrae in being longer and wider, the presence of broader posteriorly situated transverse processes, and abrupt change in zygapophyseal orientation (Jenkins 1971).

Therocephalian lumbar vertebrae have anteroposteriorly wider neural spines than those of the thoracic region, and the transverse processes are shorter and more robust. Colbert (1948) and Sigogneau (1970) did not distinguish between thoracic and lumbar vertebrae in the Gorgonopsia, but described them together as dorsals. In cynodonts, Jenkins (1971) distinguished lumbar from thoracic vertebrae by a slight increase in centrum width, development of robust transverse processes, and by the presence of synapophyses.

In all three infraorders the sacral series commences with the first vertebra having a fused rib which touches the medial surface of the iliac blade. Sacral vertebrae have lower neural spines when compared to the lumbar series and have fused holocephalous ribs which are grooved on the posterior side. In Therocephalia (Fourie 2001) and Cynodontia (Jenkins 1971) sacral zygapophyseal facets articulate at high angles, and the zygapophyses are much smaller than lumbar zygapophyses, while the situation in gorgonopsians is unknown.

Up to 14 caudal vertebrae have been reported in some therocephalian genera (Attridge 1956; Brink 1958). Isolated therocephalian and cynodont caudal vertebrae are distinguished by their small, short and robust transverse processes and only small neural spines which decrease in height posteriorly so that they are absent in the more posterior caudals. Gorgonopsian caudals have low neural spines, and the transverse processes are strong and extend as far laterally as the external iliac surface (Boonstra 1934) Amongst theriodonts, gorgonopsians have the longest tails, up to 26 vertebrae (Boonstra 1934), as compared to the 10–14 of therocephalians (Fourie & Rubidge 2007), and 16 of cynodonts (Jenkins 1971).

Ribs

Cervical ribs of therocephalians (Fourie & Rubidge 2007) and gorgonopsians (Boonstra 1934; von Huene 1950) are short with a double head whereas Jenkins (1971) described cynodont cervical ribs as short having a triangular head without distinct processes.

In therocephalians, gorgonopsians and cynodonts

thoracic ribs are dichocephalous, long and slender. Thoracic ribs of therocephalians and cynodonts differ from those of gorgonopsians (Colbert 1948; von Huene 1950) by not having the tubercle positioned on a long pedicle and by having an interconnecting sheet of bone between the two heads of the rib (Cys 1967; Jenkins 1971). Sternal segments are described for thoracic ribs of therocephalians (Fourie 2001) and gorgonopsians (Boonstra 1934) but not for cynodonts. Posterior grooves on rib shafts are present in therocephalians and cynodonts, but they are absent in gorgonopsians. Very distinct costal plates are present in the thoracic vertebrae of cynodonts (Jenkins 1971), but are lacking in gorgonopsians and therocephalians.

Therocephalian lumbar ribs have the distal end slightly expanded, while in most of the advanced cynodonts the distal end is not expanded and the proximal half of the short rib bears a broad, flange-like posterior process (costal) that overlaps and interlocks with the next posterior rib (Cys 1967; Jenkins 1971). Lumbar ribs of therocephalians are shortened relative to those of the thoracic vertebrae and have blunt ends. This reduction, which is less than that of cynodonts, is suggestive of the presence of a diaphragm (Brink 1958). Colbert (1948) noted that gorgonopsians have double-headed dorsolumbar ribs, but then added that the last four were single-headed and there are no ribs immediately anterior to the sacrum in *Lycaenops*. Boonstra (1934) also described the single-headed nature and the lack of ribs immediately anterior to the sacrum in the Gorgonopsia.

All three theriodont groups have single-headed sacral ribs but therocephalians and gorgonopsians lack the costal plates which are present in cynodonts. In gorgonopsians the first sacral rib extends far ventrally to abut below the upper half of the acetabulum, the posterior two abut higher up on the ilium (Boonstra 1934).

Caudal ribs are single-headed, very short and often fused to the vertebrae. Each rib is hourglass-shaped and dorsoventrally flattened.

Pectoral girdle

Theriodont scapulae are curved around the ribcage and bear a high, narrow blade with an expanded end. The slightly curved scapula of therocephalians is distinctive whereas a broader, straighter scapular blade with its outer surface distinctly concave is characteristic of cynodonts (Brink 1955) and gorgonopsians (Colbert 1948; Sigogneau 1970). The gorgonopsian scapula is a tall and slender bone with the dorsal part of its blade considerably expanded (Boonstra 1934), and a low ridge is present on the posterolateral side (Sigogneau 1970). An acromion process is absent in therocephalians (Fourie 2001), gorgonopsians (Boonstra 1934) and most cynodonts (Colbert 1948) but has been described for *Diademodon* (Brink 1955) and *Cynognathus* (Watson 1917). Therocephalians have a prominent ridged fossa on the lateral side of the scapular blade which appears to be absent in cynodonts (Jenkins 1971).

The medial surface of the scapular blade of both therocephalians and gorgonopsians is concave with the gorgonopsian concavity being less accentuated. In cynodonts this surface is convex (Jenkins 1971). In therocephalians the glenoid facet comprises the coracoid and scapula while in gorgonopsians (Sigogneau 1970; van Rooyen 1990) and cynodonts (Jenkins 1971) the procoracoid, scapula and coracoid together make up the glenoid cavity. An exception is the gorgonopsian, *Lycaenops*, which has a reduced coracoid region with the procoracoid not present in the glenoid facet (Cys 1967).

The position of the procoracoid foramen is variable in therocephalians (see above). Gorgonopsians (Boonstra 1934; Colbert 1948; Sigogneau 1970; Watson 1917) and cynodonts (Broom 1906; Jenkins 1971; Watson 1917) have the procoracoid foramen entirely enclosed by the procoracoid.

There are varying reports on the presence of a cleithrum in theriodonts; cynodonts do not have a cleithrum (Jenkins 1971), it is present in the gorgonopsians *Aelurognathus* and *Scylacops* (Boonstra 1934), and amongst therocephalians is reported as present in *Ericiolacerta* (Watson 1931), but in all the therocephalian specimens studied for this research we found no evidence of a cleithrum.

Some therocephalians as well as gorgonopsians (Boonstra 1934; Colbert 1948; Sigogneau 1970) do have an ossified sternum, but an ossified sternum has not yet been described for cynodonts (Jenkins 1971).

Claviculae and interclaviculae are difficult to recognize in theriodonts as there are few specimens where they are well preserved. In addition there appear to be few morphological differences amongst different genera of the same clade. Persistent minor variations are mostly due to differences in ossification. Cynodont interclaviculae are cruciate in *Thrinaxodon* (Jenkins 1971) and T-shaped in *Cynognathus* (Watson 1917) with the anterior half bearing a median tuberosity from which four ridges radiate. Therocephalia show the same feature trend where it is T-shaped in the basal genera such as *Lycosuchus* (Boonstra 1964), while in more derived genera the interclavicle is short and broad as in *Regisaurus* (Fourie & Rubidge 2007). This is also true for the Gorgonopsia (Boonstra 1934; Watson 1917).

Forelimb

The humerus of all therocephalians has a large deltopectoral crest with a deep bicipital fossa. A similar condition is found in the great majority of gorgonopsians and cynodonts. The therocephalian humeral distal end is not as wide as that of gorgonopsians or cynodonts. Of the therocephalian specimens studied, only *Bauria* has a triangular fossa for the ectepicondylar foramen as in gorgonopsians (Sigogneau 1970) and cynodonts (Jenkins 1971). The cynodont humerus shows three prominent ventral depressions; one depression is for the ectepicondylar foramen, the other for the entepicondylar foramen and the third one for radial articulation (Jenkins 1971). The olecranon fossae on the humerus in therocephalians, gorgonopsians and cynodonts are not very deep and a lip is present mediodistally.

The ulna also manifests differences. In both thero-

cephalians and gorgonopsians (Sigogneau 1970) the ulna exhibits a deep posterior depression, lateral ridge and radial depression, in cynodonts the depression is medial (Jenkins 1971). At the distal end of the ulna, the olecranon process of therocephalians (Kemp 1986) and cynodonts (Jenkins 1971) is described as weak in contrast to the robust process of gorgonopsians (Watson 1917).

Another important character on the forelimb of theriodonts is the oval and convex articulation facet of the radiale with the radius. In gorgonopsians this facet (Boonstra 1934) is smaller than that of therocephalians (Fourie & Rubidge 2007), while in cynodonts it is more rounded (Jenkins 1971).

In the manus the radiale of therocephalians is rectangular or round (Fourie & Rubidge 2007), rounded in gorgonopsians (Colbert 1948), and oval in cynodonts (Jenkins 1971). Therocephalian, gorgonopsian and cynodont ulnares are rectangular, but in cynodonts this bone has rounded corners and a slight concave dorsal surface. The intermedia of therocephalians, gorgonopsians and cynodonts all have different shapes; in Therocephalia they are oval and long (Fourie & Rubidge 2007), in Gorgonopsia they are elongated (Colbert 1948), and in cynodonts they are rectangular (Jenkins 1971).

For each of the theriodont families metacarpal IV (Hopson 1995) is the longest and I is the shortest such that IV > III > V > II > I. In therocephalians the terminal phalanges are shorter than those of gorgonopsians and cynodonts which have long slender, tapering cones. The phalangeal formula for Therocephalia is 2.3.3.3.3; Gorgonopsia is variable 2.3.4.5.3 (*Lycaenops*) (Colbert 1948), 2.3.4.4.3 (*Aelurognathus*) (Sigogneau-Russel 1989) and 2.3.4.5.3 (*Dinogorgon*) (Boonstra 1934); for cynodonts 2.3.4.4.3 *(Thrinaxodon)* (Jenkins 1971) (Parrington 1939) (*Procynosuchus*) (Hopson 1995) and later forms 2.3.3.3.3 (*Cynognathus*) (Watson 1917).

Pelvic girdle

The ilium of all theriodonts comprises a thin, moderately to greatly expanded iliac blade separated from a base (acetabulum) by a constricted neck. In therocephalians, gorgonopsians and cynodonts the ilium has a large, wide and prominent posterior process which extends back beyond the last sacral vertebra. Two anterior processes are uniquely present on all therocephalian ilia (Kemp 1978), while cynodonts (Jenkins 1971) and gorgonopsians (Boonstra 1934) only have one anterior process. The dorsal border of the ilium in all therocephalians is straight and not convex as in gorgonopsians (Boonstra 1934) and cynodonts (Jenkins 1971). This bone forms more than half of the acetabulum in the Gorgonopsia (Boonstra 1934) and only half in Therocephalia (Fourie 2001) and Cynodontia (Jenkins 1971).

In therocephalians and cynodonts the pubis and ischium have contact on both inside and outside the acetabulum, but in all the gorgonopsians (Colbert 1948) the ischium and pubis contact only within the acetabulum.

The pubis and ischium of the therocephalian genera studied lie horizontal, whereas in both cynodonts and gorgonopsians, the ischium had a vertical orientation (Colbert 1948; Cys 1967; Jenkins 1971). The ischium, like the pubis, comprises a head and a ventromedially directed rectangular plate and an oval concave acetabular facet is present for all theriodonts. Therocephalian genera may either have a pubic foramen (e.g. *Glanosuchus*) or obturator foramen (e.g. *Regisaurus*), cynodonts have only a small obturator foramen (Jenkins 1971), while in gorgonopsians the obturator foramen may be absent (Boonstra 1934), or present in the pubis as the pubic foramen (von Huene 1950).

Hind limb

The femur of therocephalians and cynodonts has the same degree of curvature in the shaft while in gorgonopsians the curvature is more pronounced. The intertrochanteric fossa of the femur is shallow in therocephalians (Fourie 2001), deep in cynodonts (Jenkins 1971) and absent in gorgonopsians (Boonstra 1934). In therocephalians the internal trochanter is situated close to the caput femoris and extends a short distance along the shaft, in gorgonopsians it is situated further from the caput femoris and extends along the entire shaft. In cynodonts the trochanter is as in therocephalians, but extends onto the shaft for only a very short distance. Both the trochanter minor and major of the therocephalians and cynodonts are low ridges wheras in the gorgonopsians they are very prominent.

The distal end of the theriodont femur bears a robust lateral condyle and a narrower medial one. The medial (anterior) condyle projects further ventrally than does the lateral condyle in both Therocephalia and Cynodontia (Jenkins 1971) and in gorgonopsians the condyles are confluent with the medial condyle (Colbert 1948). A deep patellar groove is present in therocephalians, while in cynodonts (Jenkins 1971) and gorgonopsians (Boonstra 1934) it is shallow.

The tibia has a similar morphology in all the theriodont families, but that of the Therocephalia is more slender (Cys 1967). Therocephalian and cynodont tibia are fairly straight and therefore have a small interosseal space with the fibulae, in gorgonopsians this space is large as the tibia and fibula are bowed (Colbert 1948). The oval proximal end expands laterally and somewhat anteriorly to support a large articular surface. Distally it expands in a similar fashion but less extensively. The shaft is flattened anteroposteriorly and the therocephalian and cynodont (Jenkins 1971) tibia have a shallow longitudinal groove present on the proximoposterior side of the shaft with a slight median ridge close to it.

The fibula is slender and curved laterally in all theriodonts. While the shaft of the fibula of all theriodonts has the same basic structure, the ends do differ. Therocephalian fibulae have greatly expanded proximal ends, with little expansion distally, gorgonopsians (Boonstra 1934) and cynodonts (Jenkins 1971) have both ends greatly expanded.

The shape of the calcaneum varies from square in therocephalians, disc shaped in gorgonopsians and oval in cynodonts. Two medial articulating facets for the

astragalus are present in both therocephalians (Kemp 1978) and cynodonts (Jenkins 1971). A tuber calcis is present on the calcaneum of some Therocephalia (*Regisaurus*) (Kemp 1978), Gorgonopsia and Cynodontia, but lacking in *Thrinaxodon* (Jenkins 1971).

The foot of Therocephalia has only one centrale, Gorgonopsia have two (Hopson 1995), and an irregular oval centrale is present in Cynodontia (Jenkins 1971). Of the five metatarsals, number IV is the longest in therocephalians, V the longest in cynodonts, and unknown for gorgonopsians. The pedal phalangeal formula of therocephalians (Fourie 2001) and cynodonts is 2.3.3.3.3 (Jenkins 1971), while in gorgonopsians it is variable 2.3.4.5.3 (Boonstra 1934) or 2.3.3.4.3 (Colbert 1948).

CONCLUSIONS

Boonstra (1964) described the girdles and limbs of the basal Therocephalia, but our research is the first to describe the complete dorsal view of a scylacosaurid. *Glanosuchus* can be identified by the following suite of postcranial characters: humerus lacking a distinct thinner shaft section; pelvis with large pubic foramen and lacking an obturator foramen; robust but long femur.

This description and that of Fourie & Rubidge (2007) have highlighted the similarities in postcranial morphology in different therocephalian genera and also manifested certain phylogenetic trends such as scapula morphology, position of procoracoid foramen, presence or absence of an ossified sternum, presence or absence of a pubic foramen which are set out in Table 1.

Comparison of postcranial elements in the Therocephalia, Gorgonopsia and Cynodontia has shown that diagnostic differences are present in the vertebral column, pectoral girdle and forelimb, and pelvic girdle and hind limb. There are a few single element postcranial characters which define a therocephalian, cynodont or a gorgonopsian, but a suite of characters can be used to reliably identify these taxa. These postcranial differences will be useful for broad scale identification in biostratigraphic studies when there is no associated cranial material, and also for phylogenetic studies which up till now have relied largely on cranial characters.

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ABBREVIATIONS

Figures

acet	acetabulum
a.dv.l	anterior dorsoventral line
ant.pr	anterior process
ax	axis
cap	capitulum
cap.h	caput humerus
cap.f	caput femoris
ce1	centrale 1
ce2	centrale 2
centr	centrum
clw	claw
cr	cranium
cv	cervical vertebra
dep	depression
di	distal
dp.cr	deltopectoral crest
ect	ectepicondyle
ent	entepicondyle
f	facet
fem	femur
fib	fibula
gr	groove
hum	humerus
i	intermedium
icl	interclavicle
il	ilium
isc	ischium
lm.l	lanteromedial line
lv	lumbar vertebra
man	manus
mc	metacarpal
n.a	neural arch
n.c	neural canal
n.p	neural process
n.s	neural spine
o.f	olecranon fossa
o.p.	olecranon process
pat.gr	patella groove
pes	pes
ph	phalange
post.pr	posterior process
postzp	postzygapophysis
prezp	prezygapophysis
pu	pubis
pub.for	pubic foramen
r	rib
rad	radius
re	radiale
ri	ridge
sa.b	supra-acetabular buttress
sa.n	supra-acetabular notch
sv	sacral vertebra
tib	tibia
tr.int	internal trochanter
tr.pr	transverse process
tr.maj	major trochanter
tr.min	minor trochanter
tub	tuberculum
tv	thoracic vertebra
u	ulna
ue	ulnare

Tables

Cc	coracoid
mc	metacarpal
Pc	procoracoid
Sc	scapula
?	not preserved / described

Institutions

SAM-PK K	Iziko South African Museum, Cape Town, South Africa
TM	Transvaal Museum, Pretoria, South Africa
UCMP	University of California Museum, Berkeley, U.S.A

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Dicynodont postcrania from the Triassic of Namibia and their implication for the systematics of Kannemeyeriiforme dicynodonts

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Recent years have seen a renewed interest in the postcranial anatomy of Triassic dicynodonts from Africa. This study investigates the previously undescribed dicynodont postcrania from the Omingonde Formation of Namibia. Two valid dicynodont species, based upon crania, are known from this formation: *Dolichuranus primaevus* and *Kannemeyeria lophorhinus. Dolichuranus* displays a primitive generalized cranial anatomy that has made it difficult to place in Triassic dicynodont phylogeny. Some of the postcranial specimens can be positively identified as *D. primaevus* on the basis that they were associated with skulls of this species. Two scapula morphologies can be distinguished among the postcranial specimens that are not positively associated with diagnostic cranial remains. One of these shares similarities with the scapula of *Kannemeyeria simocephalus* from South Africa and is provisionally referred to *K. lophorhinus.* The other displays unusual characters such as the absence of an acromion and a tubercle on the lateral surface of the scapula at the level where the acromion would be expected. Inclusion of the new postcranial data in a cladistic analysis of Triassic dicynodonts resolves the position of *D. primaevus* as a member of Sinokannemeyeriidae. It also causes an enigmatic unnamed postcranial taxon from equivalently aged beds in South Africa to fall within the Sinokannemeyeriidae. These results highlight the importance of including postcranial data in analyses of Triassic dicynodont relationships.

Keywords: *Dolichuranus;* dicynodont, Triassic, Namibia.

INTRODUCTION

The Triassic strata of Namibia, collectively known as the Etjo Sandstones, are found in the northern part of the country and date to the late Early to early Middle Triassic (Keyser 1973). The Triassic beds were once considered to be non-fossiliferous (Keyser 1973; Keyser 1974), but at least 25 vertebrate fossils were collected by Keyser (Keyser 1973). Among these fossils were two new medium to large dicynodont taxa, *Dolichuranus primaevus* Keyser, 1973 and *Rhopalorhinus etioensis* Keyser, 1973, along with a specimen referred to the otherwise South African species *Kannemeyeria simocephalus* (Weithofer, 1888). Keyser (1973) concluded that *Dolichuranus* was morphologically intermediate between the Late Permian taxon *Daptocephalus* and the Late Triassic taxon *Dinodontosaurus.* He found that the general shape of the skull of *Dolichuranus primaevus* was similar to that of *Kannemeyeria latirostris* Crozier, 1970, which showed a number of differences that distinguished it from other *Kannemeyeria* species (Crozier 1970). Keyser (1973) referred *K. latirostris* to *Dolichuranus* as *D. latirostris* (Crozier, 1970). Keyser & Cruickshank (1979) upheld Keyser's (1973) inclusion of *K. latirostris* in the genus *Dolichuranus.* A re-examination of *Dolichuranus primaevus* Keyser, 1973 and *Rhopalorhinus etionensis* Keyser, 1973 showed that these taxa represented two extremes of a morphological series (Keyser & Cruickshank 1979). They therefore placed *Rhopalorhinus* into synonymy with *Dolichuranus,* but still recognized two species (Keyser & Cruickshank 1979). Cooper (1980) took this one step further and suggested that if these two taxa represent extremes of a morphological series then only one species should be recognized, namely *Dolichuranus primaevus.*

Maisch (2001) suggested that *Dolichuranus* could not be assigned to a specific family because it lacked synapomorphies that characterized the four families he recognized (*viz.* Shansiodontidae, Kannemeyeriidae, Stahleckeriidae, Dinodontosauridae). He considered it an undifferentiated Triassic dicynodont taxon (Maisch 2001). He also concluded that because the postcranial skeleton is not known and the cranial osteology is incompletely known *Dolichuranus primaevus* should be considered Kannemeyeriiformes *incertae sedis* (Maisch 2001). A recent detailed study of the cranial anatomy of *Dolichuranus primaevus* also undertook a phylogenetic analysis of Triassic dicynodonts (Damiani *et al.* 2007). They suggested that *Dolichuranus* meets the requirements put down by Keyser (1973), Surkov (2000) and Maisch (2001) to be a basal member or close outgroup of the Stahleckeriidae (Damiani *et al.* 2007). The relationships of this taxon within Kannemeyeriiformes are unresolved and new data may help to resolve this problem. Since it is a rather primitive, undifferentiated taxon it is likely to have key combinations of character states that will affect our interpretation of Triassic dicynodont phylogeny.

MATERIAL

BP/1/4578 consists of partial cranial material, a complete hindlimb and some pelvic bones. The femora of this specimen were already prepared. The cranial material has been referred to *Dolichuranus* by Damiani *et al.* (2007). Locality: Mount Etjo (outcrop above Bobbejaankloof), Otjiwarongo, Omingonde Formation.

R 334: postcrania belonging to holotype of *Dolichuranus*

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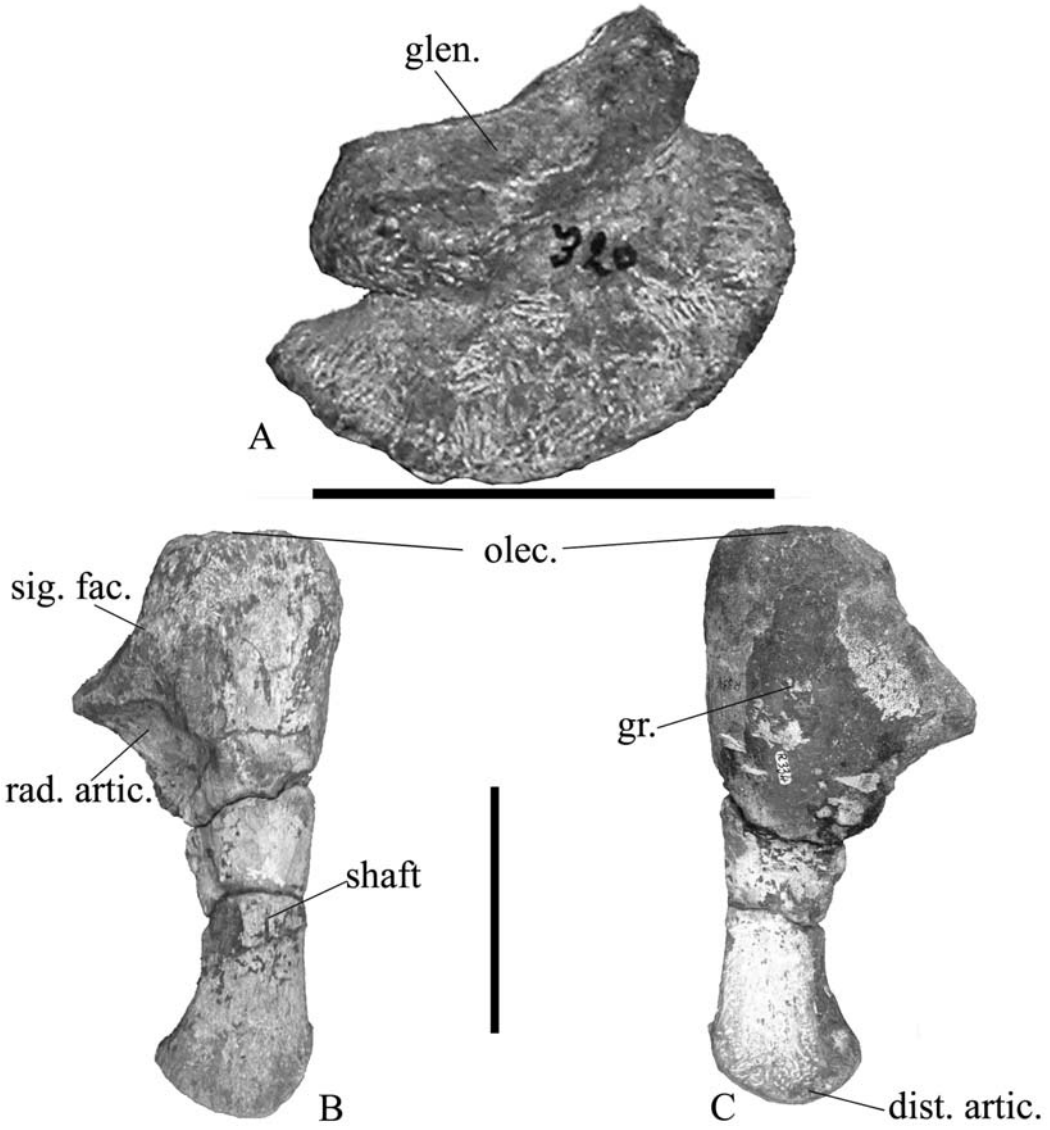


Figure 1. **A**, Lateral view of the coracoid (CGP/1/191B) of *Dolichuranus*. **B**, Lateral and **C**, medial view of the ulna (R334) of *Dolichuranus*. Scale = 10 cm

*primaevu*s. It consists of an ulna, radius and partial femur. The skull is now housed in the Council for Geosciences (CGP/1/711).

R320 consists of a tibia, fibula, coracoid and various bones of the foot. The skull (identified as *Dolichuranus primaevus*) associated with this material is catalogued as CPG/1/712.

R316 consists of incomplete material belonging to scapulae, humeri, an ilium that is fairly complete and a complete fibula. This specimen is provisionally identified as *Kannemeyeria lophorhinus.*

CGP/1/191A is a humerus belonging to a small individual. It is well preserved and has only been damaged along the dorsal border. It is tentatively identified as *Dolichuranus primaevus.*

CGP/1/191B is a small scapula. At least the proximal third of the scapula blade and the anterior border have been broken off. The bone is also broken along the plane where the distal end begins. It is tentatively identified as *Dolichuranus primaevus.*

CGP/1/412 is a second large humerus and was also used in these descriptions. It is tentatively identified as *Kannemeyeria lophorhinus.* Locality: Etjo South (Namibia).

DESCRIPTION OF THE POSTCRANIAL SPECIMENS

Dolichuranus primaevus

Pectoral girdle

Coracoid. The coracoid (R320) is small which would suggest that it belonged to a small individual (Fig. 1A). It is a complete, well-preserved bone. The glenoid articulation is a narrow, elongated oval that is wide posteriorly. Its articulating surface is concave in the middle and becomes convex posteriorly where it ends as a ridge. Below the glenoid there is a narrow groove (Fig. 1A). Distally the border of the coracoid is curved with a concave articulating surface that is divided in two: anterior one narrow and elongated and posteriorly a smaller rectangular, concave articulating surface. The medial surface is deeply concave.

Forelimb

Ulna. The complete left ulna of *Dolichuranus* is preserved in R334 (Fig. 1B,C). It is robust bone with a curved shaft. On the proximo-posterior border of the bone the surface forms a low wide flat surface. The surface is flat to slightly concave which would suggest that the olecranon was

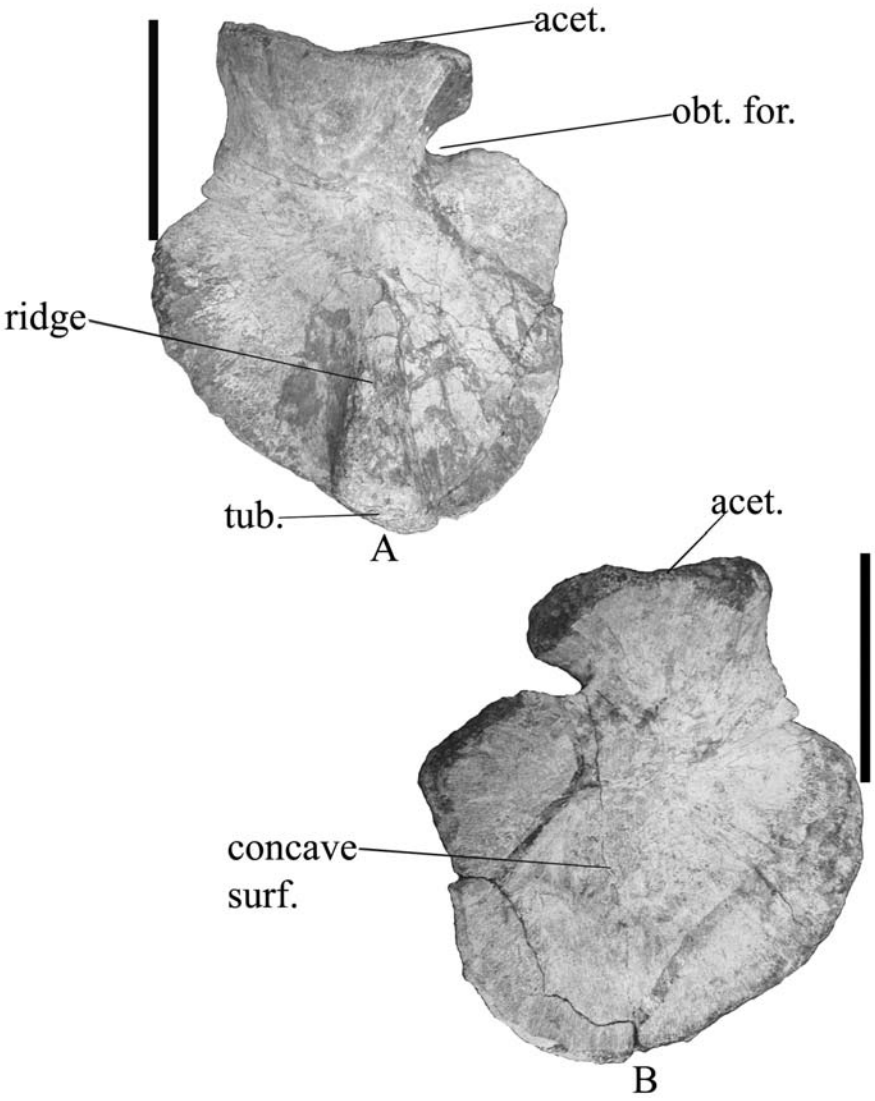


Figure 2. **A**, Lateral view and **B**, medial view of the ischium (BP/1/4578) of *Dolichuranus*. Scale = 10 cm.

most likely separately ossified. Anterior to the olecranon is the sigmoidal facet (Fig. 1B). It is directed anteriorly with an elongated, concave posterior face that is limited anteriorly by a thin ridge. The lateral face of the facet is convex and shorter than the posterior facet. It is directed laterally and its limit is demarcated by a thin ridge.

Posterior to this ridge there is a longitudinal groove that extends to the proximal end of the shaft. In front of the ridge there is an irregular oval radial facet with a deeply concave surface (Fig. 1B). The shaft is narrow with a concave anterior margin and an almost straight posterior border. Below the olecranon on the anterior surface there is a broad, concave groove that extends down the entire length of the bone to end just above the distal articulation. The distal articulation is a narrow oval with a convex surface.

Pelvic girdle

Ischium. The right ischium (BP/1/4578) is a teardrop-shaped bone that is almost completely preserved (Fig. 2). The acetabular facet forms an elongated oval that is fairly wide and more concave in the middle with raised and flat anteriorly and posteriorly. It is demarcated by a thin ridge. There is a short, fairly wide neck just below the acetabulum facet. In front of this neck there is an elongated, narrow groove that represents the posterior part of the obturator foramen. This would suggest that the obturator foramen is an elongated oval (Fig. 2A). A ridge that runs along the distal half of the bone has resulted in the anterior end of the bone being positioned at an angle to the posterior end. Laterally the surface of the bone is concavo-convex. The anterior two-thirds of the bone is flat to convex while the posterior third is narrow and concave (Fig. 2).

The ridge that is present on the distal half of the bone terminates at the distal end as a tubercle. This tubercle forms an elongated oval and is angled towards the posterior border of the bone. It is raised above the surface of the bone and narrows in the lateral direction. This surface becomes narrow laterally to form a ridge that projects up the bone to end halfway. It is on either side of this tubercle that the anterior and posterior ends of the bone are angled towards each other. Posteriorly the bone is less flared than the anterior and rises upward to form a thickened posterior end. Along the distal border of the ischium the surface is very rugose.

Medially the surface of the ischium is more deeply concave in the middle of the bone. The anterior and posterior parts of the bone become flattened (Fig. 2B).

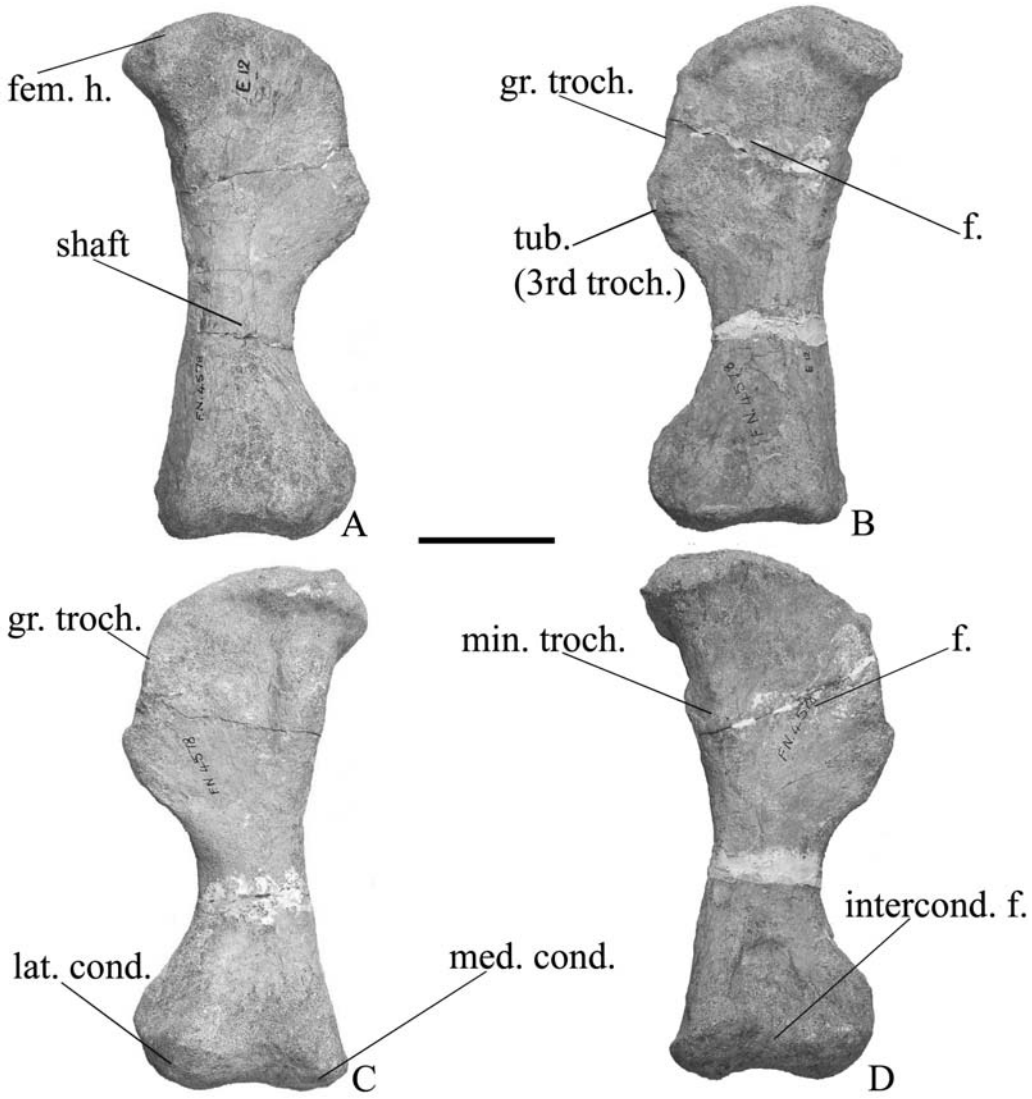


Figure 3. Left and right femora (BP/1/4578) of *Dolichuranus.* **A & B**, Dorsal view; **C & D**, ventral view. Scale = 10 cm.

Hindlimb

Femur. Both the left and right femora are preserved in BP/1/4578 and both are used to describe the femur (Fig. 3). The femur is dorso-ventrally flat, short and robust. It has a broad proximal expansion and a narrow distal expansion that is antero-posteriorly thicker than the proximal end. The medial border of the femur is thick and almost straight while the lateral border is concave.

The head of the femur overhangs the ventral surface slightly (Fig. 3C,D). When viewed from dorsally the head is triangular with the narrowest part facing laterally and it is not separated from the greater trochanter (Fig. 3A,B). Although the head of the femur is inflected medially, its articulating surface is directed dorsally. In front of the head is a very shallow, broad elliptical fossa that extends to below the greater trochanter (and the tubercle below it) to merge with the proximal end of the shaft.

Ventrally, below the head along the medial border, is an elongated tubercle which represents the minor trochanter (Fig. 3C,D). On the right femur the tubercle is divided in two with the posterior part higher than the anterior part. The posterior part of the tubercle is elongated and is separated from the anterior part by a very shallow groove. The anterior part of the tubercle is also elongated and narrow but it projects onto the anterior border. This tubercle is separated from the head by wide, shallow groove on the right femur. On the left femur the tubercle is not divided into two facets but there is a groove in the middle of the tubercle. The tubercle projects onto the medial border as a sharp ridge.

Anterior to the minor trochanter is a shallow fossa (Fig. 3C,D) that is broad and elliptical and is concave in the medial direction. Its lateral border is formed by the greater trochanter. The greater trochanter is short and dorso-ventrally broad, and its surface is reflected onto the dorsal and ventral surfaces of the right femur while on the left femur it is reflected onto the ventral surface and is twisted onto the border of the fossa on the dorsal surface. Below the great trochanter is another tubercle which represents the third trochanter that is separated from the greater trochanter by a thick ridge.

The distal end is medio-laterally narrow. A broad, concave groove passes from the distal end of the shaft in the lateral direction in front of the lateral condyle to end at the ventral border of the condyle. The lateral condyle is thicker than the medial condyle and the articulating surfaces of the condyles are directed ventrally and project only slightly onto the ventral surface (Fig. 3). Although the

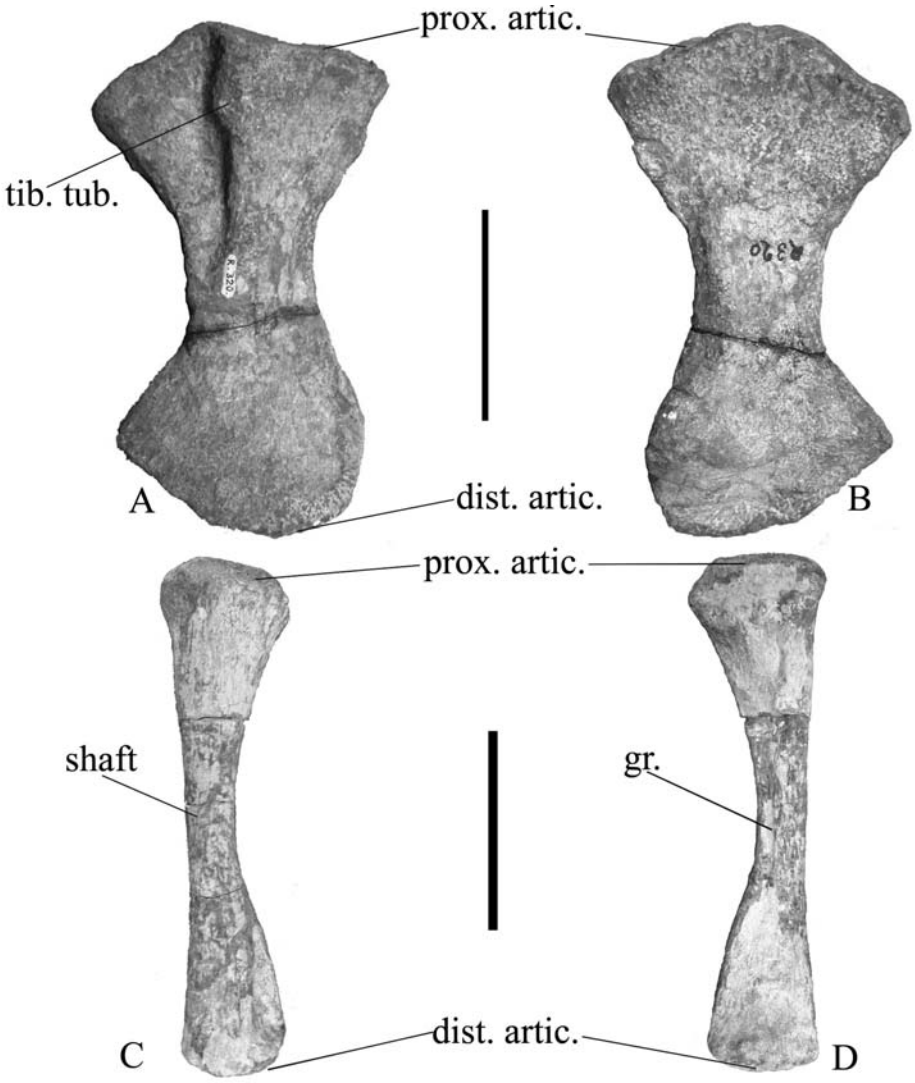


Figure 4. **A**, Anterior view and **B**, posterior view of the tibia (R320); **C**, anterior and **D**, posterior view of the fibula (BP/1/4578) of *Dolichuranus*. Scale = 10 cm.

lateral condyle's articulating surface is bigger than that of the medial condyle it ends at the same level as the medial condyle in the ventral direction. Along the ventral border the condyles are separated by a broad, shallow groove and on the ventral surface by the intercondylar fossa. On the left femur the almost circular intercondylar fossa is much shallower than the right fossa. The medial condyle is skewed in the proximo-anterior direction with a flat surface. The posterior condyle reaches the proximal end of the articulating facet, which is situated slightly below a ridge. On the left femur it is almost rectangular and is convex with the middle of the surface being concave. The articulating facet is narrow and slightly below the ridge (ridge of the condyles starts at its distal end) on the right femur and is not very convex.

Distally there is a very shallow triangular fossa (popliteal fossa) between the condyles on the dorsal surface (Fig. 3A, B). On the posterior border of the lateral condyle there is another very shallow, narrow fossa that has a concave surface that extends onto the surface of the lateral condyle. The articulating surface of the condyles does not extend onto the dorsal surface.

There is a fossa on the medial margin of the medial condyle. The fossa extends from the edge of the articulating surface onto the medial border of the right femur and has an irregular edge marked by a low sharp ridge. It has a concave surface with the deepest part closer to the articulating surface separated from the rest of the fossa by a ridge. On the left the fossa's distal end is located at the proximal edge of the medial condyle. The fossa is oblong with the deepest part distally and is located on the dorsal margin of the femur.

Tibia. The tibia (R320) is short and robust, and has suffered some damage (Fig. 4A,B). Distally the bone is distorted in the antero-posterior direction giving it a flattened appearance. Proximally the tibia appears to have a natural triangular shape which most likely has been exaggerated by flattening in an antero-posterior direction (Fig. 4A). When viewed anteriorly the middle of the proximal expansion projects above the rest of the bone. The tibial tubercle is prominent with an oval shape. Lateral to the tubercle is a broad concave groove that narrows to end on the shaft. It is limited by a narrow ridge medially. The shaft is narrow and short with slightly concave lateral and medial borders.

Distally the appearance of the tibia is possibly as a result of distortion which has resulted in it being widely expanded (Fig. 4A,B). Posteriorly the surface of the bone is almost

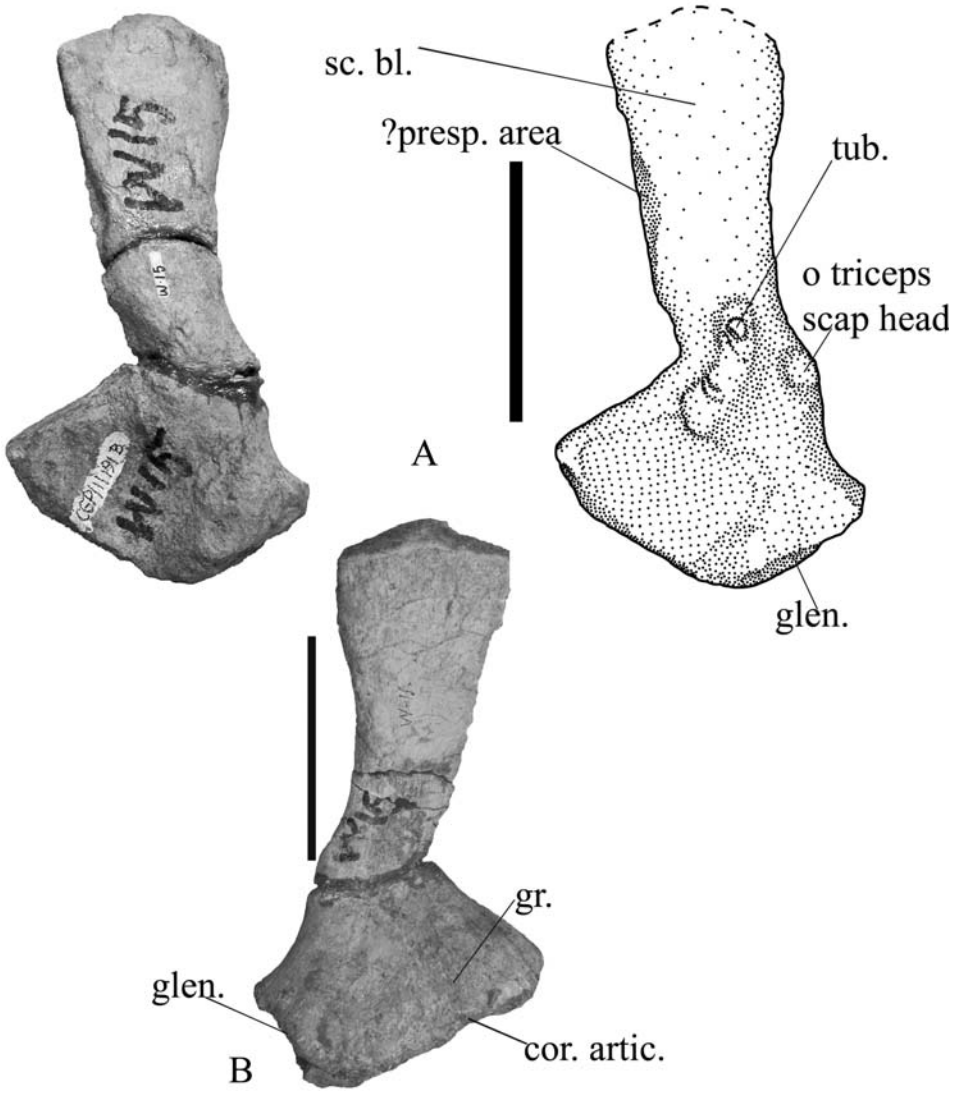


Figure 5. **A**, Lateral view and **B**, medial view of the scapula (CGP/1/191B) *cf. Dolichuranus.* Scale = 10 cm.

featureless except for a broad concave groove that extends down the entire length of the bone from just below the proximal articulation.

The proximal articulation is made up of two facets: a triangular medial facet and a narrow elongated oval lateral one. Both have concave surfaces that slope anteriorly.

Fibula. The fibula (BP/1/4578) of *Dolichuranus* is a slightly curved, gracile bone with slightly expanded ends. In anterior view the proximal expansion is slightly larger than the distal one (Fig. 4C,D). The proximal expansion is antero-posteriorly flattened while the distal expansion is antero-posteriorly thicker.

Proximally the articulating surface is oblong and convex (BP/1/4578) and slopes posteriorly becoming concave. It is demarcated by a broad rugose ridge. Just below this ridge the surface of the bone is rugose (Fig. 4C,D). Along the medial border there is a shallow elongated fossa. Below this fossa the bone surface is raised. From the proximal end the bone narrows to form the shaft. It is long and slender with a straight lateral and concave medial one (Fig. 4C,D). Distally the articulating surface is slightly convex and almost circular. This surface is demarcated by a thin ridge. Above the distal articulating surface there is a fossa along the medial border. This fossa is also surrounded by rugose bone surface.

In posterior view the surface of the proximal expansion is concave and extends to the proximal end of the shaft (R320; BP/1/4578) (Fig. 4D). A fairly deep groove passes down the bone along the medial border. Posteriorly it is demarcated by a narrow, flat ridge that is positioned towards the lateral border. This groove appears to be restricted to the shaft of the fibula.

cf. Dolichuranus primaevus

This material cannot be referred to *Dolichuranus primaevus* with certainty since the remains were not associated with any other diagnostic material. However, they differ significantly from the equivalent bones referred to *Kannemeyeria lophorhinus* and there is no evidence for a third dicynodont species in the Omingonde Formation.

Pectoral girdle

Scapula. The scapula blade (CGP/1/191B; Fig. 5) is convex laterally, antero-posteriorly narrow and the dorsal portion is angled anteriorly. Along the anterior margin of the scapula the bone is damaged proximally and appears to be incomplete (Fig. 5A). Although the anterior margin

has been damaged there is a concave area that could represent a prespinous region. Preservation suggests that the anterior margin of the scapula is complete at the level of the acromion and that there is no acromion process present on this specimen; however, at the level where one would expect to find the acromion a tubercle is present on the lateral surface. The tubercle is directed diagonally towards the posterior border and is distinctly separated from the anterior margin (Fig. 5A). The tubercle is narrow proximally and becomes wide ventrally (Fig. 5A). Near the ventral end of the tubercle is a round prominent projection. In front of the tubercle the surface is curved and slightly concave with a slightly rugose surface. The posterior border is concave and becomes convex proximally.

Approximately one-third of the way from the dorsal border is a narrow, convex tubercle. Towards the lateral surface of the posterior border is an elongated oval tubercle that has been damaged distally and which represents the origin of the scapula head of triceps. Behind this tubercle the posterior border becomes flat and it becomes narrow towards the glenoid facet. A thick, broad ridge marks the dorsal border of the glenoid facet on the lateral surface.

Ventrally the scapula is broad and is medio-laterally flattened (Fig. 5B). The ventral end thins in the anterior direction and the lateral surface is concave below the tubercle on the lateral surface at the level of the acromion. Posteriorly, on the ventral end, is the glenoid facet. The glenoid is almost round and flattened along the medial border and faces postero-ventrally (Fig. 5). The bone is medio-laterally flattened so that the coracoid articulation is wide, concave and oblong and makes up most of the ventral articulating surface than the glenoid facet. The shape of the damaged surface at the anterior tip of the distal end suggests the possible presence of a triangular tubercle.

The medial surface of the scapula blade is concave in an anterior direction and is narrowest just above the beginning of the distal end. Just above the distal end of the scapula is an elongated, concave area. On the distal end a shallow, broad groove is positioned on the medial surface of the anterior coracoid facet (Fig. 5B). The groove is more or less in the middle of the articulation and extends along the entire distal expansion. Both the coracoid and the glenoid articulations are directed ventrally.

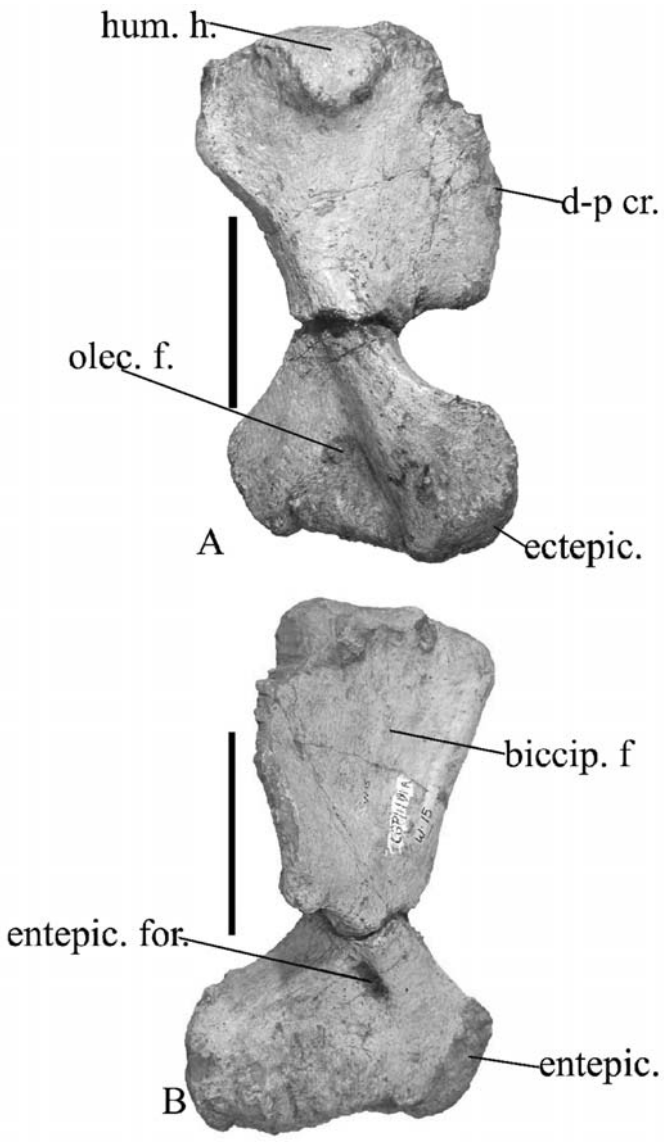


Figure 6. Dorsal view **A**, CGP/1/412; **B**, CGP/1/191A and ventral view **C**, CGP/1/412 and **D**, CGP/1/191A of the humerus *cf. Dolichuranus*. Scale = 10 cm.

Forelimb

Humerus. The proximal expansion of the humerus is narrower than the distal expansion in CGP/1/191A (Fig. 6). Proximally the expansion is antero-posteriorly is flatter and much thinner in CGP/1/191A (Fig. 6B). The proximal expansion is rounded and oblong and narrows marginally towards the shaft. In CGP/1/191A the head is positioned closer to the middle of the dorsal border. The almost triangular head of CGP/1/191A overhangs the dorsal surface to a greater degree than the ventral surface (Fig. 6A,B). Its articulating surface is directed dorsally in CGP/1/191A but also extends onto the dorsal surface of the humerus. The surface along the entire dorsal border including the head is rugose and pitted, which suggests that the surface was covered by cartilage in life (Fig. 6A,B). Posteriorly, below the dorsal border is an elongated tubercle that is visible from the dorsal and posterior views. Anteriorly and posteriorly the head is bordered by a groove with the posterior one much deeper.

Anteriorly the proximal expansion grades into the delto-pectoral crest. The delto-pectoral crest is directed anteriorly with the distal end directed medially. It is plate-like in CGP/1/191A (Fig. 6B,D) with the proximal and distal parts of the anterior border thickened. The delto-pectoral crest is directed anteriorly (Fig. 6A, B).

The anterior border of the delto-pectoral crest is thin along its entire length (CGP/1/191A ; Fig. 6B,D). Distally the delto-pectoral crest is twisted towards the biccipital fossa. The anterior surface delto-pectoral crest extends onto the dorsal surface but is limited by a ridge on the ventral surface. Below the distal end of the delto-pectoral crest on the anterior border is a narrow, elongated oval tubercle. Along the anterior surface is the entepicondylar ridge. Posterior to this ridge is the opening of the entepicondylar foramen, which has an oval opening in the large

individual and an elongated almost oblong opening in the smaller specimen.

The shaft in both individuals is short and thick. There is a distinct difference in the degree of the offset between the proximal and distal ends of the humerus. In CGP/1/191A this offset results in the ectepicondyle being directed antero-dorsally.

The distal end when viewed anteriorly is triangular, broad and thin antero-posteriorly (Fig. 6). In front of the entepicondyle ridge the surface slopes towards the ventral surface and is concave towards the ventral border. The articulation for the radius and ulna is narrow and is closer to the ectepicondyle. A triangular facet is present for articulation with the ulna. Its surface is convex proximally and becomes concave towards the ventral border. The radial facet is much smaller and is closer to the ventral border with a slightly concave surface.

In ventral view the head projects only slightly above the proximal surface. Proximally the postero-ventral 'corner' of the bone forms a thick, round border. In front of this border is an elongated tubercle that is broad proximally and narrows distally. Below the tubercle is a wide ridge that narrows where it merges with the shaft. The biccipital fossa is directed towards the delto-pectoral crest and is concave in that direction (Fig. 6). A groove starts below the biccipital fossa and ends above the entepicondylar foramen. The ventral opening of the entepicondylar foramen is oval.

The distal expansion is flared. A shallow, triangular olecranon fossa is present with thick ridges on the entepicondyle and ectepicondyle (Fig. 6C,D). The posterior border is concave below the dorsal border, while the dorsal border is dorso-ventrally thick and rounded, and it projects beyond the posterior surface. Below this the border thins towards the entepicondyle where it is very thin. In front of the dorsal projection the surface is deeply concave.

The ectepicondyle is round with a convex surface that projects dorsally. It is thicker than the entepicondyle but is proximo-distally narrower than the entepicondyle in anterior view. The ectepicondyle is lower than the entepicondyle and in CGP/1/191A it is evident that the direction of growth is antero-ventrally. The entepicondyle is proximo-distally broad and antero-ventrally thin in anterior view (Fig. 6A,B). In ventral view the articulating surface of the entepicondyle is elongated and convex, and is raised slightly above the rest of the entepicondyle in the small individual. The surface is the same in the larger individual except that it is broader proximally.

cf. Kannemeyeria lophorhinus

R316 is provisionally referred to *Kannemeyeria lophorhinus* on the basis that it shares characters with *Kannemeyeria simocephalus,* such as the presence of an acromion process and a relatively broad, straight-sided scapula blade that are not present in *cf. Dolichuranus primaevus.*

Pectoral girdle

Scapula. There are three scapulae present in R316. The left scapula is complete whereas the right one consists of two pieces (Fig. 7) while a third consist only of the proximal end of the scapula. There are also a number of fragments which represent various parts of the scapula. On the lateral surface the left scapula has been flattened so that it has a fan-shaped appearance dorsally; however, the right one has not been distorted, showing that the dorsal border is only slightly expanded and that its surface is more convex in the middle. In all the scapulae (R316) the anterior margin of the dorsal border is rounded. Just below the dorsal border the lateral surface is slightly concave. The scapula blade is fairly wide along its entire length as seen in the left scapula (Fig. 7).

About a third of the way down the anterior margin marks the beginning of the scapula spine. It is does not project far anteriorly and is not very prominent. Although the anterior border is damaged it is most likely that the spine ends at the proximal end of the acromion process (Fig. 7A,C). In all examples the acromion is broken off at the base which indicates that it is possible that the acromion was directed antero-laterally when present.

Below the acromion the bone narrows to form the distal end. Anteriorly the articulation for the coracoid is directed antero-ventrally in both the left and right scapula (Fig. 7A, C). The glenoid is directed slightly postero-ventrally with the medial wall slightly lower than the lateral which gives the oval articulating surface the appearance of facing laterally. Along the anterior margin of the glenoid there is a very small round projection.

Proximo-medially the surface is concave (Fig. 7B,D). Along the anterior border there is evidence of a very narrow concave prespinous region that possibly widens as it reaches the acromion. There is no evidence that either a tubercle or a fossa is present at the proximo-posterior border of the acromion's medial surface; however, from the posterior border of the acromion there is a groove that extend along the medial surface of the coracoid articulation to its ventral extent (Fig. 7B,D).

Forelimb

Humerus. The right humerus (R316) consists of proximal and distal ends which do not necessarily belong to the same individual while the left humerus (R316) consists of a complete bone from below the delto-pectoral crest (Fig. 8). It is possible that part of the right humerus actually represents a smaller individual (Fig. 8A,C). The delto-pectoral crest has not been preserved in proximal expansion of the right humerus. The distal end is almost completely preserved and fairly widely expanded.

On the left humerus (R316) the proximal expansion has been almost completely damaged with only the distal end of the delto-pectoral crest preserved (Fig. 8B,D). From this fragment we can deduce that the delto-pectoral crest was broad (Fig. 8D). In dorsal view it can be seen that at least the distal end of the delto-pectoral crest is twisted so that it faces antero-medially.

Although the dorsal margin of the right humerus (R316) has not been completely prepared it is evident that the head of the bone forms an inverted triangle and is located close to the posterior border of the delto-pectoral crest with a more dorsally directed articulating surface

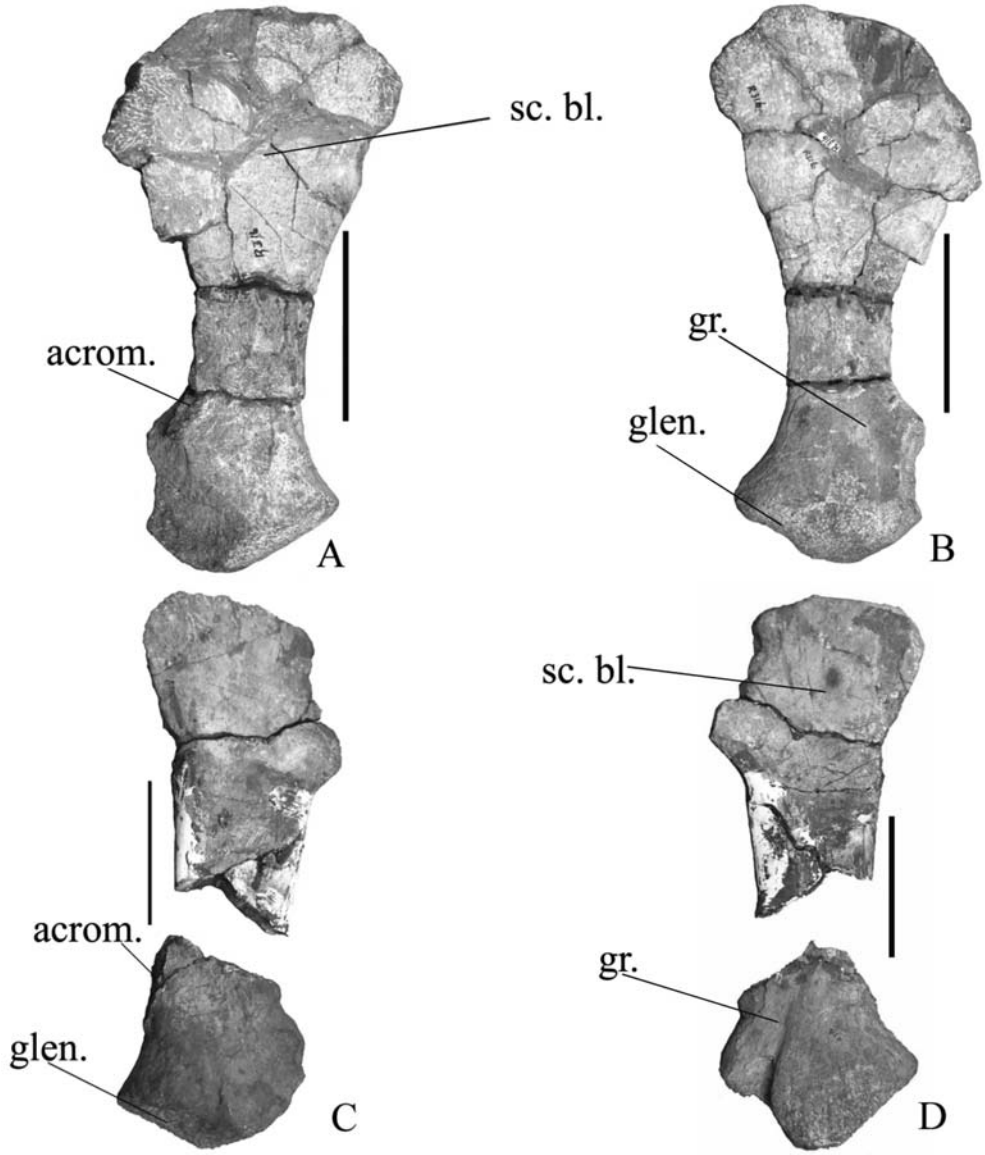


Figure 7. **A**, Lateral and **B**, medial view of the left; **C**, lateral and **D**, medial of right scapula (R316) *cf. Kannemeyeria lophorhinus.* Scale = 10 cm.

(Fig. 8A). Proximally along the posterior border of the narrow proximal expansion is a low elongated tubercle.

The head of the right humerus (R316) has not been prepared but it can be seen that the head of the bone is close to the posterior border of the delto-pectoral crest. It forms an inverted triangle but the articulating surface is directed more dorsally. The delto-pectoral crest is not preserved in this specimen but its dorsal and ventral extents are clearly visible.

Distally the humerus is widely expanded in both the left and right humeri (R316) with a wide triangular shallow olecranon fossa. The rounded ectepicondyle is larger than the entepicondyle and is raised above the dorsal surface (Fig. 8).

The biccipital fossa is incomplete on the left humerus while the right humerus (R316) it forms a narrow triangle with a concave surface (Fig. 8C,D). It narrows distally as it merges with the shaft. Distally the entepicondylar foramen forms a narrow oval slit that runs diagonally across the bone. The articulation for the ulna and the radius forms a concavo-convex surface with the radius articulation being more convex than the ulna articulation.

Pelvic girdle

Ilium. The ilia are represented by a number fragments and a single incomplete right ilium (R316; Fig. 9A). It has an incomplete anterior process while the posterior process and most of the posterior part of the iliac blade are missing. The incomplete anterior end is fairly wide and higher than the posterior process and is directed slightly laterally (Fig. 9A). Distally the blade narrows to form a short neck that grades to a short, wide acetabular (superior) ridge.

A circular acetabulum is present with incisures present along the anterior and posterior (supra-acetabular notch) margins of the lateral border. The articulating surface faces more ventrally and very slightly laterally. In front of the acetabulum the articulation for the pubis is higher and medio-laterally wider than that for the ischium (Fig. 9A).

Hindlimb

Fibula. There is a well-preserved right fibula that forms part of R316 (Fig. 9B,C). Proximally and distally the expansions are not widely expanded and are joined by a narrow shaft which is fairly straight but is curved along its medial

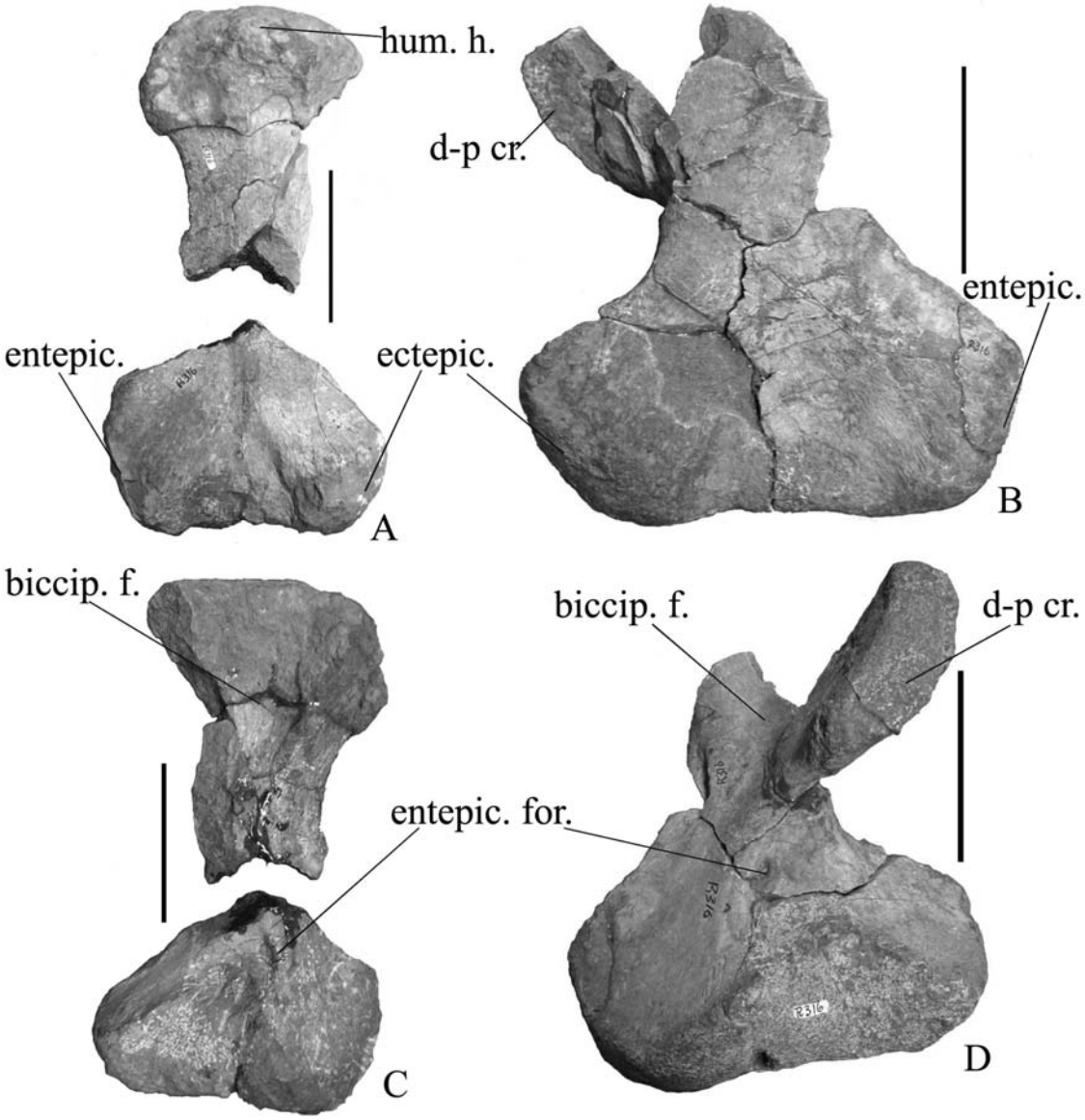


Figure 8. Dorsal view **A**, right and **B**, left and ventral view of **C**, right and **D**, left humerus (R316) *cf. Kannemeyeria lophorhinus*. Scale = 10 cm.

border. A ridge runs along the medial border on the anterior surface and becomes less distinct distally. On the posterior surface the proximal expansion is concave (Fig. 9C). A groove runs down the shaft along the medial border and it becomes wide distally. The proximal articulation is oval with a convex articulating surface that slopes medially while the distal articulation is a narrow, elongated oval with a flat to slightly convex surface.

Dicynodontia *incertae sedis*

Humerus. There is a complete humerus associated with CGP CGP/1/191A. A comparison shows that these two bones are different. It does, however, seem to share some similarities with the partial humeri currently identified as *Kannemeyeria lophorhinus.*

The proximal expansion of the humerus is narrower than the distal expansion in CGP/1/412 (Fig. 6A). Proximally the expansion is antero-posteriorly narrow in CGP/1/412 (Fig. 6A). The proximal expansion is rounded and oblong and narrows marginally towards the shaft. In CGP/1/412 the head is hemispherical and its articulating surface is directed more dorsally. The surface along the entire dorsal border including the head is rugose and pitted, which suggests that the surface was covered by cartilage in life (Fig. 6A). Posteriorly, below the dorsal border is an elongated tubercle that is visible from the dorsal and posterior views. Anteriorly and posteriorly the head is bordered by a groove with the posterior one much deeper.

Anteriorly the proximal expansion grades into the delto-pectoral crest. The delto-pectoral crest is directed anteriorly with the distal end directed medially. It is plate-like to crescent-shaped in CGP/1/412 (Fig. 6A).

The anterior border of the delto-pectoral crest is thick distally with the thickest part in the middle in CGP/1/412 (Fig. 6A). In CGP/1/412 only proximo-posterior part of the biccipital fossa is visible when viewed anteriorly. Distally the delto-pectoral crest is twisted towards the biccipital fossa. The anterior surface delto-pectoral crest extends onto the dorsal surface but is limited by a ridge on the ventral surface. Below the distal end of the delto-pectoral crest on the anterior border is a narrow, elongated oval tubercle. Along the anterior surface is the entepicondylar ridge. Posterior to this ridge is the opening of the

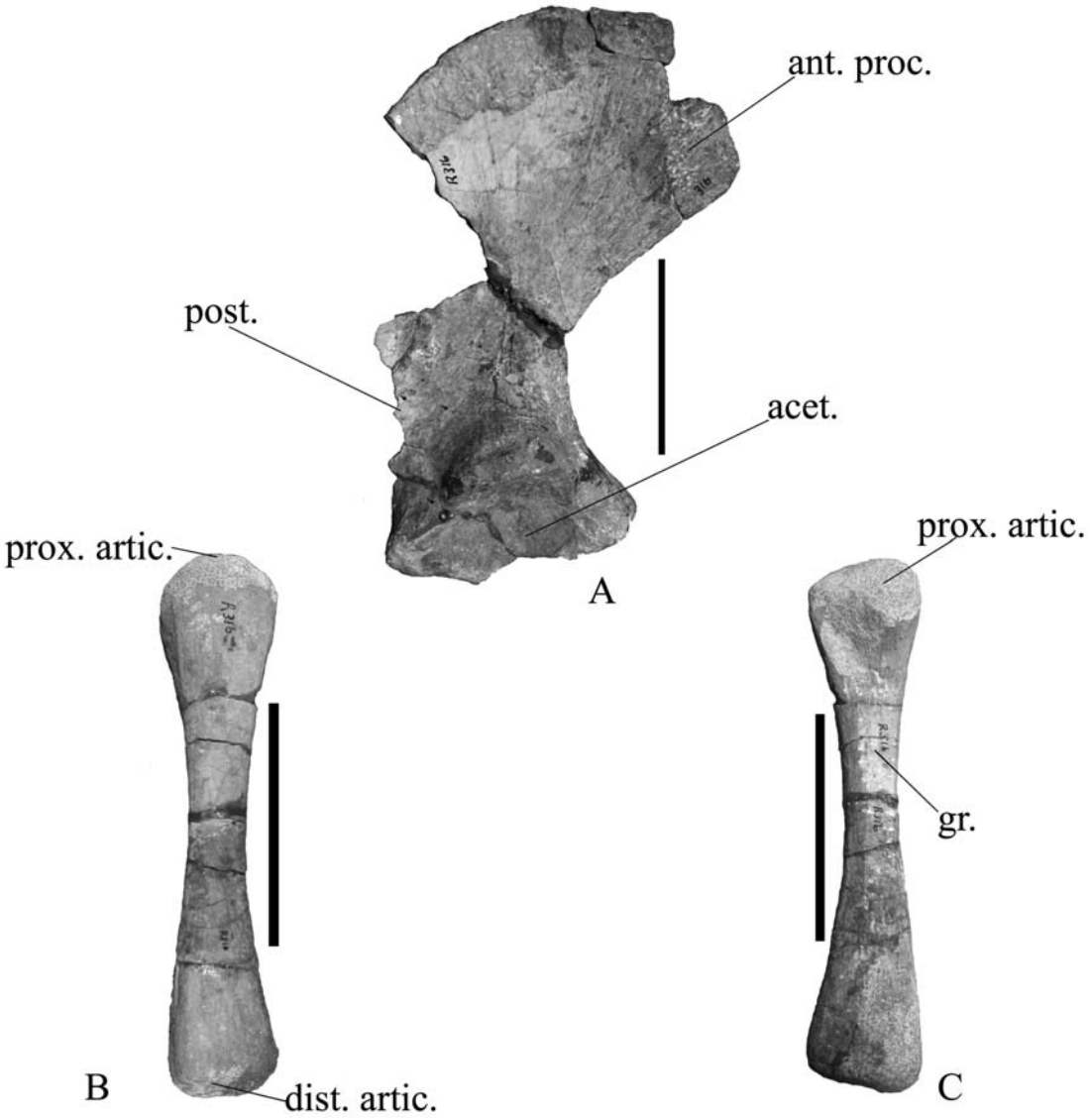


Figure 9. **A**, Lateral view of the right ilium (R316); **B**, anterior view and **C**, posterior view of the fibula (R316) *cf. Kannemeyeria lophorhinus*. Scale = 10 cm.

entepicondylar foramen, which has an oval opening in the large individual and an elongated almost oblong opening in the smaller specimen.

The shaft is short and thick. There is a distinct degree of the offset between the proximal and distal ends of the humerus which results in the ectepicondyle being directed dorsally.

The distal end when viewed anteriorly is triangular, broad and thin antero-posteriorly (Fig. 6A). In front of the entepicondyle ridge the surface slopes towards the ventral surface and is concave towards the ventral border. The articulation for the radius and ulna is narrow and is closer to the ectepicondyle. A triangular facet is present for articulation with the ulna. Its surface is convex proximally and becomes concave towards the ventral border. The radial facet is much smaller and is closer to the ventral border with a slightly concave surface.

In ventral view the head projects only slightly above the proximal surface. Proximally the postero-ventral 'corner' of the bone forms a thick, round border. In front of this border is an elongated tubercle that is broad proximally and narrows distally. Below the tubercle is a wide ridge that narrows where it merges with the shaft. The biccipital fossa is antero-posteriorly narrow, which has resulted in the fossa being deep in CGP/1/412 (Fig. 6A). A groove starts below the biccipital fossa and ends above the entepicondylar foramen. The ventral opening of the entepicondylar foramen is oval.

In CGP/1/412 the distal end faces slightly more posteriorly and the distal expansion is flared. A shallow, triangular olecranon fossa is present with thick ridges on the entepicondyle and ectepicondyle (Fig. 6A). The posterior border is concave below the dorsal border, while the dorsal border is dorso-ventrally thick and rounded, and it projects beyond the posterior surface. Below this the border thins towards the entepicondyle where it is very thin. In front of the dorsal projection the surface is deeply concave.

The ectepicondyle is round with a convex surface that projects dorsally. It is thicker than the entepicondyle but is proximo-distally narrower than the entepicondyle in anterior view. The entepicondyle is proximo-distally broad and antero-ventrally thin in anterior view (Fig. 6A, B). In ventral view the articulating surface of the entepicondyle is elongated and convex, and is raised slightly above the rest of the entepicondyle in the small individual.

The surface is the same in the larger individual except that it is broader proximally.

PHYLOGENETIC ANALYSIS

We examined the phylogenetic position of *Dolichuranus* by including the new postcranial data for *Dolichuranus* in a cladistic analysis. Only postcranial characters that could be positively ascribed to *Dolichuranus* were scored, characters of the scapula and humerus were not scored. A broad range of Triassic dicynodonts were included in this analysis (*Lystrosaurus, Shansiodon, Tetragonias, Kannemeyeria, Wadiasaurus, Rechnisaurus, Dolichuranus, Sinokannemeyeria, Parakannemeyeria, Dinodontosaurus, Placerias, Ischigualastia, Jachaleria, Angonisaurus, Stahleckeria* and '*Kannemeyeria*' *argentinensis*). An unnamed enigmatic form known only from postcranial remains from the late Early Triassic of South Africa ('morphotype B') was also included. The Triassic emydopoids *Myosaurus* and *Kombuisia* were excluded because their relationships are distant from these taxa (Angielcyzk & Kurkin 2003). The Permian *Vivaxosaurus* was included because it has been shown that it is more closely related to *Kannemeyeria* than *Lystrosaurus* (Angielczyk & Kurkin 2003). *Aulacephalodon* and *Dicynodon* (based on *D. trigonocephalus*) were employed as outgroups bringing the total number of taxa in the data matrix to 20. Characters were obtained (with some modifications) from the following sources: Damiani *et al.* (2007), Surkov *et al.* (2005), Vega Dias *et al.* (2004), Surkov & Benton (2004), Angielczyk & Kurkin (2003), Maisch (2000, 2002). All informative characters from these references were included as well as seven new characters of the postcrania, bringing the total number of characters to 85 (Appendix 1). Four of the multistate characters (10, 15, 16 and 54) represent sequential transformation series and are treated as ordered (additive). All characters were equally weighted. The authors have not had an opportunity to examine many of the relevant specimens and so have relied heavily upon the literature for character scores and for this reason the analysis should be viewed as preliminary.

The data matrix (Appendix 2) was analysed using T.N.T 1.1 (Goloboff *et al.* 2003) with the following search parameters: a traditional search using Wagner trees as the starting trees, with 100 addition sequence replicates, tree bisection reconnection was used as the swapping algorithm, saving 10 trees per replication.

The search found a single most parsimonious tree with a length of 269 steps (Fig. 10A). The tree does not represent a robust hypothesis as can be seen by the very low Bremer support values for all of the internal nodes, except *Shansiodon* + *Tetragonius* (Fig. 10B). Bootstrap values are similarly low with only two clades having a frequency of more than 50%. These are *Shansiodon* + *Tetragonius* (83%) and *Parakannemeyeria* + *Sinokannemeyeria* (52%), which is a clade that is not present in the MPT. These results indicate that a more thorough investigation of kannemeyeriiform relationships is required. Nevertheless the data are sufficient to highlight the influence that postcranial characters have for analyses of Triassic dicynodont relationships. If the postcranial data for *Dolichuranus* are excluded from the analysis a single most parsimonious tree of 267 steps results. In this tree *Dolichuranus* no longer attracts morphotype B to the Sinokannemeyeriidae which instead forms a sistergroup relationship with *Placerias,* inside the Stahleckeriidae (Fig. 11). *Dolichuranus* still nests within the Sinokannemeyeriidae, but the ancestral state reconstructions are sufficiently changed to cause the Permian *Vivaxosaurus* to nest above the Shansiodontidae as the sister-group of a clade containing *Kannemeyeria, Wadiasaurus,* Sinokannemeyeriidae and Stahleckeriidae.

DISCUSSION

In the Triassic sediments of Namibia there are two medium to large dicynodonts, namely *Dolichuranus primaevus* and *Kannemeyeria lophorhinus*. The cranial material that belongs to these taxa have been described and studied in detail (e.g. Renaut 2000; Diamiani *et al.* 2007). This study examined the postcranial material from the same unit. Unfortunately some of the postcranial material was not associated with cranial material and therefore it is not possible to definitively identify this material.

Nevertheless two scapula morphologies can be recognized and these are tentatively identified as the belonging to the two species based on cranial material. The scapula blade morph ascribed to *Dolichuranus primaevus* (exemplified by CGP/1/191B) is distinctly narrower and has a more strongly curved anterior border than that ascribed to *Kannemeyeria lophorhinus* (exemplified by R316). CGP/1/191B is also unusual in that the acromion is absent: a derived condition shared with some stahleckeriids (e.g. *Ischigualastia*; Cox 1965). In contrast R316 has an acromion and a relatively broader prespinous region to support it. CGP/1/191B shares a narrow prespinous region and a scapula spine that does not project anteriorly with the enigmatic 'morphotype B' from the *Cynognathus* subzone B of the main Karoo Basin. Morphotype B co-occurs with *Kannemeyeria simocephalus* but is known only from postcranial remains at the present time (Govender 2006; Govender & Yates, submitted). However, morphotype B retains an acromion that is not present in CGP/1/191B. Like advanced sinokannemeyeriids and morphotype B the length of the scapula of CGP/1/191B is greater than three times the width of scapula at the acromion. Similarly the humerus provisionally referred to *Dolichuranus* (CG/1/191A) shares a delto-pectoral crest set at an angle to the humeral shaft with *Sinokannemeyeria* and *Parakannemeyeria* (Sun *et al.* 1963).

The larger of the two humeri (CGP/1/412) tentatively referred to *Kannemeyeria lophorhinus* has an arc-shaped deltopectoral crest which is a derived condition shared with *Zambiasaurus* (Cox 1969; R9068; R9069), *Angonisaurus* (Cox & Li 1983; U12/1) and morphotype B. In contrast the smaller humerus (CG/1/191A) is more rectangular similar to the general kannemeyeriiforme condition (e.g. *Kannemeyeria simocephalus*; Govender 2006; Govender *et al.* 2008). The humeral head also differs between these two specimens with CG/1/412 having an antero-posteriorly expanded, hemispherical head, whereas it is less expanded and sub-triangular in CG/1/191A. These differences may be ontogenetic, but further specimens

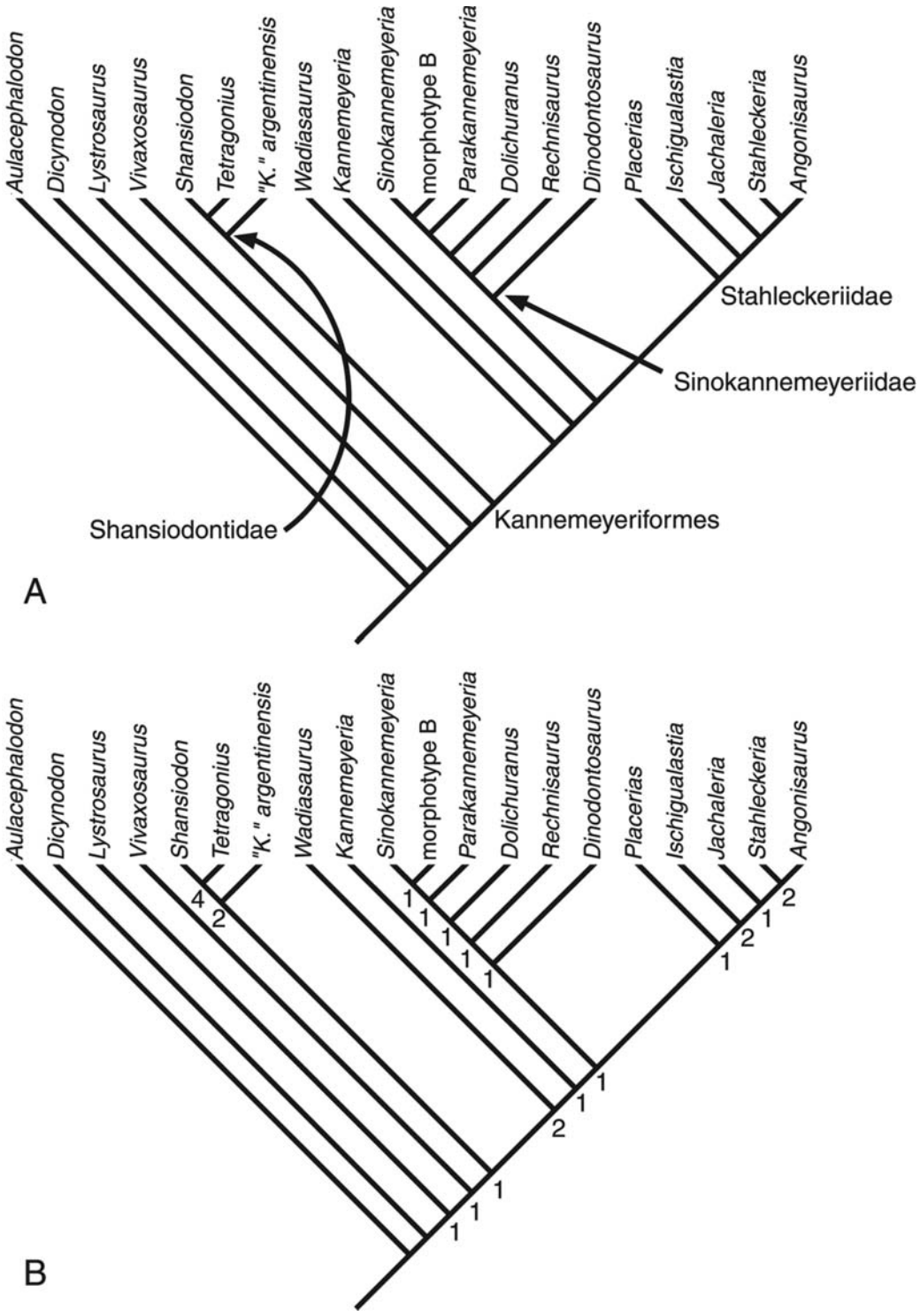


Figure 10. Single most parsimonious tree found resulting from an analysis of kannemeyeriiforme dicynodont relationships (20 terminal taxa; 85 characters). Tree has a length of 269 steps. **A**, Tree labelled with named clades; **B**, tree labelled with Bremer support values.

associated with diagnostic material are required to rule out individual variation or taxonomic mixing.

The olecranon of the ulna of *Dolichuranus* (R334) is similarly low and broad like that of *Zambiasaurus* (R9098), *Parakannemeyeria* (Sun, 1963) and morphotype B, further reinforcing a relationship with sinokannemeyeriids.

The proximal and distal expansions of the femur of *Dolichuranus* (BP/1/4578; R320) are not widely expanded as seen in *Kannemeyeria* (Govender *et al.* 2008), *Zambiasaurus* (R9118), *Ischigualastia* (Cox, 1965) and *Placerias* (Camp & Welles, 1956). Like most Triassic dicynodonts the femoral head is directed dorsally but is not offset from the rest of the bone as seen stahleckeriids (Camp & Welles 1956; Cox 1965), derived sinokannemeyeriids (Sun 1960, 1963; Young 1937) and morphotype B. The fibula (R316) does not conform to *K. simocephalus* but rather resembles that of morphotype B in that it is has slightly expanded ends with an almost straight shaft.

The specimen R316 does not resemble the other specimens from the Omingonde but tends to resemble that of *K. simocephalus,* supporting its referral to *K. lophorhinus.* The scapula blade is fairly straight, slightly wide and the

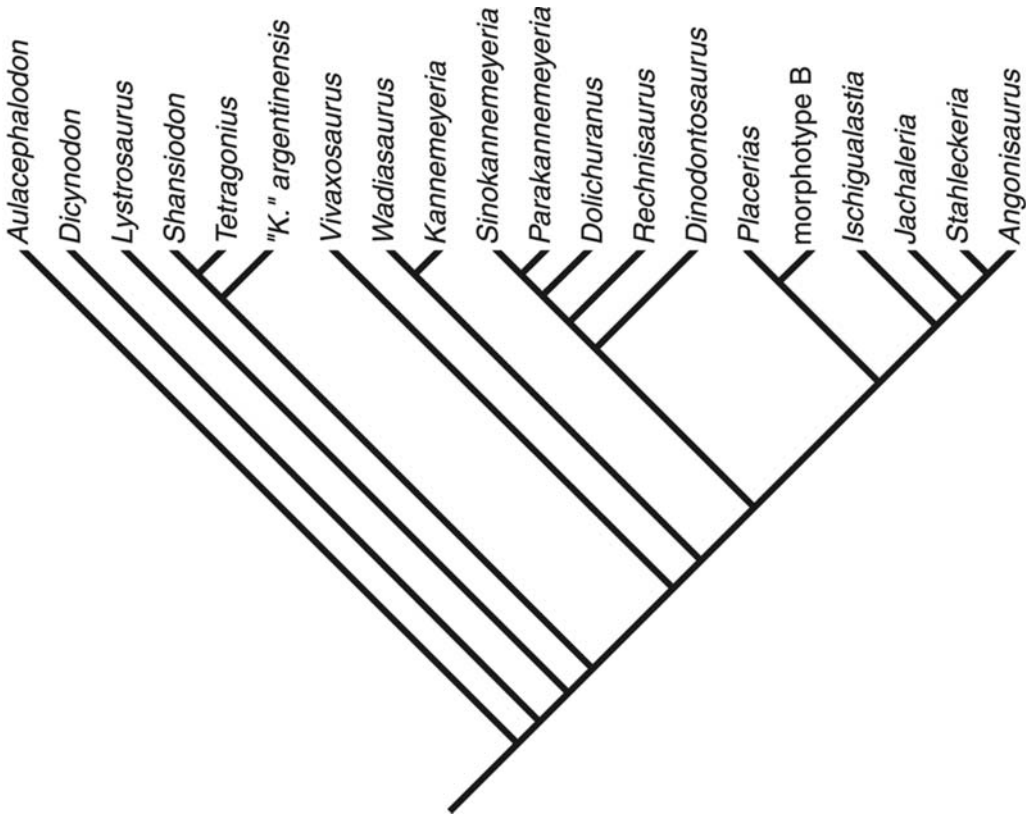


Figure 11. Single most parsimonious tree resulting from an analysis that excludes all postcranial character state data from Dolichuranus. Tree has a length of 267 steps.

acromion would have been directed antero-laterally. The proximal expansion of the right humerus is rectangular as seen in the smaller *K. simocephalus* specimen (BP/1/6160). Although incomplete posteriorly the ilium that forms part of the specimen (R316), the form of the ilium does resemble that of *K. simocephalus.* The anterior process is short antero-posteriorly but wide dorso-ventrally and it is situated higher than the posterior process. Also the acetabulum faces laterally and the superior acetabular ridge is antero-posteriorly short and wide. The only element that does not closely resemble *K. simocephalus* is a fibula which resembles that of morphotype B. Based on the above comparison we suggest that R316 represents *K. lophorhinus.*

Preliminary cladistic analysis suggests that *Dolichuranus* is a sinokannemeyeriid. Most of the character data supporting this position reside in the skull; however, the postcranial data do exert an influence on the analysis. In particular *Dolichuranus* attracts the poorly known morphotype B to the Sinokannemeyeriidae. In the absence of postcranial data from *Dolichuranus* morphotype B clusters in the Stahleckeriidae which is an unusual result, for morphotype B would then be the only stahleckeriid known from outside the Americas. A close relationship between *Dolichuranus* and morphotype B is supported by their shared presence of a third trochanter on the femur. Further derived characters supporting this relationship may be found in the scapula (a scapula blade that is three times longer than the width at the acromion) and the humerus (a deltopectoral crest that is set at an angle relative to the humeral shaft); however, these bones can only be tentatively referred to *Dolichuranus.*

CONCLUSION

The postcranial skeletons of both dicynodont species in the Omingonde can be recognized although only some material is positively associated with *Dolichuranus primaevus.* Preliminary cladistic analysis resolves *Dolichuranus* as a sinokannemeyeriid although the postcrania displays similarities to both sinokannemeyeriids and stahleckeriids. Including the postcranial characters for *Dolichuranus* in the analysis, causes the poorly known South Africa taxon, morphotype B, to group with the Sinokannemeyeriidae as well.

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INSTITUTIONAL ABBREVIATIONS

BPI	Bernard Price Institute for Palaeontological Research, Johannesburg.
CGP	Council for Geosciences, Pretoria.
R	Geological Survey of Namibia, Windhoek.

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APPENDIX 1

Character list

1. Shape of the distal margin of the caniniform process: rounded (0) or pointed (1) (modified from Vega-Dias 2004).
2. Tusks: present (0) or absent (1) (Vega-Dias 2004).
3. Position of the caniniform process: anterior to the orbit (0), underneath orbit (1) (Vega-Dias 2004).
4. Depth of the caniniform process: much shallower than the basal length (0) approximately as deep, or deeper than, the basal length (1).
5. Posterior margin of the caniniform process: not furrowed (0) with a postero-ventral furrow (1) (modified from Damiani *et al.* 2007).
6. Length of nasal symphysis: greater than 50% of the length of the nasals (0) or less than 50% of the length of the nasals (1) (Vega-Dias 2004).
7. Anterior tip of the nasal: anterior to the premaxilla-maxilla suture (0) or level with to posterior to the premaxilla-maxilla suture (1) (modified from Vega-Dias 2004).
8. Shape of the premaxillary beak in dorsal view: bluntly rounded to squared (0) or sharply pointed (1).
9. Median premaxillary ridge: short (0), elongate extending onto frontals (1) or absent (2) (Vega-Dias 2004).
10. Shape of fronto-nasal suture: irregular to straight (0) or strongly convex anteriorly (1) (Vega-Dias 2004).
11. Nasal bosses: paired, separate (0), single median boss (1), paired, meeting posteriorly (2), or absent (3) (modified from Angielczyk and Kurkin 2003).
12. Postnasal fossa behind the external naris: absent (0) or present (1) (Vega-Dias 2004).
13. Maxilla: excluded from pterygoid girder (0) or extending onto lateral surface of pterygoid girder (1) (Damiani *et al.* 2007).
14. Nasal-lacrimal contact: absent (0) or present (1) (Damiani *et al.,* in press).
15. Lacrimal-septomaxilla contact: absent (0) or present (1) (Vega-Dias 2004).
16. Shape of the prefrontal: longer than wide (0), equant (1) or wider than long (2) (Vega-Dias 2004).
17. Antorbital sulcus: present (0) or absent (1) (Damiani *et al.* 2007).
18. Adult orbit size: diameter less than 20% of the skull length (0) or greater than 20% (1).
19. Maxilla-squamosal contact: simple butt or scarf joint (0), interdigitating suture (1) (Vega-Dias 2004).
20. Posterior tips of the frontals: lateral to the parietal foramen (0), no further posterior than the anterior margin of the parietal foramen (1) or posterior to parietal foramen (2) (Damiani *et al.,* in press).
21. Posterolateral margin of the skull in lateral view: sloping anteroventrally (0) vertical (1) (Vega-Dias 2004).
22. Postorbital-squamosal contact: present (0) or absent (1) (Vega-Dias 2004).
23. Preparietal: present (0) or absent (1) (Vega-Dias 2004).
24. Intertemporal region: broad, flattened dorsal surface (0), transversely compressed intertemporal crest (1) (modified from Maisch 2001).
25. Parietal exposure on the dorsal skull roof: broad flat exposure (0), exposed only in a narrow trough (1) (Angielczyk and Kurkin 2003).
26. Ventral extent of parietal: not contacting the periotic (0) or contacting the periotic (1) (Surkov and Benton 2004).
27. Interparietal contribution to the dorsal skull roof: absent (0) narrow contribution on the rim of the skull roof (1) anteriorly extensive contribution (1) (Vega-Dias 2004).
28. Orientation of posterior process of the postorbital: facing dorsolaterally (0) vertical (1) (Angielczyk and Kurkin 2003).
29. Height of intertemporal region above orbit: less than the diameter of the orbit (0) or greater than the diameter of the orbit (1) (modified from Vega-Dias 2004).
30. Postfrontal: present (0) or absent (1) (Maisch 2001).
31. Dorsal margin of the squamosal in posterior view: notched (0) or entire (1) (modified from Angielczyk and Kurkin 2003).
32. Length of the temporal fenestra: greater than 33% of the length of the skull (0), less than 33% of the length of the skull.
33. Squamosal width: forming less than 50% of the width of the occiput (0) or forming at least 50% of the width of the occiput (1) (Vega-Dias 2004).
34. Disposition of the orbits: narrow interorbit with dorsolaterally facing orbits (0) broad interorbital region with laterally facing orbits (1) (Vega-Dias 2004).
35. Length of the prepineal region of the skull: less than the postpineal (0) or greater than the postpineal region of the skull (1) (modified from Vega-Dias 2004).
36. Skull shape in dorsal view: longer than wide (0) or as wide as long (1) (Vega-Dias 2004).
37. Height of the suspensorium: less than 60% of the skull length (0) greater than 60% of the skull length (1) (Vega-Dias 2004).

38. Skull length: well over 300 mm (0) or no more than 300mm (1) (Vega-Dias 2004).
39. Pilla antotica and trigeminal opening: pilla is present forming a notched opening for the trigemijnal nerve (0), pilla is absent so that the trigeminal opening is a horizontal hollow (1) (Surkov and Benton 2004).
40. Dorsum sella: distinct hollow (0), indistinct (1) (Surkov and Benton 2004).
41. Height of dorsum sella: under pilla antotica or less than 33% of interior endocranial cavity (0) or reaching level of pilla antotica or greater than 33% of the interior endocranial cavity (if pilla antotica is absent) (1) (Surkov and Benton 2004).
42. Carotid foramina on sella turcica: single median (0) or paired (1) (Surkov and Benton 2004).
43. Intertuberal ridge on basisphenoid: present (0) or absent (1) (Maisch 2001).
44. Basitrabecular process: terminating posterior to interpterygoid vacuity (0) or contributing to the margin of the interpterygoid vacuity (1).
45. Cultriform process: compressed and blade-like (0) or broad, nearly filling the interpterygoid vacuity (1) (Surkov and Benton 2004).
46. Shape of the interpterygoid vacuity: elongate oval (0) or broad oval to rhomboidal opening that is almost as wide as it is long (1) (Surkov and Benton 2004).
47. Mid ventral plate of the vomers: broad flat ventral surface (0) or blade like ventral surface (1).
48. Width of the pterygoid girder: longer than wide (0), as wide as long (1) wider than long and occupying half the distance between the quadrate condyles (2) (modified from Vega-Dias 2004) ordered.
49. Position of the ectopterygoid: on ventral surface of palate (0), dorsally displaced (1) or absent (2) (Damiani *et al.* 2007).
50. Symphyseal margin of the dentaries: raised with a scooped-out posterior surface (0) or level, wedge-shaped with a narrow median groove on the posterior surface (1) (modified from Angielczyk and Kurkin 2003).
51. Shape of the dentary table: lateral and medial ridges of equal height (0) or medial ridge much taller than lateral ridge and blade-like (1) (modified from Angielczyk and Kurkin 2003).
52. Size of the reflected lamina of the angular: small with a large gap between the posterior margin and the articular (0) or expanded with posterior margin closely following, if not contacting, the articular (1) (Vega-Dias 2004).
53. Coronoid emeinence: present (0) or absent (1).
54. Shape of the axis: much longer than high (0), or massive with a height:length ration of approximately 0.9 (1) (Surkov *et al.* 2005).
55. Triceps projection on the scapula: present (0) or absent (1) (Vega-Dias 2004).
56. Acromion: large projection (0) or a small knob (1) (Vega-Dias 2004).
57. Scapula blade: narrow (0) or broad (1).
58. Anteriorly projecting scapula spine attached to the acromion: absent (0) or present (1) (Vega-Dias 2004).
59. Position of the coracoid foramen: on the precoracoid (0) or on the precoracoid-scapula suture (1) (Vega-Dias 2004).
60. Precoracoid contribution to the glenoid; present (0) or absent (1).
61. Dorsal expansion of the scapula: less than 1.5 times the width of the scapula at the acromion (0) or greater than 1.5 times the width of the scapula at the acromion (2) (Vega-Dias 2004).
62. Constriction of the sternum in dorsal view posterior to the sternal bosses: absent (0) or present (1) (Vega-Dias 2004).
63. Number of sternal bosses: two (0) or four (1) (Vega-Dias 2004).
64. Twist between the transverse axes of the proximal and distal ends of the humerus: less than 60° (0) or more than 60° (1) (Vega-Dias 2004).
65. Size of the deltopectoral crest: occupying approximately 50% of the length of the humerus (0), much larger than 50% (1) or much smaller than 50% (2) (Vega-Dias 2004).
66. Length of humerus relative to the femur: less than the femur (0) or at least as long as the femur (1).
67. Proportion of the ulna that is distal to the sigmoid notch: longer than the portion proximal to the sigmoid notch (0), shorter than the proximal portion (1) or equal to the proximal portion (2) (Vega-Dias 2004).
68. Shape of the radius: elongate and slender (0), short and robust (1) (Vega-Dias 2004).
69. Anteroventral corner of the preacetabular lobe of the ilium: dorsal to the level of the acetabulum (0) extending ventral to the level of the dorsal rim of the acetabulum (1) (Vega-Dias 2004).
70. Shape of the acetabulum: dorsally notched (0) subcircular without a dorsal notch (1) (Vega-Dias 2004).
71. Dorsal projection of the ischium: not reaching the level of the ventral rim of the acetabulum (0) projecting dorsal to the level of the ventral rim of the acetabulum (1) (Vega-Dias 2004).
72. Anterior extension of the pubic tubercle: not extending as far as the level of the anterior rim of the acetabulum (0) extending anterior to the anterior rim of the acetabulum (1) (Vega-Dias 2004).
73. Shape of the femoral head in lateral view: anterior and posterior expansions of the head are equal (0) anterior expansion of the head greater than posterior expansion (1) (Vega-Dias 2004).
74. Shape of the greater trochanter of the femur: a straight ridge parallel to the shaft of the femur (0) a straight ridge set obliquely to the long axis of the femoral shaft (1) or sigmoidally curved (2) (Vega-Dias 2004).
75. Size of the greater trochanter: lateral edge no more than 33% of the length of the femur (0) lateral edge over 33% of the length of the femur (1) (Vega-Dias 2004).
76. Orientation of the coracoid facet of the scapula: facing antero-ventrally (0) or facing ventrally (1).
77. Orientation of the scapular glenoid: faces laterally (0), faces postero-ventrally (1), faces ventrally (2).
78. Profile of the deltopectoral crest: subrectangular with a straight anterior margin (0) rounded with a curved, convex anterior margin (1).
79. Olecranon ossification: part of the ulna, even in juveniles (0) develops from a separate centre of ossification (1) (Maisch 2001).
80. Shape of the olecranon process: tall, narrow and wedge-shaped (0) low, broad and rounded (1).
81. Orientation of the deltopectoral crest: anterior margin parallel with the humeral shaft (0) or set at an angle to the shaft (1).
82. Shape of the scapula blade: no more than three times longer than the width at the acromion (0) much longer than three times the width at the acromion (1) (modified from Maisch 2001).
83. Shape of the ilium: with moderate, subequal pre- and postacetabular lobes (0), preacetabular lobe markedly enlarged (1) or preacetabular lobe very enlarged while postacetabular lobe is very reduced (2) (Maisch 2001).
84. Relationship of femoral head with greater trochanter: confluent (0) or disjunct (1).
85. Third femoral trochanter: absent (0) or present (1).

APPENDIX 2

Character-taxon matrix. P = Polymorphic character (0,1), X = polymorphic character (1,2).

Aulacephalodon	00000	00000	00001	00000	00000	00100	00??0	00000	00P00	00000	000?0	0010?	10100	10?00	??000	01001	01010
Dicynodon	00000	00000	10000	01000	00011	00000	00000	0000P	00000	01000	00000	01000	0??00	00000	00001	00?00	00000
Vivaxosaurus	00000	?0000	20000	00002	00000	?2110	00001	000??	??1?0	1102?	????0	1000?	1??01	????1	?????	020??	00???
Lystrosaurus	00100	01000	P0111	20001	10000	00000	00001	10000	10000	11021	001P0	01010	10002	00000	00000	0210?	1?000
Shansiodon	00100	??01?	30100	?01?1	01?11	10?01	00?00	001?1	01???	?002?	100?1	0?00?	0??10	0000?	??000	12100	1?01?
Tetragonias	00100	00000	00111	101?1	01011	10001	00000	00101	0??11	00021	100?1	01101	00010	10000	01000	12101	10101
Kannemeyeria argentinensis	00000	11000	20101	00101	00011	?2101	00010	001??	??1??	1102?	100?1	01001	10?00	10000	01?10	01001	?0000
Wadiasaurus	0P00?	?100?	?0?00	?10??	0?011	?X12?	00000	000??	??1??	??1?1	00110	00111	??110	?201?	00011	01010	00100
Kannemeyeria	000?1	?1010	20110	01012	00011	12121	00000	00010	00110	11121	00110	00101	11?00	00000	01101	01000	00100
Dolichuranus	?0001	1?021	21000	10012	?0011	?1111	01011	000??	??1?0	01111	111??	???0?	?????	?????	??010	????1	???01
Dolichuranus (cranial only)	?0001	1?021	21000	10012	?0011	?1111	01011	000??	??1?0	01111	111??	?????	????	?????	?????	?????	?????
Morphotype B	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????	????0	1?10?	1????	?????	??111	01101	11?01
Parakannemeyeria	0001?	00001	21??0	1?00?	001?1	?001?	01011	000??	?????	??1?1	?0??1	0010?	0??10	0210?	00001	01001	0101?
Sinokannemeyeria	0001?	0000?	?1??0	1?00?	001?1	?0011	01011	000??	?????	??2??	?0?11	0010?	00010	?210?	??101	01100	1111?
Dinodontosaurus	00000	01000	?0000	01011	01010	?1?01	01001	000??	??1?1	11111	011?1	01101	00000	10101	11?21	01011	00100
Placerias	10010	0?101	?0001	0101P	01000	12?11	10000	01010	11111	10??1	01110	00101	?0012	?11??	01011	01111	10?1?
Angonisaurus	11100	??00?	20???	?10??	10111	1110?	00110	11001	01111	1?2?1	1?100	01101	?????	????1	10???	11?00	?02??
Stahleckeria	01000	10001	20?00	21010	10100	01001	10101	11010	11110	?0121	01110	0?101	00112	11111	11111	???0?	?????
Ischigualastia	11000	11111	30000	01012	01000	12111	10010	010??	??1??	1?221	011?1	21011	1?1?1	?11??	??110	00010	00210
Jachaleria	11100	10021	00001	20012	11011	?2111	10010	010??	?????	11221	????0	2101?	111??	??100	11???	01???	??1??
Rechnisaurus	0001?	01000	00?00	1?0?1	01011	??1?1	01?11	?0010	10110	??1??	???1?	?0??1	?????	?????	?????	?????	?????

Middle Pliocene Bovidae from Hominid-bearing sites in the Woranso-Mille area, Afar region, Ethiopia

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Hominid-bearing sites of the northwestern part of the Woranso-Mille research area, dated to between 3.7 and 3.8 Mya, yield 10 species of Bovidae. The evolutionary stages of the most common species fit quite well this radiometric age. The most abundant bovid is a new species of *Aepyceros,* of large size, with upright, lyrated horn-cores; it is clearly distinct from the impalas of younger sites in the same area, and from those sampled at Hadar. A new species of *Tragelaphus* is also common; its horn-cores exhibit reduced anterior keel and antero-posterior compression foreshadowing the most common form at Hadar. A single partial *Ugandax* skull, despite some primitiveness, may fit into the variation range of *U. coryndonae* from Hadar. Other tribes are rare; the virtual absence of reduncines is a major difference from younger sites, but the occurrence of a cephalophine and of *Neotragus* is worth noting. This assemblage unambiguously indicates an environment with a significant component of arboreal vegetation.

Keywords: Artiodactyla, Bovidae, Middle Pliocene, Ethiopia, eastern Africa.

INTRODUCTION

A number of fossil vertebrate localities have recently been discovered by a team led by one of us (Y.H-S.) in the Woranso-Mille (WORMIL) area, about 45 km north of Hadar in the lower Awash Valley, Afar region, Ethiopia (Fig. 1). Work at WORMIL began in 2002, and has yielded abundant mammalian faunas, together with crucial hominid remains (Haile-Selassie *et al.*, in press.). There are about 25 groups of vertebrate localities, among which five, including some of the most significant in terms of paleoanthropological discoveries, are now chronometrically dated to between 3.57 ± 0.014 and 3.82 ± 0.18 (Deino *et al.*, in press; Haile-Selassie *et al.* 2007; Haile-Selassie *et al.,* in press). These are Am-Ado (AMA), Aralee Issie (ARI), Makah Mera (MKM), Mesgid Dora (MSD) (collectively referred to as AAMM), all dated to between 3.7 and 3.77 Ma, and the slightly younger Korsi Dora (KSD), dated to the *c.* 3.5 Mya period. These five localities are situated in the northwestern part of the Woranso-Mille study area. They are older than all Hadar localities, but their ages correlate with the base of the Basal Member of the Hadar Formation (Wynn *et al.* 2008). In the early 1970s, some fossils were collected by the International Afar Research Expedition (IARE) from two localities (AL-99 and AL-100) in the same area, then called 'Ahmado'; they are presently housed in the National Museum of Ethiopia (NME). Although it is clear that the fauna from these localities is earlier than that of Hadar, the geographic and stratigraphic locations of these two localities remain too uncertain for precise correlation.

All of the bovid material studied below consists of cranial parts; very few postcranial elements of this family have been collected. Authors of family-group names follow Grubb (2001). Measurements are in mm. In descriptions, the tooth-row is taken to be horizontal. Upper teeth are in upper case, lower teeth are in lower case.

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SYSTEMATIC PALEONTOLOGY

Family Bovidae Gray, 1821
Subfamily Bovinae Gray, 1821
Tribe Tragelaphini Blyth, 1863

Genus *Tragelaphus* Blainville, 1816

Type species. Tragelaphus scriptus (Pallas, 1766), living bushbuck.

Diagnosis. Medium to large tragelaphines with spiralled horn-cores inserted close together and having an anterior keel and sometimes a strong postero-lateral one. Small to medium-sized supra-orbital pits, which are frequently long and narrow; occipital surface tending to have a flat top edge and straight sides (Gentry 1985).

***Tragelaphus saraitu* sp. nov.**, Figs 2A–E, 3, Table 1

Holotype. MSD-VP-5/2, a braincase with complete horn-cores, but lacking the cranial base, from Mesgid Dora, Woranso-Mille area, lower Awash valley, Ethiopia, 3.7–3.8 Ma (Fig. 2A).

Referred material. About 15 frontlets and horn-cores, plus numerous teeth from ARI, MKM, KSD, and MSD. A few specimens from AMA are perhaps also of this species.

Derivatio nominis. The species name 'saraitu' means kudu in the local Afar language.

Diagnosis. A *Tragelaphus* with horn-cores that are long and slender, divergent by about 90° at the base, inserted upright, strongly spiralled (almost a complete whorl), so that their lower part is strongly curved backwards, and their lowermost part is straight or slightly curved outwards (but never shows decreasing divergence). The tips are more or less parallel. The basal cross-section is intermediate in size between that of *T. moroitu* from the earliest Pliocene of the Middle Awash and that of the most common *Tragelaphus* species of Hadar; it is moderately compressed antero-posteriorly (index *c.* 0.8), with a change in outline curvature antero-laterally that may be called a keel higher

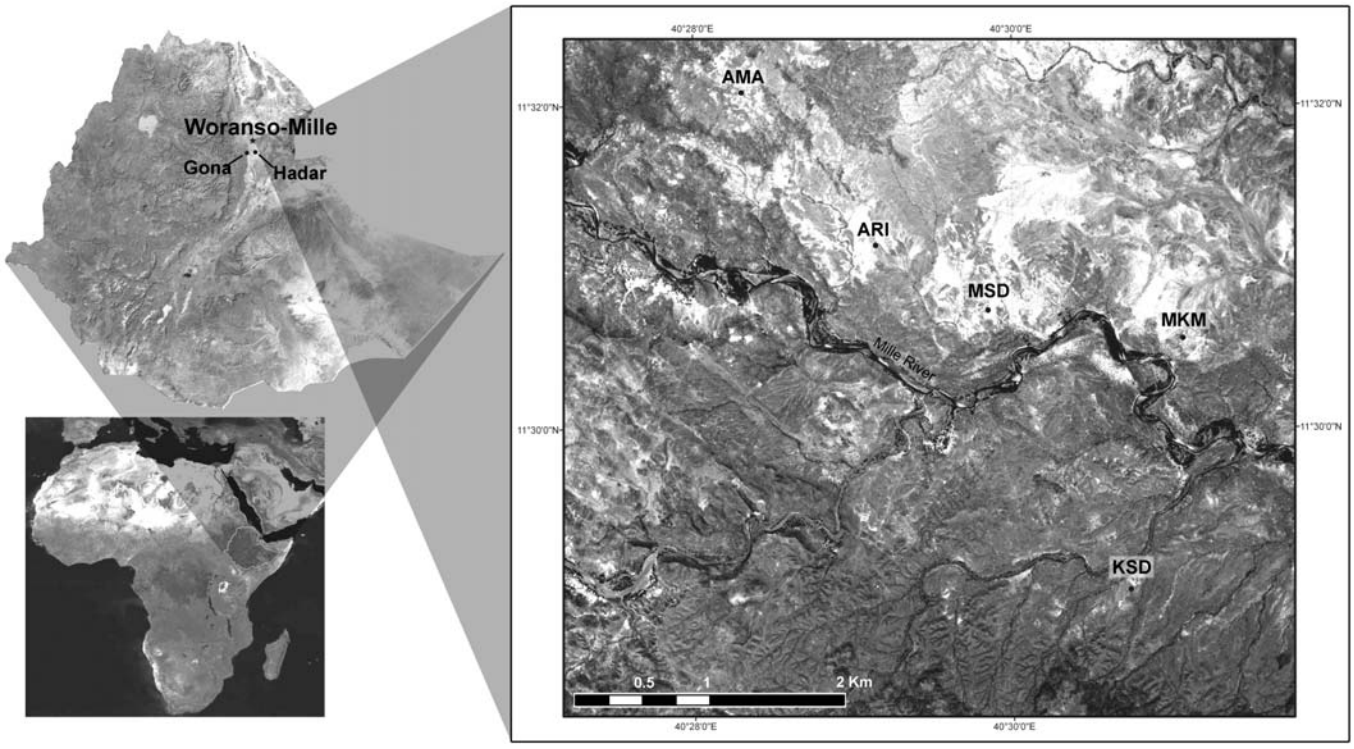


Figure 1. Location map showing major collection areas at AAMM. AMA = Am-Ado; ARI = Aralee Issie; MSD = Mesgid Dora; MKM = Makah Mera; KSD = Korsi Dora.

up, and a moderate postero-lateral keel that usually becomes more acute upwards. The occipital is trapezoidal rather than semi-circular, but with rounded upper border, and no transverse ridge above it. Lower p4 usually with an open lingual wall.

Description. The main features of this species are listed in the diagnosis. The holotype (Fig. 2A) is the only specimen with complete horn-cores, but other frontlets and horn-cores can be assigned to the same species with confidence, on the basis of their measurements, and degree of horn-core divergence, upright insertion, curvature, and cross-section shape (Fig. 3). The horn-cores of ARI-VP-3/62 share the same morphology, but are clearly more slender than the others although they are long and therefore adult; we tentatively include this specimen in the same species. Measurements are given in Table 1.

The only cranial base is that of the braincase MSD-VP-1/20 (Fig. 2C), which is certainly fully adult, as its horn-core measurements are among the largest of this species. The *foramen ovale* is circular. The basioccipital is long, as in other tragelaphines, but the anterior tuberosities are weak for this tribe, close to each other, and extend posteriorly as long ridges on either side of a very narrow central groove. No specimen includes any part of the face, although MSD-VP-8/7 has a small but well-preserved supra-orbital foramen (SOF) The damaged foramina of ARI-VP-3/62 were also likely small.

Teeth are identified on the basis of the absence of another medium to large *Tragelaphus* at these localities, but the occurrence of such another species in slightly younger sites of the WORMIL area precludes definite assignment of every tragelaphine tooth to *T. saraitu.* In any case, even if a few of them in fact belong to another species, the characters mentioned in the diagnosis would remain valid: of seven specimens of p4, five have the paraconid and metaconid separated down to the cervix, whereas the other two have a complete wall, but only one of them (ARI-VP-4/7, Fig. 2D) is in early wear, the other being much worn. The usual lack of contact between paraconid and metaconid of p4 is more like the Hadar *Tragelaphus* than like the Omo *T. nakuae,* in which more than half of the p4s are closed lingually (Gentry 1985). The mean length of seven m3s is 31 mm (range = 28–34). The lengths of three lower molar series are: 69.5 (MKM-VP-1/168), 71.3 (MSD-VP-2/161, Fig. 1E), and 74 (MSD-VP-2/44).

Comparisons. By the general course and cross-section of its horn-cores, *Tragelaphus saraitu* is reminiscent of the modern nyala (*T. angasi*), sitatunga (*T. spekei*), mountain nyala (*T. buxtoni*) and bongo (*T. euryceros*). It averages larger than the former two (the difference is greater for the teeth than for the cranium), and slightly smaller than the latter two. The nyala differs in its less spiralled, less divergent and more inclined horn-cores; those of the sitatunga differ by the same two latter characters, but their degree of spiralling is about the same as in *T. saraitu.* Those of the bongo have very weak basal divergence, and this divergence decreases from the very base, in contrast to all other species. A possible resemblance with *T. saraitu* is the presence of horns in females, as no hornless skull is known from AAMM, but this could also be due to preservation bias against hornless skulls. The mountain nyala, endemic to Ethiopia, has much more uprightly inserted horns than the other above-mentioned living species (thus resembling *T. saraitu* in this feature) but they are strongly spiralled and with re-approaching tips.

Tragelaphus saraitu can also be compared to several Pliocene eastern and South African species:

The poorly known *Tragelaphus* from the early Pliocene of

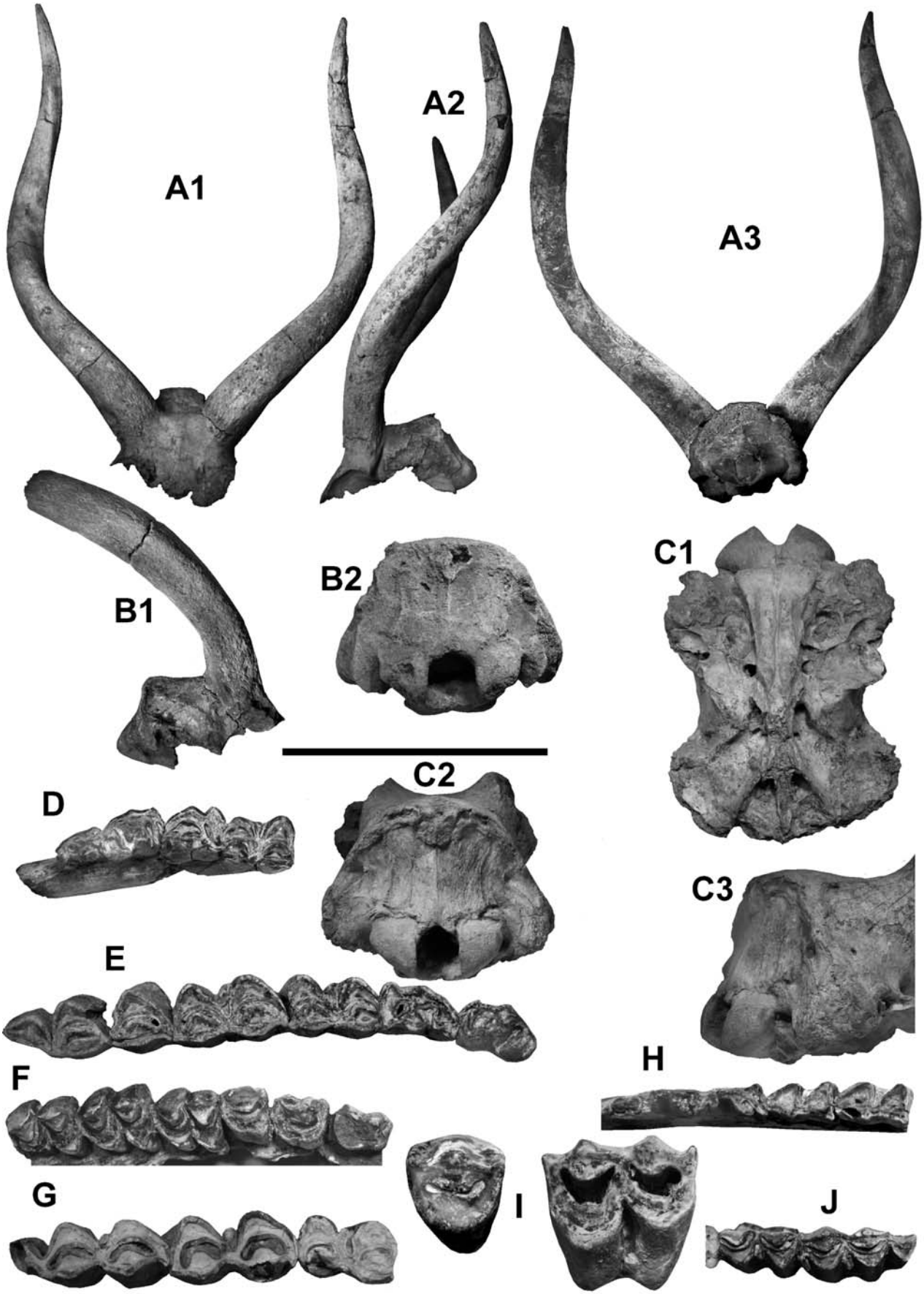


Figure 2. **A–E**, *Tragelaphus saraitu*. **A**, holotype frontlet and brain-case, MSD-VP-5/2, in (**A1**) front view, (**A2**) lateral view, and (**A3)** posterior view; **B**, brain-case, ARI-VP-3/22, in: **B1,** lateral view, and **B2,** occipital view; **C**, brain-case, MSD-VP-1/20, in (**C1**) ventral view, (**C2**) occipital view, and (**C3)** oblique right lateral view; **D**, lower tooth-row p2–m1, ARI-VP-4/7; **E**, lower tooth-row p3–m3, MSD-VP-2/161; **F**, *Tragelaphus* sp., upper tooth-row P2–M3, KSD-VP-1/9; **G**, *cf. Hippotragus* sp., lower tooth-row m1–m3, MKM-VP-1/62; **H**, *Neotragus* sp., lower tooth-row p3–m2 and roots of p2, MKM-VP-1/93; **I**, *Cephalophus* sp., upper P4, ARI-VP-1/370, and upper molar, ARI-VP-1/197; **J**, Reduncini gen. et sp. indet., m2–m3, MSD-VP-1/43. Scale = 30 cm for Fig. A, 15 cm for Figs B,C, 5 cm for Figs D–G and J, 2.5 cm for Figs H–I.

Table 1. *Tragelaphus saraitu* – measurements of the most complete specimens.

	HC APD	HC Transv.	Length along anterior curve	Width over pedicles	Width over middle of supra-orbital foramina	Minimum width over temporal fossa	Minimum width of braincase	Width over mastoids	Bicondylar width	Occipital height	Width over post. tuber. of basiocc.
ARI-VP-1/148	43.6	53.5	600	–	–	–	–	–	–	–	–
ARI-VP-3/22	51	54.3	–	–	–	60	95	128	–	66	49.5
ARI-VP-3/62	35.6	46.3	–	112	*c.* 46	–	–	–	–	–	–
MSD-VP-1/20	48.5	64.3	–	130	–	61	97	131.6	69.3	62.5	47.5
MSD-VP-3/12	41.5	56.4	–	122.5	–	–	–	–	–	–	–
MSD-VP-5/1	45	52.5	–	123	–	–	–	–	–	–	–
MSD-VP-5/2	43.7	55.7	580	120	–	50	92	124	71	60	–

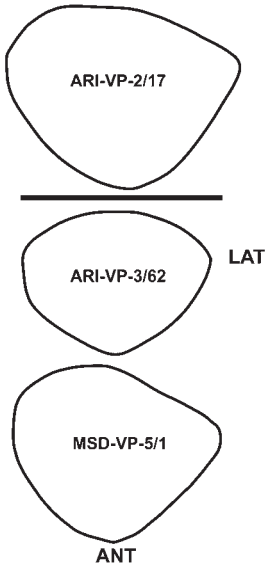


Figure 3. Cross-sections of *Tragelaphus saraitu* horn-cores. Scale bar = 5 cm.

Langebaanweg in South Africa (Gentry 1980) is smaller, and has horn-cores without antero-posterior compression, and an anterior keel which is stronger on average, and is not shifted laterally.

Tragelaphus kyaloi from the Pliocene of Kenya (Harris 1991, 2003; Harris *et al.* 2003; this name was originally spelled *kyaloae* but, being based on a male name, its genitive is *kyaloi*) is smaller, has an incipient transverse ridge across the top of the occipital, the tips of the horn-cores re-approach closely (as in *T. buxtoni*), and on the type-specimen at least (Haile-Selassie *et al.* 2009, fig. 9.10), the horn-cores have a much more rectangular basal cross-section. Although this species has been reported from several sites (East and West Turkana, Kanapoi, and Lothagam), it has not been described in great detail. Nevertheless, its type, which comes from strata not much younger than *T. saraitu,* is sufficiently distinct for specific identity to be ruled out.

Tragelaphines are rare at Laetoli. A frontlet of doubtful stratigraphic provenance (Gentry 1987, in review) was illustrated by Dietrich (1942, fig. 154) as *T.* cf. *buxtoni*; it is certainly larger than *T. saraitu* (basal perimeter 20.5 cm according to Dietrich), and has less spiralled horn-cores that are correlatively more inclined, and wholly lack an anterior keel. Although probably a member of the same broad group, this Laetoli species is certainly distinct.

Tragelaphus moroitu from the latest Miocene/earliest Pliocene of the Middle Awash (Haile-Selassie *et al.* 2009) is much smaller than *T. saraitu* (Fig. 4) and has less divergent horn-cores that are clearly more primitive in their strong anterior keel and thus slight to moderate antero-posterior compression (index A–P/transverse = *c.* 0.85 instead of 0.8). There is no doubt about the distinctness at species level, but the overall similarity of the horn-cores suggests a phyletic relationship (see below).

Tragelaphus nakuae from the Turkana basin (Gentry 1985; Harris *et al.* 1988; Harris 1991) is larger than *T. saraitu,* has a strong transverse ridge across the top of the occipital, and its horn-cores are very compressed antero-posteriorly (A–P/transverse = *c.* 0.70), less divergent, less spiralled

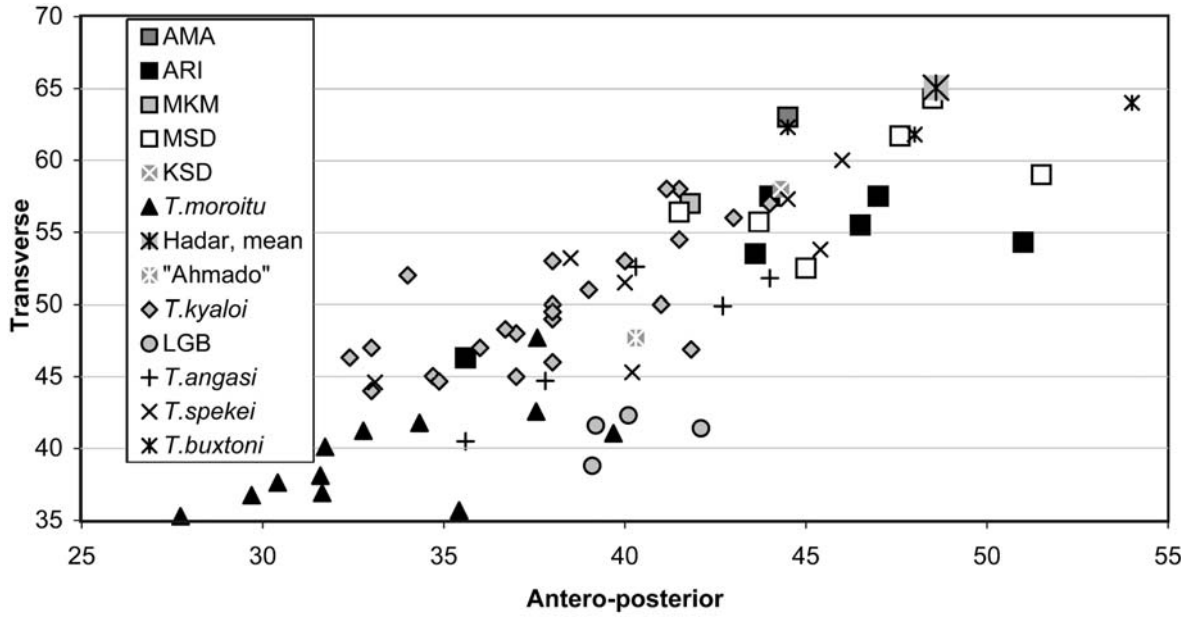


Figure 4. Plot of basal diameters of *Tragelaphus* horn-cores.

(they describe a simple curve in anterior view, and are more or less straight in lateral view), and much more inclined backwards. At Omo, more than half of the *T. nakuae* p4s have a complete lingual wall (Gentry 1985, p. 136).

The *Tragelaphus* aff. *nakuae* from Hadar (Gentry 1981) is similar to the Turkana species, but on average its horn-cores are slightly less compressed (Fig. 4; A–P/transverse = *c.* 0.75), more spiralled, and the braincase is longer with a weaker supra-occipital ridge. In these respects, it is intermediate between *T. saraitu* and *T. nakuae,* but the low inclination of the horn cores in lateral view is more like the latter species, and distinction of the common Hadar *Tragelaphus* from *T. nakuae* is perhaps not necessary. We do not see much difference between the Hadar form and the slightly younger one from Shungura upper member B, as most of the features listed by Gentry (1985, p. 133) for the latter are also found at Hadar, and the differences do not exceed intra-specific variability. We believe that the succession *T. saraitu* (AAMM) – *T.* aff. *nakuae* (Hadar) – *T. nakuae* (Omo) is a single anagenetic lineage, but it could be marked by phases of stasis and more rapid evolution. The ancestors of *T. nakuae* would thus be 'normal' tragelaphines, implying that the boselaphine-like features of this species were secondarily acquired.

Haile-Selassie *et al.* (2009) view *T. moroitu* from the latest Miocene earliest Pliocene of the Middle Awash as a likely ancestor of *T. kyaloi,* and it now seems that it could be ancestral to *T. saraitu* as well.

***Tragelaphus* sp.**

KSD-VP-1/9 is a complete upper tooth series too small to belong to *Tragelaphus saraitu* (length P2-P4 = 31.6; length M1–M3 = 40.5). The only specimen from AAMM small enough to match these upper teeth is ARI-VP-1/327, a slightly incomplete m3 (length = *c.* 18.8). No horn-core from AAMM is small enough to go with these teeth.

There is no small *Tragelaphus* at Hadar or Laetoli, but Gentry (1985) described small horn-cores from Shungura Mb C that he assigned to *Tragelaphus* ?*pricei,* a species named upon dental remains from Makapansgat by Wells & Cooke (1956). Measurements provided by these latter authors for m3 length (18, 18 and 19 mm) raise the possibility that this species is the same as that from KSD and ARI. *Tragelaphus nkondoensis* Geraads & Thomas, 1994, from Uganda, is also of similar size, so that we will not attempt specific identification for the small tragelaphine remains from KSD and ARI.

Tribe Bovini Gray, 1821
Genus *Ugandax* Cooke & Coryndon, 1970

Ugandax coryndonae Gentry, 2006

Bovini are represented by: MSD-VP-5/7 (Fig. 5A; measurements: Table 2), the posterior part of a cranium with complete left horn-core; MSD-VP-6/5, a mandible with p3–m3 (p4 missing), about 15 isolated teeth, and two astragali.

MSD-VP-5/7 originally consisted of many fragments, but

Table 2. *Ugandax coryndonae* – horn-core and skull measurements.

	HC APD	HC Transv.	Length along anterior curve	Width over pedicles	Minimum width over temporal lines	Length from horn-core to occipital
MSD-VP-5/7	83	71	250	180	71	55
	Width over mastoids	Bicondylar width	Occipital height	Width over post. tuber of basiocc.		
MSD-VP-5/7	190	96	63	62		

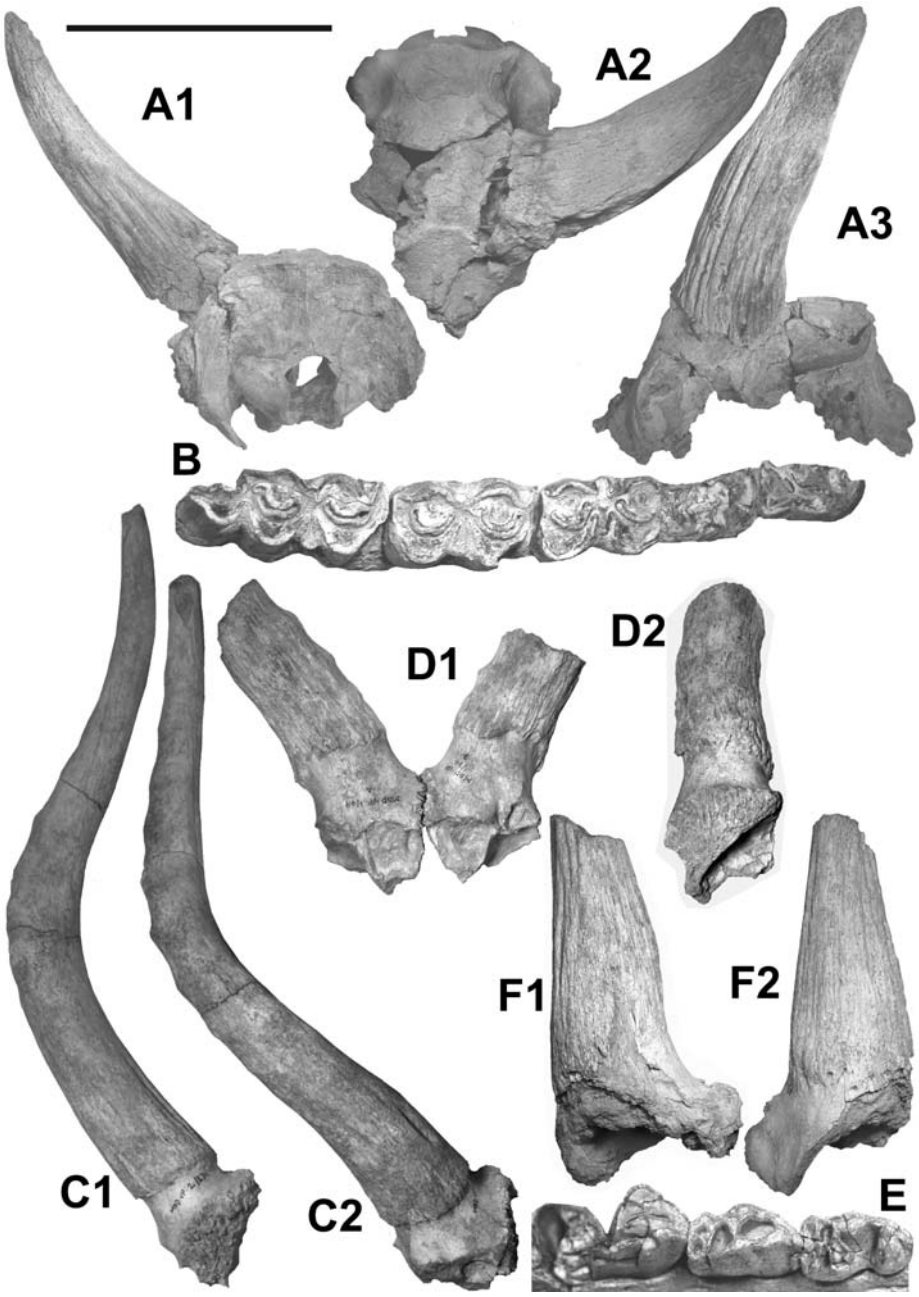


Figure 5. **A, B**, *Ugandax coryndonae*. **A**, brain-case with left horn-core MSD-VP-5/7, in (**A1**) occipital view, (**A2**) dorsal view (**A3**) left lateral view; **B**, right tooth-row p3-m3; **C–E**, *Aepyceros afarensis*. **C**, holotype right horn-core, MSD-VP-2/274, in (**C1**) medial view, (**C2**) anterior view; **D**, frontlet, MSD-VP-1/79: **D1**, anterior view of right horn-core, **D2**, medial view; **E**, lower tooth-row p3-m1, MSD-VP-4/1. **F**, *cf.* '*Damalops*' sp., right incomplete horn-core in (**F1**) anterior view, (**F2**) lateral view. Scale = 20 cm for Fig. A, 10 cm for Figs C, D, and F, 5 cm for Fig. B, 2.5 cm for Fig. E.

has been carefully and accurately reconstructed. The dorsal fronto-parietal surface is transversely flat, but slightly arched antero-posteriorly. Behind the horn-cores, it is limited by strong temporal crests that remain far apart. The brain-case is low and wide, but not extremely so. The occipital has a rather regularly rounded outline, although its top edge is only gently convex. The mastoid region is definitely less expanded laterally than in *Simatherium kohllarseni* from Laetoli (Dietrich 1942, fig. 163; Gentry 1987, pl. 10.3), *U. demissum* from Langebaanweg (Gentry 1980, fig. 8), *U. gautieri* from Kaiso (Cooke & Coryndon 1970, pl. 17B) or than in extant *Syncerus caffer*. The par-occipital processes have a strong inward curvature, as in *S. caffer*.

The horn-core slightly overhangs the anterior part of the temporal fossa. The base of the horn-core is remarkably close to the orbit for a bovine, certainly closer than in the type of *U. coryndonae* from the Denen Dora Mb. of the Hadar Fm (Gentry 2006, fig. 2), but the distance between the horn-core and the occipital is similar, so that the distance between orbit and occipital, i.e. the neurocranium, is shorter. The horn-core is rather short for a bovine, moderately inclined backwards, and moderately divergent from its counterpart at the base (by an angle of about 90°), but this divergence decreases upwards, so that the tips are parallel. The cross-section can hardly be called triangular as all sides, especially the antero-lateral and postero-lateral ones, are well rounded, with no real keel between them. These sides are also covered by deep grooves. Slightly above the base, the postero-lateral side has a flattened,

almost concave surface, as is also often found at Hadar. The frontal bone is slightly inflated in front of the anterior 'keel'.

This skull is closely similar to those of *Ugandax coryndonae* from Hadar (Gentry 2006), but differs slightly in that its horn-cores are inserted not so far behind the orbits and are less inclined backwards. Both characters (which are probably related) denote a more primitive stage for the Mesgid Dora form, in agreement with its earlier age (most *U. coryndonae* specimens at Hadar are from the Denen Dora Mb.), but do not warrant specific distinction, especially as some Hadar specimens look more similar to the Mesgid Dora form than to the type specimen of the species.

The horn-cores of the *Ugandax* sp. from the Middle Awash Late Miocene (Haile-Selassie *et al.* 2009) are remarkable by their strongly triangular cross-section, which makes them less different from boselaphines.

A frontlet from Kanapoi, unfortunately poorly preserved, was assigned to *Simatherium demissum* by Harris *et al.* (2003); its horn-cores certainly had no conspicuous postero-lateral keel, and were more medio-laterally compressed and more divergent, thus making them a poor fit as an ancestor of the Mesgid Dora form. The latter is also very different from the Laetoli *S. kohllarseni,* which lacks keels (Gentry 1987).

On MSD-VP-6/5 (Fig. 5B), the p3 (length = 20.6+) has a narrow metaconid crest (epicristid) extending disto-lingually, but a wide valley remains between it and the paraconid. The molars have strong localized lingual ribs and pinched labial lobes. The length m1–m3 is 90, but this is an overestimate because of gaps between the teeth. MSD-VP-2/139 is an m3 (length = 40.3) showing the same characters. MSD-VP-2/158 is probably a p3 (length = 26); its talonid is narrower than the trigonid, and the metaconid is more transverse, but it is too large for a hippotragine. Upper molars also have pinched lingual lobes.

There is a good deal of variation in the morphology of lower bovine premolars at Hadar, as at Omo (Gentry 1985, fig. 6); even the lower tooth-row AL165-10 from the Sidi Hakoma Mb., that Gentry (1981) had distinguished as more primitive, does not look very different from the other Hadar specimens. A larger sample from AAMM would be needed to discover any evolutionary difference from the Hadar tooth sample, but the differences in horn-core insertion are clear, and suggest that the Hadar form is more derived.

Subfamily indet.
Tribe Reduncini Knottnerus-Meyer, 1907

Reduncini gen. et sp. indet.

Reduncines are extremely rare in the Woranso-Mille area, and only a few teeth have been recovered from the sites considered here. The best specimen is MSD-VP-1/43, a mandible fragment with m2–m3 (Fig. 2J; length of m3 = 22.2). The molars are confidently identified as reduncine due to the presence of a strong goat fold and transversely elongated ectostylid, but they look less mesio-distally compressed than in later forms, the central enamel islands have the shape of an open V, and the labial lobes are not pinched. MKM-VP-1/172 is a p4 (13.5 × 7.6) which is brachyodont for a reduncine but is otherwise typical of this tribe, with transverse talonid cristids and a labially salient hypoconid.

AMA-VP-2/2, ARI-VP-2/74 and MKM-VP-1/6, all lower molars, have a more modern morphology, but the former two have a different facies, and could be derived from slightly younger strata.

The very limited amount of available material prevents any generic assignment, but at least some of the reduncine teeth are more primitive than expected for their age; they are, for example, more primitive than those from the roughly contemporaneous sites of Koro Toro (Geraads *et al.* 2001), and even than those from the earlier site of Kollé (Geraads *et al.* 2009); this confirms that various reduncine lineages evolved at different rates (Haile-Selassie *et al.* 2009; Geraads *et al.* 2009).

Subfamily Hippotraginae Sundevall in Retzius & Lovén, 1845
Tribe Hippotragini Sundevall in Retzius and Lovén, 1845

cf. *Hippotragus* sp.

We assign 10 specimens to this tribe, with various degrees of confidence. The most secure identifications are those of two well-worn p4s, MKM-VP-1/36 and MKM-VP-1/226, both from the right side (length × width = 16.3 × 10.7 and 16.3 × 10.4, respectively). At this wear stage, the parastylid is not distinct from the paraconid that remains separated by a narrow grove extending down to the cervix from a bulbous pillar-shaped metaconid, typical for this tribe. Identification of lower molars, such as those of MKM-VP-1/63 (Fig. 2G) is less straightforward; pinching of their labial lobes is only incipient, ectostylids are high but small, and goat folds are weak and do not reach the top of the crown. None of these features excludes alcelaphines, but when these characters are associated in lower molars, they fit better as hippotragines. The only upper teeth, MKM-VP-1/7, have small but transversely elongated entostyles, and also a hint of pinching of the lingual lobes.

The incomplete horn-core ARI-VP-1/84 is straight in anterior view and moderately curved backwards, but its orientation cannot be determined. It is transversely compressed (basal dimensions = 48 × 37.3), oval in cross-section, with no keel or torsion, no transverse ridges, and a slightly flattened lateral side. There is a single large sinus in the pedicel, and the post-cornual fossa is very shallow. Again, none of these features rules out alcelaphines, but it is so similar to *Hippotragus* or *Tchadotragus* (Geraads *et al.* 2008; Geraads *et al.* 2009) that Hippotragini is a much more likely identification. It is certainly distinct from the straight horn-cores of the species known as *Praedamalis deturi* from Hadar and Laetoli. Other eastern African sites of similar age have yielded few hippotragines. Harris *et al.* (2003) described a horn-core fragment from Kanapoi as *Hippotragus* sp., but it could in fact be reduncine. There are

some specimens from Omo (Gentry 1985) and the Middle Awash Late Miocene (Haile-Selassie *et al.* 2009) that are of similar size, but those from the latter sites were probably shorter.

Tribe Alcelaphini Brooke in Wallace, 1876

cf. *'Damalops'* sp. (new genus Gentry, in press)

Alcelaphines are not common elements in the AAMM localities. There are only three horn-cores, of which only one, MSD-VP-1/8 (Fig. 5F), is reasonably complete and can be oriented. Enough of the frontal bone is preserved to indicate that it was inserted rather uprightly, with little divergence from its counterpart. It is quite short for its basal size, with the antero-posterior diameter quickly decreasing upwards, and is straight in lateral view, but with a slight outward curvature, especially marked on its medial side, in anterior view. The basal cross-section is almost circular (47.6 × 45.7), and the base of the horn-core is lower laterally than medially, but there is no tendency towards a splayed out expansion of this base, as is often seen in specimens from Hadar. The antero-lateral side of the horn-core is convex and there are no transverse ridges. The frontal sinus certainly penetrates into the horn-core, and the post-cornual fossa is virtually absent.

Most alcelaphine dental remains are isolated teeth. Metrics from these specimens suggest that two species coexisted at Mesgid Dora, where an M3 (MSD-VP-2/80: 25.8 × 17) probably belongs to a smaller form than an M1 or M2 (MSD-VP-5/28: 25.3 × 19). Thus, assignment of all specimens to either form is impossible. These dental remains are less characteristic than those of modern alcelaphines. Upper molars may have lingual expansions at the mesio-lingual and disto-lingual corners of the crown, giving the occlusal surface a more rectangular outline than in modern alcelaphines, and this is matched by a tendency to form small goat folds on lower molars, also unknown in modern forms. The lingual wall of the p4 is closed in 5 out of 6 specimens, but open down to the cervix in the longest tooth (MKM-VP-1/175; L = 16.2). It is almost closed in two other teeth, of small size (MSD-VP-2/107; L = 13.3 and MSD-VP-1/63, L = 13.8); they could be p3s, or p4s of the smaller species if two species are really present, but all these measurements are in the range of the '*Damalops*' '*sidihakomae*' from Hadar (Vrba 1997). This advanced stage of lingual closure of p4 compares better with Hadar specimens, where four out of six p4s show lingual closure, than with specimens from Maka and Wee-ee (Vrba 1997) where only one out of four does. No specimen shows whether a p2 was present.

It is unfortunate that alcelaphines are so rare in the AAMM sites, because they probably attest a poorly known early stage in the evolution of the eastern African '*Damalops*', referred to a new genus by Gentry (in press). The single well-preserved horn-core looks much like an alcelaphine frontlet, 1959.233, from Laetoli (Gentry & Gentry 1978, pl. 22, fig. 1) that is considered by Gentry (in review) as close to the Ethiopian *'Damalops*', but both the Mesgid Dora and Laetoli forms differ from later *'Damalops' 'sidihakomae'* in their shorter horns lacking transverse ridges. However, the horn-cores are also relatively long, and with transverse ridges, on a frontlet from Aramis (Vrba 1997). Vrba (1997) also referred frontlet KNM-KP-71 from Kanapoi to this lineage, but this is debatable, because its horn-cores, albeit badly preserved, are smaller but relatively longer.

Subfamily Antilopinae Gray, 1821
Tribe Antilopini Gray, 1821
Genus *Gazella* Blainville, 1816

***Gazella* sp.**

Antilopines are extremely rare in the AAMM sites. From the localities considered here, only the basal part of a horn-core, KSD-VP-1/25, probably belongs to a female *Gazella.* It is a supra-orbital, slightly curved backwards, and has an almost circular cross-section (A–*P* = 20.5, Transverse = 19.6). A few teeth from ARI and KSD also belong to this tribe.

Tribe Aepycerotini Gray, 1872

Genus *Aepyceros* Sundevall, 1847

Type species. Aepyceros melampus (Lichtenstein, 1812), living impala.

Diagnosis. Horn cores little compressed, long and often with transverse ridges. They diverge proximally, then change course in their centre and have more or less parallel distal parts. This lyrated course never becomes strong enough to be spiralled. Females hornless. Frontals hollowed internally and slightly raised between the horn bases, small supraorbital pits. The teeth and limb bones of the living species have a number of unique or distinctive characters (Gentry, in review).

***Aepyceros afarensis* sp. nov.**, Figs 5C–E, Table 3

Holotype. MSD-VP-2/274, a virtually complete left horn-core from Mesgid Dora Vertebrate Locality 2, Woranso-Mille area, lower Awash valley, Ethiopia, 3.7–3.8 Ma (Fig. 5C).

Referred material. Almost 30 horn-cores, mostly basal parts, and numerous dentitions from the localities of Aralee Issie, Makah Mera and Mesgid Dora.

Diagnosis. An *Aepyceros* of large size, matched only by the Laetoli *Aepyceros* and the modern *A. melampus.* Horn-cores with well-marked transverse ridges, very uprightly inserted on long pedicles, almost spiralled, with almost no backward curvature at the base (or even with a slight forward one), but with a strong backward curvature higher up; divergence moderate at the base but increasing for the first few centimetres before decreasing thereafter. The cross-section is but slightly compressed transversely, with its main axis strongly oblique with respect to the sagittal plane, a stronger convexity postero-laterally that never amounts to a keel, but sometimes a longitudinal grove.

Sinuses in the frontal bone are large, but less extensive than in *A. melampus,* not extending high into the pedicle; post-cornual fossa roughly circular, and very deep. Premolar series less reduced than in latter forms.

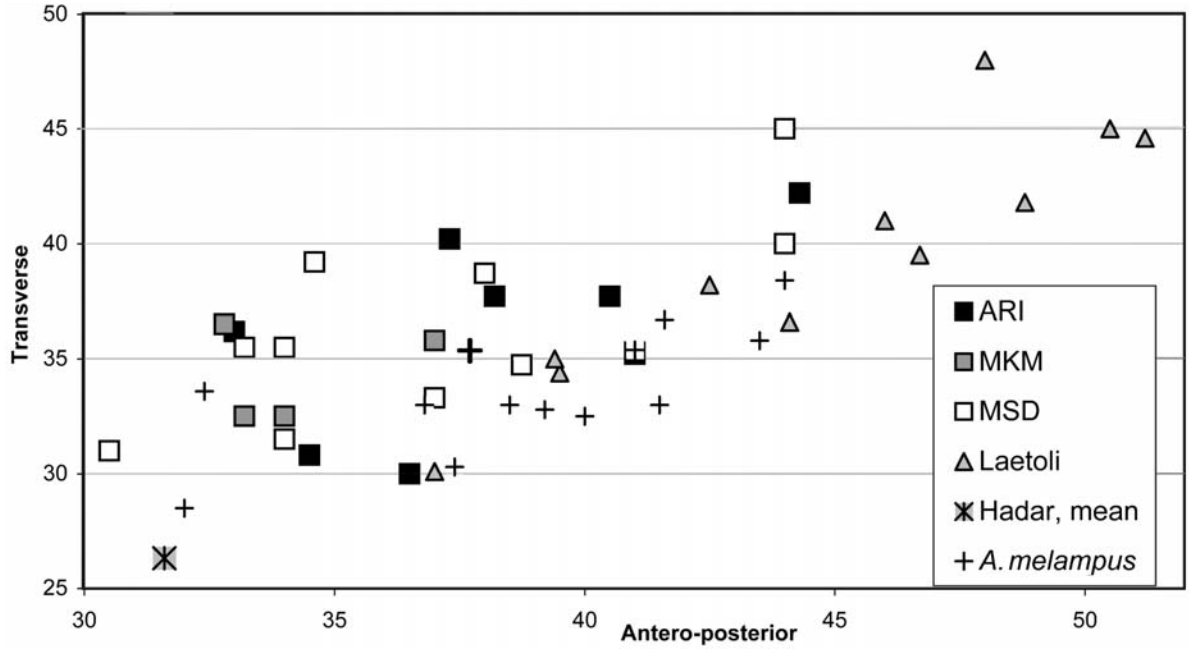


Figure 6. Plot of basal diameters of *Aepyceros* horn-cores. The larger, bold '+' is the mean of 11 specimens (Gentry 1985); they look less compressed than those measured by us, but this is probably only due to a different measurement technique, as the strong inclination of the main axis of the cross-section make them difficult to orientate.

Table 3. *Aepyceros afarensis* – measurements of horn-cores and frontlets.

	HC APD	HC Transv.	Width over pedicles	Width over middle of supra-orbital foramina
ARI-VP-1/44	41	35.2	92	59
ARI-VP-1/214	41	35.3	81	–
ARI-VP-3/172	37.3	40.2	85	–
ARI-VP-2/46	33	36.2	–	*c.* 52
ARI-VP-4/12	44.3	42.2	*c.* 100	–
MSD-VP-1/14	44	45	*c.* 104	–
MSD-VP-1/79	38	38.7	83.5	54
MSD-VP-2/108	33.2	35.5	*c.* 80	–
MSD-VP-2/274	34.7	38.7	*c.* 88.5	–

Table 4. Lengths of premolar row and m3 in *Aepyceros*.

	L p2–p4	L m3
ARI-MSD-MKM	28.6 (MSD-VP-1/19)	23.3 (mean of 9)
A. melampus		
LZMO 1940-1145	23.7	26.1
LZMO 1996-645 (p2 absent in life)	18.2	22.2
LZMO 1962-389	25.0	25.0
A. shungurae holotype	21.3	19.7

Description. The main features of the horn-cores are listed in the diagnosis. The upright insertion (in lateral view, the angle between the posterior border of the horn-core and the fronto-parietal plane is greater than 90°: Figs 5C1, 5D2), lack of clear basal backward curvature, if any, and increasing divergence upwards (Figs 5C2, 5D1), are characteristic enough for horn-core basal parts to be distinguished from other *Aepyceros,* including those from slightly younger sites in the Woranso-Mille area. Measurements are given in Table 3.

A number of teeth also belong to *Aepyceros.* The only complete lower premolar row is MSD-VP-1/19. Its p4 is not unlike that of *Tragelaphus,* but it is smaller than that of *T. saraitu.* In addition, the p2 of MSD-VP-1/19, as inferred from its root, is too small for a tragelaphine. The p4 of this specimen is almost identical to the p4 of MSD-VP-4/1 (Fig. 5E), which is associated with an *Aepyceros* m1. The premolar row is less reduced than in the modern form and than in *A. shungurae* from the Turkana basin (Table 4). No specimen from Laetoli (Gentry, in review) or Lothagam (Harris 2003) is complete enough to estimate this proportion. The four available p4s have only a narrow bridge between paraconid and metaconid that does not reach the top of the crown; the lingual wall is thus less fully formed than in *A. melampus* and the metaconid is less preponderant in its formation. There is only one p4 of *Aepyceros* at Laetoli (Gentry, in review, fig. 5), and it is similar to that of the modern form.

Specific distinctions among Pliocene *Aepyceros* are not easy. *Aepyceros afarensis* differs:

- from living *A. melampus* in its much longer premolar row (although we were able to measure only three specimens of modern impala, the difference is so clear that it can be taken for granted), and in its horn-cores that are less compressed (but some modern specimens may also have an almost circular cross-section; Fig. 6), and more upright (in lateral view, the angle between the posterior border of the horn-core and the fronto-parietal plane never exceeds 90° in the modern form). However, horn-cores are rather similar, and were it not for premolar differences, *A. afarensis* could have been included in *A. melampus*; but of course we know nothing of other possible cranial differences;
- from *A. shungurae* from the Shungura Fm at Omo in its much larger size, more upright insertions and stronger spiralling of the horn-cores;

- from an unnamed species in the same Fm (Gentry 1985, p. 175) in its larger size, much stronger spiralling, much greater basal divergence, and more upright insertion of the horn-cores;
- from the Hadar *Aepyceros* in its much larger size, longer, more spiralled and much more upright horn-cores;
- from the *Aepyceros* of the Upper Laetolil beds (Dietrich 1942, fig. 45; Gentry 1987, pl. 10.8; Gentry, in review) in the more upright insertion of its horn-cores, and in the increasing divergence and lack of clear backward curvature basally. In spite of similar size and geological age, these species are clearly distinct.
- from *A. premelampus* of Lothagam (Harris 2003) in its larger mean size, in the longer pedicles, and presence of transverse ridges and more upright insertions. However, published descriptions of this species are not detailed enough for in-depth comparisons;
- from the rare and poorly known *A.* cf. *premelampus* from the Middle Awash Mio–Pliocene (Haile-Selassie *et al.* 2009) in its larger size, more upright insertion and deeper post-cornual fossa.

Aepyceros afarensis is still very incompletely known, but we prefer to distinguish it at species level because it is clearly, and unexpectedly, distinct from the *Aepyceros* of other Woranso-Mille localities, some of which are probably not much younger, although not yet securely dated. It is also distinct from the *Aepyceros* of the geographically close Hadar Formation at Hadar, including the specimens from the Basal Member, which ranges in age from 3.42 to >3.8 Ma (Wynn *et al.* 2008); however, *Aepyceros* fossils from the Basal Member come from localities sampling its upper part, and are thus certainly younger than the ARI, MKM and MSD ones. *Aepyceros afarensis* therefore appears to have had restricted time and geographic ranges. It adds to the diversity of fossil *Aepyceros,* the evolution of which, far from consisting of a single lineage leading to the modern impala, now appears to have included numerous variations upon a basic pattern.

Subfamily indet.
Tribe Neotragini Sclater and Thomas, 1894
Genus *Neotragus* Hamilton Smith, 1827

***Neotragus* sp.**

Inclusion of this genus in the subfamily Antilopinae has been questioned (Agnarsson & May-Collado 2008), and it is perhaps distinct from other genera recognized as Neotragini.

Description and comparisons. MKM-VP-1/93 (Fig. 2H) is a mandible with p3–m2 (length p2–p4 = *c.* 15), and MSD-VP-5/10 is a mandible with p4, m2 and m3 (length m1–m3 = 24.6; length of m3 = 9.7). They are quite similar in size and morphology, and there is little doubt that they belong to the same taxon, much smaller than *Raphicerus,* which is the most commonly reported 'neotragine'. On p4, the metaconid has a long oblique cristid directed towards the entoconid, itself very long, more or less parallel to the posterior hypoconid cristid, and reaching the disto-lingual corner of the tooth. This tooth is long, but the anterior premolars are shorter, resulting in a relatively short premolar series. The molars are antilopine-like; the third lobe of m3 is not much enlarged. KSD-VP-1/32 is a maxilla with P4-M2 which is of the right size and morphology to go with the above-mentioned mandibles.

These dental remains match in size and morphology those of the living suni of sub-equatorial eastern Africa, *Neotragus moschatus* (which is slightly larger than other species of the genus, and sometimes assigned to a different genus, *Nesotragus*), and we are confident in referring these remains to this genus, which, as far as we know, has never been reported as a fossil. West African forms (*Neotragus s. str.*) are forest dwellers, but *Neotragus moschatus* lives in thick bushes.

Subfamily Cephalophinae Blyth, 1863
Genus *Cephalophus* Hamilton Smith, 1827

***?Cephalophus* sp.**

We tentatively assign to this genus two upper teeth, a premolar (probably P4), ARI-VP-1/370 (9.7 × 11.7), and a molar, ARI-VP-1/197 (14.6 × 14), perhaps of the same individual (Fig. 2), and a lower molar, ARI-VP-3/225 (12.8 × 8.9). The premolar is small compared to the upper molar, quite brachyodont, and has a rounded lingual lobe and a salient labial pillar. The upper molar is less brachyodont, has a small entostyle, rounded but slightly pinched lingual lobes, strongly outbowed labial folds, and no mesostyle. This latter character is the most decisive for inclusion of these 'boödont' teeth in the Cephalophinae. In this subfamily, the mesostyle is small but present in the upper part of the crown, but vanishes in worn teeth. This also occurs in some 'Neotragini', but that group has 'aegodont' teeth, quite unlike these ones. The lower molar also has strong pillars and rounded labial lobes, but no hint of a goat fold, and is therefore definitely not reduncine. These teeth are almost certainly cephalophine, but we are cautious about this assignment, because in the past, specimens referred to *Cephalophus* have more than once been misidentified. This species would be of about the same size as the Laetoli cephalophine (Gentry 1987, in review).

CONCLUSIONS

The distribution of bovid species from the AAMM and KSD localities is given in Table 5. The low diversity at AMA is obviously related to the smaller number of collected specimens, but the high diversity at KSD is worth noting. The other three sites do not differ significantly in terms of their bovid composition.

Figure 7 shows the number of dental and cranial (mainly horn-core) remains found in the AAMM group of localities. As in other eastern African sites, dental remains of Alcelaphini and, to a lesser extent, of Bovini, are relatively more common than horn-cores, while the reverse is true of *Aepyceros* and Tragelaphini. This is doubtless a taphonomic bias due to the horn-cores of the latter groups being solid and more robust, whereas those of the Alcelaphini are more easily broken (in part because of their large basal sinus). Similarly, the robustness of alcelaphine

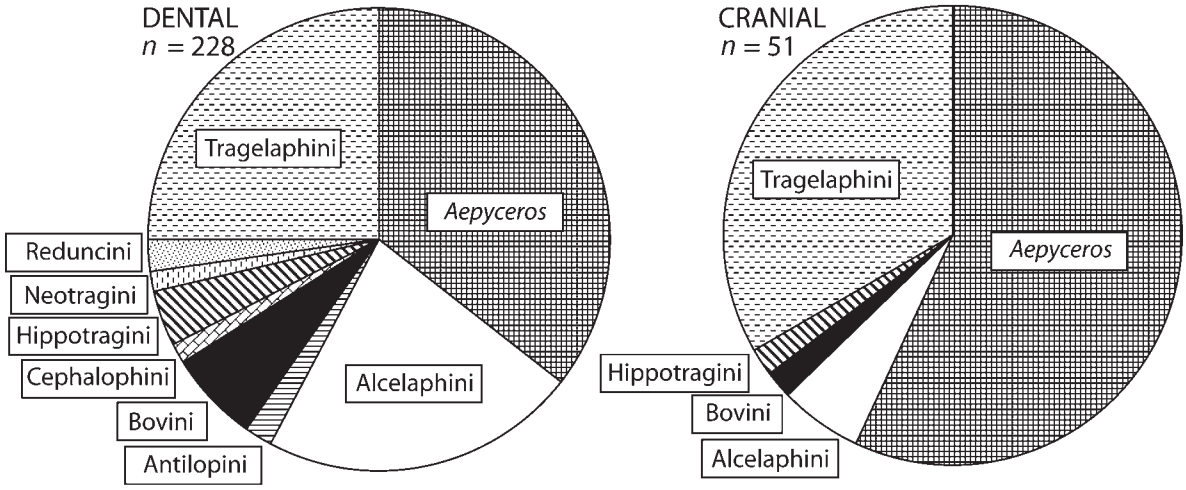


Figure 7. Proportions of the various bovid taxa in the AAMM localities, calculated from the number of identified teeth (**left**) or cranial remains, mostly horn-cores (**right**).

Table 5. Distribution of the various bovid species in the AAMM and KSD localities (the first row gives the total number of bovid cranial and dental remains in each group of localities).

	AMA	ARI	MKM	MSD	KSD
	7	110	77	82	11
Tragelaphus saraitu	*cf.*	+	+	+	+
Tragelaphus sp.		?			+
Ugandax coryndonae	*cf.*	*cf.*	*cf.*	+	
Reduncini gen. et sp. indet.	+	?	+	+	
cf. Hippotragus sp.		+	+	?	
cf. '*Damalops*' sp.		+	+	+	+
Gazella sp.		+		+	+
Aepyceros afarensis		+	+	+	+
Neotragus sp.			+	+	+
?*Cephalophus* sp.		+			

teeth, which preserve better than those of other groups, increases this bias. Therefore, the true relative abundance of the Alcelaphini lies probably between that of their horn-cores and that of their teeth. In any case, it is clear that the AAMM bovid associations are dominated by tragelaphines and impalas, alcelaphines being significantly less common, bovines rare, and other groups virtually absent. The habitat of such an assemblage, very poor in antilopines and reduncines, was certainly neither open savannah nor grassland. Impalas are not very habitat-specific, as they can browse or graze, but usually favour woodland fringes, while tragelaphines are well known to favour bushes and thickets. Their abundance points unambiguously towards a moderate to high degree of vegetation cover, such as dense woodland with bushes, although the presence of alcelaphines implies some clear patches. This inference is compatible with the evidence from other mammalian taxa from these localities.

The slightly younger site of Korsi Dora yielded only 15 identifiable bovid specimens, but the composition of this assemblage differs from the AAMM ones, as it includes four antilopine remains, including the only *Gazella* horn-core, a neotragine, and a maxilla of *Tragelaphus saraitu* and yet another small species of *Tragelaphus*. Sample size is too small to choose between a taphonomic bias and/or a real ecological difference. Further investigation of the KSD-VP-1 assemblage might help in distinguishing between these options.

The bovid fauna cannot contribute to the dating of the AAMM sites as these have been accurately dated by radiometric methods, but it is worth noting that the Bovidae, at least those that are represented by enough material, are clearly distinct from those of the Sidi Hakoma Member of the Hadar Fm, which is only 0.3–0.4 Ma younger. Ancestor-descendant relationships are likely for *Ugandax*, *Tragelaphus* and '*Damalops*', and less likely for the *Aepyceros*. It is noteworthy that none of these taxa remains unchanged, thus demonstrating significant rates of evolution between *c.* 3.5–3.8 Mya.

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ABBREVIATIONS

AAMM Am-Ado + Aralee Issie + Makah Mera + Mesgid Dora
A-P Antero-posterior

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Partial hominin tibia (StW 396) from Sterkfontein, South Africa

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Comparison of a proximal hominin tibial fragment, StW 396 from Sterkfontein Member 4, South Africa, with the StW 514a tibia, also from Member 4 and attributed to *Australopithecus africanus,* indicates a degree of morphological variability that may represent the extremes of intraspecific variability or even exceed what one would expect from intraspecific variation alone. The morphology of StW 396 is human-like which suggests adaptations towards stability at the knee, whilst that of StW 514a is interpreted as being more mobile and ape-like (Berger & Tobias 1996). Four features separate the two morphological patterns. In StW 514a the attachment area of m. semimembranosus is strongly localized, whereas in StW 396 the posteromedial border is notched near the base of the lateral intercondylar tubercle; thirdly, the lateral tibial condyle of StW 514a is supero-inferiorly thin, whereas in StW 396 the lateral condyle is supero-inferiorly thickened and the contrast between the condyle and the shaft is less pronounced; lastly the articular surface of the medial condyle of StW 396 is anteroposteriorly broad and highly concave as opposed to the narrower, flatter surface of StW 514a. The degree of variability of the two specimens possibly suggests differing functional adaptations and may thus support an hypothesis suggesting that two hominin species may be represented within Sterkfontein Member 4.

Keywords: hominin, tibia, Sterkfontein, *Australopithecus africanus.*

INTRODUCTION

The fossil tibia StW 514a from the Sterkfontein Formation, Gauteng, South Africa, is argued to possess ape-like proximal tibial morphology (Berger & Tobias 1996). The specimen is regarded as belonging to an australopith from Member 4, which has been estimated to be 2.4–2.8 Ma (Vrba 1985; Delson 1988; Partridge & Watt 1991; McKee *et al.* 1995; Kuman & Clarke 2000; Pickering *et al.* 2004). Berger *et al.* (2002), in a revision of the *Australopithecus*-bearing deposits of Sterkfontein, interpreted Member 4 more likely to fall between 1.5–2.5 Ma. These revised age estimates have been refuted by Clarke (2002).

StW 514a has a close association with large numbers of cranio-dental remains attributed to australopiths (Moggi-Cecchi *et al.* 2006), suggesting a high probability that the tibia should be assigned to this taxonomic group, and most probably to the species *Australopithecus africanus* (Berger & Tobias 1996). More recently we have analysed another proximal tibial fragment from Member 4 (StW 396) and we find that, in certain functionally important features, this specimen differs from StW 514a. Berger & Tobias (1996) described the convex anteroposterior curvature of the lateral tibial condyle of StW 514a as possibly being associated with a more chimpanzee-like locomotor function when compared to the flatter lateral tibial condyle of *A. afarensis.* Latimer *et al.* (1987) have observed that joints become flatter as size increases as a result of a response to increased transarticular loads accompanied by larger body mass. They suggest that variation observed among hominins, both within and between species, reflects size alone rather than function (Latimer *et al.* 1987). Recently, Organ & Ward (2006) in a detailed study, compared the three-dimensional surface areas of the lateral tibial condyle of humans and apes with those of *A. afarensis* (A.L. 129b, A.L. 288-1aq, A.L. 333–42, A.L. 333X-26) and *A. africanus* (StW 514a). Their results neither support the hypotheses that *A. africanus* and *A. afarensis* differ in condylar topology or that joint surfaces become flatter with increased transarticular load accompanying increased body size. Organ & Wards' (2006) arguments are compelling and their methods would have been useful in solving the problem of the StW 396 proximal tibial fragment if a lateral condyle was present. However, the remainder of this specimen appears to vary enough from StW 514a to justify further consideration. Following is a description of StW 396 and a comparison of its morphology with that of StW 514a that highlights the morphological differences between these two specimens. The implications of the differences are discussed, with special reference to the claim of Clarke (1985, 1994, 2009) that two different hominin taxa may possibly be represented in Sterkfontein Member 4.

DESCRIPTION

StW 396 is a fragment of the proximal epiphysis and diaphysis of a right hominoid tibia including the medial condyle and intercondylar eminence (Fig. 1). This tibial fragment was recovered in August 1986 by the Sterkfontein excavation team under A.R. Hughes, grid square O/45 at a depth of 18'4'–19'7' (5.6–6.0 m) in partially decalcified sediments that Clarke (2006) attributes to the deepest fossil-bearing levels of Member 4. The specimen comprises a complete medial condyle, a small part of the lateral condyle, most of the intercondylar eminence, the posterior intercondylar area, and a short length of the posterior and medial parts of the shaft. The apices of both the medial and lateral intercondylar tubercles are damaged. The articular surface of the medial condyle is markedly concave, the greatest depth being located just lateral to

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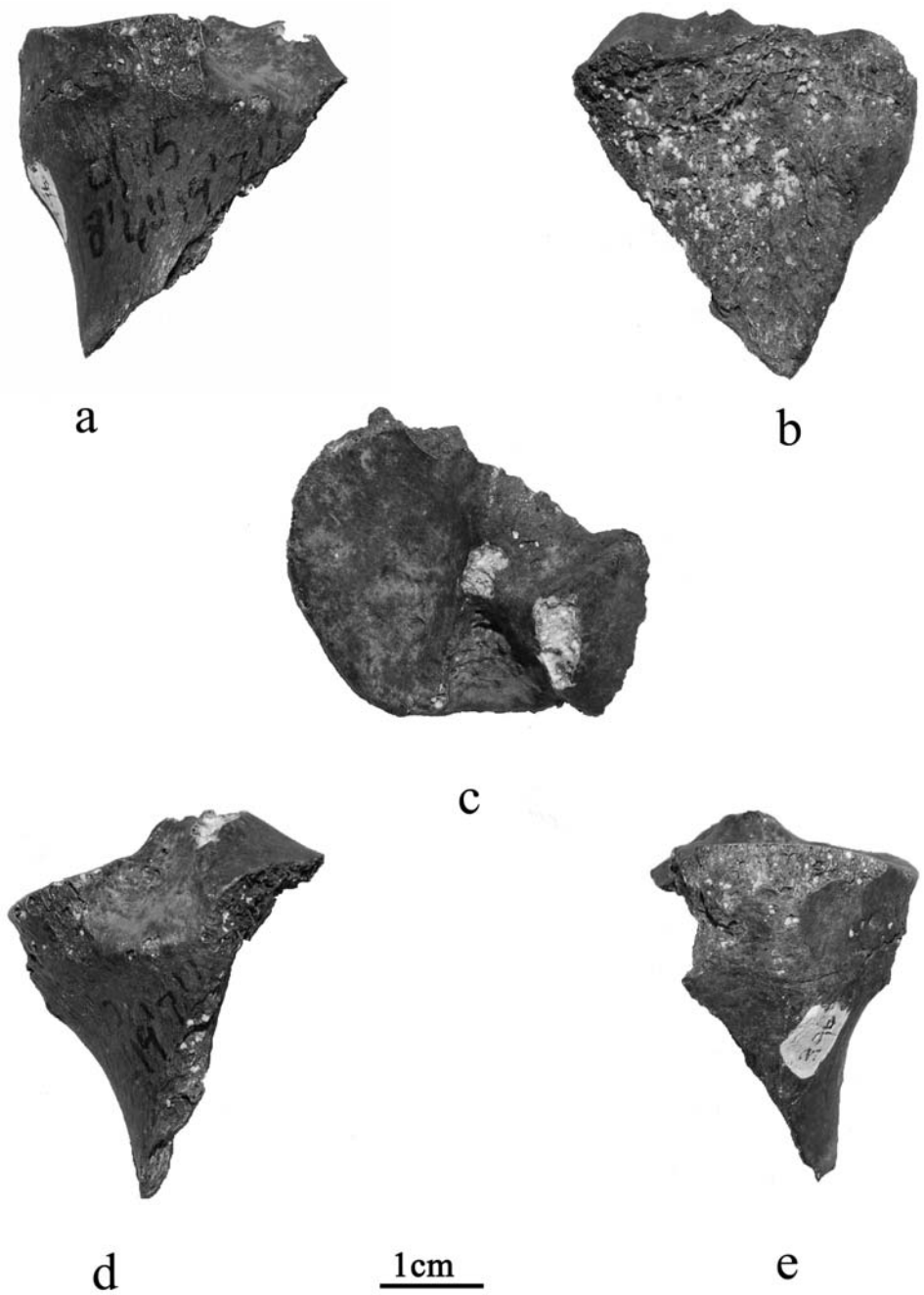


Figure 1. StW 396 proximal tibial fragment from Sterkfontein: **a**, posterior; **b**, anterior; **c**, superior; **d**, lateral; **e**, medial.

the mediolateral midpoint of the condyle. A small area of pitting is present in the middle of the posterior part of the medial condyle that most likely represents slight osteoarthritic degeneration. The maximum mediolateral diameter of the medial condyle is 24.4 mm; the anteroposterior diameter cannot be determined. The intercondylar tubercles are high, and a line between their apices is oriented at an angle of approximately 30 degrees to the mediolateral line of the plateau. Most of the lateral condyle is missing except for a steeply sloping area applied to the lateral face of the lateral intercondylar tubercle. The steepness of this slope reflects the appreciable elevation of the intercondylar tubercles above the articular condylar surfaces. The posteromedial border of the lateral condyle is curved and slightly notched at the base of the lateral intercondylar tubercle and appears to have been long, although damage obscures its most posterior extent. On the posteromedial edge of the specimen, just below the most medial edge of the medial condyle, is an anteroposteriorly elongate, depressed area that represents the attachment of m. semimembranosus. The intracapsular area at this point is deep, extending almost 17.0 mm below the lip of the medial condyle. The transition between the intracapsular area of the medial condyle and the shaft is not marked and is distinguished only as a slight but definite lateral sloping of the shaft below the intracapsular area. The remainder of the lateral half and the anterior portion of the specimen are missing. The specimen is fully adult, with no traces of the epiphyseal plate remaining.

DISCUSSION

In descending order of importance, four features suggest a marked difference in morphology between

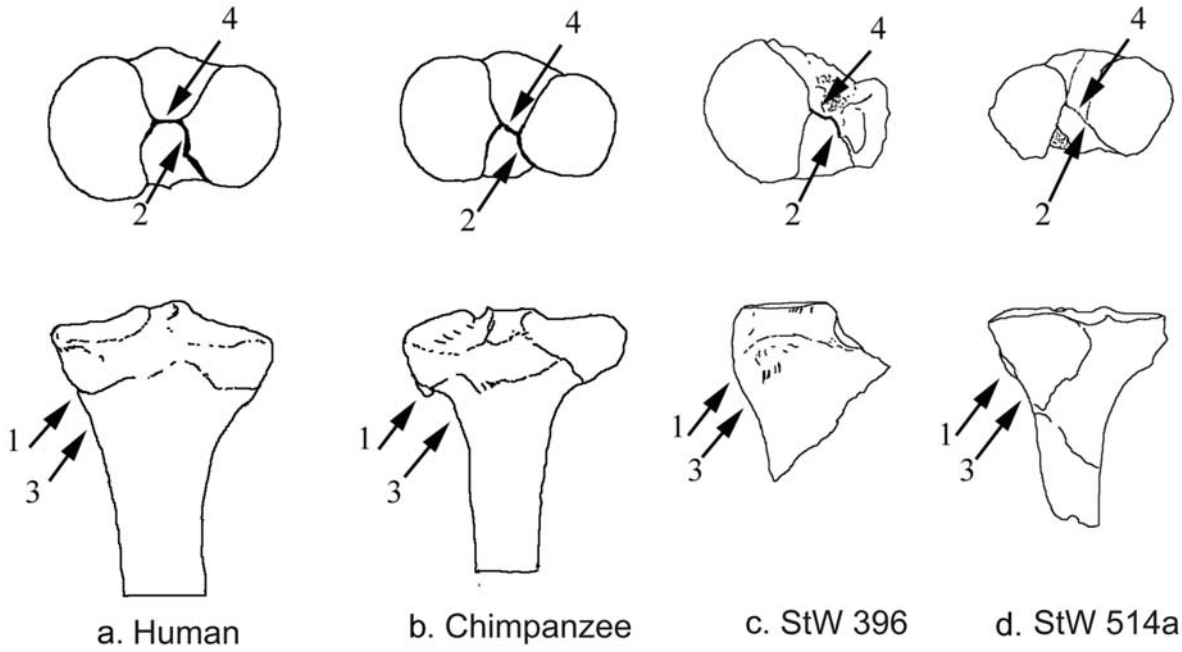


Figure 2. Dorsal and posterior views of proximal tibiae. The attachment area of m. semimembranosus is an indistinct, horizontal groove as in humans (**a**, '1'), whereas in StW 514a (**d**, '1') the attachment area is strongly localized as in apes (**b**, '1'). The posteromedial border of the lateral tibial condyle in StW 396 is slightly notched (**c**, '2'), whereas unnotched in StW 514a as in apes (**b**, **d**, '2'). In StW 396 the contrast between the condyle and the shaft is less pronounced as in humans (**a, c,** '3') whereas, the medial tibial condyle of StW 514a and chimpanzee is supero-inferiorly thin (**b, d,** '3'). An ape-like feature in StW 396 is that a line joining the intercondylar tubercles is oriented at a greater angle to the mediolateral centre-line of the plateau (**d,** '4') than one would expect in modern humans (**a,** '4'), similar to chimpanzees (**b,** '4') and StW 514a (**d,** '4').

the StW 396 and StW 514a tibiae (Fig. 2):

(1) In the StW 396 specimen, the attachment area of m. semimembranosus is an indistinct, horizontal groove as in humans, whereas in StW 514a the attachment area is strongly localized as in apes. Aiello & Dean (1990) have stressed the importance of this feature in distinguishing ape morphology from that of humans and the distinction appears consistent in our sample of comparative material consisting of humans, chimpanzees, gorillas, orangutans and a bonobo (Table 1).

(2) The posteromedial border of the lateral tibial condyle in StW 396 appears long and is slightly notched near the base of the lateral intercondylar tubercle, thereby indicating a semicircular lateral meniscus as is found in most humans (Senut & Tardieu 1985; Tardieu 1986; Holliday & Dugan 2003), whereas the posteromedial border is short, straight and unnotched in StW 514a as in apes. Senut & Tardieu (1985) pointed out that modern humans have two lateral meniscal insertions, differentiating them from apes and many earlier hominins. They also used this feature to differentiate fossil taxa, claiming two Plio-Pleistocene hominin taxa can be delimited, one modern (*Homo*), the other chimpanzee-like (*Australopithecus*). Holliday & Dugan (2003), however, in testing this feature's taxonomic utility in a much larger sample of human tibiae, found that some modern humans lack this notch, its absence cannot therefore be used to exclude a fossil tibia from *Homo.*

(3) In StW 396 the medial condyle is supero-inferiorly thickened and the contrast between the condyle and the shaft is less pronounced, thus creating a human-like appearance of this area, whereas the medial (and lateral) tibial condyle of StW 514a is supero-inferiorly thin, creating an ape-like shelved appearance of the tibial plateau. We recognize that we are dealing here with a possibly continuous variable, the assessment of which is thus highly subjective; moreover, it has previously been pointed out that variation of this feature in modern hominoids is extreme (Lovejoy *et al.* 1982; Berger & Tobias 1996), yet we are impressed by the fact that the two Sterkfontein proximal tibiae appear to represent opposite poles in the range of variation observed in humans and in apes.

Table 1. Approximate intercondylar tubercle angles of fossils, humans and apes measured between the mediolateral line of the tibial plateau to the highest point of the intercondylar tubercles. The great apes are of both wild shot and zoological garden origin.

Group	Intercondylar tubercle angle
StW 396	30°
StW 514a	40°
AL 288-1AQ[a]	45°
Homo sapiens (n = 24)	11.92° (S.D. = 9.8; range: 0–35°)
Pan troglodytes (n = 4)	33.75° (range: 30–40°)
Pan paniscus (n = 1)	30°
Gorilla gorilla (n = 3)	41.67° (range: 40–45°)
Pongo pygmaeus (n = 2)	37.5° (range: 35–40°)

[a]Good-quality cast (Cs 1573B) of 'Lucy' *Australopithecus afarensis.*

(4) The articular surface of the medial condyle of StW 396 is anteroposteriorly long and highly concave as opposed to the narrower, flatter surface in StW 514a. Again, while comparable measurements of StW 514a could not be made, the medial condylar articular surface of StW 396 is clearly relatively broader in relation to its estimated length.

The only 'ape-like' feature of the StW 396 tibia is that a line joining the intercondylar tubercles is oriented at a greater angle to the mediolateral centre-line of the plateau than one would expect in modern humans (Fig. 2).

Modern humans, however, vary a great deal in this morphology and in certain tibiae (e.g. A92, A330 and A757) in the Raymond Dart Collection of Human Skeletons, University of the Witwatersrand, we have observed angulation of the tubercles to a degree seen in StW 396 (Table 1) being about 30 degrees to the mesiolateral line of the plateau.

The morphology of the StW 396 tibia may be described as being more derived than primitive. The total morphology may be said to represent an adaptation to a human-like bipedal gait with the consequent ability to hyper-extend and 'lock' the knee. This morphology is in striking contrast to that described for the StW 514a tibia (Berger & Tobias 1996). In that specimen, it was concluded that the proximal tibial morphology indicated a knee joint which was less stable than those of humans, and more mobile with appreciable rotational capacity as in the extant African apes.

The degree of variation between the two Sterkfontein specimens may suggest differing functional adaptations, namely in the case of StW 514a, emphasis on mobility at the knee, and in the case of StW 396, emphasis on human-like stability. Both specimens have been obtained from seemingly *in situ* breccia in a deep part of Member 4 of the Sterkfontein Formation. Thus, the depth below datum of the ape-like StW 514a tibia was 5.6–6.0 m. In a 28 m total depth of the Sterkfontein Formation, these figures would place both tibiae in the second oldest bed (Bed B) of Member 4 (Partridge 1978; Stiles & Partridge 1979). Stratigraphically, therefore, the individuals represented by the two tibiae were near contemporaries, unless StW 396 proves after all to have been intrusive from younger sediments. Their discrepant morphological traits, albeit based on only two fragmentary specimens, compel us to consider whether the more human-like tibia StW 396 could possibly stem from the same taxon as that to which the chimpanzee-like tibia StW 514a belongs. At this stage, there is very little fossil evidence from which to infer the degree of intraspecific variability of the lower limb of *A. africanus,* or, for that matter, of any of the early hominin taxa.

If our interpretation of the morphological and biomechanical patterns of the two tibiae is correct, it would seem most unlikely that the disparate patterns of knee-joint would occur in normal, healthy members of the same species. For example, neither gender dimorphism nor individual variation would be expected to be associated with two functional morphs of this nature. On the contrary, the studies of Senut & Tardieu (1985) indicate that precisely such differences as we believe are manifest between StW 398 and StW 514a occur between members of various hominoid taxa, extant and extinct.

We are drawn to the view that the two Sterkfontein Member 4 tibiae may indeed have belonged to members of two different taxa. The question is if there is any evidence from cranial and dental remains that more than one taxon is represented in the very large Member 4 sample of nearly 650 catalogued hominin specimens? A hypothesis of multiple hominin species at Hadar, Ethiopia, has arguably, been supported by the tibial condyle morphology of small *A. afarensis* fossils (Senut & Tardieu 1985; Zihlman 1985; Tardieu 1986, 1999). Organ & Ward (2006) draw attention to a number of studies that do not support this hypothesis, suggesting that the Hadar australopith assemblage represents a single species (e.g. Stern & Susman 1983; McHenry 1986; Jungers 1988; Richmond & Jungers 1995; Lockwood *et al.* 1996; Lague 2002). There is a growing impression that the inferred diversity of taxa suggests that there was also a considerable degree of locomotor diversity among early hominins (Harcourt-Smith & Aiello 2004).

Based on qualitative anatomical comparisons, Clarke (1985, 1994, 2009) has suggested that two species are present within the Sterkfontein Member 4 assemblage. One species is *A. africanus* Dart, while the other, as yet unnamed, presents a morphology that Clarke suggests is possibly ancestral to the robust australopithecine lineage. However, as yet no thorough statistical analysis of the craniodental subsets have been published, although such features as maxillary molar and pre-molar morphology are thought to play a major part in distinguishing the subsets (Clarke, 1994). At present, the case for two species being represented by the Member 4 hominin cranial and dental specimens can by no means be considered to be established. Furthermore, there appears to be no stratigraphic separation between Clarke's proposed two subsets; thus examples of his 'pre-*Paranthropus*' group stem from both Beds B and C (Partridge 1978).

Reason has previously been seen to recognize a mosaic of derived and primitive features in the fossil hominin specimens from Sterkfontein Member 4. These include traits in the cerebral cortex (e.g. Falk 1983, 1989; Tobias 1987), the basicranium (e.g. Tobias 1967; Dean & Wood 1982), the spinal column (Benade 1990), the shoulder region (Berger 1994), the hip (Häusler & Berger 2001) the knee (Berger & Tobias 1996; Organ & Ward 2006) and the foot (Deloison 2003; Zipfel *et al.* 2009).

Within this complex of regional morphological patterns, the tibia StW 514a with its chimpanzee-like traits can be comfortably accommodated. Only the human-like tibia StW 396 is difficult to place. On the prevailing single-species hypothesis, StW 396 may oblige us to extend the range of intraspecific variability of the proximal tibial morphology. On a two-species hypothesis, either of the Member 4 tibiae may need to be accommodated in a taxon other than *A. africanus.* Since mosaic evolutionary trends are evident in the lower limbs of early hominins (e.g. Lovejoy *et al.* 1982; Susman *et al.* 1984; Senut & Tardieu 1985; Harcourt-Smith & Aiello 2004; Clarke & Tobias 1995; Kidd & Oxnard 2005; Susman & deRuiter 2005; Zipfel & Kidd 2006; DeSilva 2008), it cannot be assumed that the more human-like StW 396 is necessarily the 'odd man out' requiring to be classified in a different taxon. In this regard, we strike a cautionary note; the two tibial specimens are incomplete and, on a two-species hypothesis, we should remain in the statistically and populationally invidious position of dealing with sample sizes of a single specimen in each of the putative subsets.

Although we are at present unable to link any specific Member 4 cranial or dental material directly with any postcranial specimens, our analysis of the StW 396 and

StW 514a tibiae suggests possible support for a two species hypothesis.

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Technical note

New Cenozoic fossil- bearing site abbreviations for collections of the University of the Witwatersrand

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INTRODUCTION

The University of the Witwatersrand houses significant faunal and floral fossil collections. These contain a range of Palaeozoic, Mesozoic and Cenozoic vertebrates, invertebrates, trace fossils and plants, representing an almost continuous record of life on earth. Cataloguing and recording this large collection poses some significant curatorial problems. For the Palaeozoic and Mesozoic collections, primarily from the Karoo, a simple abbreviation and numbering system has been adopted, a number being allocated to each fossil when accessioned by the curator. This is practically possible as, for example, in the case of the Karoo vertebrates (assigned BP/1) housed at the Bernard Price Institute for Palaeontological Research (BPI), a South African Heritage Resources Agency (SAHRA) permit is granted to the institution rather than to any particular site or scientist. The BPI abbreviations are listed in Table 1. The accession of material is thus continuous, databases are up to date and available to all, and the possibility of duplication of accession abbreviations and numbers is practically eliminated. In addition, there is an added advantage that these collections may be incorporated into national databases (e.g. Nicolas 2007) containing all the fossil repositories with the view of creating future international databases. As soon as material is identifiable, it is accessioned, and becomes part of the larger collection.

With Cenozoic fossil collections, more specifically Late Miocene to Late Pleistocene fauna, excavations are carried out according to the archaeological model and SAHRA permits are granted to specific sites and scientists. This gives the permit holder the freedom to manage the site as he or she sees fit within the guidelines set out by the SAHRA. As a result, collections have received a variety of abbreviations created on a number of, often inconsistent, criteria. This has the potential for duplication of fossil accession allocations and confusion between sites, both nationally and internationally.

In this paper, we give examples of abbreviations used both at the University of the Witwatersrand and elsewhere and present a new abbreviation and numbering system for Cenozoic fossil-bearing sites to be used by the University of the Witwatersrand, together with the rationale for this decision.

Table 1. The list of collections currently housed at the Bernard Price Institute for Palaeontological Research at the University of the Witwatersrand.

Name of BPI collection	Catalogue series
Karoo Vertebrate Collection	BP/1/
Palaeobotanical Collection	BP/2/
Cenozoic Mammal Collections (site-specific collections)	BP/3/
Recent Comparative Faunal Collection	BP/4/
Maguire Collection of Putative Stone Artefacts (Makapansgat)	BP/5/
Ichnological (Trace Fossil) Collection	BP/6/
Sedimentological Collection	BP/7/
Collection of Bone Histology Slides	BP/8/
Invertebrate Collection	BP/9/
Palynology Collection	BP/10/
Collection of Fossil Casts	BP/11/
Teaching Collection	BP/12/
Collection of Teaching Slides	BP/13/
McLachlan Collection of Dwyka Fossils	BP/14/
Stromatolite Collection	BP/15/
Fossil Wood Collection	BP/16/
Cave of Hearths Collection	BP/17/
Comparative Collection of Recent/Extant Flora	BP/18/

WHAT DO THOSE ABBREVIATIONS MEAN?

As African Cenozoic fossil sites often yield, or potentially yield, early hominids, we will focus on these so-called 'hominid sites'. In the past there have been no 'hard and fast' rules for deciding on which abbreviations to use. In most cases the letters indicate where the fossil was found and/or the repository at which the fossil is kept. The letters are followed by a number indicating the number of fossils found in a series. For instance, KNM-ER 3733 was the 3733th specimen found in East Rudolf (= Koobi Fora) and is kept at the Kenya National Museum. In another instance the letters may indicate the place where the fossil was found and the type of fauna it represents. For example O.H. 8 (Olduvai Hominid 8) is the eighth hominid found at Olduvai. Some examples of African hominid site allocations are given in Table 2.

Table 2. Examples of common East and West African hominin-bearing site abbreviations.

Abbreviation	Locality/Institution
AL	Afar Locality, Ethiopia
ARA-VP	Aramis Vertebrate Paleontology, Ethiopia
BOU-VP	Bouri Vertebrate Palaeontology, Ethiopia
KNM-ER	Kenya National Museum, East (Lake) Rudolf, Kenya
KNM-WT	Kenya National Museum, West (Lake) Rudolf, Kenya
KP	Kanapoi, Kenya
KT	Koro Toro, Chad
OH	Olduvai Hominid, Tanzania
TM	Toros-Menalla, Chad

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PROBLEMS WITH UNIVERSITY OF THE WITWATERSRAND'S PRESENT SITE ACCESSION SYSTEM

The University of the Witwatersrand houses a remarkable range of fossils, more specifically, the material from more than sixty Miocene, Pliocene and Pleistocene sites, at least seven of these being significant early hominid localities. With the freedom of site permit holders to accession their excavated material, there is much variation in how this is done. In most instances, the abbreviations are linked only to the common name of the site (Table 3). For the famous locality of Sterkfontein (Broom & Schepers 1946), representing a single site, there are at least six different abbreviations allocated to different groups of fossils depending on the type of material and/or project carried out (e.g. Pickering). We do not suggest that there is anything wrong with this in principle, but feel that if this practice continues, over time, it could lead to confusion, difficulty in integrating databases and most importantly, the potential for duplication. Examples of duplication are the abbreviation 'TM', associated with the Transvaal Museum in Pretoria and with Toros Manalla in Chad, also 'SAM' used by both the South African Museum and South Australian Museum. Cranial fauna from Makapansgat has been assigned the abbreviation 'M' as a prefix to the fossil number, but the post-crania have the abbreviation as a suffix. This means that, for the same site, there are two fossils assigned to each number, the only difference being that one is assigned the abbreviation as a prefix (crania) and the other as a suffix (post-crania). This was not a problem with pre-computer cataloguing which occurred when these catalogues were created. For modern searchable electronic databases, however, this poses a major challenge as there are literally thousands of fossils with duplicate numbers.

Table 3. Examples of some common South African hominin-bearing site abbreviations.

Abbreviation	Locality/Institution
BC	Border Cave
GVD	Gladysvale
GVH	Gladysvale Hominid
C	Coopers
M	Makapansgat
MLD	Makapansgat Limeworks Deposit
DN	Drimolen
DNH	Drimolen Hominid
BP/3/	Bernard Price Institute Cenozoic Mammal
PL	Plovers Lake
T	Taung
StW	Sterkfontein, Witwatersrand Hominid
Sts	Sterkfontein Type Site
SWP	Sterkfontein Witwatersrand Primate
SKX	Swartkrans
ST	Swartkrans, Transvaal Museum
TM	Transvaal Museum
K	Kromdraai

A NEW SYSTEM FOR THE UNIVERSITY OF THE WITWATERSRAND

After careful consideration of fossil abbreviations and numbering used internationally, it was decided that a system similar to that used, for example in East Africa, be adopted. The abbreviation 'U.W.' (University of the Witwatersrand) indicates the repository responsible for or in any way associated with the material, followed by a number allocated to the site, followed by the number allocated to the fossil. To ensure continuity, a U.W. number has been allocated to all sites historically and currently associated with the University of the Witwatersrand (Table 4). This does not change the current *status quo* of established sites historically using a particular abbreviation and numbering system. The 'renumbering' of the sites serves only as a reference of the approximate chronological order of the noting, discovery and/or establishment of the sites so that future sites are numbered appropriately. For example U.W. 1, the first site discovered under the auspices of the University of the Witwatersrand is the 'Type Site' of *Australopithecus africanus* at Taung (Dart 1925). The 'Taung Child' (Taung 1), could therefore also be allocated as U.W. 1-1. It should be noted that the sites with their new U.W. numbers listed in Table 4 also contain a number of sites that have as yet not been excavated and also sites where the excavated material is housed at institutions other than the University of the Witwatersrand. The reason for their inclusion is that the sites have either been discovered or noted by individuals associated with Wits, or a permit holder/associate of the site is or has been employed at the university, but the site permit specifies that the material is curated elsewhere. Examples of such sites are Luleche (Adams *et al.* 2007) and a number of sites on Bolt's Farm (Thackeray *et al.* 2008). This does not imply that the material must or should be curated at the University of the Witwatersrand, nor that another institution housing the material is compelled to use U.W. numbers. The sites listed merely create an initial record of localities historically associated with the University of the Witwatersrand and also provide a U.W. number if required in future.

The main purpose of developing a new abbreviation and numbering system is not to change established sites, but to have a standardized abbreviation and a site number assigned by the University, rather than a 'random' abbreviation only, given by the site permit holder, discoverer or researcher. The disadvantage of this new system is that the name of the site is not obvious or indicated by a fossil accession number. However, even with the site abbreviations in use to date, it is not always clear as to what these abbreviations mean or their interpretation may be ambiguous. An example of this is a case of a hominin tooth in a piece of breccia marked 'BF' held at the University of the Witwatersrand. Bolt's Farm is the first locality that comes to mind, but this has to date not been confirmed, and the provenance is as yet still uncertain. Nevertheless, the new system avoids confusion, as the common site locality name may still be used in conjunction with the U.W. number, for example, reference can be made to U.W. 3 (Gladysvale) or U.W. 21 (Sterkfontein) (See Table 4). When a significant fossil is unprovenanced with limited information about the specimen, a U.W. number may also be assigned to such a

Table 4. Late Miocene to late Pleistocene palaeontological site details and their University of the Witwatersrand (U.W.) numbers.

U.W. no.	Reference no.	Common name	Locality/region	Coordinates	Geological context	First report
U.W. 1	None	Taung type site	Buxton Limeworks	27.6167S, 24.6167E	Thabaseek Tufa	Dart (1925)
U.W. 2	None	Hrdlička deposits	Buxton Limeworks	28.6167S, 24.6167E	Thabaseek Tufa	Hrdlička (1925)
U.W. 3	SAAN – 0001	Gladysvale	John Nash Reserve	25.9000S, 27.7000E	Dolomitic cave, Eccles Form.	Broom & Schepers (1946)
U.W. 4	SAAN – 0003	Kemps cave	Krugersdorp	26.0806S, 27.7056E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 5	SAAN – 0004	Minaars cave; Hadeco	Sterkfontein Valley	25.9900S, 27.7731E	Dolomitic cave, Monte Cristo Form.	Brain (1981)
U.W. 6	SAAN – 0005	None	Sterkfontein Valley	25.9881S, 27.8039E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 7	SAAN – 0006	None	Sterkfontein Valley	25.9853S, 27.7692E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 8	SAAN – 0007	None	Sterkfontein Valley	25.9671S, 27.7335E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 9	SAAN – 0008	None	Sterkfontein Valley	25.9812S, 27.7764E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 10	SAAN – 0009	None	Sterkfontein Valley	25.9543S, 27.7793E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 11	SAAN – 0010	None	Sterkfontein Valley	25.9525S, 27.7985S	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 12	SAAN – 0011	None	Sterkfontein Valley	25.8275S, 28.0131E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 13	SAAN – 0012	None	Sterkfontein Valley	25.8492S, 28.0132E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 14	SAAN – 0013	None	Sterkfontein Valley	25.8035S, 28.0657S	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 15	SAAN – 0014	None	Sterkfontein Valley	25.8032S, 28.0531E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 16	SAAN – 0015	None	Erasmia	25.8039S, 28.0525E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 17	SAAN – 0016	Legolo	Erasmia	25.8060E, 28.0508S	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 18	SAAN – 0017	None	Pelindaba	25.8161S, 27.9693E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 19	SAAN – 0018	None	John Nash Reserve	25.8895S, 27.7761E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 20	SAAN – 0019	None	John Nash Reserve	25.8442S, 27.8464E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 21	SAAN – 0020	Sterkfontein	Sterkfontein Valley	26.0317S, 27.7350E	Dolomitic cave, Monte Cristo Form.	Broom & Schepers (1946)
U.W. 22	SAAN – 0021	Swartkrans	Sterkfontein Valley	26.0167S, 27.7239E	Dolomitic cave, Monte Cristo Form.	Broom & Schepers (1946)
U.W. 23	SAAN – 0022	Kromdraai	Sterkfontein Valley	26.0106S, 27.7503E	Dolomitic cave, Monte Cristo Form.	Broom & Schepers (1946)
U.W. 24	SAAN – 0023	Coopers A	Sterkfontein Valley	26.0128S, 27.7468E	Dolomitic cave, Monte Cristo Form.	Broom & Schepers (1946)
U.W. 25	SAAN – 0023	Coopers B	Sterkfontein Valley	27.0128S, 27.7468E	Dolomitic cave, Monte Cristo Form.	Broom & Schepers (1946)
U.W. 26	SAAN – 0023	Coopers C	Sterkfontein Valley	28.0128S, 27.7468E	Dolomitic cave, Monte Cristo Form.	Broom & Schepers (1946)
U.W. 27	SAAN – 0023	Coopers D	Sterkfontein Valley	29.0128S, 27.7468E	Dolomitic cave, Monte Cristo Form.	Berger *et al.* (2003)
U.W. 28	None	None	Thabazimbi Valley	Unknown	Unprovenanced	This publication
U.W. 29	None	Makapan Historic Cave	Makapan Valley	24.1500S, 29.1831E	Malmani Dolomites	Van Riet Louw (1954)
U.W. 30	None	Makapan Limeworks	Makapan Valley	24.1500S, 29.1831E	Malmani Dolomites	Dart (1952)
U.W. 31	None	Makapan Cave of Hearths	Makapan Valley	24.1500S, 29.1831E	Malmani Dolomites	Van Riet Louw (1954)
U.W. 32	None	Makapan Buffalo Cave	Makapan Valley	24.1478S, 29.1722E	Malmani Dolomites	Broom (1937)
U.W. 33	None	Border Cave	Ingwavuma	21.1000S; 31.5900E	Howies Poort Stratum	Cooke *et al.* (1945)
U.W. 34	UCMP Loc. V-67256	Kraal Pit (Pit 1)	Bolt's Farm	26.0286S, 27.7173E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 35	UCMP Loc. V-67257	H Cave (Pit 2)	Bolt's Farm	26.0281S, 27.7173E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 36	UCMP Loc. V-67258	Kaffir Beer/Cobra Cave (Pit 3)	Bolt's Farm	26.028S, 27.7171E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 37	UCMP Loc. V-67259	Garage Ravine Cave (Pit 4)	Bolt's Farm	26.0319S, 27.7155E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 38	UCMP Loc. V-67260	Smith Cave (Pit 5)	Bolt's Farm	26.0287S, 27.7166E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 39	UCMP Loc. V-67261	Baboon Cave (Pit 6)	Bolt's Farm	26.0327S, 27.7113E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 40	UCMP Loc. V-67262	Elephant/Bridge Cave (Pit 7)	Bolt's Farm	26.032S, 27.7127E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 41	None	Rodent Cave (Pit 8)	Bolt's Farm	26.0292S, 27.7163E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 42	None	No name (Pit 9)	Bolt's Farm	26.0285S, 27.7173E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 43	UCMP Loc. V-67263	Grey Bird Pit/Main Quarry (Pit 10)	Bolt's Farm	26.0267S, 27.7309E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 44	None	U Cave (Pit 11)	Bolt's Farm	26.0302S, 27.7316E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 45	12A	No name (Pit 12A))	Bolt's Farm	26.0304S, 27.7133E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 46	12B	No name (Pit 12B)	Bolt's Farm	26.0309S, 27.7133E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 47	None	Arm Pit (Pit 13)	Bolt's Farm	26.0287S, 27.7165E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 48	UCMP Loc. V-67264	Bench Mark Pit (Pit 14)	Bolt's Farm	26.0291S, 27.7163E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 49	None	Aves Cave (Pit 15)	Bolt's Farm	26.0291S, 27.7161E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 50	UCMP Loc. V-67288	Tit Hill Pit (Pit 23)	Bolt's Farm	26.0346S, 27.7128E	Dolomitic cave, Monte Cristo Form.	Cooke (1991)
U.W. 51	None	Dart deposits	Buxton Limeworks	27.6167S, 24.6167E	Thabaseek Tufa	McKee & Tobias (1994)
U.W. 52	None	Tobias Pinnacle deposit	Buxton Limeworks	28.6167S, 24.6167E	Thabaseek Tufa	McKee (1994)
U.W. 53	FEP 38-2	Berger Cave complex	Buxton Limeworks	29.6167S, 24.6167E	Thabaseek Tufa	McKee (1994)
U.W. 54	FEP 38-15	Unnamed Soluton Cavity	Buxton Limeworks	30.6167S, 24.6167E	Thabaseek Tufa	Cooke (1990)
U.W. 55	FEP 38-16	Unnamed Soluton Cavity	Buxton Limeworks	30.6167S, 24.6167E	Thabaseek Tufa	Cooke (1990)
U.W. 56	FEP 38-25	Unnamed Soluton Cavity	Buxton Limeworks	31.6167S, 24.6167E	Thabaseek Tufa	Cooke (1990)
U.W. 57	FEP 38-1	Lucky Moon Cave complex	Buxton Limeworks	33.6167S, 24.6167E	Norlim Tufa	McKee (1993)
U.W. 58	FEP 38-28	Peabody Cave	Buxton Limeworks	34.6167S, 24.6167E	Norlim Tufa	Cooke (1990)
U.W. 59	None	LSN Cave	Buxton Limeworks	35.6167S, 24.6167E	Norlim Tufa	McKee (1994)
U.W. 60	None	Innominate Cave	Buxton Limeworks	36.6167S, 24.6167E	Norlim Tufa	McKee (1994)
U.W. 61	None	Cut-through Alley	Buxton Limeworks	37.6167S, 24.6167E	Norlim Tufa	McKee (1994)

Continued on p. 80

Table 4 (*continued*)

U.W. no.	Reference no.	Common name	Locality/region	Coordinates	Geological context	First report
U.W. 62	None	Quinney cave	Buxton Limeworks	38.6167S, 24.6167E	Norlim Tufa	McKee (1994)
U.W. 63	None	Black Earth Cave	Buxton Limeworks	39.6167S, 24.6167E	Norlim Tufa	McKee (1994)
U.W. 64	None	Equus Cave	Buxton Limeworks	40.6167S, 24.6167E	Oxland Tufa	Grine & Klein (1985)
U.W. 65	None	Peabody's Equus Site	Buxton Limeworks	41.6167S, 24.6167E	Oxland Tufa	Peabody (1954)
U.W. 66	None	Blom Cave	Buxton Limeworks	42.6167S, 24.6167E	Oxland Tufa	McKee (1994)
U.W. 67	None	Acacia Cave	Buxton Limeworks	43.6167S, 24.6167E	Oxland Tufa	McKee (1994)
U.W. 68	FEP 38-29?	Satan Cave	Buxton Limeworks	44.6167S, 24.6167E	Oxland Tufa	McKee (1994)
U.W. 69	None	Oxland Mammal Site	Buxton Limeworks	45.6167S, 24.6167E	Oxland Tufa	McKee (1994)
U.W. 70	FEP 38-12	Blue Pool Cave	Buxton Limeworks	46.6167S, 24.6167E	Oxland Tufa	McKee (1994)
U.W. 71	None	Spiers' Cave	Buxton Limeworks	47.6167S, 24.6167E	Oxland Tufa	Broom (1946)
U.W. 72	None	Tobias Cave	Buxton Limeworks	48.6167S, 24.6167E	Oxland Tufa	Humphreys (1978)
U.W. 73	None	Alcove Cave	Buxton Limeworks	49.6167S, 24.6167E	Blue Pool Tufa	McKee (1994)
U.W. 74	None	None	Buxton Limeworks	Unknown	Unprovenanced	This publication
U.W. 75	SAAN – 0024	Drimolen	Rhino Game Reserve	25.9681S, 27.7564E	Dolomitic cave, Monte Cristo Form.	Keyser et. al. (2000)
U.W. 76	SAAN – 0025	Plovers Lake A	Sterkfontein Valley	25.9936S, 27.7764E	Dolomitic cave, Monte Cristo Form.	Brain (1981)
U.W. 77	SAAN – 0025	Plovers Lake B	Sterkfontein Valley	25.9936S, 27.7764E	Dolomitic cave, Monte Cristo Form.	Brain (1981)
U.W. 78	SAAN – 0026	Bones Cave	Sterkfontein Valley	25.9756S, 27.7783E	Dolomitic cave, Monte Cristo Form.	Brain (1981)
U.W. 79	SAAN – 0027	Wonder Cave	Sterkfontein Valley	25.9703S, 27.7720E	Dolomitic cave, Monte Cristo Form.	Brain (1981)
U.W. 80	None	None	Cape St. Francis	Unknown	Unprovenanced	This publication
U.W. 81	None	Kalkbank	Kalkbank	23.5167S, 29.3500E	Fluvial Sandstone	Dart & Kitching (1958)
U.W. 82	None	None	Sudwala	Unknown	Unprovenanced	This publication
U.W. 83	None	Goldsmith's	Bolt's Farm	26.0386S, 27.7103E	Dolomitic cave, Monte Cristo Form.	Mokokwe (2005)
U.W. 84	SAAN – 0028	None	John Nash Reserve	25.8992S, 27.7984E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 85	SAAN – 0029	None	Motstetsi Farm	25.9131S, 27.8281E	Dolomitic cave, Monte Cristo Form.	Berger & Brink (2007)
U.W. 86	SAAN – 0030	Motstetsi	Motstetsi Farm	25.9025S, 27.8267E	Dolomitic cave, Monte Cristo Form.	Berger & Lacruz (2003)
U.W. 87	SAAN – 0031	Gondolin	Skurweberg	25.8303S, 27.8635E	Dolomitic cave, Monte Cristo Form.	Watson (1993)
U.W. 88	None	Malapa	John Nash Reserve	25.5339S; 27.4757E	Dolomitic cave, Monte Cristo Form.	This publication
U.W. 89	None	None	John Nash Reserve	25.5728S; 27.4649E	Tufa cave	This publication
U.W. 90	None	Luleche	Skurweberg	25.8332S, 27.8560E	Dolomitic cave, Eccles Form.	Adams *et al.* (2007)
U.W. 91	None	Femur Dump	Bolt's Fram	26.0347S, 27.7127E	Dolomitic cave, Monte Cristo Form.	Thackeray *et. al.* (2008)
U.W. 92	None	Alcelaphenae Site	Bolt's Farm	26.0336S, 27.7135E	Dolomitic cave, Monte Cristo Form.	Thackeray *et. al.* (2008)
U.W. 93	None	Waypoint 160	Bolt's Farm	26.0339S, 27.7139E	Dolomitic cave, Monte Cristo Form.	Sénégas *et. al.* (2002)
U.W. 94	None	Machine Cave	Bolt's Farm	26.0352S, 27.7110E	Dolomitic cave, Monte Cristo Form.	Thackeray *et. al.* (2008)
U.W. 95	None	Dom's Site	Bolt's Farm	26.0339S, 27.7136E	Dolomitic cave, Monte Cristo Form.	Thackeray *et. al.* (2008)
U.W. 96	None	X Cave	Bolt's Farm	26.0299S, 27.7148E	Dolomitic cave, Monte Cristo Form.	Thackeray *et. al.* (2008)
U.W. 97	None	Y Cave	Bolt's Farm	26.0294S, 27.7151E	Dolomitic cave, Monte Cristo Form.	Thackeray *et. al.* (2008)
U.W. 98	None	None	Bolt's Farm	Unknown	Dolomitic cave, Monte Cristo Form.	This publication
U.W. 99	None	Hermanus Cave	Hermanus	Unknown	Unprovenanced	This publication
U.W. 100	None	None	Boesmansklip	Unknown	Unprovenanced	This publication

specimen or specimens; after all, the specimen has come from somewhere, albeit that the exact locality is currently unknown. More accurate information may be found on such specimens in future, in the interim it has been accessioned and catalogued and therefore 'exists' and has a reference for future research. For localities that have more than one site, for example, Buxton Limeworks (Taung), Coopers and Bolt's Farm (See McKee 1994; Broom & Schepers 1946; Thackeray *et al.* 2008), each site receives its own U.W. number.

It is difficult if not impossible to find a practical abbreviation and numbering system that has or will never be replicated elsewhere. Similar to U.W., the abbreviations UW (University of Wyoming), Uw (University of Utrecht Wood) and UWBM (University of Washington Burke Museum) are used on fossils. For this reason, periods have been inserted in the University of the Witwatersrand abbreviation (U.W. as opposed to UW). Even without this, or the same abbreviation adopted by another institution in future, the use of a site number, followed by the specimen number is unlikely to be replicated in exactly the same manner elsewhere.

In terms of assigning catalogue numbers to fossils, we encourage scientists and curators to number these consecutively, regardless of what type of fossil (or artifact) it is. This implies that, for example, non-primate and primate (including hominin) fauna be incorporated into the same catalogue. This refers to a curatorial database; of course, for research purposes, these can be subdivided into separate catalogues or lists. It is also suggested that each fossil, even if presumed to be from the same individual, be given its own number. This allows each element to have its own number, rather than the same number (for the individual) with sub-letters such as a, b, c ,etc. This suggestion of numbering each fossil separately creates a biologically sound principle, that a specimen may have been misidentified and at a later stage not deemed to be part of a particular individual. This would prevent confusion and the need to renumber specimens. It follows that new material, later to be conclusively identified as part of a previously (incorrectly) identified individual, keep its 'place' in the catalogue and simply be noted as part of the previously identified individual. Furthermore, such a system readily allows the easy association of individual elements from a skeleton, simply by referring to their unique accession number. As an additional source of reference, an alterna-

tive name may be assigned to an important specimen, or specimens, in order to link them to each other. For example, at the new site of Malapa (U.W. 88) in the Cradle of Humankind, a number of elements, each having their own accession number, but belonging to the same partial hominin individual is also known as MH 1 (Malapa Hominin 1), indicating the first hominin found at Malapa. Other names may also be given to important specimens in order to make them unique and easily identifiable to the scientific community.

CONCLUSION

A new system of abbreviation and numbering of fossil sites associated with the University of the Witwatersrand has been presented. The fossil locality number is allocated by the University Curator of Collections. Any alternative names or numbers are still given at the discretion of the fossil site permit holder. The list of sites and their U.W numbers in Table 4 will be updated from time to time and published as a source of reference. This list is by no means complete and may also contain inadvertent errors which, if identified will be corrected in future. It does, however, highlight the remarkable number of sites associated with the University of the Witwatersrand.

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REVIEWED EXTENDED ABSTRACTS

South American Middle Triassic continental faunas with amniotes: biostratigraphy and correlation

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South America has an extensive record of continental Triassic, in which several groups of vertebrates are represented (Bonaparte 1982; Langer *et al.* 2007). This record encompasses a diversified fauna of archosauriforms, including basal dinosauriforms, and the oldest dinosaurs, along with abundant rhynchosaurs and mammal-like therapsids (dicynodonts and cynodonts). The Middle Triassic constitutes an important transitional period, when significant changes in amniote faunas occurred. South American deposits of this age yielded a diversified fauna of dinosauriforms, as well as the first records of traversodontids, one of the most successful groups of non-mammaliaform cynodonts. In addition, the diversity of dicynodonts recovered from the Permo/Triassic extinction event, and the group is recorded globally in Laurasia and Gondwana (Surkov 2000).

Five Middle Triassic faunal assemblages, including amniote body fossils, have been recognized in South America, three in Argentina and two (or possibly three) in Brazil (Table 1). The Puesto Viejo Local Fauna represented by the upper levels of the Puesto Viejo Group, San Rafael Basin, south of Mendoza Province (= Puesto Viejo Formation, see Stipanicic *et al.* 2007) includes the dicynodonts *Kannemeyeria argentinensis* and *Vinceria* sp. (but see Renaut & Hancox 2001 for a different interpretation of *K. argentinensis*) and the cynodonts *Pascualgnathus polanskii, Cynognathus crateronotus,* and the recently discovered *Diademodon tetragonus* (Bonaparte 1982; Martinelli *et al.,* in press).

The Puesto Viejo Local Fauna was correlated with the *Cynognathus* Assemblage Zone (AZ) of South Africa (Bonaparte 1982) suggesting an Olenekian (e.g. Bonaparte 1982; Lucas 1998) or Anisian age (Bonaparte 1967). The Puesto Viejo Local Fauna is strongly reminiscent of African paleofaunas, such as those of the Burgersdorp Formation of the Karoo Basin and the Omingonde Formation of Namibia (Kitching 1995; Smith & Swart 2002). These similarities include the occurrence of *Cynognathus* and *Diademodon,* the two most common cynodonts in the *Cynognathus* AZ of South Africa (Kitching 1995). In the last decade, the *Cynognathus* AZ has been informally divided into three subzones, based mainly on its temnospondyl amphibian taxa (Hancox *et al.* 1995), but also supported by other tetrapods (Abdala *et al.* 2005). Faunal comparison suggests the temporal correlation of the upper assemblage of the Puesto Viejo Group with subzones B and C of the *Cynognathus* AZ, where both *Cynognathus* and *Diademodon* are known. The record of the traversodontid *Pascualgnathus* in the Puesto Viejo Local Fauna represents an important difference between the South American and South African assemblages.

Taking into account all these points it seems possible to consider the upper fauna of the Puesto Viejo Group as Anisian in age, although the record of traversodontid cynodonts in this unit may suggest a Late Anisian age (Fig. 1). Radiometric dates are problematic. Valencio *et al.* (1975) reported variations between 230 ± 10 Ma and 236 ± 10 Ma for ignimbrites and 232 ± 10 Ma for basalts from the lower levels of the Puesto Viejo Group (i.e. Quebrada de



Figure 1. Stratigraphic chart, showing correlations between terrestrial Middle Triassic faunas from South America. Timeframe after the Geological Time Scale 2004 (Gradstein & Ogg 2004). Abbreviations: *Dinod, Dinodontosaurus*; *Hyperod, Hyperodapedon.*

Table 1. Tetrapods from South American Middle Triassic faunas. 'A' indicates taxon more abundant in the fauna. Uncertainty as to the identity of *Kannemeyeria*/Kannemeyeriidae follows Renaut & Hancox (2001).Chañares fauna modified from Rogers *et al.* (2001); *Dinodontosaurus* Assemblage Zone fauna modified from Langer *et al.* (2007).

1) ANISIAN FAUNAS
Puesto Viejo Local Fauna, Argentina
Therapsids
Dicynodontia
?*Kannemeyeria argentinensis*
Vinceria sp.
Cynodontia
Cynognathus crateronotus
Pascualgnathus polanskii A
Diademodon tetragonus
Cerro de Las Cabras Fauna, Argentina
Therapsida
Dicynodontia
Vinceria andina
?Kannemeyeriidae
Cynodontia
Andescynodon mendozensis A
Rusconiodon mignonei
Cromptodon mamiferoides
2) ANISIAN TAXA IN BRAZILIAN TRIASSIC
Cynodontia
Luangwa sudamericana
Rhynchosauria
'Mariante' rhynchosaur
3) LADINIAN FAUNAS
Chañares fauna, Argentina
Therapsida
Dicynodontia
Dinodontosaurus platiceps
Dinodontosaurus platygnathus
Dinodontosaurus brevirostris
Cynodontia
Chiniquodon theotonicus
Massetognathus pascuali A
Probainognathus jenseni
Archosauriformes
Proterochampsidae
Chanaresuchus bonapartei
Gualosuchus reigi
Tropidosuchus romeri
Archosauria
Crurotarsi
Tarjadia ruthae
Rauisuchidae
Luperosuchus fractus
Crocodylomorpha
Gracilisuchus stipanicicorum
Ornithodira
Lagerpeton chanarensis
Lewisuchus admixtus
Marasuchus lilloensis
Pseudolagosuchus major
Dinodontosaurus Assemblage Zone fauna, Brazil
Therapsida
Dicynodontia

Dinodontosaurus pedroanum A

Stahleckeria potens

cf. Ischigualastia
Cynodontia
Chiniquodon theotonicus
Massetognathus ochagaviae
Traversodon stahleckeri
Protheriodon estudianti
Protuberum cabralensis
Parareptilia
Owenettidae
Candelaria barbouri
Archosauriformes
Proterochampsidae

?*Chanaresuchus*/?*Gualosuchus*
Archosauria
Crurotarsi

Rauisuchidae
Prestosuchus chiniquensis
'*Karamuru vorax*'
Barberenasuchus brasiliensis
?Rauisuchidae/?Dinosauria
Spondylosoma absconditum
Santa Cruz do Sul fauna, Brazil
Therapsida
Cynodontia
Santacruzodon hopsoni A
Massetognathus sp.
Menadon-like traversodontid
cf. Probainognathus
Chiniquodon sp.
Archosauriformes
Proterochampsidae
Unnamed proterochampsid

los Fósiles Formation; Stipanicic *et al.* 2007), which are generally considered as Lower Triassic. Considering the Geologic Time Scale 2004 (Gradstein & Ogg 2004), these dates would imply a Late Anisian-Ladinian age for the lower levels of the Puesto Viejo Group.

Another South American faunal association often interpreted as contemporaneous with the Puesto Viejo Local Fauna (e.g. Bonaparte 1982, 2002) is the Cerro de Las Cabras fauna (= Río Mendoza Local Fauna). There is some disagreement concerning its age: plant fossils indicate Early Triassic to early Middle Triassic (Morel *et al.* 2003) while palynology suggests late Middle Triassic to early Upper Triassic (Zavattieri & Arcucci 2007). In the Cerro de Las Cabras Formation, Cuyo Basin, north of Mendoza Province, body fossils are represented only by therapsids (Tables 1 & 2), among them the dicynodont *Vinceria andina* and the cynodonts *Andescynodon mendozensis, Rusconiodon* mignonei and *Cromptodon mamiferoides* (Bonaparte 1982). Zavattieri and Arcucci (2007) also reported a dicynodont maxillary fragment assigned to Kannemeyeriidae. Archosauriforms in the Cerro de Las Cabras Formation are represented by footprints and trackways of crurotarsan archosaurs (Marsicano *et al.* 2004; Table 2).

Vinceria is the only genus shared between the Puesto Viejo and the Cerro de Las Cabras faunas (e.g. Bonaparte 1982; Marsicano *et al.* 2001). The cynodont *Cromptodon* is represented by a tiny lower jaw with postcanines very similar to those of *Aleodon* from the Manda Formation in Tanzania, which is generally considered as Anisian in age (Abdala & Ribeiro 2003). Both the Puesto Viejo and Cerro de Las Cabras faunas present traversodontid cynodonts, but recent cladistic analyses of this group showed different placements for *Andescynodon* and *Pascualgnathus.* In Abdala & Ribeiro (2003) they formed a monophyletic

Table 2. Diversity and abundance of amniotes represented in Middle Triassic faunas from South America. Abbreviations: ARC, archosauriforms; CYN, cynodonts; DIA, diapsids; DIC, dicynodonts; PRT, parareptiles; TH, therapsids; TRC, traversodontid cynodonts. Archosauriforms in the Cerro de Las Cabras fauna are represented by footprints and trackways of crurotarsan archosaurs (Marsicano *et al.* 2004). Numbers in brackets indicate the quantity of taxa of the group represented in the fauna.

	Puesto Viejo	Cerro de Las Cabras	Chañares	*Dinodontosaurus* Assemblage Zone	Santa Cruz do Sul	Mariante
Taxa	TH	TH ARC	TH ARC	TH ARC PRT	TH ARC	TH DIA
Diversity	CYN (3)	CYN (3)	ARC (10)	CYN (5) ARC (5)	CYN (5)	
Abundance	TRC DIC	TRC	TRC	DIC	TRC	

group in a basal politomy of traversodontids. A more comprehensive study by Abdala *et al.* (2006) produced hypotheses in which *Pascualgnathus* is basal to *Andescynodon.* In both studies the traversodontids from the discussed faunas are basal to those from the Middle Triassic deposits of the Ischigualasto-Villa Unión Basin (i.e. *Massetognathus* from the Chañares Formation). Judging by the phylogenetic relationships of the traversodontids in Abdala *et al.* (2006), the cynodont assemblage from the Cerro Bayo of Potrerillos can prove to be somewhat younger than that of the upper fauna of the Puesto Viejo Group, possibly latest Anisian, but indeed older than the Ladinian Chañares fauna (Fig. 1). Recent radiometric dating near the top of the Río Mendoza Formation, below the Cerro de Las Cabras Formation, indicate an age of 243 ± 5 Ma (Avila *et al.* 2006), corresponding to the Anisian (*sensu* Gradstein & Ogg 2004). In addition, recent dating of the lower and middle levels of the Potrerillos Formation, which overlies the Cerro de las Cabras Formation, indicates 239.2 ± 4.5 Ma, 239.7 ± 2.2 Ma and 230.3 ± 2.3 Ma (Spalleti *et al.* 2008). All the radiometric dates are therefore consistent with an Anisian age for the Cerro de las Cabras fauna.

The South American faunas of Ladinian age are remarkably diverse if compared with older ones. Not only therapsids are represented but also procolophonoids and a large number of archosauriforms (Tables 1 & 2).

In the fauna from the Chañares Formation, Ischigualasto-Villa Unión Basin, San Juan and La Rioja provinces, central western Argentina, archosauriforms includes proterochampsids, rauisuchians, crocodylomorphs and ornithodirans (Marsicano *et al.* 2001). Archosauriforms are represented by at least ten taxa (Table 2), showing greater species diversity than cynodonts and dicynodonts combined (Rogers *et al.* 2001). Three species of dicynodonts (all included in the genus *Dinodontosaurus*) and three cynodonts are members of the fauna (Table 1). The traversodontid *Massetognathus pascuali* is, by far, the most abundant taxon (Table 2), representing approximately 58% of the identified specimens of this faunal assemblage (Rogers *et al.* 2001).

In the lacustrine levels of the Los Rastros Formation that overlie the Chañares and Ischichuca formations, amniotes are known only by indeterminate archosaur remains (Forster *et al.* 1995) and footprints and trackways of therapsids and archosauriforms (putative dinosaurs and crurotarsal archosaurs; Marsicano *et al.* 2004). The Los Rastros Formation is well known for its rich record of pollen and fossil plants, whereas recent contributions have described invertebrate fossils (insects and conchostracans), actinopterygian fishes, and temnospondyl amphibians (Martins-Neto *et al.* 2005, 2006; López-Arbarello *et al.* 2006; Mancuso & Marsicano 2008). Radiometric dates from tuffs at the base of the Ischigualasto Formation (Rogers *et al.* 1993) indicate an age of 227.8 ± 0.3 Ma, corresponding to the limit between Middle and Upper Triassic (*sensu* Ogg & Gradstein 2004; but see Muttoni *et al.* 2004, for a different opinion about the Middle/Late Triassic boundary). Consequently, the underlying Los Rastros and Chañares formations are usually interpreted as Ladinian in age (e.g. Rogers *et al.* 2001; Mancuso & Marsicano 2008; see Fig. 1). Palaeofloristic studies, however, suggested a lower Middle Triassic age (probably Anisian) for the Chañares, Ischichuca and Los Rastros formations (Spalleti *et al.* 1999). In contrast, pollen associations from the Ischichuca Formation, comparable to the Ipswich microflora from Australia, suggested a Late Ladinian to Carnian age for this unit, implying a younger, minimally Carnian, age for the Los Rastros Formation (Zavattieri & Melchor 1999).

The *Dinodontosaurus* AZ of the Santa Maria Formation, Paraná Basin, Rio Grande do Sul State in southern Brazil is commonly considered contemporaneous with the Chañares assemblage, sharing several taxa at genus level with the Argentinean fauna. The *Dinodontosaurus* AZ has procolophonoids in addition to the groups above mentioned for the Chañares fauna (Tables 1 & 2). In the Brazilian fauna the diversity of cynodonts and archosauriforms (five taxa each) is higher than that of dicynodonts (three taxa), while procolophonoids are only represented by the owenettid *Candelaria barbouri* (Cisneros *et al.* 2004). Dicynodonts are the most abundant tetrapods in the *Dinodontosaurus* AZ (Table 2), representing 61% of occurrences in the fauna (Schultz *et al.* 2000).

In an outcrop of the Santa Maria Formation usually considered within the *Dinodontosaurus* AZ (e.g. Schultz *et al.* 2000) a rhynchosaur, known as the 'Mariante rhynchosaur', was found associated with dicynodonts (Tables 1 & 2). This is the only South American record of rhynchosaurs in levels considered as Ladinian in age, and the only joint occurrence of those two groups in the

Brazilian Triassic. A recent phylogenetic analysis of rhynchosaurs by Montefeltro (2008) indicates a close relationship between the 'Mariante rhynchosaur' and Anisian taxa from India and Tanzania (see also Langer *et al.* 2007). In addition, the traversodontid cynodont *Luangwa sudamericana,* collected from an unknown locality in the Brazilian Triassic (Abdala & Sa-Teixeira 2004), is closely related to the congeneric taxa known from the Anisian of Zambia and Namibia (Kemp 1980; Abdala & Smith 2007). Based on the presence of the 'Mariante rhynchosaur' and *Luangwa sudamericana* in Brazilian beds, Abdala and Sa-Teixeira (2004) suggested an Anisian age for some of the faunas of the Santa Maria Formation, which would thus be older than the *Dinodontosaurus* AZ (Fig. 1).

The recently discovered fauna from Santa Cruz do Sul, also known as 'Santuario Schoenstatt', in outcrops of the Santa Maria Formation, has a remarkable abundance of cynodonts. Apart from one specimen assigned to Proterochampsidae, the rest of the rich deposit yielded only cynodonts (Tables 1 & 2). Among these, there are three different traversodontids: a) *Santacruzodon hopsoni* (Abdala & Ribeiro 2003); b) a taxon with affinities to *Menadon* from Madagascar and to Carnian forms (i.e. *Exaeretodon*); and c) *Massetognathus* (Schultz & Langer 2007). A fourth traversodontid, represented by a tiny portion of the maxilla with four postcanines, whose pattern was initially considered as resembling those of *Boreogomphodon* from the U.S.A., is now considered a juvenile of *Santacruzodon,* with remarkably worn teeth (Abdala, pers. obs.). Carnivorous cynodonts are documented by a couple of chiniquodontid specimens and by a tiny mandibular fragment, bearing a single tooth, assigned to *cf. Probainognathus* (Soares & Abdala 2008). Faunal resemblances of Santa Cruz do Sul to other Triassic faunas include chiniquodontids which are known in Ladinian and Carnian faunas of South America and were most recently recorded in a putative Anisian fauna from Namibia (Abdala & Smith 2007). *Massetognathus* and *Probainognathus* are also represented in the Ladinian Chañares fauna from Argentina. Yet, the more significant similarities are with the late Ladinian/early Carnian 'Isalo II' fauna from Madagascar, which yielded chiniquodontids and two traversodontids that resemble forms from the Santa Cruz do Sul fauna (Flynn & Wyss 2002; Abdala & Ribeiro 2003; Langer *et al.* 2007). The presence of Ladinian traversodontids along with taxa resembling Carnian forms was interpreted as supporting a transitional position for the Santa Cruz do Sul fauna, between the Ladinian *Dinodontosaurus* AZ and the Carnian *Hyperodapedon* AZ dominated by rhynchosaurs (Fig. 1), an thus coincident with the age proposed for the Malagasy assemblage.

An overview of the global distribution of tetrapods of Anisian age shows the first record of traversodontid cynodonts in Africa and South America, where they are diverse and, in some cases, abundant (Table 2). This group, however, is curiously absent from the extensive and highly fossiliferous Karoo Basin of South Africa, lying in a paleolatitude of approximately 55°S, and from the upper Fremouw fauna in Antarctica which is further south. The only record of Mid Triassic traversodontids from Laurasia is based on two isolated postcanines discovered in ?Upper Anisian/Ladinian beds from Russia (Battail & Surkov 2000). The large carnivorous *Cynognathus* and the large gomphodont *Diademodon,* abundant in the Anisian beds of the Karoo, are common in Gondwana and absent from Laurasian faunas. Dicynodonts are represented by four families (*sensu* Maisch 2001) in the Anisian of Gondwana: kannemeyeriids, shansiodontids, dinodontosaurids, and stahleckeriids, whereas only the last two families are known in the Ladinian. In Laurasia, shansiodontids, dinodontosaurids and, perhaps, kannemeyeriids (Maisch 2001) are represented in the Russian ?Late Anisian/Ladinian (Shishkin *et al.* 2000) and in the Middle Triassic of China.

The only record of rhynchosaur in the Middle Triassic of Brazil is suggestive of a putative Anisian age for some beds of the Santa Maria Formation (Fig. 1). Rhynchosaurs are recorded in the Anisian of Gondwana (e.g. India and Tanzania) and particularly well represented in Anisian faunas from the United Kingdom (Benton *et al.* 1994). It is remarkable that this group is not represented at all in the rich Ladinian faunas from Argentina and Brazil, although it is known from a partially coeval fauna from Madagascar (Langer *et al.* 2000).

With the record of parareptiles and several archosauriforms, along with therapsids (Table 2), the Ladinian faunas from Argentina and Brazil document an increase in diversity compared with those from the Anisian. Representatives of the latter are always dominant: traversodontid cynodonts in Chañares and Santa Cruz do Sul and dicynodonts in the *Dinodontosaurus* AZ (Table 2). Archosauriforms show a remarkable diversification in the Ladinian of South America, including endemic proterochampsids, rauisuchians, and dinosauromorphs, the latter two groups with a respectable diversity.

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Taxonomic re-evaluation of tapinocephalid dinocephalians

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Tapinocephalid dinocephalians are morphologically the most diverse Middle Permian herbivorous tetrapod group from South Africa. Although they were the first large and the most successful therapsid group to have existed at that time on land, they all became extinct by the Middle to Late Permian (Boonstra 1971). They are well represented in South Africa (Boonstra 1963; Boonstra 1969; Rubidge 1991) and are less diverse in Russia (Tchudinov 1983; Ivachnenko 2003), Zimbabwe (Boonstra 1946; Lepper *et al.* 2000; Munyikwa 2001) and possibly Brazil (Langer 2000). They are most abundant in the *Eodicynodon* and *Tapinocephalus* assemblage zones of the Beaufort Group of South Africa (Haughton & Brink 1954; Boonstra 1963, 1969; Rubidge 1991, 1995), which are considered to be the equivalents of Russian Zone I and Zone II (Efremov 1938, 1952) and the *Titanophoneus* Superzone (Ivachnenko *et al.* 1997). Boonstra (1969) used the following characters to define South African tapinocephalid dinocephalian: (1) absence of canine, (2) intermeshing upper and lower incisors, (3) crushing heel and talon on all teeth and (4) moderately to greatly developed pachyostosis. By contrast the most recently described tapinocephalid, *Tapinocaninus pamelae,* has a canine tooth in both upper and lower jaws (Rubidge 1991). This character is also present in the Russian tapinocephalid *Ulemosaurus svijagensis* (Riabinin 1938; Efremov 1940).

Taxonomically, tapinocephalid dinocephalians were first considered to be a new family of the Dinosauria (Owen 1876). After Seeley (1894) used the term 'Dinocephalia' for *Delphinognathus* (Seeley 1892) and *Tapinocephalus* (Owen 1876), they were placed in the order Anomodontia. Broom (1905a,b) upgraded the taxon to the order Dinocephalia and described a tapinocephalid *Pelosuchus.* In following years Broom (1911, 1912, 1914) added three more genera, *Moschops, Taurops* and *Moschognathus* to the group. Watson (1914) revised the Dinocephalia and recognized the following genera: *Pnigalion, Mormosaurus, Lamiosaurus.* Later, Haughton (1915a,b) added the genera *Struthiocephalus* and *Moschosaurus* to the Dinocephalia. Broom (1923) recognized the suborders Titanosuchia and Tapinocephalia. Gregory (1926) proposed three subfamilies for the South African tapinocephalid dinocephalians, namely Moschosaurinae (including *Moschosaurus*), Moschopinae (including *Delphinognathus, Moschops, Moschognathus, Taurops, Pnigalion* and *Lamiasaurus*) and Tapinocephalinae (*Tapinocephalus, Mormosaurus* and *Struthiocephalus*). Later, three new genera, *Taurocephalus* (Broom 1928), *Criocephalus* (Broom 1928) and *Keratocephalus* (von Huene 1931), were assigned to the taxon. Boonstra (1936) reconsidered the taxonomy of South African tapinocephalids and elevated Gregory's (1926) subfamilies to family level and also added one more subfamily as follows: Moschosauridae (including *Moschosaurus*), Moschopidae (including *Delphinognathus, Moschops, Moschognathus, Pnigalion* and *Lamiosaurus*), Tapinocephalidae (*Tapinocephalus, Taurops* and *Keratocephalus*) and Mormosauridae (*Mormosaurus, Taurocephalus* and *Struthiocephalus*).

After a detailed revision of dinocephalian taxonomy, Boonstra (1969) further synonomised the following genera: *Taurops* and *Moschognathus* with *Tapinocephalus* and *Moschops; Pnigalion* with *Moschops*; *Moschosaurus* with *Struthiocephalus*; *Pelosuchus* with *Keratocephalus,* and included *Lamiosaurus* in titanosuchids. This new taxonomy included the latest founded new genera *Avenantia* (Boonstra 1952a), *Riebeeckosaurus* (Boonstra 1952c), *Struthiocephaloides* (Boonstra 1952d) and a new subfamily to Gregory (1926), while discarding its taxon Moschosauridae after synonymizing *Moschosaurus* with *Struthiocephalus.* Boonstra (1969) grouped South African tapinocephalids in four subfamilies; Struthiocephalinae (including *Struthiocephalus, Struthiocephalellus, Struthionops* and *Taurocephalus*), Moschopinae (including *Moschops, Delphinognathus, Avenantia*), Tapinocephalinae (including *Tapinocephalus, Mormosaurus, Phocosaurus* and *Keratocephalus*) and Riebeeckosaurinae (*Riebeeckosaurus*), on the basis of the degree of pachyostosis and the length of the snout. Subfamilies Struthiocephalinae and Riebeeckosaurinae included taxa having long snouts. However, Riebeeckosaurinae is represented only by *Riebeeckosaurus* (Boonstra 1952b), which does not have preserved snout. Genera comprising the subfamilies *Moschopinae* and *Tapinocephalinae* are all considered to have short snouts. However the moschopin *Avenantia* has no preserved snout. The original descriptions of the tapinocephalin *Tapinocephalus* (Owen 1876) and *Phocosaurus* (Seeley 1888) are based mainly on postcranial material Boonstra (1955a, 1956). The associated cranial material of *Phocosaurus* was known only much later (Boonstra 1956). The holotype material of *Phocosaurus* (Seeley 1888) was first described as *Pareiasaurus* by Owen (1876a), and was later referred to *Tapinocephalus* by Lydekker (1890). Watson (1914) referred it again to *Phocosaurus.*

King (1988, p. 10) included genera in the subfamilies Tapinocephalinae and Moschopinae into the tribe Tapinocephalini, considering that 'pachyostosis as a character is variable within the subfamily and not a foolproof guide to relationship'. She considered tapinocephalid dinocephalians in three tribes without any synonymization as follows: Struthiocephalini, Tapinocephalini, Riebeeckocephalini. Because she considered *Struthionops* to be short-snouted, King (1988) assigned it to the tribe Tapinocephalini rather than Struthiocephalini. This taxonomy also includes the only Russian tapinocephalid, *Ulemosaurus,* also in the tribe Tapinocephalini.

Tchudinov (1983) considered two groups of Dinocephalia, Titanosuchia and Tapinocephalia, the last including Tapinocephalidae as the only family. In this taxonomy *Ulemosaurus* (Riabinin 1938) was assigned to genus *Moschops* (Tatarinov 1965; Tchudinov 1983), which was previously considered to be closely related to *Moschops*

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Table 1. Currently recognized tapinocephalid dinocephalian genera listed according to date of description.

Genus	Species	Synonym	Institution* housing holotype	Institution* housing referred specimens
Tapinocephalus	*Tapinocephalus atherstonei* Owen, 1876	*Taurops macrodon* Broom, 1912	AMNH	SAM, TM, BPI
Delphinognathus	*Delphinognathus conocephalus* Seeley, 1892		SAM	AMNH
Phocosaurus	*Phocosaurus megischion* Seeley, 1888		BMNH	SAM
Moschops	*Moschops capensis* Broom, 1911 *Moschops koupensis* Boonstra, 1957 *Moschops whaitsi* (Broom, 1914) Boonstra 1969 *Moschops oweni* (Watson, 1914) Boonstra 1969	*Moschognathus whaitsi* Broom, 1914 *Pnigalion oweni* Watson, 1914 *Moschoides romeri* Bryne,1937 *Agnosaurus pienaari* Boonstra, 1952b	AMNH, SAM	SAM, BPI
Mormosaurus	*Mormosaurus seeleyi* Watson, 1914		BMNH	SAM
Struthiocephalus	*Struthiocephalus whaitsi* Haughton, 1915a	*Struthiocephalellus* Boonstra, 1955b *Moschosaurus longicesps* Haughton, 1915b *Struthiocephalus kitchingi* Brink, 1957 *Struthiocephalus milleri* Olson &Broom, 1937 *Struthiocephalus rheederi* Broom, 1937 *Struthiocephalus akraalensis* Boonstra, 1952e	SAM, FMNH	SAM, BPI
Taurocephalus	*Taurocephalus lerouxi* Broom, 1928		AMNH	
Criocephalus	*Criocephalus* Broom, 1928		KM	SAM
Keratocephalus	*Keratocephalus moloch* von Huene, 1931	*Pelosuchus priscus* Broom, 1905b	UT	SAM
Ulemosaurus	*Ulemosaurus svijagensis* Riabinin, 1938		PIN	
Struthiocephaloides	*Struthiocephaloides cavifrons* Boonstra, 1952f		SAM	
Struthionops	*Struthionops intermedius* Boonstra, 1952g		SAM	
Avenantia	*Avenantia kruisvleiensis* Boonstra, 1952		SAM	SAM
Riebeeckosaurus	*Riebeeckosaurus longirostris* Boonstra, 1952		SAM	
Tapinocaninus	*Tapinocaninus pamelae* Rubidge, 1991		NMQR	ROZ K

*Institutional abbreviations: AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London; BPI, Bernard Price Institute for Palaeontology, Johannesburg; FMNH, Field Museum of Natural History, Chicago; KM, McGregor Museum, Kimberley; PIN, The Museum of the Paleontological Institute of the Russian Academy of Sciences, Moscow; SAM, Iziko South African Museum; NM, National History Museum, Bloemfontein; UT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen; ROZ K, Roy Oosthuizen; TM, Transvaal Museum, Pretoria.

(Riabinin 1938; Efremov 1940). Ivakhnenko (1994, 2003) later placed *Ulemosaurus* in a new family, Ulemosauridae, together with the South African genus *Tapinocaninus* (Rubidge 1991). The latter genus, based on five skulls, is considered the most basal tapinocephalid (Rubidge 1991).

Recent studies on the stratigraphic ranges of tetrapod taxa in the Beaufort Group have revealed a large number of genera of tapinocephalid dinocephalians (all considered to be herbivores) in the *Tapinocephalus* Assemblage Zone relative to the number of herbivorous genera from any other assemblage zones of the Beaufort Group (Nicolas 2007; Rubidge 1995). This, together with the fact that most of the tapinocephalid genera are based on very fragmentary material and have not been researched for more than 30 years, is a clear indication of the necessity for a taxonomic revision of this group. Our preliminary assessment suggests that some of the holotypes are juvenile specimens, and that there is thus further synonymization in this chequered group are expected.

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Additional evidence of early hominid bone tools from South Africa. First attempt at exploring inter-site variability

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Introduction

There are four basic views of early hominid bone tool culture in South Africa: the first that there isn't one (Kuman 2005), the second that bone tools were used to extract tubers as part of a vegetarian dietary adaptation (Brain & Shipman 1993, 2004), the third that they were used mainly to forage for termites in mounds (Backwell & d'Errico 2001; d'Errico *et al.* 2001), and the fourth that they were involved in both tuber- and termite-digging activities (van Ryneveld 2003). The use of bone tools by early hominids was first proposed by Schmidtgen (1929). The idea was seconded by Breuil (1932, 1938) and Bastin (1932), and culminated in Dart's (1957) 'Osteodontokeratic culture of *Australopithecus'*. Later research contested the 'Osteodontokeratic' hypothesis (Klein 1975; Shipman & Phillips 1976; Maguire *et al.* 1980), citing evidence that hyaenas were more likely the modifiers and accumulators of bones in caves. This created scepticism as to whether early hominids truly used bone tools, but at the same time stimulated a wide range of research. Taphonomic studies have revealed that a number of natural processes can produce pseudo bone artefacts, for example vascular grooves have been shown to mimic cut marks (Shipman & Rose 1984) and engravings (d'Errico & Villa 1997), and some types of wear on teeth have been misinterpreted as carved notches (Gautier 1986). Other mimics include natural breakage and wear of deer antler (Olsen 1989) and elephant tusk tips (Haynes 1991; Villa & d'Errico 2001), gnawing or digestion by carnivores, rodents or herbivores (Pei 1938; Sutcliffe 1973, 1977; Binford 1981; Villa & Bartram 1996; d'Errico & Villa 1997), fracture for marrow extraction by hominids and carnivores (Bunn 1981, 1983; Gifford-Gonzalez 1989; Backwell & d'Errico 2004), trampling (Haynes 1988; Olsen & Shipman 1988), root etching (Binford 1981), weathering (Brain 1967), and the abrasive action of sediment (Brain 1981; Lyman 1994). In order to distinguish between pseudo and true tools it is necessary to adopt an interdisciplinary approach that combines analysis of bones modified by known agents, taphonomic analysis of the fossil assemblages from which the purported bone tools derive, microscopic studies of possible traces of manufacture and use, experimental replication of purported tools, and quantification of wear patterns. Our ongoing research on minimally modified bone tools has led to the development of a number of diagnostic criteria that provide a useful framework in which to assess new potential evidence.

Here we focus on the site of Drimolen, located 7 km north of Sterkfontein. Discovered by Keyser in 1992 (Keyser 2000a,b; Keyser *et al.* 2000), the Drimolen cave deposits are estimated to date to between 1.5 and 2 Mya, based mostly on faunal correlation with Swartkrans Member 1 (Brain 1993). Excavations have yielded 79 hominid specimens of which only two are firmly attributed to *Homo* sp. The remainder are attributed to *P. robustus* and nearly half of these are juveniles. Other large mammal taxa represented at the site include cercopithecines, carnivores and bovids (Keyser *et al.* 2000). There is an abundance of small to medium-sized bovids, and notable absence of suids and equids. Twenty-three bone fragments were earmarked in the field as possible bone tools, and of these 22 were made available for study.

Materials and methods

We previously examined 35 reference collections of bone modified by known non-human agents (hyaena, dog, leopard, cheetah, porcupine, river gravel, spring water, plain flooding, trampling) in search of mimics of modifications recorded on the Swartkrans specimens interpreted as bone tools (Backwell & d'Errico 2001, 2004). Bones from these collections was analysed at macro- and microscopic scale using optical and scanning electron microscopy. Research on the recognition of shaping techniques includes the reproduction and microscopic analysis of marks produced with different techniques and motions (d'Errico *et al.* 1984; d'Errico & Backwell 2003; Backwell & d'Errico 2004). We have also created and microscopically analysed a reference collection comprising experimentally manipulated, transported (d'Errico 1993a,b) and utilized bones (Backwell & d'Errico 2004). Our comparative collection was recently increased to include material from the open-air site of Kalkbank (Mason 1958), which has yielded a bone assemblage described by Dart & Kitching (1958) as containing Osteodontokeratic tools. In our analysis of this collection we focused on shaft fragments morphologically and dimensionally similar to those identified as bone tools from Swartkrans and Drimolen, and analysed them with the same procedures used for the Drimolen purported bone tools. The tips of the Drimolen specimens and 14 pieces from Kalkbank were moulded with Coltene President light body dental elastomer, and cast using Araldite M resin. All original specimens from Drimolen and transparent replicas of their tips, as well as the Kalkbank specimens were examined microscopically, and selected pieces photographed with a motorized multifocus microscope equipped with a digital camera.

Results

Microscopic analysis of the Drimolen specimens revealed that 14 of the 22 pieces analysed bear the same wear pattern recorded on the Sterkfontein and Swartkrans bone tools (Backwell 2000; Backwell & d'Errico 2001, 2008; d'Errico *et al.* 2001), namely a single smoothed end covered with individual striations confined to an average

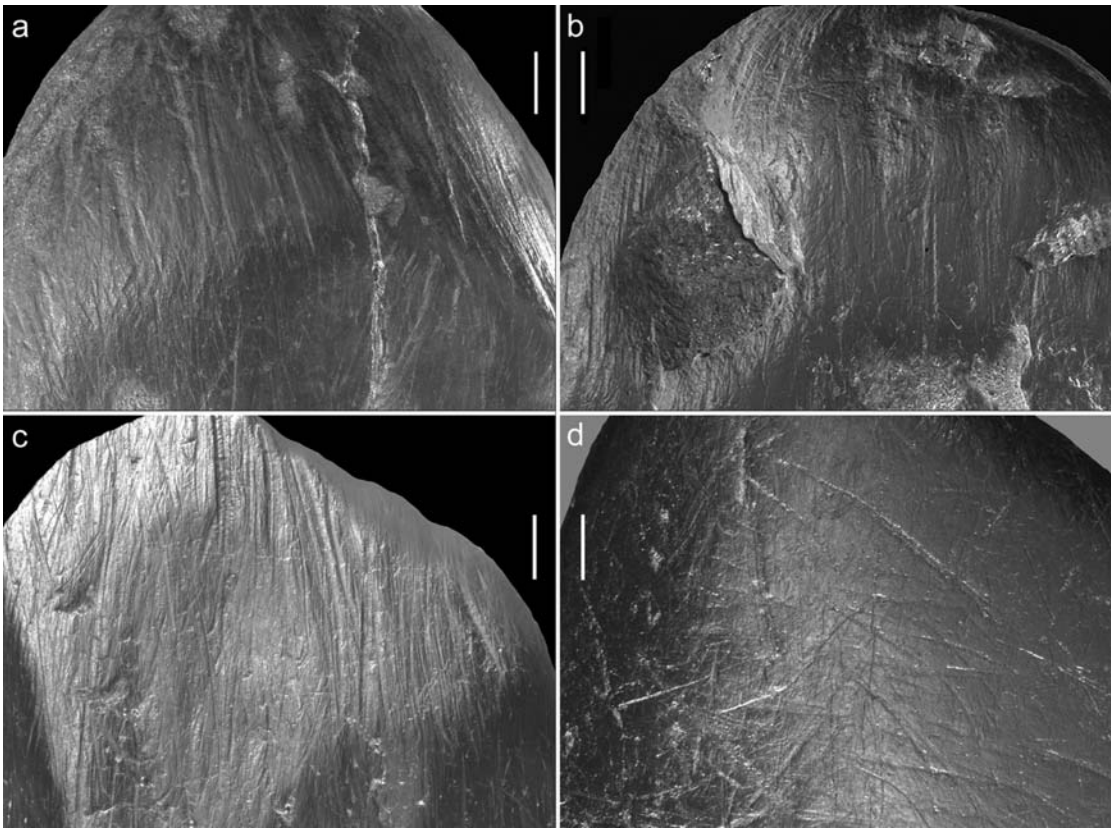


Figure 1. Transparent resin replicas of wear patterns on Swartkrans, Drimolen and experimental bone tool tips photographed in transmitted light. **a**, Bone tool from Swartkrans Member 2 (SKX 1142). **b**, Newly identified bone tool (DN 414) from the early hominid site of Drimolen showing rounded tip covered with longitudinal striations and flake scars smoothed by use wear. **c**, Experimental bone tool used to dig in a termite mound. **d**, Bone tool used in Brain's experiment to dig up *Scilla marginata* bulbs. Note the similarity in the orientation and width of the striations in (a), (b) and (c). Scale bars = 1 mm.

of *c.* 30 mm from the tip (Fig. 1). The pattern comprises striations oriented parallel or sub-parallel to the main axis of the object, decreasing in number away from the tip. A few striations oriented perpendicular to the main axis, generally posterior to the longitudinal parallel ones, are also recorded on some specimens. The eight Drimolen specimens interpreted as pseudo tools lack evidence of a wear pattern. Many shaft fragments from Kalkbank exhibit smoothing and rounding of the tips, but this generally extends over the entire piece. Microscopic analysis did not reveal a single piece from this site bearing the wear pattern observed on the Swartkrans and Drimolen bone tools. On the Drimolen specimens retained as tools we recorded the same variables as those taken on the 84 specimens from Swartkrans, and the single piece from Sterkfontein. These relate to mammal size class, type of bone used, fracture patterns, shape and size of the bone flake, including compact bone thickness and the length and position of the worn area, and orientation and position of striations on the worn tip.

At Sterkfontein and Swartkrans the tools derive mostly from mammal size classes II-III and III–IV. At Drimolen class III–IV is under-represented. The use of more robust bone fragments at Swartkrans is also reflected in the high number of fragments with a compact bone thickness in excess of 10 mm. As at Swartkrans, the large majority of Drimolen tools derive from long bone shaft fragments. The four exceptions – two mandible fragments, a rib and a horn core – are not unlike the trend observed at Swartkrans, where one mandible, seven ribs, and 14 horn cores out of 84 pieces were used as tools. The choice for weathered, elongated, straight bone flakes (as opposed to small spirally fractured fresh fragments) is also evident at Drimolen, where almost all the shaft fragments bear longitudinal breakage. As at Swartkrans, almost all Drimolen tools are represented only by their tips, which prevents analysis of intra- and inter-site length variation. However, analysis of the width and thickness of long pieces at 5, 10, 15 and 20 mm from the tip reveals a remarkable dimensional similarity between the three sites. The slightly more slender trend observed at Drimolen is in accordance with the low incidence of size class III–IV mammal shafts used as tools. The length of the worn area on the Drimolen specimens falls well within the range of that observed at Swartkrans, with the majority of the wear ranging between 20 and 40 mm. The lack of pieces with a very short or long worn area at Drimolen is most likely a function of the small sample size. At all three sites the occurrence and location of differently oriented striations shows an abundance of longitudinal relative to oblique, and rarity of transverse striations. Microscopic inspection of the worn tips has highlighted another feature that parallels what we have observed at Swartkrans. The only horn core from Drimolen records an area close to the tip covered with parallel striations perpendicular to the main axis. These closely match those described on six horn cores from Swartkrans (d'Errico & Backwell 2003), interpreted as possible evidence of grinding, for the purpose of

re-sharpening the functional area of the tool. Finally, among the pieces interpreted as bone tools, two have punctures probably produced by small carnivores and one piece shows damage consisting of shallow grooves reminiscent of porcupine gnawing. Carnivore damage is recorded on one of the bone tools from Swartkrans (d'Errico & Backwell 2003), where it is quite clearly covered with use-wear.

Discussion and conclusion

Besides the wear pattern, the Drimolen bone tools exhibit a number of features similar to those recorded on the Sterkfontein and Swartkrans bone tools. The only difference being the rarity of very robust pieces at Drimolen. This may be due to the small size of the sample, different availability of weathered shaft fragments, or a preference for slightly smaller fragments at Drimolen. Limited availability of large bone is supported by the few very large mammals reported for this site, but a preference for smaller bone tools is not supported, as indicated by the strong similarity in tool tip morphometry between sites, in spite of the use of thinner blanks at Drimolen. This may be clarified in future, when results of taphonomic analysis of the faunal assemblage from this site become available. More detailed contextual information may also elucidate why, in three instances, bone tools have been found in very close proximity, and why others cluster in a 4 m^2 area, within a 50 cm depth of each other. Spatial analysis of hominid and other mammal remains, bone and possible stone tools, is also required to help address the question of who used the Drimolen bone tools. The association of a high number of *Paranthropus* remains with bone tools, and the recovery of only two stone tools at Drimolen supports the hypothesis, first proposed by Brain & Shipman (1993) and followed by us (2001, 2003), that *P. robustus* may have used the South African bone tools. Based on the female aggregation practices present in chimpanzees and gorillas, and the fact that both are proposed as models for early hominid cultural and social behaviour (d'Errico *et al.* 2001; Lockwood *et al.* 2007), we hypothesize that if *P. robustus* was the user of the bone tools, the foraging activity in which they were used was conducted mainly by females.

The absence of knapped bone flakes in South Africa, and of digging implements in East Africa, lends support to the hypothesis that two distinct bone tool traditions existed in Africa between 1 and 2 Mya (Backwell & d'Errico 2004), either as variations of a single species behaviour (*Homo erectus*), or due to manufacture by different hominid taxa (*H. erectus* and *P. robustus*). Considering that only a single piece is reported from Sterkfontein, this hypothesis is based on the findings from only two sites, Swartkrans and Olduvai. The existence of an additional South African Plio-Pleistocene site yielding the same type of bone tools as those from Swartkrans demonstrates that the Swartkrans bone tools are not an isolated case, and that the digging activity in which they were used, which we posit was mainly termite foraging, was relatively widespread and well established in the region. Based on available information on fauna, geochronology and site formation processes at Swartkrans and Drimolen (Vrba 1982; Brain 1993; Watson 1993; Turner 1997; Keyser *et al.* 2000; Curnoe *et al.* 2001; de Ruiter 2003), this cultural tradition lasted unchanged for at least 300 000 and possibly as long as one million years.

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Tetrapod burrows in the southwestern main Karoo Basin (Lower Katberg Formation, Beaufort Group), South Africa

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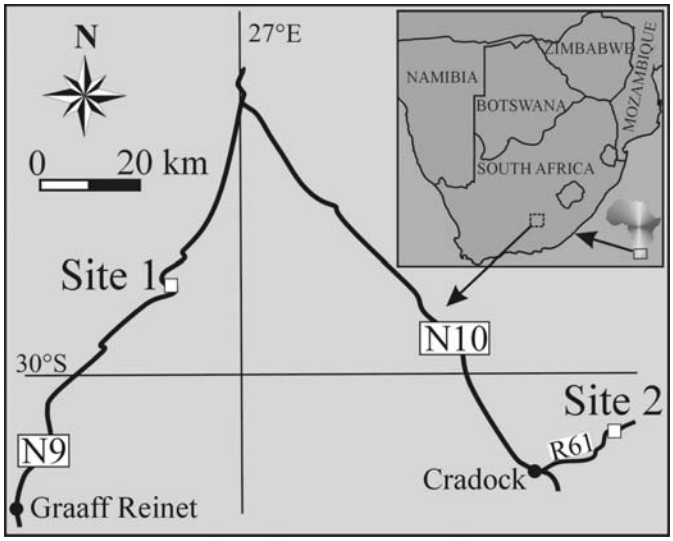


Figure 1. Locality map showing the two study sites in the Eastern Cape (South Africa). Site 1 (GPS 31°50′39.30″S, 24°52′15.54″E) is situated along the N9 national road, some 90 km from Site 2 (GPS 32°6′18.12″S, 25°47′42.78″E) which is found along road R61.

Introduction

Large, cylindrical, inclined tetrapod burrows are preserved in two stratigraphic zones immediately above of the Permo-Triassic (P/T) boundary as well as ~100–110 m above it in the southern main Karoo Basin (Eastern Cape, South Africa) (Fig. 1). Considering that the P/T boundary event is regarded as the most dramatic mass extinction in the Earth's Phanerozoic history, not only the environmental conditions that lead to it, but also those that followed this mass extinction and resulted in the Early Triassic biodiversity recovery, are of prime interest (Smith & Botha 2005).

Analysing the morphology and stratigraphic distribution of these burrows and associated sedimentary facies may improve (a) the understanding of the ethological reasons of the burrow making at and shortly after the P/T boundary event; as well as (b) the interpretation of the Early Triassic palaeoenvironment in the southwestern Karoo Basin. Some of these large, cylindrical burrows, especially those that are directly above the P/T boundary, have been mentioned (Retallack *et al.* 2003; Botha & Smith 2007a,b), but their morphology has never been described in detail. In this contribution, we document some of these large cylindrical burrows and consider their significance as environmental indicators in the Early Triassic of the main Karoo Basin.

The Katberg Formation

The described burrows are found in sandstones and siltstones of the Katberg Formation (Lower Triassic, Beaufort Group, Karoo Supergroup), at two localities situated some ~90 km apart (Fig. 1). The burrows are located at ~70 m from the base of the formation at Site 1 and ~45 m at Site 2, and in both sites, ~100–110 m above the P/T boundary, representing a sedimentary record of ~1 Ma in duration (Griesbachian to early Dienerian) (Ward *et al.* 2005; Szurlies 2007).

In the southern Karoo, the Katberg Formation is characterized by multistoried, fine- to medium-grained sandstones and mudstones (Fig. 2). The architecture of the sandstone stories shows lateral to downstream accretion of channel forms and bars. The accretionary surfaces are associated with channel lags overlain by intraformational mud-pebble and calcareous-nodule conglomerates. Main sedimentary structures in the sandstones include horizontal lamination, parting lineations, cross-bedding, soft-sediment deformations and massive beds with well-developed sole marks (Fig. 3). Mudstone intervals are either horizontally bedded with millimetre- to centimetre-thick intercalations of very fine sandstones or characterized by remnant horizontal bedding that alternates with irregular patches of sandy-clayey siltstones. The mudstones contain shallow and smooth erosional surfaces, as well as laterally traceable surfaces marked by sand-filled desiccation cracks at several levels (Fig. 4). These features are in agreement with previous palaeoenvironmental interpretations of the Katberg Formation that suggested a relatively high energy braided fluvial setting under relatively warm, dry climatic conditions (SACS 1980; Hiller & Stavrakis 1984).

Observations

Burrows consist of inclined shafts with a single opening that leads to a subhorizontal, rounded terminus (Fig. 5A, B,C,D). Burrow diameter range from ~25 to ~40 cm, with an average of ~30–35 cm. Individual burrow diameters are fairly consistent along the length of the burrow, and only very rarely seem to slightly taper downward (to an apparent minimum diameter of ~12 cm). Chambers or other enlargements are absent, and while the burrow terminus is rounded, it does not form a terminal chamber as it has the same diameter as the burrow itself. Cross-sectional burrow shape is circular-to-subcircular, and medial ridge in the burrow floor is absent.

These simple burrows are non-branching, non-connected, non-cross-cutting, and lack evidence for any coiling or spiralling, however may curve gently in any direction in the level of the terminus. Burrows descend at an angle of ~30° before levelling out in the rounded terminus. Burrow axis may have a deviation of up to 5°, but show no change in the inclination with depth. Preserved burrow lengths range from 0.5 m to greater than 3 m; maximum vertical depth is 1.5 m (average ~1 m, minimum 0.5 m).



Figure 2. Road-cutting in the Lower Triassic of Katberg Formation showing extended tabular sandstones and vertically accreted mudstones (siltstones and claystones). Person for scale.

Burrow sides and bases are well-defined as the massive and lithologically distinct burrow fill contrasts the lithology of the surrounding beds. These inclined structures are particularly apparent where they obliquely truncate the stratification of the host rocks (Fig. 5A,B,C).

Burrow fills are invariably unstratified (massive), and consist of coarse silt, very fine- to fine-grained sandstone and locally poorly-sorted, fine-grained claystone parabreccias. In spite of careful inspection, bone material has not been identified in the fill of the burrows. Burrow fills are surrounded by a <5 mm thin clay lining which in cross-section consists of packed clay flakes parallel to the burrow wall (and at high angle to the stratification in the host sediment).

The outer burrow walls are generally smooth with rare and subtle indentations of a few cm. Burrow walls are often covered by well-preserved transverse and longitudinal scratch marks which seem to be higher in density in the side of the burrow walls (Fig. 6A,B). The most common scratch marks are elongated triangular ridges (replicas of grooves) on the outer burrow wall with their long axis roughly perpendicular to the axis of the burrow.

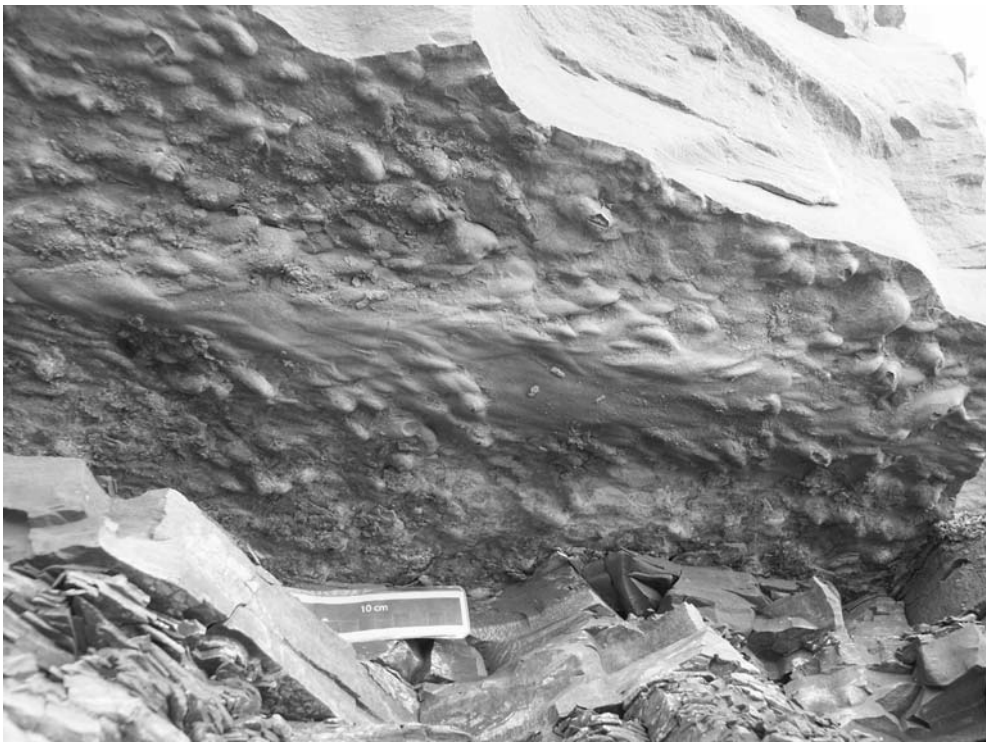


Figure 3. Sole marks at the base of medium-grained sandstones are most commonly flute marks and gutter casts. Scale in centimetres.



Figure 4. Mudstones both within and between the multistorey sandstones often contain desiccation cracks of up to 50 cm in depth. Person for scale.

Interpretation

Based on comparisons to fossil and modern burrows (e.g. Hasiotis *et al.* 1999; Groenewald *et al.* 2001; Miller *et al.* 2001; Damiani *et al.* 2003; Sidor *et al.* 2008), these structures are interpreted as burrows of vertebrates with fully or partly fossorial life style. The burrow morphology, in particular the uniform burrow diameter and lack of terminal chamber may suggest a reverse mode of excavation and that the burrow probably functioned as resting, hiding, aestivating shelter, and unlikely as a permanent dwelling, breeding or nesting structure.

Preservation of the burrows and scratch marks on their

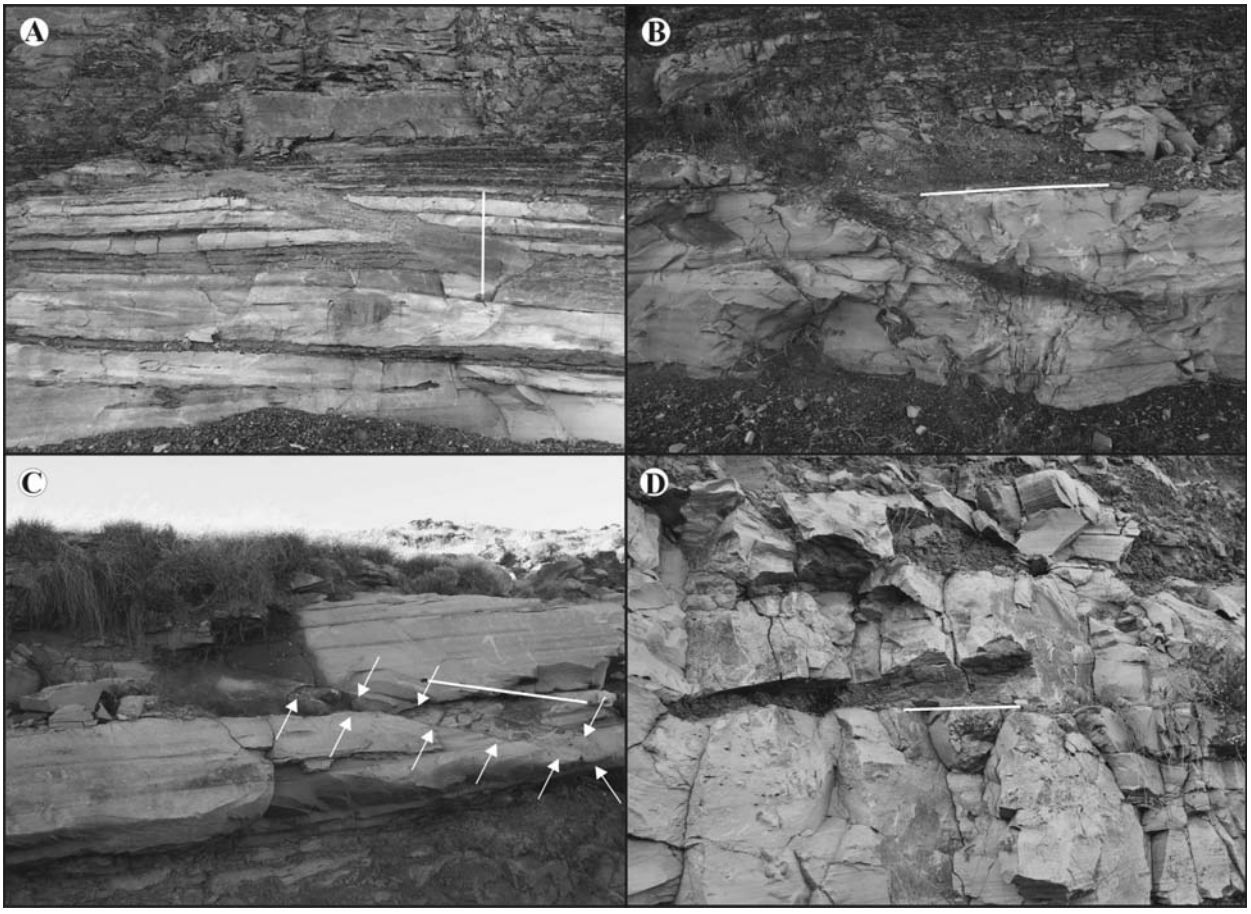


Figure 5. Large-diameter, low-angle inclined trace fossils in the lowermost Triassic Katberg Formation interpreted as subterranean therapsida burrows. Scale tape measure = 1 m in A, B, C and 0.5 m in D.

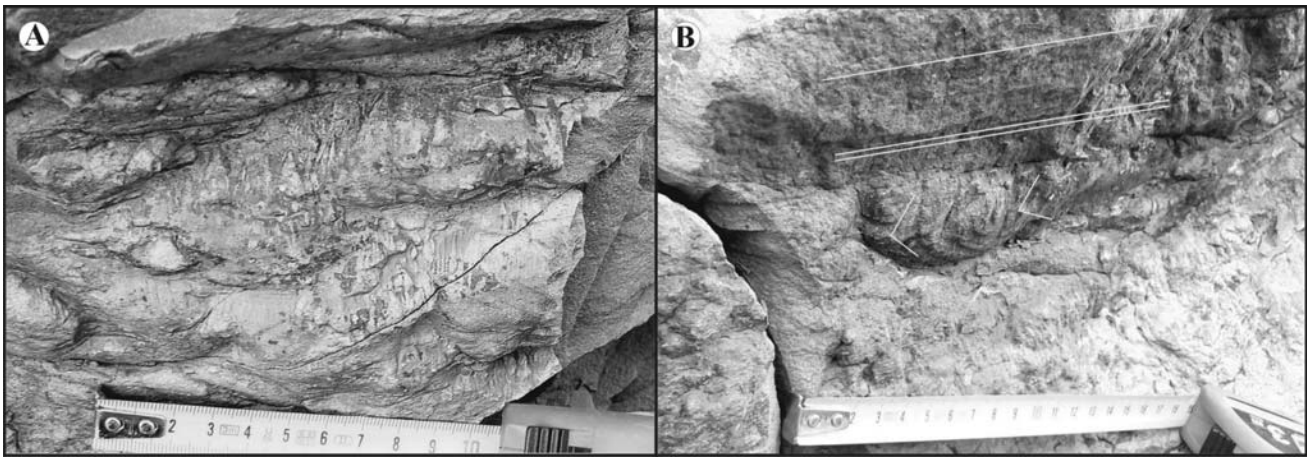


Figure 6. Vertical, triangular (**A**) and horizontal (**B**) scratch marks on burrow surfaces. Scale in centimetres.

outer burrow wall as well as absence of any deflected or offset laminae in the surrounding sediments suggest that the host medium was sufficiently firm to prevent the deformation of host strata or caving in of the open burrow, but moist enough to preserve scratch marks. Clay lining may indicate that the animals plastered their burrow internally, probably not only to reinforce the structure, but maybe also to slow dehydration of burrow, creating a buffered, sheltered (insulated) microenvironment at depths where daily temperature variations were less significant. Constructed burrow linings, massive burrow fill of sandstone and/or claystone parabreccias and lack of evidence for active backfilling (e.g. internal menisci) show that these lined structures were open burrows which were subsequently and passively filled in by probably in relatively high energy, rapid mass movement deposits.

Structures on the outer burrow wall record methods of excavation, and they indicate that penetration into the substrate occurred by scraping of the host sediment. The triangular ridge-like impressions on the outer burrow wall suggest a trace-maker animal with pointy claws and/or specialized beak or teeth with spikes of 2–3 mm terminus size for scratch digging. The orientation of scratch marks, and the apex of the scratch triangles pointing away from the direction of scratching movement collectively imply that excavation occurred sideways in a mostly downward direction within the burrow.

Possible tracemakers

Current palaeontological studies (e.g. Smith & Botha 2005; Botha & Smith 2007a,b; Abdala *et al.* 2006) suggest that in the Earliest Triassic of the main Karoo Basin, taxa including dicynodonts (*Lystrosaurus murrayi, L. declivis*) and cynodonts (e.g. *Thrinaxodon liorhinus, Galesaurus, Progalesaurus*), show features and preservational conditions congruent with fossorial lifestyle. Among these, prime burrow-maker candidates, however, remain *L. murrayi* and *L. declivis* not only based on their size, relative abundance and physiological adaptations (e.g. significant bone wall thickness, spatulate structure of the claws), but also due to fact that several of their articulated skeletons were found *in situ* in large, scratched, but undescribed burrows (Retallack *et al.* 2003). However, the lack of associated bone material within the structures described here only permits their attribution to mammal-like therapsids that possibly produced these structures to escape surface environmental conditions, which based on the associated sedimentary structures (e.g. high abundance of very large desiccation cracks) were, at least episodically, extremely hot.

Conclusion

In summary, these newly described structures are considered here possibly therapsid burrows that have been constructed as shelters to generate a microenvironment which allowed their occupants to extend the limits of their habitat under extreme ecological conditions characterized by lack of water and possibly episodic high temperatures. This is in agreement with previous suggestions (e.g. Smith 1987; Groenewald *et al.* 2001; Damiani *et al.* 2003; Retallack *et al.* 2003; Abdala *et al.* 2006; Botha & Smith 2007a,b) that large vertebrate burrows in the Earliest Triassic of South Africa assisted the tracemakers in surviving the harsh environmental conditions associated with the P/T mass extinction. The stratigraphic reoccurrence of these vertebrate burrows in spatially separated, but coeval sites in the South Africa, at some 100–110 m above the P/T boundary, may suggest that harsh environmental conditions have persisted at least on a semi-regional scale and reoccurred shortly after the P/T mass extinction event.

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Nodular preservation of trilobite fossils from the Bokkeveld Group, Eastern Cape Province, South Africa

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Introduction

Invertebrate fossils and fossiliferous nodules within the Bokkeveld Group (Cape Supergroup) were recorded in the Cederberg area from the early nineteenth century (Rogers 1937; Cooper 1982; Theron 1972; MacRae 1999). These fossils have since been collected and described from various other localities within the Cape Fold Belt (Johnson 1976; MacRae 1999; Oosthuizen 1984).

The preservation of fossils within the Bokkeveld varies greatly. In general, specimens are better preserved within nodules compared with the surrounding shales, which reflects the early diagenetic origin of these nodules (Theron & Johnson 1991). Some nodules have been known to contain very well preserved invertebrate fossils (Theron 1972; Oosthuizen 1984), many of which are described as type specimens. Although preservation of fossil material as moulds predominates (Oosthuizen 1984), some original skeletal material in the form of phosphatic inarticulate brachiopods is preserved (Almond 2005). Rare preservation of skeletal carbonate is known from accumulations of shelly debris (*op cit.*). Studies on the original mineralogy of trilobite exoskeletons have shown that these are usually composed of calcite (Wilmot & Fallick). Fresh fossil samples often display pyritic encrustations (Theron 1999). Within the Bokkeveld the composition of trilobite fossil material specifically has not been studied. Also, very little attention has been paid to the nodular structures themselves and to possible reasons for better preservation of fossils within them compared to within the surrounding shales. The following short note aims to highlight some macro- and micro-structural and mineralogical differences between trilobite material found within shales and nodules.

The lower Bokkeveld shales were deposited on a storm-influenced clastic shoreline controlled by cyclical eustatic sea-level fluctuations (Cooper 1982; Broquet 1992; Cotter 2000). These lithologies were subjected to advanced stages of diagenesis grading into low grade metamorphism (de Swardt & Rowsell 1974). Nodular structures within them are considered to be early diagenetic in origin (Theron 1972).

Materials and methods

Nodules were collected from the Gydo Formation, within the Ceres Sub-group, at various localities in the Cockscomb/Steytlerville area. Where possible, nodules were collected in situ and their GPS locations were taken (see Browning 2009). Some limitations of this study should be noted from the outset. In the absence of equipment needed for detailed chemical and isotope analysis, it was decided to adopt a different approach to nodule examination. Limited chemical analysis in the form of XRD (X-ray diffraction) was carried out on the central regions of both nodules and shale. However the majority of the work entailed petrographic analysis of thin sections, together with careful observations and photography of macro-structural features and field observations.

Results

Macro-structure

The nodules are clearly more resistant to weathering than the surrounding shales in which they occur. They are typically spheroidal, ranging from oblate to prolate in form, and range in size from 30–130 mm (long axis). Nodule shape is controlled by that of the enclosed organic remains in 40% of nodules, while the shapes of the remaining nodules are not influenced by enclosed organic remains (Browning 2009). Nodular cross-sections usually reveal a series of colouration zones which mimic their roughly circular to elliptical shape. These colouration zones indicate that the nodules are weathered and vary from burnt orange to deep purple-maroon. Fossil material within nodules varies but is usually dark grey in colour (Fig. 1). Fossil material within shales also varies but is typically burnt orange in colour and often associated with the growth of fine mica (sericite?) crystals.

X-ray diffraction (XRD)

The XRD results obtained from the analysis of nodules and host shales are presented in Table 1. On average the shales contained higher percentages of sericite compared to the nodules. The average nodule contains more quartz than the average shale does. The feldspar median percentages of shales and nodules are very similar.

The results obtained from the XRD analysis of selected nodules in the Western Cape (Cederberg) by Almond (1996), are shown in Table 2. Differences were noted in the chemistry of the nodules from the Western and Eastern Cape localities (Tables 1 & 2). These variances may be real or they may be an artefact of the degree of weathering. The most noticeable difference between Eastern and

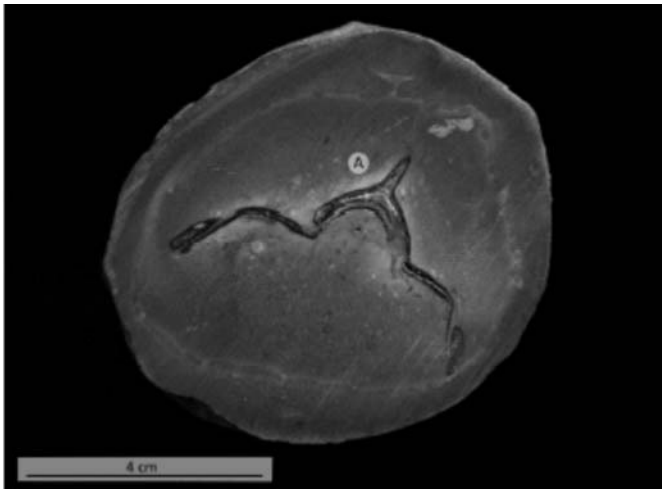


Figure 1. Macro-photograph of a transversely sliced surface of a nodule showing a cross-section through a trilobite carapace (A).

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Table 1. Preliminary XRD results showing the percentage of dominant minerals found within shales and nodules.

Sample no.	Seriate	Quartz	Chlorite	Feldspar
Nodule (5)	30	28	36	5
Nodule (017)	39	33	17	12
Nodule (03H)	12	63	26	n/d
Nodule median %	30	33	26	8.5
Shale 2	39	28	22	11
Shale 3	52	20	10	10
Shale median %	45.5	24	20	10.5

Western Cape nodules is the apatite content. Apatite is the dominant mineral recorded in the Western Cape nodules, while the Eastern Cape nodules did not contain any apatite (at least not within the detectable limits of the analysis). When the combined percentage of mica found within the Eastern and Western Cape samples is compared, the Eastern Cape nodules have higher percentages of mica. This suggests a greater degree of weathering in these nodules. The nodules of the Eastern Cape are enriched in quartz with respect to the Western Cape samples. A slightly higher percentage of quartz was recorded in Western Cape nodules containing trilobite remains, compared with the quartz content of the nodules that did not contain trilobite fragments. The Eastern Cape nodules contained an unidentified feldspar. The Western Cape samples contained feldspar that has been identified as plagioclase. Plagioclase has been identified in some Bokkeveld shales (de Swart & Rowsell, 1976). A high percentage of calcite was present in one Western Cape sample identified as a 'carbonate nodule'. Calcite was not identified in XRD analyses of the Eastern Cape samples.

Petrography

The minerals contained within trilobite carapaces in shales and nodules differ. Within nodules, quartz, together with some minor opaque minerals, is the only replacement mineral (Fig. 2). Within shales, the trilobite carapace material was composed of equal proportions of quartz, hematite and biotite (Fig. 3). Opaque minerals were also present as minor constituents. Hematite was found in the central portions of the carapace, while quartz and biotite dominate the outer portions of the carapace. Fossils found within nodules are generally more deformed towards the nodule margins than they are in the centre of the nodule.

Discussion

The colour zoning within nodules probably results from varying levels of oxidation of opaque and iron minerals within the nodule matrix. It appears that the presence of quartz within both the nodule structure and as a replacement of the trilobite carapace within the nodule, makes these structures more resistant to weathering than surrounding shales. These results could be clarified by the investigation of a wider variety of faunal groups as well as a more extensive chemical analysis of a range of nodules.

There are clearly differences in the nature of minerals which replace fossil material in the shales and within nodules. As previously stated, most fossil material within the Bokkeveld is preserved as moulds and casts. The direct replacement of trilobite carapaces by quartz is therefore unlikely. Quartz and other replacement minerals were more probably deposited later in the diagenetic process, as a secondary infilling of a mould. The presence of a gap in the axial ring and furrow regions of the carapace where the cuticle is thickest (Fig. 2) further supports

Table 2. XRD results for Western Cape nodules (Almond 2006).

Sample	Calcite	Apatite	Mica	Smectite	Quartz	Chlorite	Plagioclase
Orbiculoidea	n/d	59	9	5	24	4	n/d
Metaconularia	n/d	68	5	n/d	21	5	n/d
Shelly remains	n/d	58	10	10	19	3	n/d
Trilobite concretion	n/d	55	7	2	29	6	n/d
'Carbonate' nodule	68	n/d	8	n/d	9	13	3
Median %	68	59	7.5	5	22.5	5	3

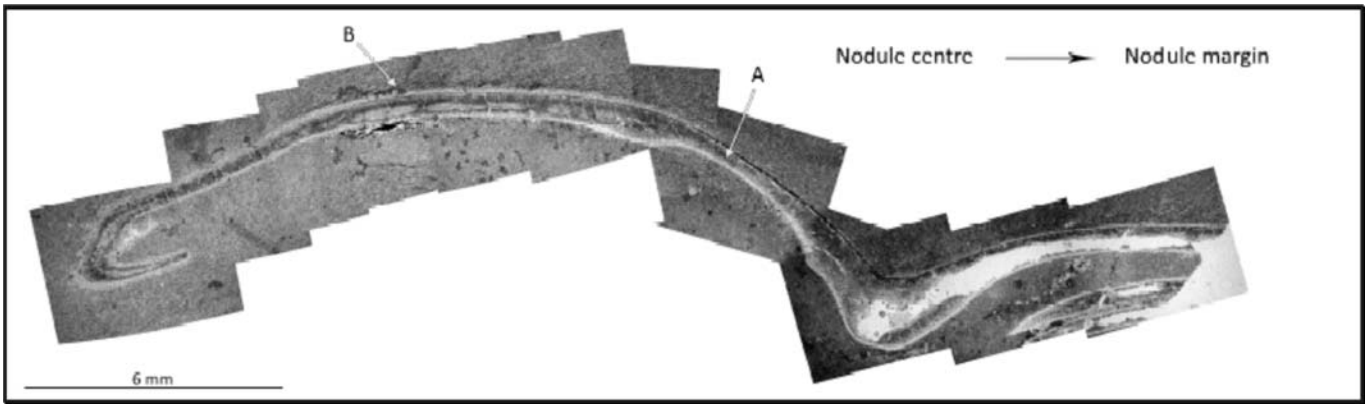


Figure 2. A photomicrograph composite composed of various images of a transverse section through a single thoracic tergite of a trilobite within a nodule. Quartz is the dominant replacement mineral (A). The images were taken under plane polarized light. Note the excellent preservation of the carapace and the formation of cleavage near the upper surface of the fossil (B).

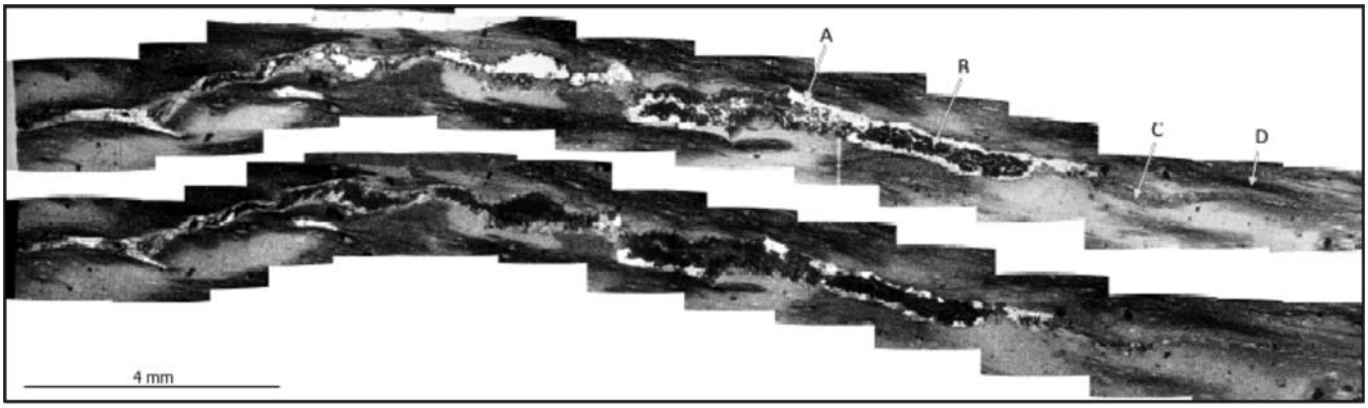


Figure 3. A photo-composite image composed of photomicrographs taken of a longitudinal section through successive thoracic tergites of a trilobite carapace within shale. The upper composite was taken under plane polarized light while the lower one was taken under cross-polarized light. The general shape of the carapace can still be seen although deformation is evident. Minerals within the carapace include quartz (A), hematite (B) and biotite (C). Minor amounts of other white micas are found in association with biotite. Biotite seems to develop preferentially at the thinner margins of the fossil. Hematite is mostly found in the central portions of the carapace and generally shows a close association with quartz. Cleavage can clearly be seen in the shale matrix surrounding the carapace (D). Cleavage intensity varies as do colouration zones within the shale.

this idea. Within the shales, the predominance of biotite in the outer regions of the carapace, suggests that this mineral initially coated the surfaces of the empty mould. This initial coating could then have been followed by the infilling of the remaining empty spaces by quartz and later haematite although these observations need to be confirmed by more extensive studies. The increase in deformation towards the nodule margins compared with the central regions implies nodule growth during compaction and supports the early diagenetic origin.

Nodules from the Cockscomb area are predominantly composed of quartz while nodules from some Western Cape localities (Almond 1996) within the same formation are mainly composed of apatite. The reasons for this variation along strike are not known. It is interesting to note, however, that similar compositional variations have been documented for nodules located in the Armorican Massif of France (Becq-Giraudon *et al.* 1992; Loi & Dabard 2002). The analysis of these 'French nodules' recorded variations in bulk quartz composition of between 40 and 85% and the quartz percentages presented were directly proportional to the apatite content within the nodules. Given this variation, the difference in bulk mineral composition between the Cockscomb and Western Cape nodules may simply reflect a natural variation and not imply vastly different diagenetic or depositional environments of formation.

Conclusion

Although preservation of invertebrate fossiliferous material is better within nodular structures, material within the shales of the Bokkeveld are not as deformed or poorly preserved as would be expected for lithologies subjected to the known levels of diagenesis and metamorphism. The reason for this appears to be mineralogical, with variations in both mineralogy and overall nodule composition being the main contributing factors. The composition of nodules analysed from the Western and Eastern Cape varied significantly. These findings need to be clarified with more detailed analysis of general as well as isotope chemistry.

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The early fossil record of perching birds (Passeriformes)

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Introduction

The fossil record of the perching birds or passerines (Passeriformes) is very scarce and not well studied, but new discoveries and reinvestigations during the past few years supplement an earlier critical review by Olson (1985) and enable conclusions on the composition of Cenozoic passerine avifaunas. For a better understanding of the significance of the recent findings a short introduction of current hypotheses on the phylogeny of passerines is necessary. Passeriformes are an enormously diverse and species rich group comprising more than half of all the modern bird species described (Sibley & Ahlquist 1990; Schodde & Mason 1999). Monophyly of Passeriformes is well supported by several morphological characters (Raikow 1982), but the reconstruction of the phylogenetic relationships within this clade was only recently promoted by the application of DNA sequence analyses (Ericson *et al.* 2002a,b, 2003; Barker *et al.* 2002, 2004; Harshman *et al.* 2007). According to these studies, three major clades can be distinguished, i.e. Acanthisittidae, Oscines and Suboscines (Fig. 1).

The New Zealand wrens (Acanthisittidae) are restricted to New Zealand. Only two species of a more specious radiation survived to the present, but three additional species were described from late Pleistocene and early Holocene deposits in New Zealand (Millener 1988; Millener & Worthy 1991). Molecular-based analyses revealed that Acanthisittidae are the sister group of a clade comprising the Oscines and Suboscines (Ericson *et al.* 2002a; Barker *et al.* 2002) (Fig. 1). This particular clade was named Eupasseres by Ericson *et al.* (2003).

Suboscines have their centre of distribution in South and Central America. However, a few species of broadbills (Eurylaimidae) and pittas (Pittidae) inhabit the tropical and subtropical areas of the Old World. Surprisingly, Old World Suboscines have a representative overseas: *Sapayoa aenigma,* which occurs in the Chocó region of Panama, western Colombia and Ecuador, is not closely related to suboscine tyrant flycatchers of South America as previously thought, but turns out to be deeply nested within the broadbill clade (Fjeldså *et al.* 2003; Chesser 2004; Moyle *et al.* 2006).

The third major clade is that of the songbirds (Oscines). Several molecular based hypotheses suggest that this group originated in Australia (Barker *et al.* 2002, 2004; Ericson *et al.* 2002a), because several basal songbird groups are mainly restricted to Australia and New Guinea (Fig. 1). Although some of the Australian taxa might be misclassified according to more recent studies (e.g. Irestedt & Ohlsen 2008), the 'out of Australia' hypothesis gains strong support (see also Sibley & Ahlquist 1990; Schodde & Mason 1999). This is even more remarkable, because the Australian passerine avifauna was traditionally supposed as being solely composed by subsequent dispersals from Asia (Mayr 1944).

Gondwanan origin for Passeriformes?

The current DNA sequence-based phylogenetic hypotheses and the distribution of the major groups are considered to support the hypothesis of a Gondwanan origin of Passeriformes (Barker *et al.* 2002, 2004; Ericson *et al.* 2002). Thus the break-up of the southern continents in the late Cretaceous is proposed to have caused the separation of the three major passerine lineages. Ericson *et al.* (2002), for example, assumed that the lineage of Acanthisittidae became separated when New Zealand was split up from rest Gondwana, 82–85 My ago. A relation between the split-up of the Gondwanan continent during the Cretaceous and the diversification of passerines was also suggested by Cracraft (1973, 2001), Sibley & Ahlquist (1990) and Hedges *et al.* (1996), but these authors based their hypotheses on different data sets and on meanwhile outdated assumptions.

However, there is as yet no fossil evidence for crown group passerines prior to the early Eocene, implying a 30 My gap in the fossil record for passeriforms. Furthermore, the few and fragmentary passerine fossils known from the Eocene cannot be assigned to any of the three major passerine lineages (see below).

The early fossil record of Passeriformes

There is much evidence that previous records of passerines from the early Cenozoic were based on misidentifications. *Palaeospiza bella* was initially described as a primitive songbird from the late Eocene of the Florissant Beds (Wetmore 1925), but was recently identified as a stem-lineage representative of extant mousebirds (Coliidae) (Mayr 2001: 428; Ksepka & Clarke 2009). *Neanis schucherti* from the early Eocene of the Green River Formation is not a passerine as suggested earlier (Shufeldt 1913), but a representative of Gracilitarsidae. These tiny, zygodactyl and long-legged birds are probably stem-lineage representatives of woodpeckers, barbets, honeyguides and allies (Piciformes) (Mayr 2005a,b). Similarly, *Palaegithalus cuvieri* from the late Eocene of France is now referred to another zygodactyl group of stem-lineage Piciformes, the Sylphornithidae (Mayr 1998, 2005a).

Harrison & Walker (1977) described *Primoscens minutus* from the early Eocene of the London Clay as the earliest-known passerine bird (see also Harrison 1982), but comparisons with more complete specimens support its assignment to Zygodactylidae (Mayr 2004, 2008). Despite their zygodactyl toe arrangement – i.e. fourth toe pointing backwards, which is characteristic for Piciformes, Psittaciformes (parrots) and Cuculidae (cuckoos) – Zygodactylidae are now discussed as stem-lineage representatives of Passeriformes (Mayr 2004, 2008).

For the time being, the earliest fossil record for passerines

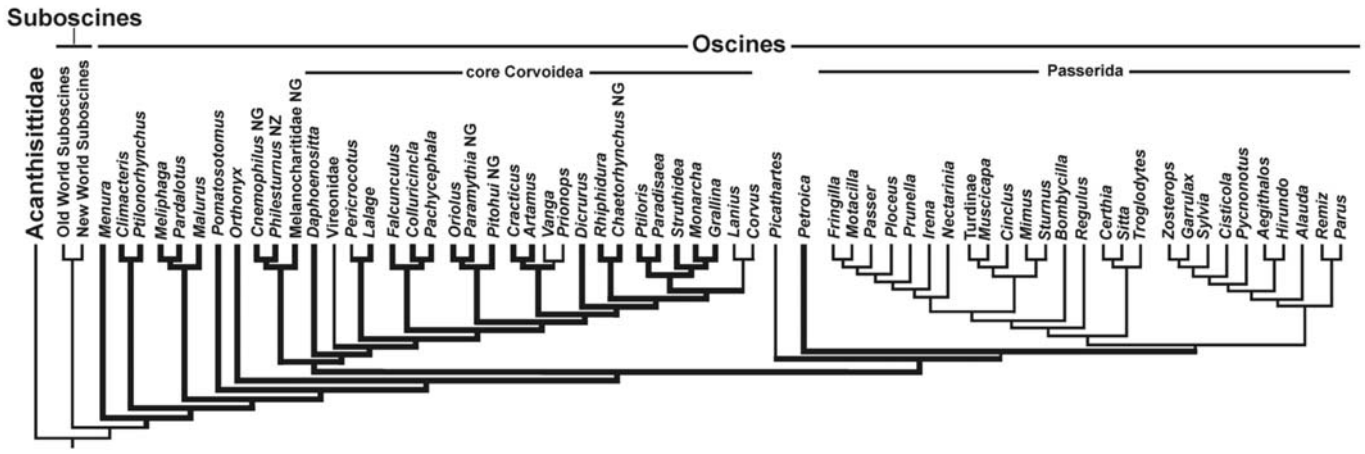


Figure 1. Phylogenetic relationships of Passeriformes based on the DNA-sequence analyses of Barker *et al.* (2004). Lineages of primarily Australian songbird taxa as well as a few taxa restricted to New Guinea (NG) and New Zealand (NZ) are highlighted in bold. Because all of the basal songbird taxa are restricted to or have their centre of distribution in the Australo-Papuan region, an Australian origin of Oscines seems evident. This hypothesis is not challenged by more recent analyses (e.g. Irestedt & Ohlsen 2008) that are in conflict with the branching pattern presented here.

dates from the early Eocene of Australia (Boles 1995a, 1997). It is based on a proximal carpometacarpus and two distal tibiotarsi discovered at Murgon, Queensland (Tingamara local fauna). The fragmentary nature of these specimens does not yet allow further phylogenetic assignments. Mayr (1998) and Louchart (in litt.) call attention to the fact that the fossils in question remain to be compared with Zygodactylidae.

In the northern hemisphere, fossil passerines are unknown until the Oligocene. Not a single passerine has been identified among the numerous avian remains from Eocene fossil sites in Europe and North America, such as Messel Pit, London Clay, Quercy or Green River Formation (Mayr 2005a). Until recently, few fragmentary bones of songbirds and indeterminate passeriforms, respectively, from the late Oligocene of France rated as the earliest passerine record (Mourer-Chauviré *et al.* 1989, 2004). Meanwhile, these findings were complemented by new discoveries of fossils in France and Germany, which also indicate a more complex evolutionary history of passerines than previously thought.

An isolated cranium with lower jaw and an almost complete skeleton of a passerine were found in early Oligocene deposits of southern Germany, and described as *Wieslochia weissi* (Mayr & Manegold 2004, 2006a) (Fig. 2). These are the first associated remains of an early Cenozoic passerine

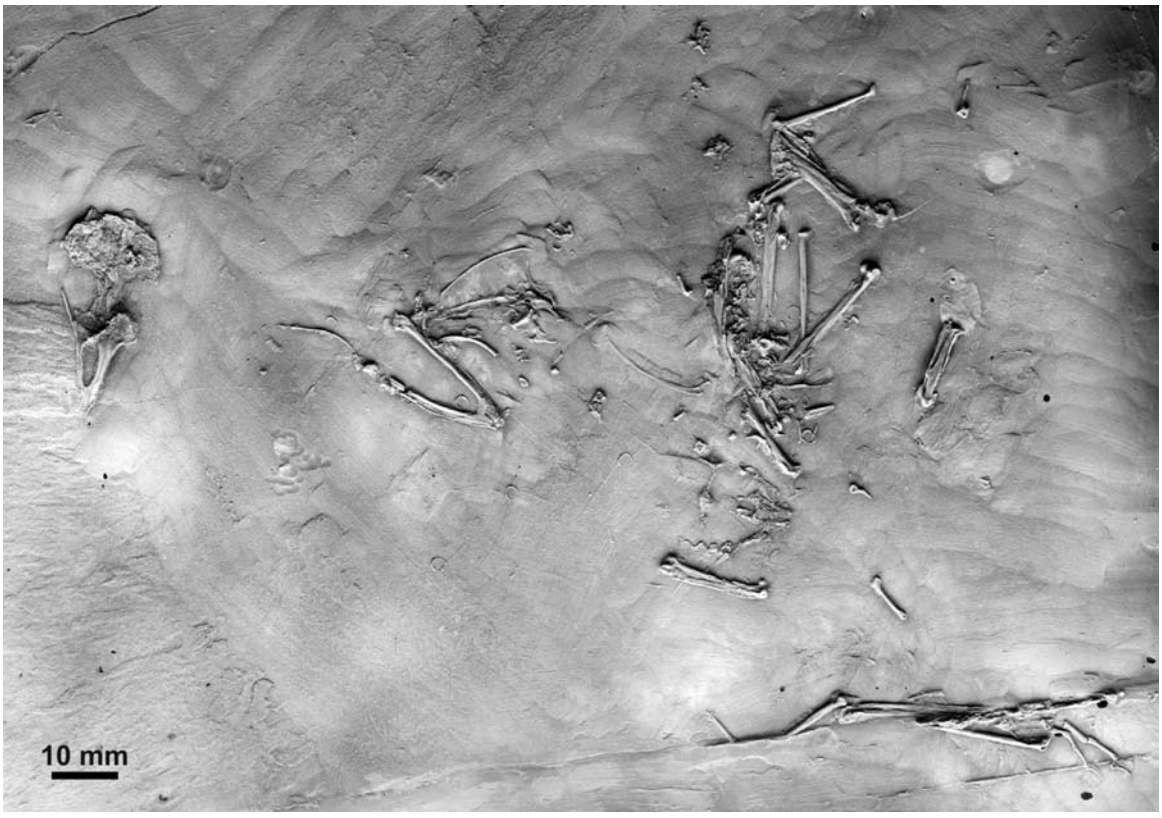


Figure 2. *Wieslochia weissi,* from the early Oligocene of Frauenweiler, Germany. It is to date the earliest record for Passeriformes in the northern hemisphere (Mayr & Manegold 2004, 2006a). Photograph by S. Tränkner.

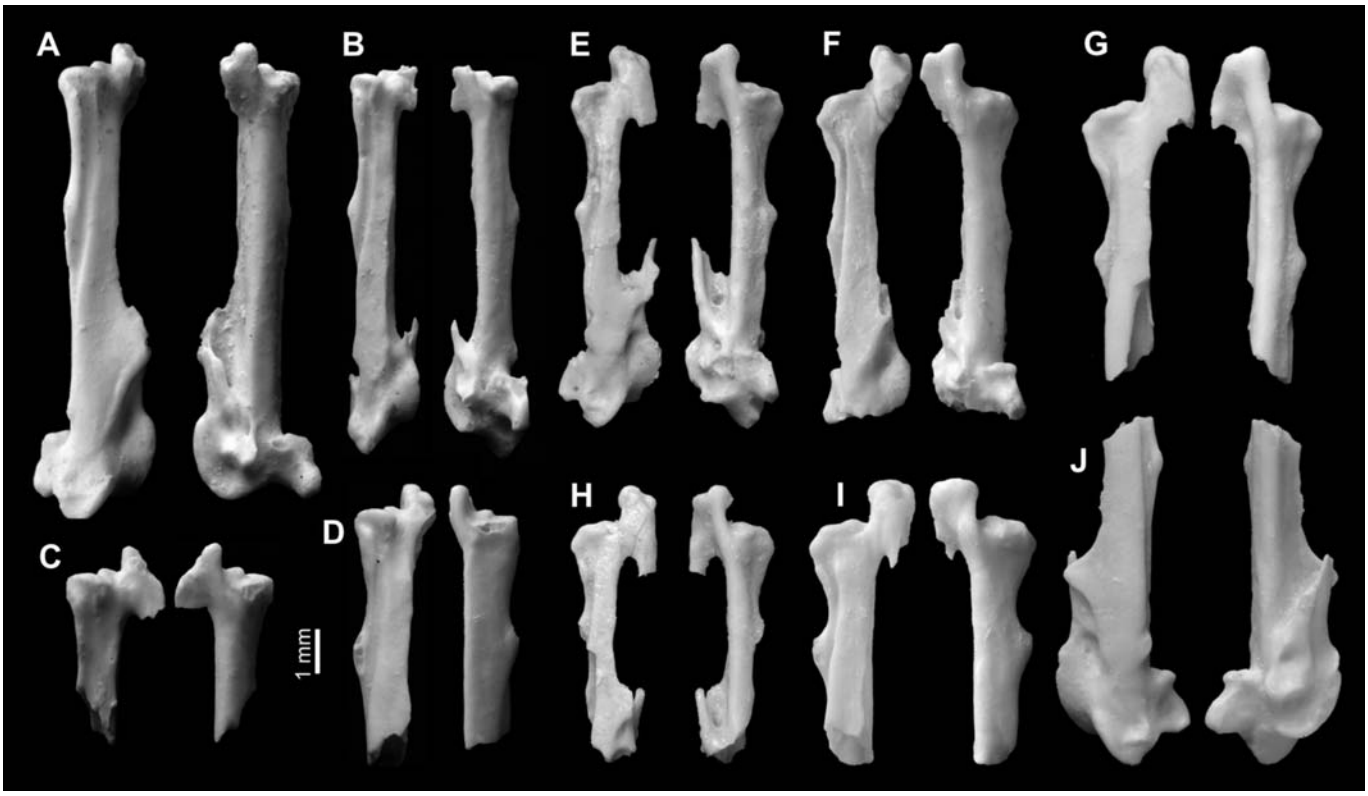


Figure 3. Isolated carpometacarpi from the late Oligocene of Herrlingen, Germany, in dorsal (left) and ventral (right) aspect. Carpometacarpi (**A**–**D**) can be assigned to Suboscines, (**E**–**I**) to Oscines. Carpometacarpus (**J**) might belong to another, primitive passeriform lineage (Manegold 2008a). Photograph by S. Tränkner.

described so far. *Wieslochia weissi* was a comparatively small bird, approximately of same size as a modern house sparrow (*Passer domesticus,* Passeridae). The specimens are six to ten million years older than the aforementioned fossils from France, and *Wieslochia* is clearly not a representative of crown group Oscines. Actually, a few characters indicate that this species might be outside Eupasseres (Mayr & Manegold 2006a).

Contemporaneously with *Wieslochia* was an as yet unnamed passerine from the early Oligocene of France (Mayr & Manegold 2006b). Only an isolated wing skeleton is known, but this shows derived features otherwise only known for Suboscines. Thus, it might be referable to a suboscine bird, but additional material is needed for more detailed conclusions. Another passeriform bird of the same age from the same French locality was mentioned by Roux (2002), but that specimen is still undescribed.

There is still a big gap of several million years in the fossil record of passeriforms, but from the late Oligocene onwards, passerines are very abundant in corresponding deposits in the northern hemisphere. Fissure fillings in southern Germany dating from the late Oligocene provided the earliest evidence for the coexistence of Oscines and Suboscines as well as a surprisingly high diversity of perching birds (Manegold 2008a). Remains of at least two suboscine and about ten oscine species could be identified, but there were possibly representatives of another, now completely extinct passerine lineage at the same locality too (Manegold 2008a) (Fig. 3). Enigmatic passerines are also known from the mid Miocene of Germany and France (Manegold *et al.* 2004). They lack a derived character on the tarsometatarsus apomorphic for Eupasseres which might indicate that the fossils are not part of this clade.

There are no records of early Cenozoic songbirds from Africa and Asia, and the oldest New World songbirds are of early Miocene age (Olson 1985; Noriega & Chiappe 1993). A partial skeleton from the Early to Middle Miocene of Japan is the oldest record for passerines in Asia (Kakegawa & Hirao 2003). The authors abstain from a more detailed classification of the conspicuously small specimen, but the lack of a processus dentiformis on the well-preserved carpometacarpus indicate that the fossil belongs to the core Corvoidea *sensu* Barker *et al.* (2004), a group comprising bush-shrikes, cuckoo-shrikes, shrikes, orioles, monarchs, crows, ravens and others (Fig. 1).

As far as the pre-Pliocene record is concerned, only few passerine fossils could be assigned to extant subordinated clades within Oscines and Suboscines, respectively (Olson 1985). For northern Africa, remains of a proximal humerus and an almost complete carpometacarpus from the middle Miocene of Morocco were tentatively referred to the modern common nightingale (*Luscinia* cf. *megarhynchos,* Oscines) (Brunet 1961), but this identification was justifiably questioned by Olson (1985). Passeriform remains from the early Miocene of Africa south of the Sahara are listed by Pickford (1986) for two fossil sites in Koru/Songhor/Muhoroni Area, western Kenya, but no further information or illustrations are available.

Fossil broadbills (Eurylaimidae, Suboscines) are known from the early Miocene of Bavaria, Germany (Ballmann 1969). *Certhiops rummeli,* the earliest fossil representative of a clade comprising extant nuthatches and treecreepers (Certhioidea, Oscines) showing adaptations for climbing

was discovered in a contemporaneous and close by fossil locality (Manegold 2008b).

In the southern hemisphere, evidence for fossil representatives of lyrebirds (*Menura*) and logrunners (*Orthonyx*) dates from the early Miocene of Australia (Boles 1993, 1995b). Remains of several species of honeyeaters (Meliphagidae) were described from the middle to early late Miocene of Australia (Boles 2005) and suggest an already high diversity of passerine birds at that time. A fragmentary scapula from the early to middle Miocene of New Zealand was tentatively assigned to the butcherbirds (Cracticidae) by Worthy *et al.* (2007). Cracticidae are no longer part of New Zealand's avifauna, but today restricted to Australia and New Guinea. So far, only a single passerine is described from the early Miocene of South America. A fragmentary humerus shows suboscine features, but could not be further identified (Noriega & Chiappe 1993).

Discussion

The fossil record of passerines does not contradict the DNA sequence based hypotheses that this clade originated and diversified in the southern hemisphere. However, the proposed late Cretaceous age for the three major passerine lineages seems to be less convincing from a palaeontologist's perspective, although several molecular clock estimates received similar assumptions (Cooper & Penny 1997; Van Tuinen & Hedges 2001). Interestingly, more recent molecular clock estimates considering latest insights into the fossil record of birds for calibrating splits found no solid molecular evidence for an extensive pre-Cenozoic radiation of Neoaves (Ericson *et al.* 2006), though assuming that the split between Oscines and Suboscines occurred during the Paleocene. Unfortunately, Acanthisittidae were not included in that particular analysis. A Cretaceous age for the major passerine lineages is not in concordance with the fossil record of birds in general and with that of passerines in particular. Bird fossils from the late Cretaceous and the Paleogene were identified as stem-lineage representatives of modern taxa, but no crown-group representatives of any modern family-level taxa are known from pre-Oligocene deposits (Mayr 2005a). The only known stem-lineage representatives of Passeriformes, the Zygodactylidae, appear for the first time in the early Eocene of Europe and North America (Mayr 2008). Enigmatic fossils like *Wieslochia* also indicate that additional and now extinct passerine lineages dwelled in the northern hemisphere, probably before the dispersal of suboscine and oscine birds.

The evidence for Suboscines in the northern hemisphere already inspired new hypotheses on the biogeography of the extant *Sapayoa*, the Old World suboscine in the New World (Fjeldså *et al.* 2003; Moyle *et al.* 2006), but the relationships of the Miocene broadbills of the different suboscine species from the late Oligocene are still obscure. The dramatic increase in diversity and abundance of songbirds in the northern hemisphere during the Oligocene might be correlated with the contemporaneous approach of the Australian continental plate to Eurasia (Hall 1998; Smith *et al.* 1994) facilitating the dispersal of many songbird lineages (Ericson *et al.* 2002a,b). Sustained northward moving of Australia permitted further faunal exchanges between Australia and Eurasia by the formation of the Indo-Australian Archipelago during the Miocene (Olson 1988; Briggs 1995), but detailed reconstructions of the biogeography of selected groups within the songbirds is still in the beginning, and the study of fossil passerines might be crucial in such attempts.

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Review and analysis of African sauropodomorph dinosaur diversity

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Introduction

Sauropodomorphs were a major Mesozoic terrestrial radiation of gigantic, herbivorous dinosaurs. Their remains have been discovered on all continents and by the close of the Triassic they had achieved a global distribution (Galton & Upchurch 2004). African sauropodomorphs are known from the Carnian (Late Triassic; Raath 1996), right through to the Maastrichtian (Late Cretaceous; Curry Rogers & Forster 2001), thus spanning the entire known temporal range of dinosaurs. In addition, their remains have been recovered from 16 different African countries, ranging across the entire continent (Fig. 1). Here, the sauropodomorph diversity from each geological Epoch will be summarized, with a concluding analysis of African sauropodomorph diversity through time.



Figure 1. Map of African sauropodomorph localities.

Late Triassic

The Late Triassic of Africa is almost entirely dominated by remains from South Africa. These include numerous basal sauropodomorphs (*Eucnemesaurus* and *Plateosauravus,* as well as undiagnostic remains; Van Hoepen 1920; Haughton 1924; Yates 2003, 2007a; Galton *et al.* 2005), several indeterminate prosauropods (including remains from Zimbabwe; Raath 1996), as well as *Azendohsaurus* from Morocco (originally described as an ornithischian and then reinterpreted as a prosauropod; Dutuit 1972; Gauffre 1993a), which is now considered a non-dinosaurian archosauriform (Irmis *et al.* 2007). Additionally, two South African taxa originally considered as prosauropods (*Melanorosaurus* and *Blikanasaurus;* Haughton 1924; Galton & van Heerden 1985) have more recently been resolved as basal sauropods (Upchurch *et al.* 2004, 2007; Yates 2007b). A third South African Triassic sauropod (*Antetonitrus*) was named by Yates & Kitching (2003).

Early Jurassic

The Early Jurassic is dominated by the South African and Zimbabwean prosauropod *Massospondylus* (Owen 1854), which is known from over 80 skeletons (Galton & Upchurch 2004). Barrett (2004) noted the presence of another diagnostic Early Jurassic South African sauropodomorph, though this is considered a new species of *Massospondylus* (Barrett, in press) and is not included as a distinct taxon in the diversity analysis. As well as various indeterminate sauropodomorph remains, there are also recently excavated skeletons from South Africa that have been suggested to represent three new sauropodomorph taxa, including a basal sauropod (Yates *et al.* 2007). The Zimbabwean taxon *Vulcanodon* was originally identified as a prosauropod (Raath 1972) but has subsequently been demonstrated to be a basal sauropod (Cruickshank 1975; Upchurch *et al.* 2004). Gauffre (1993b) named a second species of *Melanorosaurus* (*M. thabanensis*) based on an isolated femur from Lesotho; however, Yates (2007b) recently expressed doubt as to the validity of this species and it is here considered a *nomen dubium.* Another basal sauropod, *Tazoudasaurus,* is known from the Toarcian of Morocco (Allain *et al.* 2004).

Middle Jurassic

By the Middle Jurassic, African sauropodomorphs were composed entirely of sauropods, with prosauropods seemingly having become extinct. The first Madagascan remains are known from this time period, with the basal eusauropod *Archaeodontosaurus* (Buffetaut 2005) and the titanosauriform *Lapparentosaurus* (Bonaparte 1986; Upchurch *et al.* 2004) roughly contemporaneous alongside material described by Lydekker (1895) as '*Bothriospondylus madagascariensis*'. This latter material represents a derived non-neosauropod eusauropod which is distinct from the other named Madagascan taxa (Mannion, in press). The basal macronarian *Atlasaurus* is known from Morocco (Monbaron *et al.* 1999), as are also remains originally described as '*Cetiosaurus mogrebiensis*' (Lapparent 1955), which are in need of revision and are currently considered undiagnostic. Most recently, Mahammed *et al.* (2005) described a basal eusauropod, *Chebsaurus,* from Algeria.

Late Jurassic

Currently known Late Jurassic African sauropods are restricted to Tanzania and Zimbabwe. Most remains were collected during the German Tendaguru expeditions of 1909–1913. Diplodocoids (*Australodocus, Dicraeosaurus* and *Tornieria*), *Brachiosaurus,* the putative titanosaur *Janenschia* and a taxon of unknown affinities (*Tendaguria*) are all known from Tanzania (Fraas 1908; Janensch 1914; Wild 1991; Bonaparte *et al.* 2000; Remes 2007). Material

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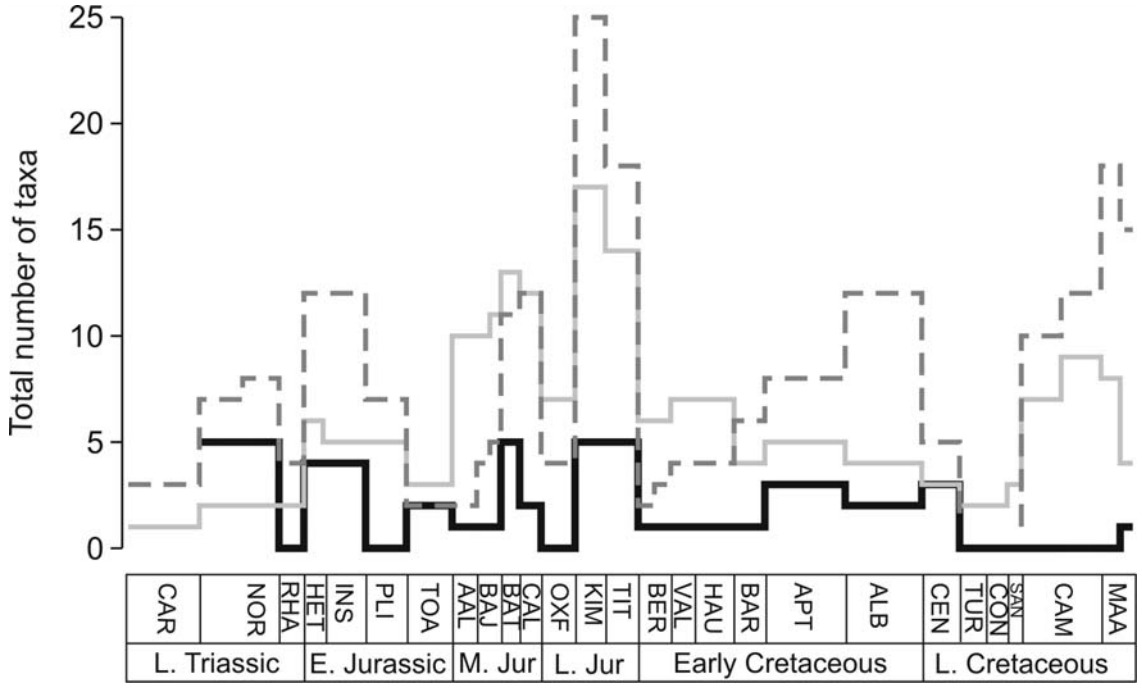


Figure 2. African sauropodomorph diversity through time. Solid black line represents African sauropodomorph taxic diversity. Dashed grey line represents global sauropodomorph taxic diversity. Solid grey line represents a phylogenetic diversity estimate of global sauropod diversity. These last two diversity curves are based on Barrett & Upchurch (2005) and Upchurch & Barrett (2005). Geological timescale based on Gradstein *et al.* (2005).

from Zimbabwe has also been referred to several of these genera (Raath & McIntosh 1987).

Early Cretaceous

The first sauropod material known from Malawi is preserved in Early Cretaceous deposits. This is represented by the titanosaurs *Malawisaurus* and *Karongasaurus* (Haughton 1928; Jacobs *et al.* 1993; Gomani 2005). *Rebbachisaurus* is known from Morocco (Lavocat 1954) and another rebbachisaurid (*Nigersaurus*) has been described from Niger (Sereno *et al.* 1999). Also described from Niger is the eusauropod (or basal macronarian; Upchurch *et al.* 2004) *Jobaria* (Sereno *et al.* 1999). Material described from Niger, Tunisia and Algeria as '*Rebbachisaurus tamesnensis*' (Lapparent 1960) may be a mixture of *Nigersaurus* and *Jobaria*. A brachiosaurid ('*Brachiosaurus nougaredi*') was also named by Lapparent (1960) based on Algerian remains, but is not here considered valid. Lastly, indeterminate sauropod material is known from South Africa, Cameroon and Kenya (Weishampel *et al.* 2004, and references therein; Sertich *et al.* 2005; De Klerk 2008).

Late Cretaceous

Valid, named Late Cretaceous taxa are composed entirely of titanosaurs, with *Aegyptosaurus* and *Paralititan* both described from the Cenomanian of Egypt (Stromer 1932; Smith *et al.* 2001), and *Rapetosaurus* known from the late Maastrichtian of Madagascar (Curry Rogers & Forster 2001). Indeterminate remains (predominantly of titanosaurs, but also including some possible diplodocoids) are also known from Angola, Morocco, Niger, Sudan, Swaziland and Tanzania (Weishampel *et al.* 2004, and references therein; Pereda Suberbiola *et al.* 2004; Jacobs *et al.* 2006; O'Connor *et al.* 2006).

Discussion and conclusions

Thirty-one African sauropodomorphs are considered generically distinct, spanning the full temporal interval that dinosaurs existed and including representatives of all the main sauropodomorph clades. An African sauropodomorph taxic diversity curve (Fig. 2) shows peaks in the Norian (Late Triassic), Hettangian-Sinemurian (Early Jurassic), Bathonian (Middle Jurassic) and Kimmeridgian-Tithonian (Late Jurassic), as well as a shallower peak in the mid-Cretaceous. The curve also suggests that the Pliensbachian-Bajocian (Early-Mid Jurassic), Oxfordian (Late Jurassic), and much of the Cretaceous were periods of apparent lower diversity.

In general, this matches quite closely with diversity curves based on global taxic and phylogenetic diversity estimates (i.e. Barrett & Upchurch 2005; Upchurch & Barrett 2005; Fig. 2), although the African diversity curve unsurprisingly shows lower diversity levels based on only sampling from one continent. The main difference is the lack of any known African taxa for much of the Late Cretaceous, in comparison to global values. Upchurch & Barrett (2005) used dinosaur-bearing formations (DBFs) to help tease apart genuine global diversity signals from preservational biases. During the Cretaceous, DBFs were at their highest; however, the number of DBFs for the African Late Cretaceous (based on Weishampel *et al.* 2004) is extremely low, thus this low diversity may be an artefact of a poor African Late Cretaceous rock record. The overall closeness in fit suggests that African sauropodomorphs were at least as diverse as in other areas of the world, and followed similar fluctuations temporally.

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Micromammals from the Middle Stone Age (92–167 ka) at Cave PP13B, Pinnacle Point, south coast, South Africa

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Introduction

This paper presents the preliminary results of an analysis of micromammal assemblages recovered from three excavation areas in Cave 13B at Pinnacle Point (from this point referred to as PP13B), namely the 'eastern', 'western' and the 'LC-MSA' areas. The geological context of the site, dating, excavation and stratigraphy of these areas are described in detail in Marean *et al.* (2004, 2007) and Marean *et al.* (in press), and are dealt with only briefly here. All the Optically Stimulated Luminescence (OSL) dates quoted in this paper were carried out by Zenobia Jacobs at the School of Earth and Environmental Sciences, University of Wollongong, Australia. In this paper, we report age ranges as the maximum spread of all employed dating techniques, which include OSL and uranium-thorium on speleothems, with 1 sigma error added on to either side of the age. Some spreads are corrected and/or narrowed by other dating techniques. For example, a series of highly precise uranium-thorium ages shows the cave was closed to human occupation beginning ~92 ka, providing limits to the OSL age spreads.

Background

The LC-MSA area

In the northeastern area archaeological sediments are called the LC-MSA (Lightly Cemented Middle Stone Age). The LC-MSA is attached to the cave wall and is capped by a flowstone. The LC-MSA consists of multiple lenses of burning, within which are faunal bone, shellfish, lithics and ochre. The LC-MSA is divided into three stratigraphic aggregates. These aggregates are the LC-MSA Lower, LC-MSA Middle and the LC-MSA Upper, which reflect a relatively homogeneous set of formation processes. LC-MSA Lower is the oldest facies, is the archaeologically richest, and has the least cemented layers (Marean *et al.* 2007; Marean *et al.*, in press). At the bottom of the currently sampled horizons is water-rounded bedrock. The excavations in this area were limited as the amount of preserved sediment is small.

Micromammals were found throughout the LC-MSA aggregates, although, to date, sample sizes sufficient for analysis were found only in the LC-MSA Lower sediments dated by OSL to 153 to 174 ka, placing it in MIS stage 6. However, our 3D sea level model (Marean *et al.*, 2007) shows the coast was only close enough for shellfish collection around 167 ka, and thus this further constrains the age spread for the LC-MSA Lower.

The eastern area

In the eastern area the various stratigraphic facies identified and used for analysis are depicted in Table 1 (from the bottom to the top of the sequence), along with the OSL dates obtained for that horizon, and the number of individual micromammal specimens (NISP) recovered. The Shelly Brown Sand and Upper Roof Spall were separated in excavation, however, the excavators now consider them contemporary due to the overlapping age estimates and the fact they grade into each other.

The Lower Roof Spall Facies, which represents an MSA horizon, is at the base of the excavations and rests on bedrock. Archaeological finds are scarce and tend to be concentrated towards the top of this facies. The deposits lie between the bedrock, forming a thick fill which thins out over the tops of the boulders. Cemented patches are found and are more common in the southerly parts of the excavated area. The Upper Roof Spall Facies represents a richer archaeological horizon than the Lower Roof Spall Facies and contains lithics, shellfish and fauna and grades into the Shelly Brown Sand. This facies thickens appreciably from south to north. In the southernmost area, the Upper Roof Spall Facies contains both isolated and connected burnt areas which become increasingly more complex and inter-woven towards the northern side of the facies. Within these areas stratified hearths with associated lithics and fauna are found. On top of the Upper Roof Spall Facies and Shelly Brown Sand are the Truncation Fill, the modern Redeposited Disturbance, and the Surface Sediments.

As Table 1 illustrates, micromammal assemblages of sufficient size for analysis were recovered from only the Lower Roof Spall Facies and the Upper Roof Spall Facies, although sample size was very poor in the latter.

The western area

In the western area of the site the deposits appear to resemble a midden or dump. However, micromorphological evidence is somewhat contradictory as combustion features appear to be in situ, but do not appear to be hearths, as seen in the eastern area and LC-MSA (Karkanas & Goldberg, in press). Some of the sediments have strong anthropogenic signatures, whereas others appear to be geogenic in origin. There are areas with substantial geogenic disturbance as a result of faulting, slippage, or subsidence, and there were at least two events of erosion or anthropogenic cutting of MSA sediments.

Table 1. OSL dates and NISP for the eastern area facies.

	Dates	NISP
Surface sediment	Modern	2
Re-deposited Disturbance	Modern	1
Truncation Fill	No OSL dates available, but possibly dates between 35-39 ka	7
Shelly Brown Sand	92–98 ka	1
Upper Roof Spall Facies	92–98 ka	17
Lower Roof Spall Facies	106–114 ka	27

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Table 2. Sequence of stratigraphic relationships of the western area facies in sequence of formation (after Marean *et al.,* in press).

Facies name		Age of horizons within facies
Boulder Beach		–
Laminated Facies		375–451 ka, probably MIS 11
Light Brown Silt Facies (abbreviation: LB Silt)		153–375 ka, maybe MIS 11 or just after
Dark Brown Sand Facies (abbreviation: DB Sand)	DB Sand 2 DB Sand 3 DB Sand 4	92–102 ka 92–102 ka 117–375 ka – probably just postdates the LC-MSA Lower in MIS 6
Light Brown Grey Sand Facies (abbreviation: LBG Sand)	LBG Sand LBG Sand 2 LBG Sand 3	94–134 ka 117–166 ka 152–375 ka (Note: LBG Sand 2 and 3 also probably just postdate LC-MSA Lower in MIS 6)
Light Brown Sand Facies (abbreviation: LB Sand)		92–94 ka
South Pit Fill		Modern
North-east Fill		Modern
Surface Sediments		Modern

There has also been a modern disturbance in at least one area. Maximum and minimum age spreads have been developed and Table 2 illustrates a simplified sequence of the various western area facies. The Laminated Facies is composed of a thick series of sediments which lie at the base of archaeological deposits. The Dark Brown Sand Facies contains series 4a to 4c. DB Sand 1 was later identified as representing the same horizon as DB Sand 2 and was eventually grouped with it.

Materials and methods

Stratigraphic Units (lenses, features, and other discrete sedimentary units) were initially identified during excavation, and then later verified by projecting 3D total station shots of the units onto section drawings and photographs, by generating 3-D point clouds, and lastly using micromorphological observations to develop reconstructions of the sequence of deposition, alteration, and erosion of the various facies. The stratigraphic units were grouped into larger stratigraphic aggregates, which reflected a homogeneous set of formation processes. The micromammal assemblages from each stratigraphic aggregate were analysed as a unit.

The use of the methodology initially proposed by Andrews (1990) and Fernandez-Jalvo & Andrews (1992) for the analysis of micromammal assemblages has become more or less standardized (e.g. Manthi 2002; Matthews 1999, 2002, 2006; Matthews *et al.* 2006; Dewar & Jerardino 2007) and was used for recording the breakage and taphonomy of the PP13B assemblages. Only selected results from the taphonomic analysis of the PP13B assemblages, pertaining directly to the identity of the accumulating agent/s are presented in this paper, which concentrates on the paleoenvironmental implications of the micromammals in PP13B.

From this point onwards, the three molars of the murid mandible will be referred to as the $M_{1–3}$, and the three maxillary molars, as the $M^{1–3}$, respectively.

Taphonomy

Identifying the predator/s or agents responsible for accumulating a fossil micromammal assemblage is essential if reliable palaeoenvironmental information is to be extracted (Matthews 1999; Matthews *et al.* 2006). Variation within a fossil micromammal assemblage over time may be attributable to changes in the identity of the predator responsible for the accumulation, rather than environmental change. Also, different predator species have different requirements for selecting prey species from the available local micromammal population.

A most useful tool for identifying the predator/s involved in a micromammal accumulation is the pattern of digestion on enamel and dentine of incisors. The following categories describe and record incisor digestion on both isolated and *in situ* incisors. Incisors that suffered damage and that could not be properly assessed were excluded.

Class 0: No visible digestion on the incisor. The early stages of digestion may not be detectable with a light microscope and it is possible that some incisors falling into this category sustained very light, but indiscernible digestion.

Class 1 (light): Light etching and removal of the upper layers of small areas of enamel and/or dentine.

Class 2 (moderate): The area of digestion may not be much greater than Class 1, but the digestion has penetrated much deeper through enamel layers, down to, or very close to dentine. The dentine shows a deeper degree of penetration and loss.

Class 3 (heavy): The area of digestion is more extensive than Class 2 digestion, with complete removal of enamel in areas, and digestion and removal of underlying dentine.

Class 4 (extreme): Extreme digestion of both enamel and dentine, with some teeth having all enamel removed and much dentine removed. The edges of dentine or enamel may be collapsing in on themselves.

Samples of incisors from modern barn owl and spotted eagle owl pellets were examined to provide a comparative database.

Identification

Murid M^1 and M_1 teeth (*in situ* and isolated) were identified to species whenever possible, and these were used to quantify the different species present in the fossil assemblages. An exception was made in the case of Otomyinae (the vlei rats), where the more diagnostic M^3 rather than the M^1 was used to quantify this murid subfamily. Occasionally, breakage, wear or digestion of the tooth precluded identification. Teeth of uncertain identification were not used for analysis.

Differentiating between *Otomys saundersiae* and *Otomys irroratus* was frequently difficult due to great variability in size and shape of the laminate teeth of these two species. Some specimens could not be allocated with certainty to either species and were thus recorded simply as *O. saundersiae/O. irroratus.*

General diversity

The Shannon Wiener index of general diversity was used to assess diversity of the fossil micromammal assem-

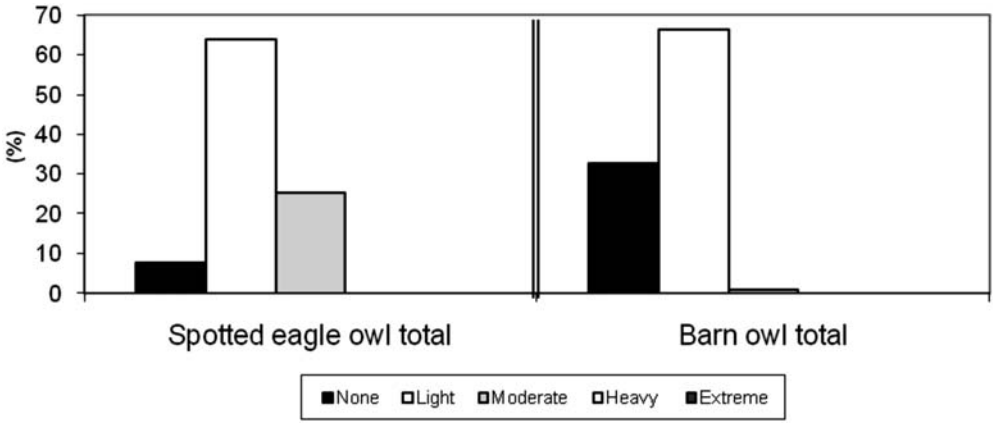


Figure 1. Incisor digestion patterns of modern spotted eagle owl and barn owl pellet assemblages from the south coast.

blages. This index accounts for both the number of taxa present, and relative frequency (evenness of representation) of each taxon (Cruz-Uribe 1988). The Shannon Wiener index is calculated using the equation:

$$H = -\Sigma\, P_i \log_e P_i ,$$

where $P_i = n/N$, that is, the proportion of the total sample represented by each species.

Results

Taphonomy

Figure 1 shows the incisor digestion patterns typical of modern barn owl (*Tyto alba affinis*) and spotted eagle owl (*Bubo africanus*) pellet assemblages. The characteristic incisor digestion patterns of spotted eagle and barn owls were verified by studying several modern comparative assemblages (Matthews, unpubl. report). The results from two barn owl, and three spotted eagle owl pellet assemblages are averaged in Figure 1 to facilitate comparisons with the fossil assemblages. These owl species roost on the floor or on ledges of caves and rocky overhangs, and are thus the most likely contributors to the fossil micromammal assemblages in PP13B. The only small carnivore likely to build up an accumulation of scats in a cave is the small-spotted genet (*Genetta genetta*), which frequently uses caves and rocky overhangs as midden areas, however, this predator was excluded on the basis of incisor digestion patterns.

The barn owl assemblages were distinguished from those of the spotted eagle owl on the basis that a far higher proportion of incisors showed no digestion, and very few incisors fell into the 'moderate' digestion category. Neither the barn or spotted eagle owl assemblages contained incisors that showed heavy or extreme digestion, although incisors with these advanced degrees of digestion do occasionally occur in pellet assemblages from both owl species (T.M., pers. obs.).

Figure 2 shows the incisor digestion patterns found in various fossil assemblages from the western, eastern and northeastern areas of PP13B. The number of incisors in each facies is shown above the individual bar graphs. Facies which contained very few or no incisors are omitted.

Incisor digestion patterns in the LC-MSA Lower suggests that a barn owl was responsible for the accumulation of the micromammal assemblages. The sample of incisors in the LC-MSA Upper is too small for comment. In the eastern

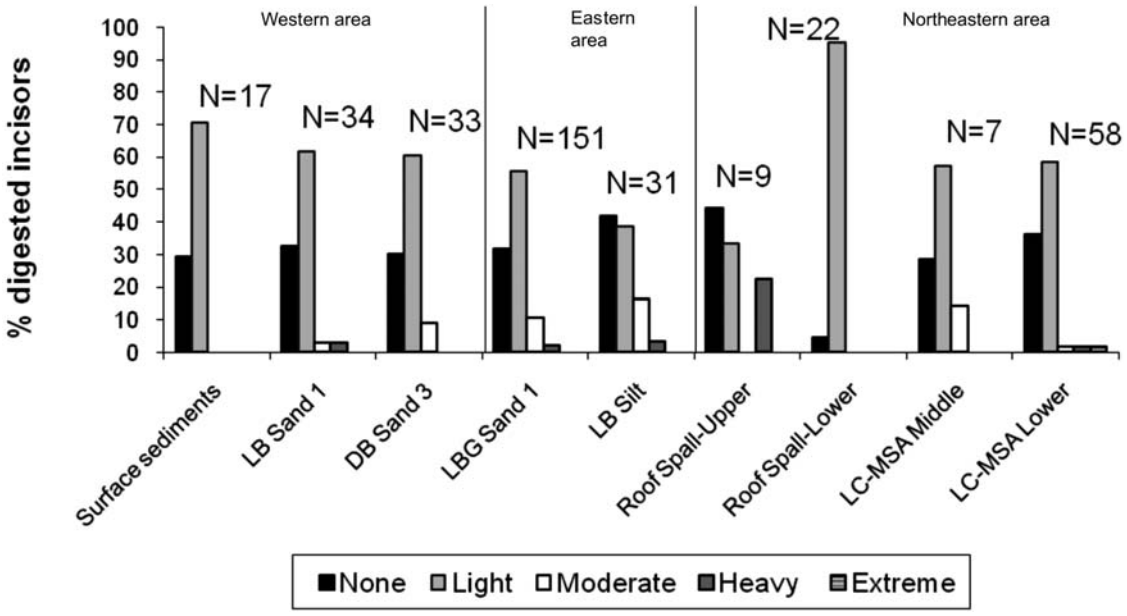


Figure 2. Incisor digestion patterns in the east, western and northeastern areas of PP13B.

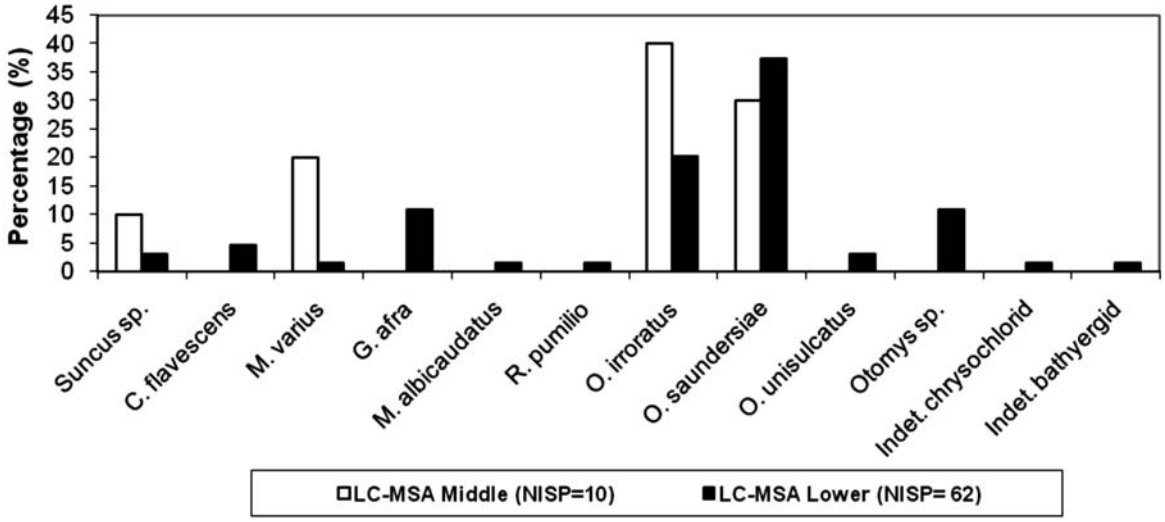


Figure 3. The micromammalian population from the LC-MSA Middle and Lower Facies.

area poor incisor sample size precludes identification of the predator, although digestion patterns are closer to the barn owl than the spotted eagle owl. in the western area barn owl predator activity is clearly suggested by incisor digestion patterns in all facies. LB Silt differs slightly in the high percentage of incisors showing moderate digestion, but this will be discussed later.

Identification

The proportional representation of micromammalian taxa found in the LC-MSA Middle and LC-MSA Lower Facies is shown in Fig. 3, and those of Roof Spall-Upper and Roof Spall-Lower (eastern area) in Fig. 4. The values pertaining to these figures may be seen in Appendix A. The NISP in all the following figures was calculated by counting the number of upper and lower first molars (isolated and *in situ*). Figure 5 illustrates micromammal percentage representation in the western area assemblages containing a NISP of 28 or more, namely LB Sand 1, DB Sand 3, LBG Sand 1 and LB Silt.

Table 3 shows the number of each micromammal species present in the western area facies, including those depicted in Fig. 5.

General diversity (*H*)

Table 4 gives micromammal diversity for the various facies of PP13B and, for the purposes of comparison, Table 5 shows the general diversity in several micromammal- bearing south and east coast archaeological sites (after Avery, 1986).

Discussion

Sample size in the LC-MSA Middle Facies is too small for paleoenvironmental analysis and species which are present are catholic in their ecology. Otomyinae dominate the micromammal assemblages, a feature seen in the majority of facies throughout the western area as well. Sample size in the LC-MSA Lower is larger, but once again no clear pattern of environmental conditions emerges from the ensemble of species represented. Incisor digestion patterns suggest that a barn owl was responsible for the accumulation of this facies. Barn owls are generalist feeders and produce pellet assemblages that provide a broad sample of the micromammal population living within the hunting range of the owl (Andrews 1990; Avery *et al.* 2005) so predator bias with regard to selection of prey species should not be affecting the suite of species to any marked

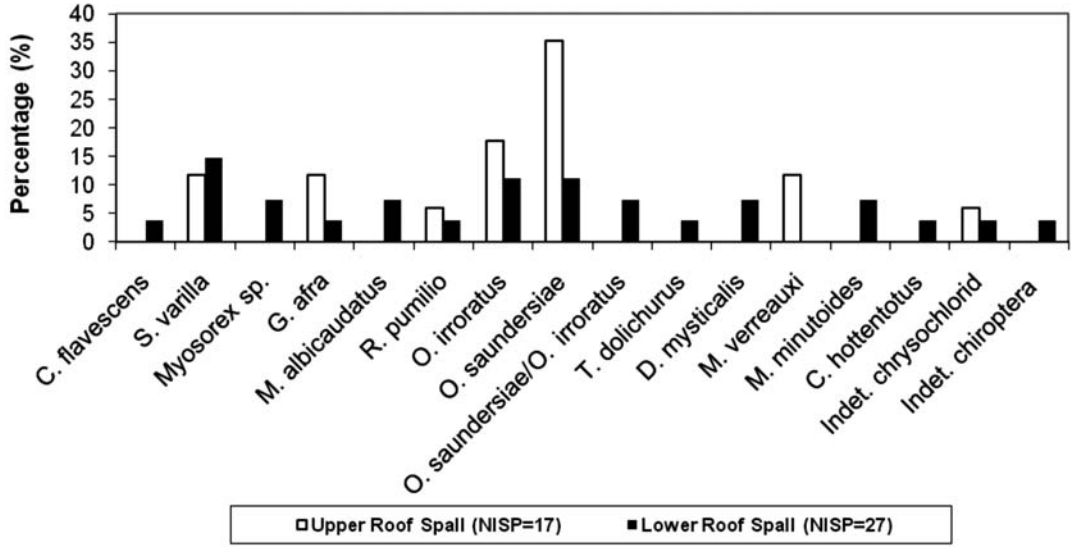


Figure 4. The micromammalian population from the Upper Roof Spall and Lower Facies.

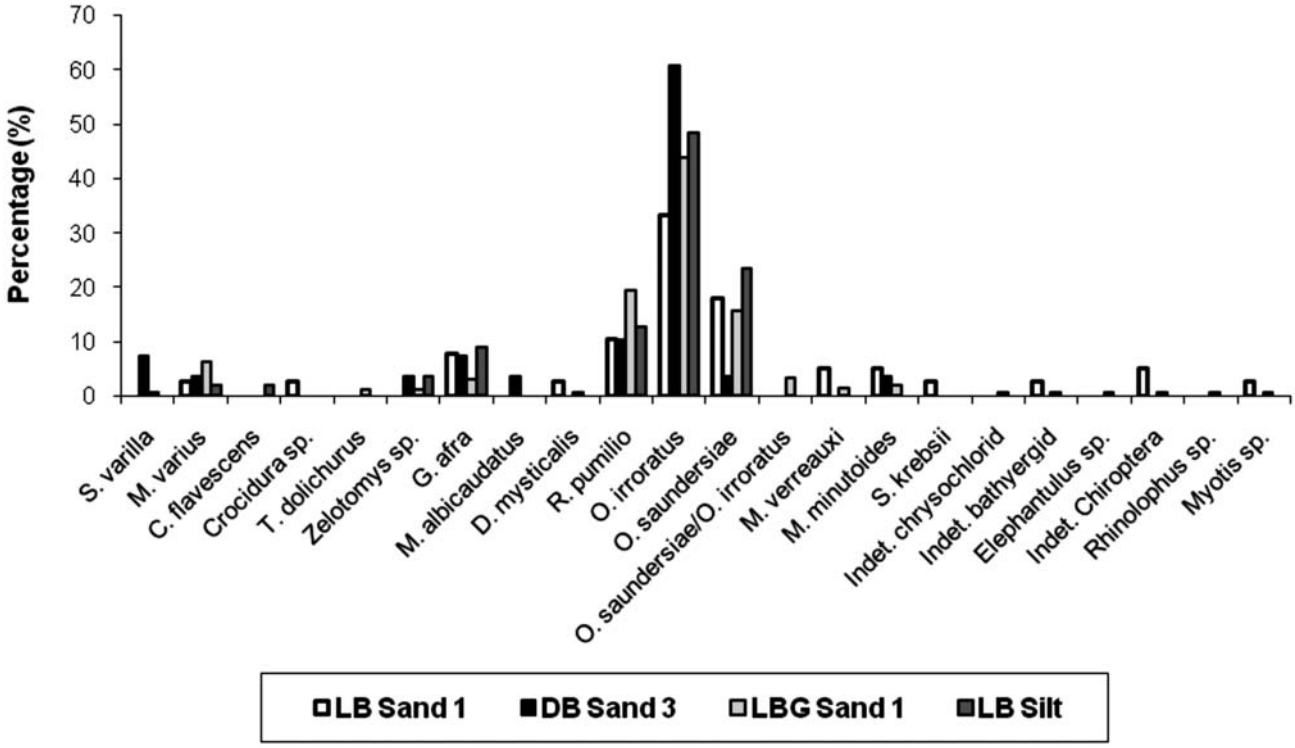


Figure 5. The micromammalian population in larger (NISP ≥ 28) samples from the western area facies.

degree. The fact that all the species present are species found in a variety of habitats and are thus presumably adaptable to changing conditions may in itself be significant, but this must be substantiated by further research into micromammal assemblages from other Pinnacle Point cave sites.

The fact that *O. saundersiae* dominates in the LC-MSA Lower Facies, and *O. irroratus* throughout most of the western area facies, may indicate relatively drier conditions in the LC-MSA, but this interpretation is tentative as both these *Otomys* species are frequently found together in modern comparative barn owl assemblages from the south coast (Avery *et al.* 2005; Matthews, unpubl. report). This suggests that these two species can occupy the same areas simultaneously, although they may inhabit different microhabitats. Changes in relative proportions of the two species may thus have little to do with changes in rainfall/environment over time. The presence of *Otomys unisulcatus,* albeit in very low frequencies (this species was represented by one mandible and one isolated M_1), does lend some credence to the suggestion that conditions were somewhat drier in the LC-MSA as *O. unisulcatus* is known to shun damp situations (De Graaff 1981). It is not found along the southern coast today, but is distributed some distance inland from the coast. During the formation of the LC-MSA Lower and Middle the coastline was further away than it is today, but still within several kilometres of PP13B. However, species which might be expected to reflect drier, more sparsely vegetated or sandier environments, such as *S. krebsii, A. namaquensis* and *G. afra* are not found in greater abundance in these older facies, so the picture is not clear. In addition, the soricid, *Crocidura flavescens,* which is generally associated with dense vegetation and reportedly shows a preference for relatively moist environments, appears only in the older facies of all three areas (i.e. the LC-MSA Lower in the northeastern, the Roof Spall Lower sediments in the eastern, and in LB Silt in the western area). The absence of this species during later periods at Pinnacle Point was confirmed by the micromammal assemblages from PP9C (PP9C lies along the coast approximately 100 m north of PP13B) which are currently undergoing analysis. The implications of this are presently uncertain.

There are a couple of species not found in the LC-MSA Lower that the eastern and western areas hold in common. These are the woodland mouse, *T. dolichurus* and the chestnut climbing mouse, *D. mystacalis*. *T. dolichurus* provides evidence for the presence of a woodland/forest/thicket environment in the vicinity over 114 ka up until at least 92 ka (as indicated from its appearance in the eastern area in the Roof Spall Lower Facies at 114 ka, and in the western area in LBG Sand 1 and DB Sand 4a). Today this species is found on the eastern coast in Albany thicket, and may indicate that this biome extended further down the south coast in the past. *D. mystacalis* requires a habitat of tall grasses and rank vegetation. Such grasses could be provided by both a fynbos, or more typically grassland, habitat. This suggests that vegetation was denser during MIS 5 than the preceding MIS 6 (as represented by the LC-MSA Lower Facies).

Steatomys krebsii is found only in the western area of PP13B, in surface sediments. In the fossil sediments only one specimen was recovered from LB Sand 1. Avery (1977) noted that on the basis of fossil evidence from Boomplaas A, *S. krebsii* arrived at the south coast at the onset of the Holocene. The appearance of *S. krebsii* in the western area suggests that this species was present in the Mossel Bay area around 100 ka.

In the eastern area, two horizons dated from 92–98 ka (Upper Roof Spall) and 106–114 ka (Lower Roof Spall)

Table 3. The micromammals from the western area facies.

Genus and species	South Pit Fill	Northeast Fill	LB Sand 1	DB Sand 2	LB Sand 2	DB Sand 3	LBG Sand 3
S. varilla						2	
M. varius		1	1		2	1	1
C. flavescens				1			
Crocidura sp.			1				
Zelotomys sp.						1	
G. afra			3	2		2	
M. albicaudatus					2	1	
S. krebsii			1				
D. mystacalis			1		1		
R. pumilio			4	4	1	2	
O. irroratus	1		13	8	3	17	
O. saundersiae			7	4	1	1	
M. verreauxi			2		1		
M. minutoides			2			1	
Indet. chrysochlorid	1			1			
Indet. bathyergid			1				
Indet. Chiroptera			2				
Myotis sp.			1				
NISP	2	1	39	20	11	28	1

Genus and species	DB Sand 4a	LBG Sand 1	LBG Sand 2	DB Sand 4b	DB Sand 4c	LB Silt and LB Silt G	Laminated Facies
Suncus sp.		1				1	
S. varilla							1
M. varius		13				1	
C. flavescens						1	
Indet. soricid						1	
T. dolichurus	1	2					
Zelotomys sp.		2				2	
G. afra		6				5	
D. mysticalis		1					
R. pumilio	2	41			2	7	
O. irroratus	4	92	4	1	11	27	1
O. saundersiae	1	33			4	13	
O. saundersiae/O. irroratus		7	3				
M. verreauxi		3					2
M. minutoides		4					
Indet. chrysochlorid		1					
Myotis sp.		1					
Indet. bathyergid		1					
G. capensis					1		
Elephantulus sp.		1					2
Indet. Chiroptera		1					
Rhinolophus sp.		1				?1	
NISP	8	210	7	1	18	59	6

contained micromammals, but only the latter horizons contained a sample size sufficient for analysis. The pattern of incisor digestion is closer to that of the spotted eagle owl rather than the barn owl, although incisor sample size is unsatisfactorily small and the identity of the predator/s is uncertain. The diversity of species is high considering the relatively small sample, and suggests that the predator/s took a broad selection of prey species. The pattern of species representation of the Roof Spall Lower was unusual in that it shows none of the peaks and dominance of 1–3 taxa commonly seen in barn and spotted eagle owl pellet assemblages. Roof Spall Lower shows a pattern of low percentage representation from a number of different species, and a diversity which is relatively high compared to other areas in PP13B.

Incisor digestion patterns indicate that a barn owl was responsible for deposition of micromammals in all western area facies containing larger samples. LB Silt contains more incisors in the moderate digestion category than observed in modern barn owl assemblages, but a high percentage of undigested incisors suggests the predator is also a barn owl. This is supported by the fact that the frequency of micromammal species found in LB Silt is similar to those in the surrounding facies. It may be that a young barn owl was contributing to the assemblage as

Table 4. Micromammal diversity in the various facies of PP13B.

	H	No. of species	NISP
Western area			
Surface sediments	2.15	11	20
LBG Sand 1	1.78	17	207
LB Silt	1.57	9	57
LB Sand 1	2.13	12	39
DB Sand 3	1.46	9	28
DB Sand 2	1.54	9	20
Eastern area			
Upper Roof Spall	1.76	7	17
Lower Roof Spall	2.58	13	27
LC-MSA area			
LC-MSA Lower	1.98	12	63

Table 5. Diversity *H* in fossil micromammal assemblages from south and east coast archaeological assemblages (values after Avery (1986) unless otherwise indicated).

Archaeological site	Shannon Wiener index of general diversity (*H*)	Age/age range covered by micromammal-bearing deposits
Klasies River Mouth	1.9–2.3 (the majority of assemblages fell below 2.2) (Avery 1987)	Late Pleistocene
Die Kelders 1	2.27–1.75	MSA
Die Kelders 1	2.10	LSA
Boomplaas	2.44–1.69	Last Glacial Maximum
Nelson Bay Cave	1.62–1.42	18 000–5 000
Border Cave	1.97–2.74 (Avery 1992)	134 000–24 000
Byneskranskop I	2.48–2.14	Holocene

young owls digest bones and teeth of prey to a greater degree than adults (Andrews 1990).

In the western area there is a lower diversity of species in the facies of small samples (as would be expected), relative to the larger samples. Nevertheless, the general pattern of species representation is very similar, with *O. irroratus* dominating, and *R. pumilio* and *O. saundersiae* occurring in far lower frequencies, and representing the second or third most common species. *O. irroratus* is one of the two vlei rat species that are associated with moist and marshy habitats; however, they are also found in drier habitats such as grassy hillsides.

The western area micromammals differ from those of the other two areas in that shrews (the Soricidae), as a group, are poorly represented in the western area and make up only 6.8% of the micromammals, as opposed to 25% in the eastern area, and 13.15% in the northeastern area. The western area also contains three species which do not occur in the LC-MSA and eastern areas, namely, *Zelotomys woosnami, Elephantulus edwardi,* and *Georychus capensis.* All these species are generally associated with sandy substrates and/or rocky areas and sparse vegetation.

In terms of distribution, *Zelotomys* was the most surprising find at PP13B as this species is currently confined to arid and semi-arid areas of the subregion and in the Kalahari region of South Africa (Stuart & Stuart 2001). Levinson (1985) notes that *Zelotomys* is likely to have undergone a habitat change since 250 ka as this species shows very few marked desertic adaptations, such as enlarged bullae, long hind legs, or a bushy tip to the tail. The presence of this species on the south coast in PP13B deposits certainly suggests that, in the past, this species lived in very different environments compared to its modern habitat. *Zelotomys* was found in DB Sand 3, LBG Sand 1, and LB Silt, indicating its presence in the area from early in MIS 6, to around 92 ka. A *cf. Zelotomys woosnami* was identified in the late Middle Pleistocene site of Hoedjiespunt 1 (Saldhana, west coast, Western Cape Province), but this find was less surprising as it is still found in the west coast region today, albeit several hundred kilometres to the north (Matthews *et al.* 2005).

Some features common to all PP13B micromammal assemblages were noted. The gerbilline, *Gerbilliscus afra,* appears in consistently low frequencies in many facies in all three areas of PP13B. This species is known to be associated with sandy soil rather than any particular type of vegetation and suggests the presence of a sandy component in the surrounds of PP13B over a long period of time, with a surprising lack of variation in the proportion of *G. afra* in the landscape. In a study made of modern barn owl roost collections throughout the western cape, *G. afra* was frequently found to be one of the top two best represented species and occurred in percentages which ranged from 20.1–80.9% (Avery *et al.* 2005). In several of the west coast fossil sites dating from Late Pleistocene to Holocene, two species of gerbilline (*G. afra* and *Gerbillurus paeba*), four soricid species, and three species of Otomyinae were always represented, although one particular gerbilline or otomyine species usually dominated in terms of overall numbers (Matthews *et. al.* 2005). The pattern at PP13B is very different, and *G. afra* is the only gerbilline represented, and appears in very low frequencies of 4–9% in various areas of PP13B. The fact that it is common in modern, but not fossil, barn owl assemblages may be related to the fact that it thrives in environments anthropogenically modified by farming. *G. afra* was not found in the Klasies River assemblages, but was found in similarly low levels in LSA levels of De Kelders at 4.1% (Avery 1979).

In absolute terms the western area of PP13B contained the highest number of micromammalian taxa with some twenty species represented, the eastern area contained 16, and the LC-MSA yielded 12 species. General diversity is highest in the eastern area in Lower Roof Spall, in the western area in LB Sand 1, and in the LC-MSA in LC-MSA Lower. Small sample size hampers the interpretation of diversity in some of the smaller assemblages (diversity and richness of a fossil sample are highly correlated with sample size (see Cruz-Uribe 1988; Denys 1999; Manthi 2002; Matthews 2004) but low general diversity appears to be a real feature of LB Silt, and possibly DB Sand 3. It is uncertain how to interpret this as, in a study by Avery (1999b), proportions of micromammalian taxa from barn owl pellets were analysed with climatic variables in order to investigate the relationship between the two. Diversity indices were not found to be closely related to any climatic factors. It is thus uncertain how to interpret changes in diversity between the various facies. Diversity in the surface sediments is higher than in any of the fossil assemblages, with the exception of Lower Roof Spall. Both Lower Roof Spall and LB Sand 1 show a relatively high diversity relative to the other PP13B facies, and also to Nelson Bay Cave and Border Cave. The relatively high diversity appears to be a real feature of these assemblages rather than an artefact of sample size as these facies represent comparatively small samples. Upper Roof Spall also shows a high diversity given the small sample size.

In terms of comparison with the younger sites such as Byneskranskop I and Die Kelders 1 general diversity is relatively low in the PP13B facies, with the exception of Lower Roof Spall, LB Sand 1 and LC-MSA Lower. Avery (1987) noted that an index *H* of 2.2 appears to be a fairly consistent cut-off point between Holocene interglacial scores and Late Pleistocene glacial scores in South Africa, with the latter generally falling below 2.2. The PP13B facies show a similar pattern to the Late Pleistocene glacial sites, with the exception of the eastern area which contains a relatively high general diversity and which indicates that diversity has fluctuated quite considerably over time.

In Avery et al.'s (2005) comparative study of 27 Barn owl roost sites (multiple collections were made at some of these sites) from the Western Cape, *H* ranged from 1.39 to 2.58. In terms of this, and also, in comparison with modern owl pellet data from the south coast (Matthews unpubl. report), the range of variability of general diversity seen in the PP13B micromammals falls within that of modern barn and spotted eagle owl pellet assemblages. Differences between the PP13B facies could be related to differences in the season, or in the area in which the owl was hunting, as well as climatic change.

In terms of density, the micromammal assemblages enjoyed an inverse relationship with shellfish (Antonieta Jerardino, pers. comm.), and were scarce when shellfish were abundant. This suggests that owls were occupying the cave when people were absent. A low general diversity was observed in large mammal assemblages from the site (Amy Rector, pers. comm.).

The density of micromammal remains in PP13B suggests that the owls responsible for micromammal accumulations did not roost in the cave for long periods so it is likely that the micromammals offer a glimpse of the micromammal population in the area over a brief period of time. The reasons for the lack of long-term visits are uncertain, but it is unlikely that lack of prey was the reason as there were clearly a variety of prey species available as indicated by the diversity index in several facies. The short occupation periods are also puzzling given that Taylor (2002) found that once barn owls selected a nest site, they keep it for life (strong site fidelity is a characteristic of hole-nesting species). In a study of occupancy in relation to site quality in barn owls (*Tyto alba*) in south Scotland, Taylor (2002) found that sites with the lowest amount of preferred foraging habitat and lowest long-term breeding success were occupied just as often as sites with opposite characteristics.

Conclusions

It is impossible to extrapolate any definite picture of the paleoenvironment reflected by micromammals from the LC-MSA Facies as species present are all catholic in their habitat requirements. Whether there was selection for species which are adaptable and opportunistic must be substantiated by further research into micromammal assemblages from other Pinnacle Point cave sites bracketing the LC-MSA Lower in age, and from similarly aged deposits. There are some faunal differences between micromammal assemblages from the LC-MSA and the eastern and western areas and it appears that vegetation was less dense during MIS 6 compared to MIS 5. Further research into micromammal assemblages dating to both MIS 5 and MIS 6 should aid in establishing if this impression is correct.

Not only is there no indication for marked environmental change over the long time period represented by the western area facies, but there is surprising consistency in the pattern of species abundance over time. The degree of consistency is quite remarkable, even considering that the same predator, a barn owl, was responsible for the accumulation of almost all the assemblages.

In the eastern area the pattern of species representation of Roof Spall Lower was unusual, and general diversity is high for a relatively small sample. Some evidence suggests that the environment was less open and moister during deposition of eastern area sediments, but differences in micromammal populations between eastern and western facies of similar age could conceivably be linked to different hunting strategies of owls, sampling different micro environments near the cave.

Zelotomys was the most surprising find in PP13B and serves as a reminder that using habitat requirements of extant species to extrapolate that of their fossil relatives may be problematic. The presence of *Zelotomys* in PP13B deposits suggests that this species enjoyed a far wider distribution in the past, and adaptation to arid environments occurred recently in its evolutionary history. Apparently, prior to 92 ka, *Zelotomys* had very different ecological requirements to that of today.

On-going research into the micromammalian assemblages from other Pinnacle Point archaeological sites aims to place the PP13B micromammalian assemblages within context, and to provide a well elucidated continuum of how micromammal populations on the south coast reacted to paleoenvironmental and paleoclimatic change over time.

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APPENDIX A

The micromammal fauna from the eastern area of PP13B

	Surface sediments	Re-deposited Disturbance	Truncation Fill	Shelly Brown Sand	Upper Roof Spall	Lower Roof Spall	Section Cleanings
Thamnomys dolichurus						1	
Gerbilliscus afra					2	1	1
Mystromys albicaudatus						2	
Dendromus mysticalis						2	
Suncus varilla					2	2 *cf.* 2	cf.
Myosorex varius							2
Myosorex sp.						2	
Rhabdomys pumilio					1	1	
Otomys irroratus	1		1	1	3	3	1
Otomys saundersiae		1	4		6	3	
Myomyscus verreauxi	1				2		
Mus minutoides						2	
Crocidura flavescens	*					1	
Aethomy namaquensis			1				
O. saundersiae/O. irroratus					2		
Cryptomys hottentotus						1	
Indet. chrysochlorid					1	1	2
Indet. Chiroptera			1			1	

* = represented by teeth other than the M^1 or M_1, or by maxillary fragments.

The micromammal fauna from the northeastern area of PP13B

	LC-MSA Middle	LC-MSA Lower
Suncus sp.	1	2
Myosorex varius	2	1
Crocidura flavescens	0	3
Gerbilliscus afra	0	7
Mystromys albicaudatus	0	1
Rhabdomys pumilio	0	1
Otomys irroratus	4	13
Otomys saundersiae	3	24
Otomys unisulcatus	0	2
O. saundersiae/O. irroratus	0	7
Cryptomys hottentotus	0	1
Indet. bathyergid	0	1
Indet. chrysochlorid	0	1

Brachyceran assemblages (Insecta: Diptera) as indicators of terrestrial palaeoenvironments in the Late Mesozoic

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Introduction

Brachyceran flies are characterized by their high diversity, rapid evolution, broad distribution and rather frequent occurrence in fine-grained lacustrine sediments and in fossilised resins, but rarely in marine deposits. The diversification of brachyceran Diptera started during the Early Jurassic and continued successfully over the Middle–Late Jurassic, Cretaceous and the Cainozoic (Blagoderov *et al.* 2002). The confinement of brachyceran fly taxa to particular deposits, regions and time intervals make these flies useful in biostratigraphy and correlation of non-marine deposits. Indeed, several levels can be traced during the Jurassic and Cretaceous, where brachyceran faunas changed considerably. The stratigraphic position of these levels is sometimes unclear, and their confident correlation with units and boundaries of the International Stratigraphic Chart (Ogg *et al.* 2008) is not always possible. Alternatively, the composition of Mesozoic brachyceran faunas seems to be partially influenced by changing local or regional palaeoenvironments. Although there are some extinct families, most are extant. This presents an opportunity to use presumed ecological characteristics of their representatives for reconstructing palaeoenvironments at sites of their burial (e.g. Coram *et al.* 2000).

Material

Over 1000 brachyceran compression fossils and inclusions in fossilised resins from more than 60 Jurassic and Cretaceous localities worldwide have been examined (Figs 1, 2). Assemblages from the following oryctocoenoses (revealed death assemblages) have been considered the most representative and have been analysed numerically for the purpose of this study (Fig. 3): Karatau-Mikhailovka (southern Kazakhstan; Callovian–Kimmeridgian), 'basalmost Cretaceous of Mongolia' (several localities of similar age), Purbeck and Wealden (England; Berriasian–Barremian), Baissa (Transbaikalia; Valanginian–Hauterivian), Bon-Tsagaan (Mongolia; Barremian–Aptian), Obeshchayushchiy (Russian northern Far East; Cenomanian), Orapa (Botswana; Cenomanian–Turonian). Brief characteristics of localities and further references are provided elsewhere (Rayner *et al.* 1996; Zherikhin *et al.* 1999; Mostovski & Martínez-Delclòs 2000; Mostovski *et al.* 2000; Rasnitsyn & Quicke 2002; Brothers & Rasnitsyn 2003; Gernon *et al.* 2009). The figured specimens are deposited in the collections of the Paleontological Institute, Russian Academy of Sciences, Moscow (PIN), and the Bernard Price Institute for Palaeontological Research, University of Witwatersrand, Johannesburg (BP).

Results

Karatau-Mikhailovka

This locality yielded almost 500 identifiable remains of brachyceran flies that belong to the following families (Fig. 3A): Stratiomyidae (5 specimens or 1.1% of the total assemblage), Xylomyidae (1/0.2%), Xylophagidae *sensu lato* (66/13.9%), Rhagionidae (246/51.7%), Rhagionempididae (28/5.9%), ?Vermileonidae (1/0.2%), Archisargidae (22/4.6%), Eremochaetidae (5/1.1%), Kovalevisargidae (4/0.8%), Therevidae (37/7.8%), Asilidae (4/0.8%), Asiloidea fam. indet. (21/4.4%), Apystomyiidae (1/0.2%), Nemestrinidae (17/3.6%), Rhagionemestriidae (1/0.2%), Acroceridae (4/0.8%), Hilarimorphidae (1/0.2%), Scenopinidae (2/0.4%), Empididae: Protempidinae (9/1.9%), Eomyiidae (1/0.2%).

'Basalmost Cretaceous of Mongolia'

Several localities of a presumably similar age are listed under this name: Gurvan-Erenii-Nuru (10 Rhagionidae, 3 Eremochaetidae, 1 Bombyliidae, 3 Empididae), Hotont (1 Empididae), Hara-Hutul (1 Rhagionidae, 1 Therevidae, 1 Asiloidea indet., 9 Empididae), Manlay (1 Eremochaetidae, 1 Stratiomyidae), Myangad (1 Rhagionidae), Tsagaan-Tsav (2 Empididae), Ulaan-Tolgoy (1 Empididae). If assemblages from these localities are taken as one, the families' contributions are as follows (Fig. 3B): Stratiomyidae, 2.8%; Rhagionidae, 33.3%; Eremochaetidae, 11.1%; Bombyliidae, 2.8%; Empididae, 44.4%; Therevidae, 2.8%; Asiloidea indet. 2.8%.

Purbeck and Wealden

Purbeck and Wealden deposits of southern England yielded 51 identifiable brachyceran specimens. Deposits of the Lulworth Formation (Lower Purbeck) consisted of a depauperate assemblage consisting of Rhagionidae (2 specimens/33.3%), Athericidae (1/16.7%), Rhagionemestriidae (2/33.3%), and Empididae (1/16.7%). The Durlston Formation (Middle Purbeck) yielded Rhagionidae (11 specimens/61.1%), Tabanidae (1/5.6%), Empididae (5/27.8%), Opetiidae (1/5.6%). The Lower Weald Clay of England yielded Xylophagidae (1/4.8%), Rhagionidae (4/19%), Athericidae (1/4.8%), Empididae (15/71.4%); whereas the Upper Weald Clay brought Rhagionidae (2/33.3%), Athericidae (2/33.3%), Rhagionemestriidae (1/16.7%), Empididae (1/16.7%).

Baissa

This Lower Cretaceous Laggerstätt was sampled bed by bed (Zherikhin *et al.* 1999), and revealed a rich brachyceran fauna (221 specimens) (Fig. 3C): Stratiomyidae (6/2.7%), Rhagionidae (25/11.3%), Vermileonidae (1/0.5%), Tabanidae (1/0.5%), Athericidae (1/0.5%), Eremochaetidae (9/4.1%), Nemestrinidae (5/2.3%), ?Bombyliidae (2/0.9%), Mydidae (6/2.7%), Therevidae (1/0.5%), Asilidae (6/2.7%),

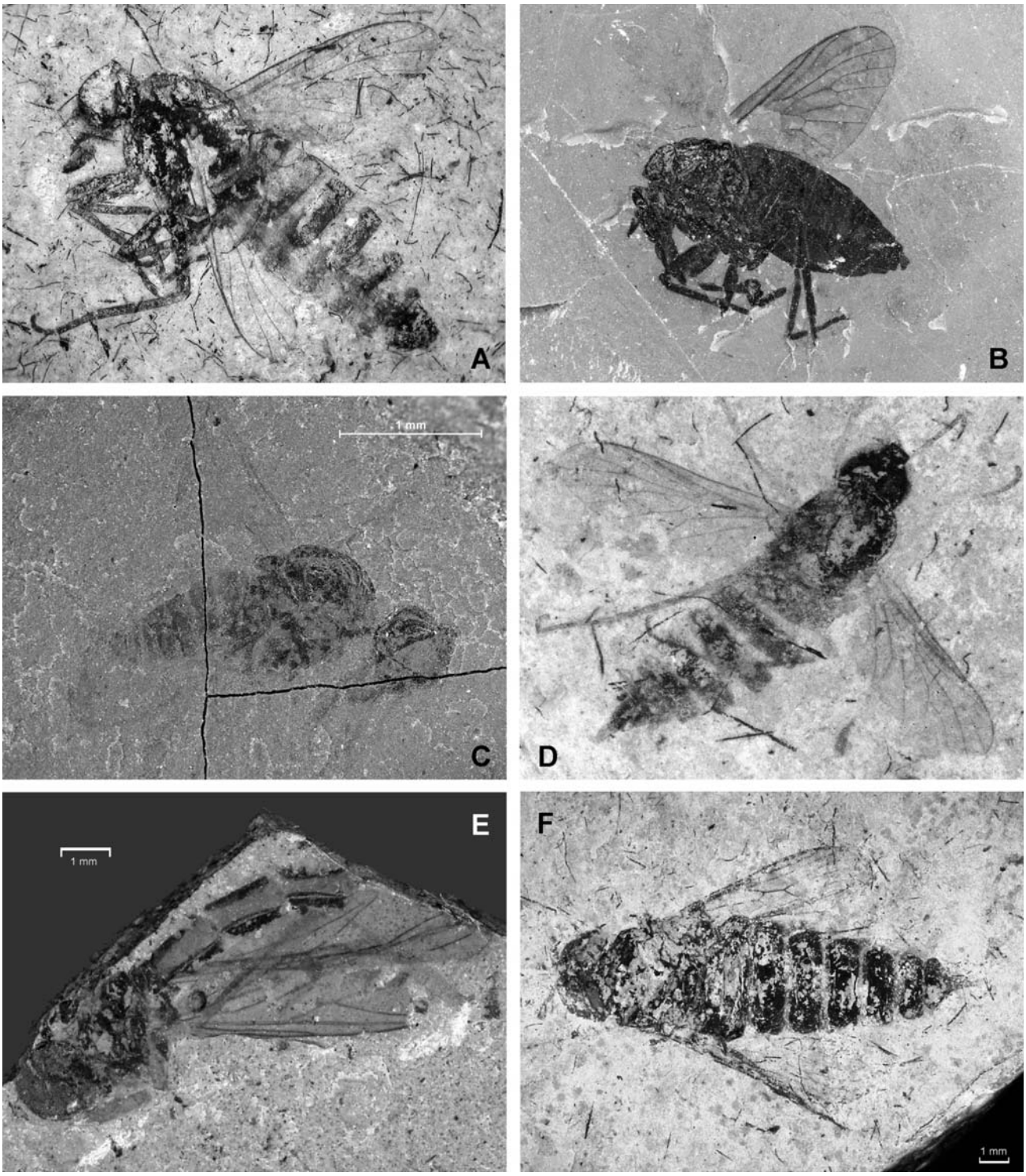


Figure 1. Compression fossils of Mesozoic brachyceran flies. **A**, *Protorhagio ponomarenkoi* Mostovski, 2008 (Rhagionidae), holotype PIN-2239/2182, Middle–Upper Jurassic of Karatau, Kazakhstan; **B**, *Palaeoarthroteles mesozoicus* Kovalev & Mostovski, 1997 (Rhagionidae), PIN-3063/1436, Upper Jurassic or Lower Cretaceous of Daya, Transbaikalia; **C**, Rhagionidae indet., BP/2/26852, Upper Cretaceous of Orapa, Botswana; **D**, *Probolbomyia modesta* Ussatchov, 1968 (Rhagionempididae), PIN-1789/120, Middle–Upper Jurassic of Karatau, Kazakhstan; **E**, *Eremomukha* (*Eremocreta*) cf. *sorosi* Mostovski, 1997 (Eremochaetidae), PIN-4210/5212, Lower Cretaceous of Baissa, Transbaikalia; **F**, *Archinemestrius litigiosus* Mostovski, 1998 (Nemestrinidae), holotype PIN-2784/79, Middle–Upper Jurassic of Karatau, Kazakhstan.

Asiloidea fam. indet. (5/2.3%), Hilarimorphidae (3/1.4%), Empididae (90/40.7%), Platypezidae (30/13.6%), Ironomyiidae: Sinolestinae (29/13.1%), ?Sciadoceridae (1/0.5%).

Bon-Tsagaan

This locality yielded 49 identifiable brachyceran specimens. The following brachycerans were found (Fig. 3D): Rhagionidae (7/14.3%), Eremochaetidae (3/6.1%), Rhagionemestriidae (1/2%), ?Bombyliidae (1/2%), Therevidae (2/4.1%), ?Mydidae (4/8.2%), Asiloidea fam. indet. (1/2%), Empididae (6/12.2%), Platypezidae (9/18.5%), Ironomyiidea: Sinolestinae (15/30.6%).

Obeshchayushchiy

Cenomanian deposits of this locality yielded the following brachyceran assemblage (89 specimens) (Fig. 3E):

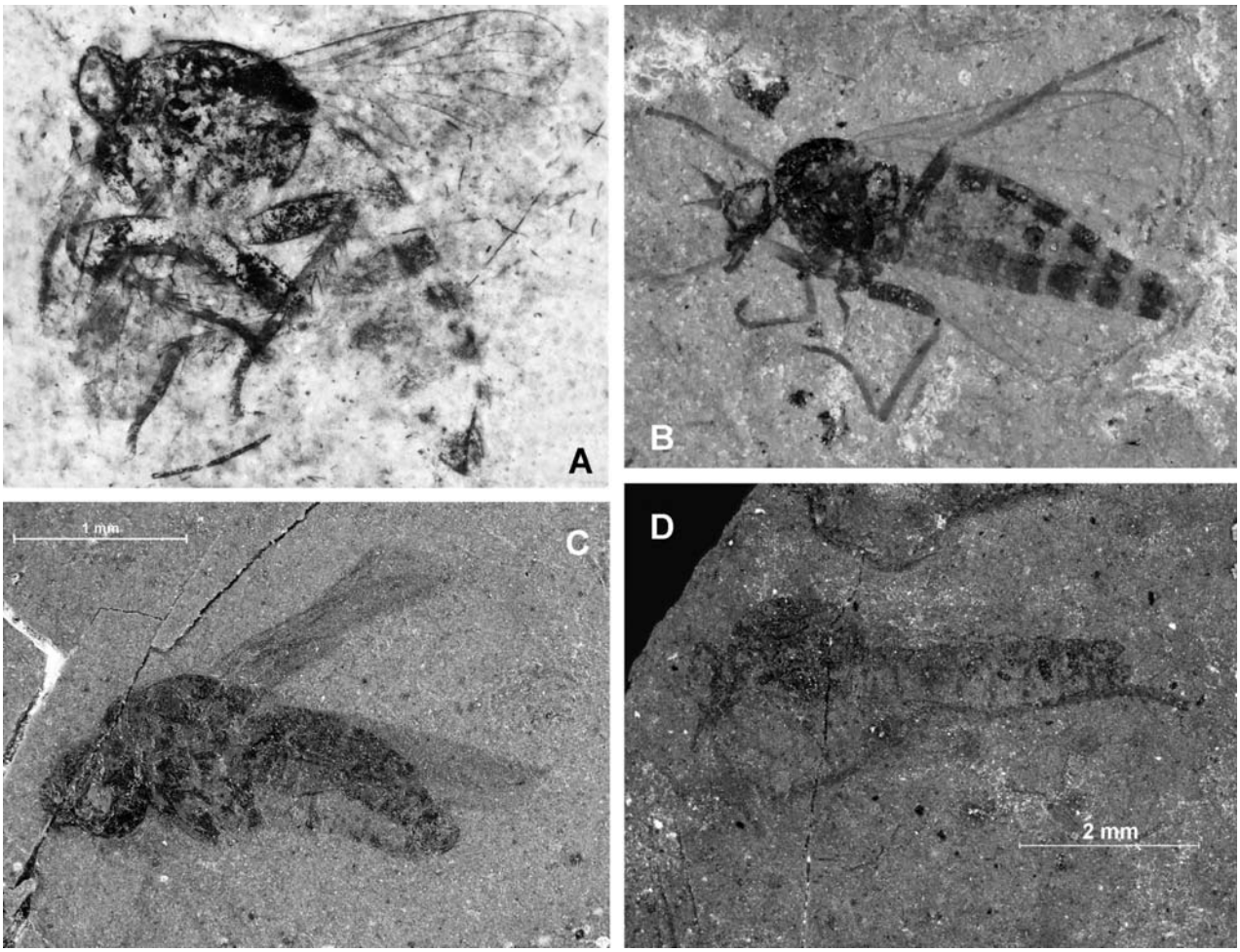


Figure 2. Compression fossils of Mesozoic brachyceran flies. **A**, *Rhagiophryne bianalis* Rohdendorf, 1964 (Therevidae), PIN-2997/3490, Middle–Upper Jurassic of Karatau, Kazakhstan; **B**, Empididae indet., PIN-4210/6375, Lower Cretaceous of Baissa, Transbaikalia; **C**, Empididae indet., BP/2/26872, Upper Cretaceous of Orapa, Botswana; **D**, Empididae indet., BP/2/25974, Upper Cretaceous of Orapa, Botswana.

Stratiomyidae (4/4.5%), Rhagionidae (3/3.4%), Asiloidea (5/5.6%), Empididae (39/43.8%), Platypezidae (3/3.4%), Ironomyiidae: Sinolestinae (27/30.3%), Platypezoidea indet. (7/7.9%), Phoridae: Prioriphorinae (1/1.1%).

Orapa

This is the only southern African Upper Cretaceous locality that has yielded a rich insect assemblage. Brachyceran flies are, however, scarce (12 specimens, Fig. 3F) and represented by almost only two families, Rhagionidae (3 specimens/25%; Fig. 1C) and Empididae (8/66.7%; Figs 2C, 2D), with one poorly preserved impression possibly belonging to Stratiomyidae (8.3%).

Discussion and conclusions

The above assemblages clearly differ from each other in their taxonomic composition and ratios of particular families. The Jurassic Karatau assemblage is distinctive in a high number of extinct families and the dominance of Rhagionidae; the rhagionids are exceptionally diverse and represented by archaic forms (Fig. 1A). The relative abundance of stiletto flies (Therevidae, 7.8%) (Fig. 2A) supports a reconstruction of a warm to hot and (semi)arid climate at that time; this is also confirmed by a minor share of Empididae, although they are represented in this locality by extinct Protempidinae which climatic preferences are uncertain. All other assemblages belong to a more advanced 'empidid' type, with the share of this family varying from 12–67%. The diversification of Empididae, as well as the appearance and diversification of Platypezidae and Ironomyiidae (Sinolestinae), are characteristics of the Cretaceous stage of dipteran evolution. Extant Empididae are predators; it has been noted that members of this family generally prefer mesic local environments, even in regions with generally arid or semi-arid climate (e.g. Smith 1969; Chvála 1983). Having assumed that ecological preferences of empidids have remained largely unchanged, their ratio in various assemblages was used to establish a relative humidity in corresponding palaeoenvironments. The first attempt to employ empidids in palaeoreconstructions for Purbeck and Wealden deposits, Baissa, Bon-Tsagaan and Obeshchayushchiy was made elsewhere (Coram *et al.* 2000). It has been shown that the empidid ratio increases in localities or during periods when warm and humid climate prevailed based on other studies. Empidids also dominate the Orapa assemblage (Figs 2C, 2D), although the latter is extremely poor in brachyceran fossils. However, this fully supports a previous reconstruction of a wet climate in the central Botswana at the beginning of the Late Cretaceous (Waters 1990; Rayner *et al.* 1991). The brachyceran assemblage of the basalmost

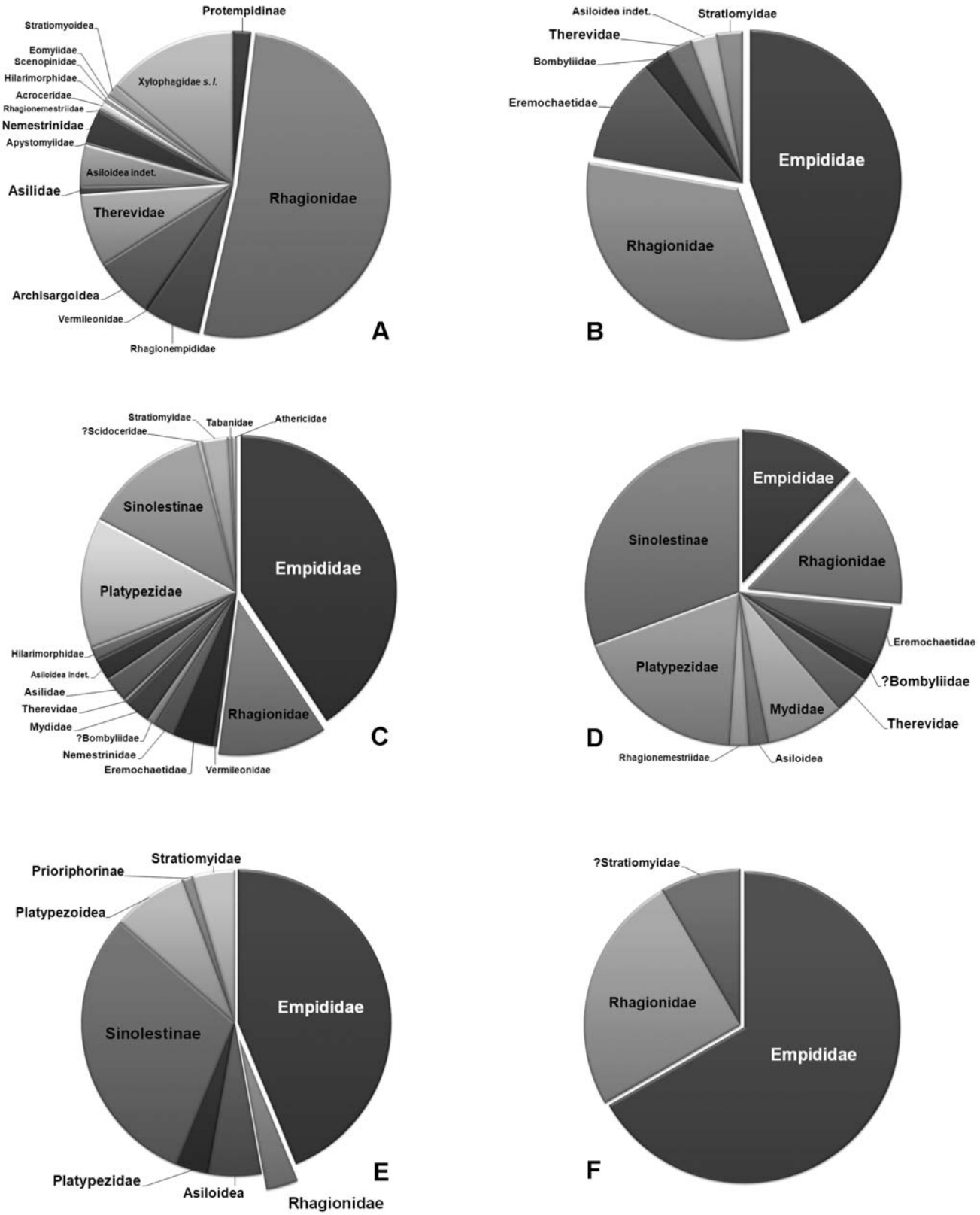


Figure 3. Composition of brachyceran assemblages in some Mesozoic localities. **A**, Callovian–Kimmeridgian Karabastau Formation of Karatau; **B**, 'basalmost Cretaceous of Mongolia'; **C**, Lower Cretaceous Zaza Formation of Baissa; **D**, Barremian–Aptian Hurilt Beds of the Bon-Tsagaan Group; **E**, Cenomanian Ola Formation of Obeshchayushchiy; **F**, Cenomanian–Turonian of Orapa.

Cretaceous of Mongolia is remarkable for its unusually high (for Cretaceous) share of Rhagionidae (33.3%), while Empididae still dominate (44.4%). Apparently, the rhagionids did not immediately lose their dominant position with the transition over the Jurassic/Cretaceous boundary. The high proportion of empidids suggests humid conditions near burial sites, which supports general palaeogeographic reconstructions (Zharkov *et al.* 1998).

Data collected at the Baissa locality all for reconstruction of the environmental conditions during the development of the palaeolake. Two main terrestrial insect fossil assemblages are recognized, one being restricted to the middle

part of the section (Beds 25 to 13) and another occurring in the lower part of the section and reappearing in the uppermost beds. Some aquatic insects demonstrate a similar distributional pattern. The mid-section assemblage is more diverse and enriched in more thermophilous taxa, and a warming episode during the deposition of the middle part of the section was postulated (Zherikhin *et al.* 1999). While empidids (Fig. 2B) constitute 40.7% of the total brachyceran assemblage in Baissa, their distribution in different parts of the section varies substantially. The family constitutes 34% in the the assemblage of the 'cold' beds (39–27 and 9–2), whereas it reaches 41% in the 'warm'-bed assemblage, with a maximum of 46% in Bed 22. Such a distribution suggests the transition from drier conditions to more humid environments during the history of the palaeolake. (The uppermost part – Beds 9–2 – is separated from the rest of the section by a fault, and its correct correlation remains debatable.) This interpretation contradicts data obtained from studies on cockroaches (Vršanský *et al.* 2002), where more warm and (semi)arid conditions were postulated for Beds 25–13 of the Baissa sequence. However, representatives of the family Empididae seem to be more sensitive to changes of humidity than to ambient temperatures, unlike cockroaches.

Other brachyceran flies do not show such strong climatic preferences, but may be indicative of other aspects of palaeoenvironments. Thus, long proboscid flies like Nemestrinidae (Fig. 1F) and Mydidae could act as pollinators (Labandeira *et al.* 2007). Parasitic flies were represented in the Late Mesozoic by the Archisargidae, Eremochaetidae, Acroceridae, Apystomyiidae, Bombyliidae *sensu lato,* and Nemestrinidae. Many Archisargidae and Eremochaetidae (Fig. 1E) had a contrasting colour pattern, apparently were good fliers capable of hovering, and possessed a needle-like ovipositor; representatives of extinct Nemestrinidae demonstrate shortened and elongated ovipositor, which suggests a broad spectrum of their hosts. Cretaceous flat-footed flies (Platypezidae) apparently were connected with fungi, like their modern representatives. Quite diverse Cretaceous Sinolestinae have been assigned to Ironomyiidae with some reservations; they share varying portions of the total dipteran fauna based on locality, which suggest a still unknown factor that might influenced their distribution. Rare were presumed haematophagous flies represented by Tabanidae, Athericidae and, possibly, some Rhagionidae; all dipterans with mouthparts adapted for bloodsucking are unknown before the Early Cretaceous (Lukashevich & Mostovski 2003). Ancient Asilidae show a remarkable general resemblance to present-day robber flies, which are predatory and prefer open, often dry landscapes. Extant Acroceridae are parasites of spiders, and an extreme rarity of acrocerids in the palaeontological record correlates well with the utmost rarity of spider compression fossils (Selden *et al.* 2009), although both phenomena can be explained taphonomically.

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Nannoplankton in the manganese deposits of the Mozambique Ridge and Mozambique Basin, southwestern Indian Ocean

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Introduction

During the SO-183 cruise of the RV *Sonne* (Jokat 2006), dredging of the Mozambique Ridge and the Jaguar seamount in the Mozambique Channel resulted in the collection of a suite of manganese nodules and encrustations (Watkeys *et al.* 2006). In this paper the age of the manganese mineralization is obtained from nannofossil assemblages that occur as cores to nodules, as basal layers to the manganese encrustations, and as interlayers within the encrustations. Nannofossils are proved to be very useful tool for the identification of the age of deposits (Bosman *et al.* 2007), especially when very small quantities of sediments are available for analysis.

Material and methods

The nannoplankton assemblages come from samples collected from three localities on the Mozambique Ridge and one on the Jaguar seamount. The preservation of nannofossils is generally good and moderate. Standard techniques of nannoplankton identification and description of assemblages were employed for all 21 samples (Bosman *et al.* 2007; Green *et al.* 2008). In this study we have used the most popular scheme by Gartner (1977) for Pleistocene biostratigraphic zonation. The definition of the Pliocene/Pleistocene boundary we recognize by the first occurrence of *Gephyrocapsa oceanica* s.l. (Green *et al.* 2008). The standard zonation by Martini (1971) has been used for the Pliocene interval. Rio *et al.* (1990) proposed a very detail Pliocene–Pleistocene zonation for the Mediterranean region.

Results and conclusions

Almost all samples contained representative nannoplankton assemblages, which include 62 species, with 10 species being reworked from Upper Cretaceous, Upper Oligocene, Middle Miocene, and Lower Pliocene (Table 1, Fig. 1).

In general, all samples can be referred to various parts of the interval of Zones NN15–NN21 (Gartner 1977; Martini 1971) or Zones MNN14–MNN21 (Rio *et al.* 1990), i.e. their origin can be dated by the Early Pliocene–Holocene.

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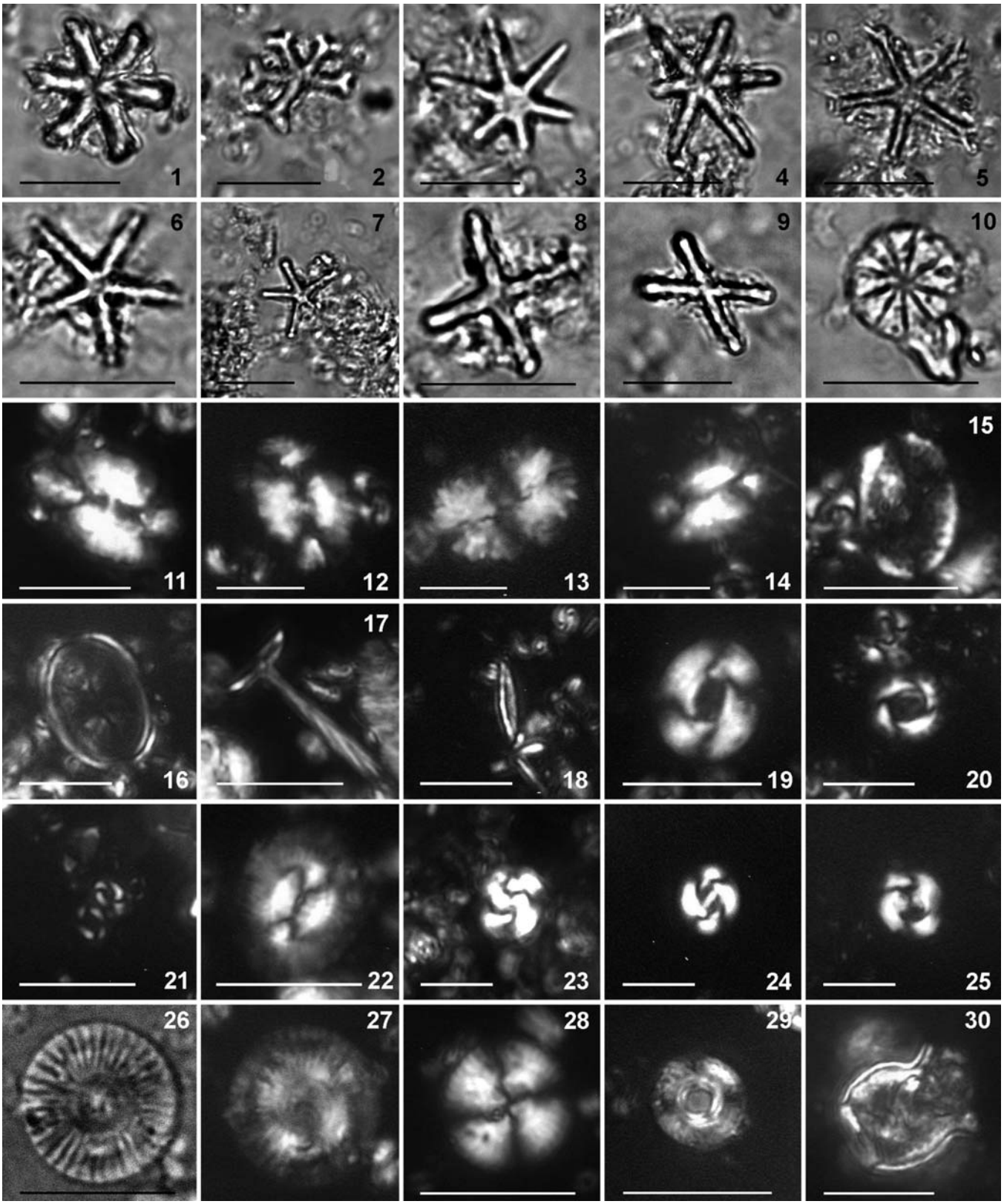


Figure 1. Calcareous nannoplankton from the Mozambique Ridge and the Jaguar seamount in the Mozambique Channel. All illustrations are light micrographs. The abbreviations 'pol' and 'tr' denote polarized and transmitted light, respectively. Scale bar of samples 1–10, 15, 17, 19, 22, 26–30 is 10 μm. Scale bar of samples 11–14, 16, 18, 20, 21, 23–25 is 5 μm. **1**, *Discoaster surculus,* sample 05–34, tr; **2**, *D. variabilis,* sample 05–34, tr; **3**, *D. brouweri,* sample 05–36, tr; **4**, *D.* cf. *brouweri,* sample 05–34, tr; **5**, *D. pentaradiatus,* sample 05–36, tr; **6**, *D. quinqueramus,* sample 05–34, tr; **7**, *D. asymmetricus,* sample 05–37, tr; **8**, *D. tamalis,* sample 05–36, tr; **9**, *D. blackstockae,* sample 05–43, tr; **10**, *Hayaster perplexus,* sample 05–34, tr; **11**, *Helicosphaera sellii,* sample 05–48, pol; **12**, *H. sellii,* sample 05–43, pol; **13**, *H. kamptneri,* sample 05–48, pol; **14**, *H. carteri,* sample 05–48, pol; **15**, *Pontosphaera discopora,* sample 05–43, pol; **16**, *Syracosphaera pulchra,* sample 05–38, pol; **17**, *Rhabdosphaera claviger,* sample 05–53, pol; **18**, *Scapholithus fossilis,* sample 05–34, pol; **19**, *Reticulofenestra pseudoumbilicus,* sample 05–34, pol; **20**, *Pseudoemiliania lacunosa,* sample 05–38, pol; **21**, *Emiliania huxleyi,* sample 05–01, pol; **22**, *Coccolithus pelagicus,* sample 05–36, pol; **23**, *Gephyrocapsa carribbeanica,* sample 05–53, pol; **24**, *G. oceanica,* sample 05–48, pol; **25**, *G.* sp., sample 05–48, pol; **26**, *Calcidiscus macintyrei,* sample 05–48, tr; **27**, *C. macintyrei,* sample 05–48, pol; **28**, *C. leptoporus,* sample 05–36, pol; **29**, *Umbilicosphaera sibogae,* sample 05–36, pol; **30**, *Scyphosphaera* cf. *globulata,* sample 05–37, pol.

Table 1. Taxonomic list of calcareous nannofossils from the samples of the manganese deposits of the Mozambique Ridge and Mozambique Basin with abundance (Liu *et al.* 1996) and preservation observations (Shafik *et al.* 1998). A, abundant; C, common; F, few; R, rare; RR, very rare; G, good; M, moderate; P, poor; r, reworked. Nannofossil Zones: H.s., *Helicosphaera sellii*; s.G., small *Gephyrocapsa*.

| Station | Average depth (m) | Sample | Preservation | *Amaurolithus* cf. *A. bizarrus* | *Amaurolithus delicatus* | *Calcidiscus leptoporus* | *Calcidiscus macintyrei* | *Chiasmolithus grandis* (reworked) | *Coccolithus miopelagicus* (reworked) | *Coccolithus pelagicus* | *Cribrosphaerella ehrenbergii* (reworked) | *Dictyococcites* sp. | *Discoaster asymmetricus* | *Discoaster berggrenii* (reworked) | *Discoaster blackstockae* | *Discoaster brouweri* | *Discoaster deflandrei* (reworked) | *Discoaster pentaradiatus* | *Discoaster quinqueramus* (reworked) | *Discoaster* sp. | *Discoaster surculus* | *Discoaster tamalis* | *Discoaster variabilis* | *Discoasteroides tubifera* | *Emiliania huxleyi* | *Fohsphaera profunda* | *Gephyrocapsa caribbeanica* | *Gephyrocapsa ericsonii* | *Gephyrocapsa oceanica* | *Gephyrocapsa* sp. | *Gephyrocapsa* sp. (large) | *Gephyrocapsa* sp. (small) | *Hayaster perplexus* | *Helicosphaera carteri* | *Helicosphaera kamptneri* | *Helicosphaera sellii* | *Helicosphaera wallichii* | *Kamptnerius magnificus* (reworked) | *Pontosphaera discopora* | *Pontosphaera japonica* | *Pontosphaera multipora* | *Pontosphaera* sp. | *Prediscosphaera cretacea* (reworked) | *Pseudoemiliania lacunosa* | *Reticulofenestra gelida* | *Reticulofenestra pseudoumbilicus* | *Reticulofenestra* sp. | *Reticulofenestra* sp. (small) | *Reticulofenestra umbilica* (reworked) | *Rhabdosphaera clavigera* | *Rhabdosphaera procera* | *Scapholithus fossilis* | *Scyphosphaera amphora* | *Scyphosphaera cantharellus* | *Scyphosphaera* cf. *globulata* | *Scyphosphaera pulcherrima* | *Scyphosphaera* sp. | *Sphenolithus moriformis* (reworked) | *Syracosphaera pulchra* | *Syracosphaera* sp. | *Thoracosphaera heimii* | *Thoracosphaera saxea* | *Umbellosphaera irregularis* | *Umbilicosphaera rotula* | *Umbilicosphaera sibogae* | Nannofossil zones (Gartner, 1977; Martini, 1971) | Nannofossil zones (Rio *et al.*, 1990) |
|---|---|---

Calcareous nannofossils from the stratotype section of the Upper Cretaceous Mzamba Formation, Eastern Cape, South Africa

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Introduction

Cretaceous deposits are scattered along the eastern and southern margins of South Africa (Shone 2006), partially filling the accommodation space provided when the Falkland Plateau was withdrawn from the Natal Valley during Gondwana break-up (Watkeys 2006). The Mzamba Formation is an Upper Cretaceous shallow-marine succession, which crops out in a narrow, discontinuous coastal strip from the north-eastern Eastern Cape to southern KwaZulu-Natal; it is equivalent to the St Lucia Formation of the coastal plain of northern KwaZulu-Natal (Dingle *et al.* 1983). The fossiliferous Mzamba Formation has been studied since 1853 (for review of previous works on Mzamba fossils see, for example, Kiel & Bandel (2003) and McMillan (2008)), but its exact age remains debatable. Klinger & Kennedy (1980) described the (u)Mzamba Formation formally and suggested its Middle Santonian–Early Campanian age, with the Santonian/Campanian boundary established in the middle of the section at the level corresponding to the boundary between Greyling's (1992) Beds N16 and N17. Using sequence stratigraphy, Greyling (1992) delineated the Santonian/Campanian boundary at the base of her Bed N13, having noted that the identification of this boundary is impeded due to the paucity of leading macrofossils in the deposit. McMillan (2003) gave a comprehensive review of foraminiferal stratigraphy of the Cretaceous successions in South Africa, including the Mzamba Formation. He proposed an Early Santonian age for the lower half of the formation, and an Early Campanian age for its upper half; however, the stratigraphic position of the unconformity that should exist between the Early Santonian and the Early Campanian parts was not established precisely but was suggested to lie within the interval between the top of Klinger & Kennedy's (1980) bed A7 and the base of bed A15 which corresponds to Greyling's (1992) beds N15–16 and N25. Recently, McMillan (2008) re-evaluated foraminiferal assemblages of the Mzamba Formation type section and suggested the Middle to Late Santonian age for the lower half of the lower Mzamba succession up to and including Klinger & Kennedy's (1980) bed A8; the position of the Santonian–Campanian boundary remained unclear due to inaccessibility to the relevant part of the section, but was suggested to lie between the beds A9 and A12 (effectively A15). The analysis of the calcareous nannofossils presented here adds to this stratigraphic conundrum and offers another variant of zonal sequencing in the stratotype section.

Materials and methods

The stratotype section (Greyling's (1992) sections N1 & N2, 31°06′13.6″S, 30°10′40.8″E; Fig. 1) was sampled on 11 May 2008 at low tide, which facilitated the access to the lowest beds. Samples were taken at 0.05–0.3–0.5 m intervals, except for the lowermost part of the succession that was covered with beach sand and the uppermost part, which was inaccessible at the time. Greyling's (1992) profile of the unit stratotype has been used to map samples (Fig. 2). The lowermost part of the sequence (samples 1/1–1/8) was sampled at an outcrop 60 m south of N1. Subsamples (*ca.* 100–200 g) were crushed and concen-

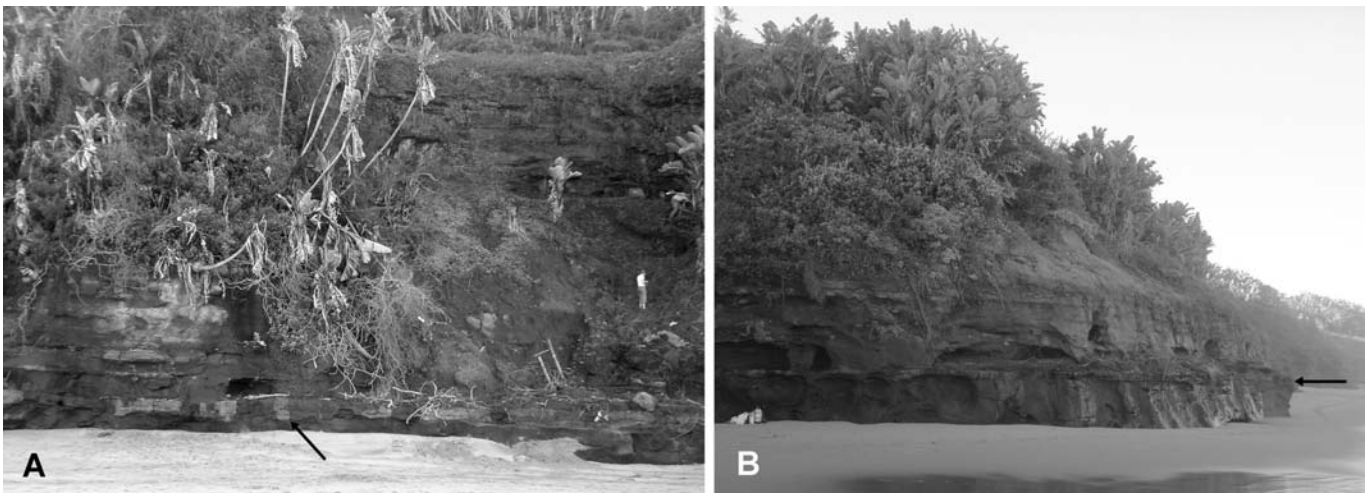


Figure 1. Cliff exposure of the lectostratotype of the Mzamba Formation: **A**, Greyling's N1 section; **B**, Greyling's N2 section. The level of Bed 7 is arrowed.

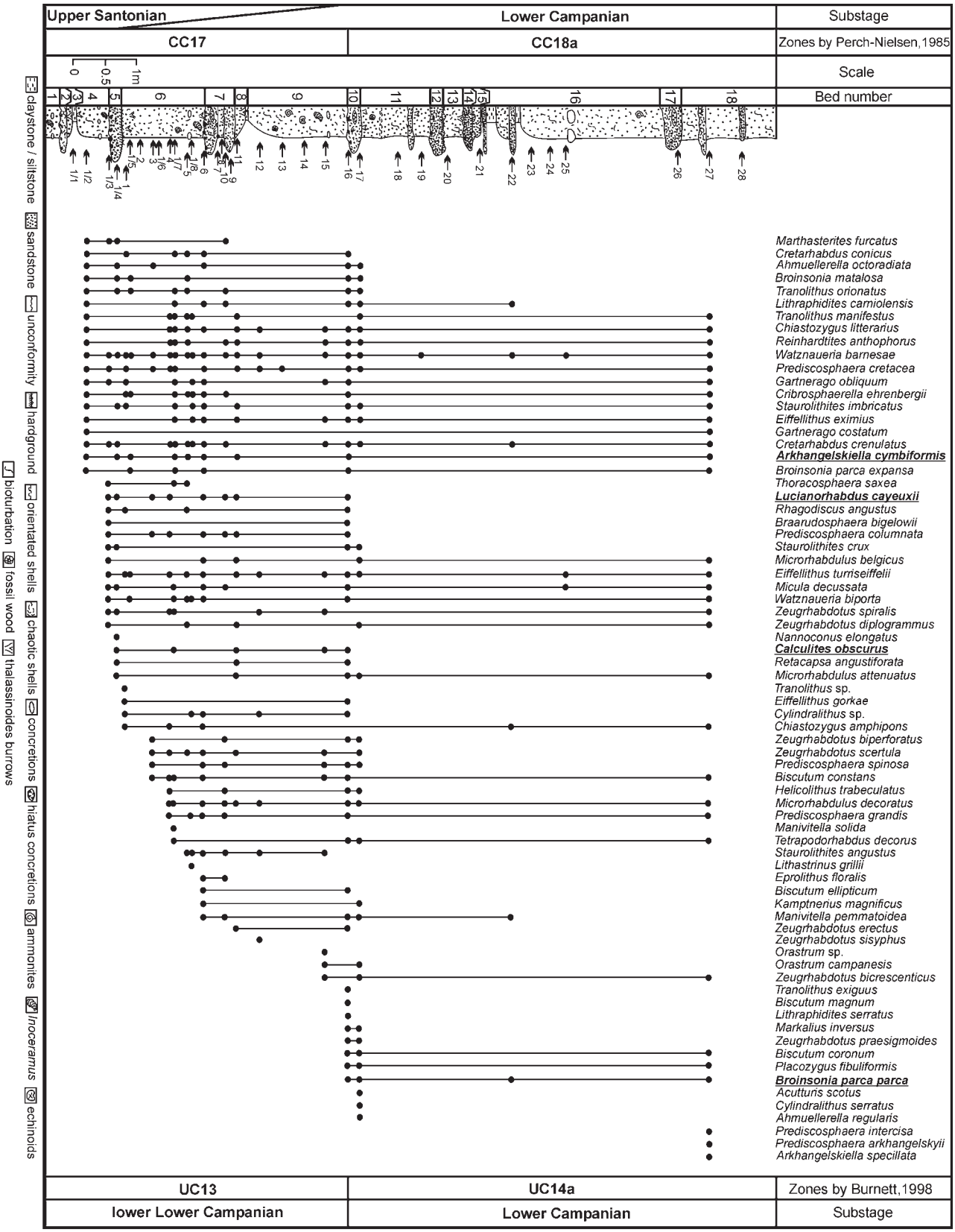


Figure 2. Distribution of calcareous nannofossils from the stratotype section of the Mzamba Formation. The unit stratotype profile is re-drawn after Greyling (1992).

trated, and smear slides (22 × 32 mm) were made in Canada Balsam (Ovechkina 2007). The slides were systematically examined for nannoplankton which was then identified and photographed using light microscope (Zeiss Axioskop) with crossed Nicols at ×1200–1920 magnification with immersion.

The calcareous nannofossil assemblage identified in the stratotype section of the Mzamba Formation includes 73 species (Figs 2–4). Nannofossils are well preserved but extremely rare throughout the section (1–5 specimens of each species per one smear slide). Samples 1/1, 1/6, 2, 7–9, 14, 18, 20, 21, 23, 24, 26, 28 yielded no nannofossils.

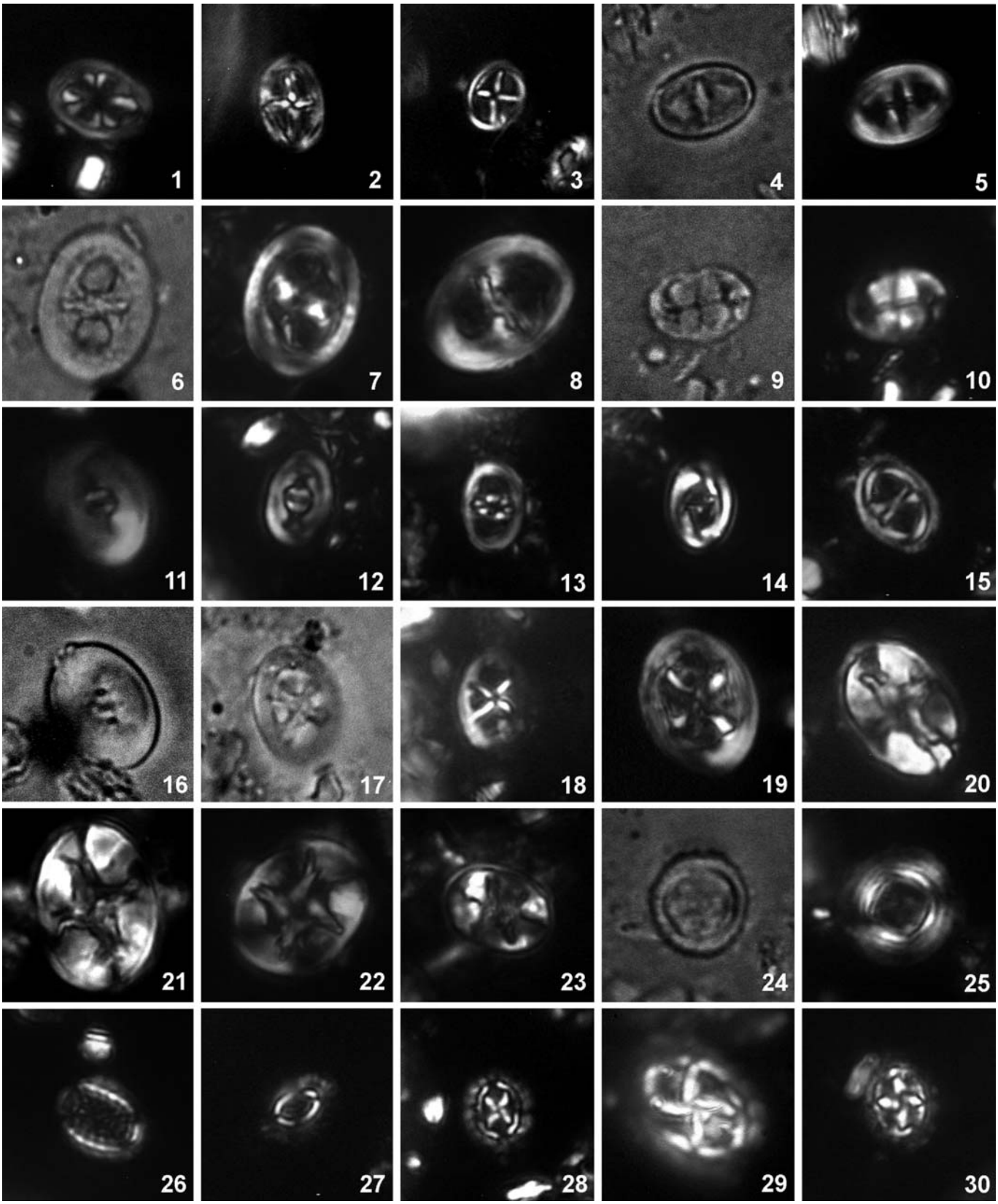


Figure 3. Calcareous nannoplankton from the Mzamba Formation. All illustrations are light micrographs. Abbreviations 'pol' and 'tr' denote polarized and transmitted light, respectively. The magnification for all images is ×2300. **1**, *Ahmuellerella octoradiata,* sample 16, pol; **2**, *Staurolithites imbricatus,* sample 17, pol; **3**, *S. crux,* sample 16, pol; **4**, *Tranolithus manifestus,* sample 17, tr; **5**, *T. manifestus,* sample 17, pol; **6**, *Reinhardtites anthophorus,* sample 16, tr; **7**, *R. anthophorus,* sample 16, pol; **8**, *Zeugrhabdotus scertula,* sample 15, pol; **9**, *Tranolithus orionatus,* sample 16, tr; **10**, *T. orionatus,* sample 16, pol; **11**, *Zeugrhabdotus biperforatus,* sample 17, pol; **12**, *Z. bicrescenticus,* sample 17, pol; **13**, *Z. erectus,* sample 16, pol; **14**, *Z. spiralis,* sample 15, pol; **15**, *Placozygus fibuliformis,* sample 17, pol; **16**, *Zeugrhabdotus biperforatus,* sample 17, tr; **17**, *Chiastozygus amphipons,* sample 27, tr; **18**, *Ch. amphipons,* sample 27, pol; **19**, *Ch. litterarius,* sample 17, pol; **20**, *Eiffellithus eximius,* sample 16, pol; **21**, *E. eximius,* sample 17, pol; **22**, *E. turriseiffelii,* sample 15, pol; **23**, *E. gorkae,* sample 16, pol; **24**, *Cylindralithus serratus,* sample 17, tr; **25**, *C. serratus,* sample 17, pol; **26**, *Cribrosphaerella ehrenbergii,* sample 10, pol; **27**, *Biscutum magnum,* sample 16, pol; **28**, *Prediscosphaera cretacea,* sample 6, pol; **29**, *P. grandis,* sample 16, pol; **30**, *P. spinosa,* sample 10, pol.

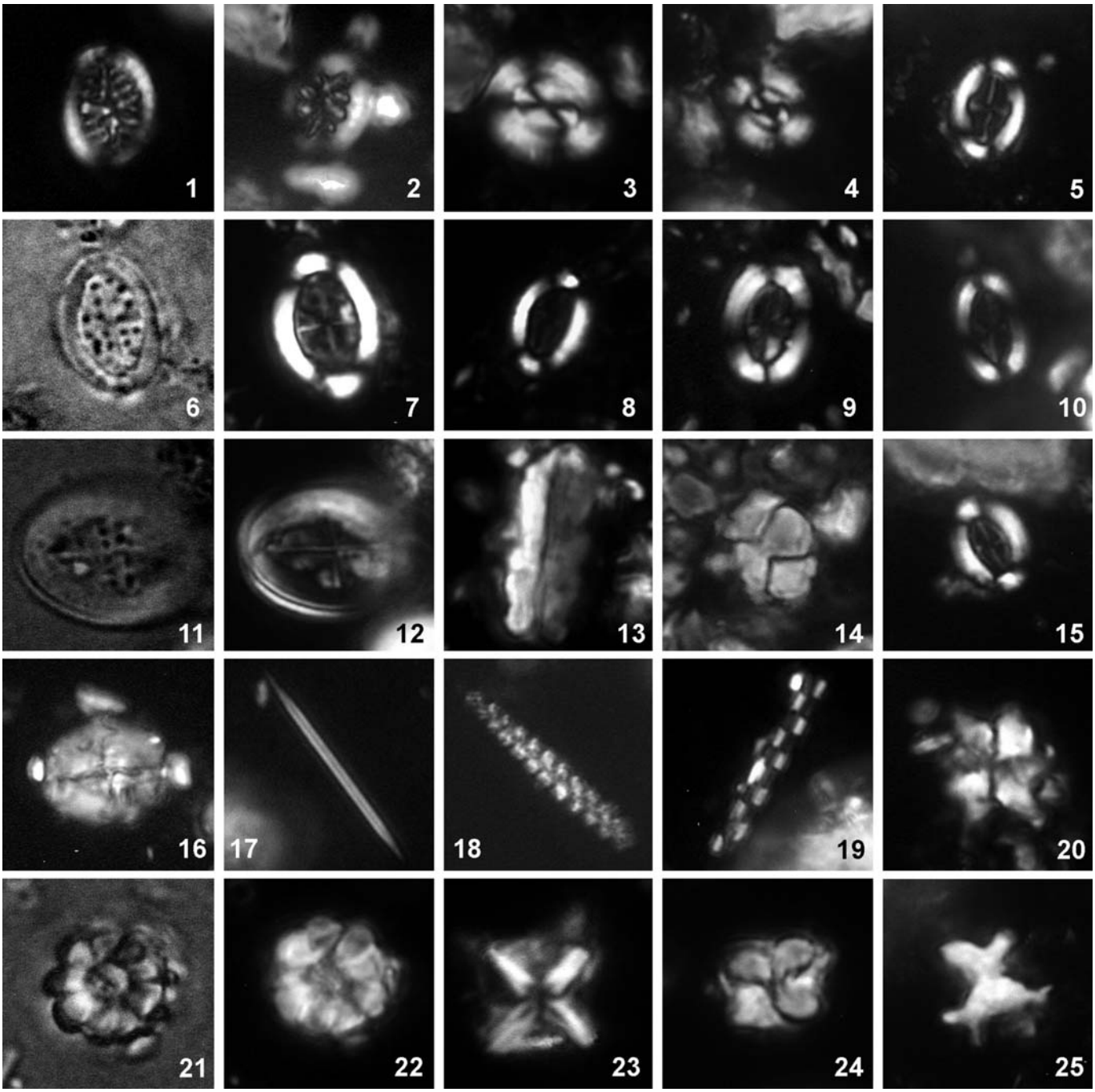


Figure 4. Calcareous nannofossils from the Mzamba Formation. Abbreviations as in Fig. 3. The magnification for all images is ×2300. **1**, *Cretarhabdus crenulatus,* sample 16, pol; **2**, *Retacapsa angustiforata,* sample 16, pol; **3**, *Watznaueria barnesae,* sample 27, pol; **4**, *W. biporta,* sample 16, pol; **5**, *Broinsonia matalosa,* sample 16, pol; **6**, *Arkhangelskiella cymbiformis,* sample 6, tr; **7**, *A. cymbiformis,* sample 6, pol; **8**, *Broinsonia parca expansa,* sample 1/7, pol; **9**, *B. parca parca,* sample 16, pol; **10**, *B. parca parca,* sample 16, pol; **11**, *Gartnerago obliquum,* sample 6, tr; **12**, *G. obliquum,* sample 6, pol; **13**, *Lucianorhabdus cayeuxii,* sample 10, pol; **14**, *Calculites obscurus,* sample 11, pol; **15**, *Broinsonia parca parca,* sample 17, pol; **16**, *Orastrum campanensis,* sample 17, pol; **17**, *Lithraphidites carniolensis,* sample 17, pol; **18**, *Microrhabdulus belgicus,* sample 17, pol; **19**, *M. decoratus,* sample 10, pol; **20**, *Lithastrinus grillii,* sample 1/8, pol; **21**, *Eprolithus floralis,* sample 6, tr; **22**, *E. floralis,* sample 6, pol; **23**, *Micula decussata,* sample 27, pol; **24**, *M. decussata,* sample 6, pol; **25**, *Marthasterites furcatus,* sample 1/3, pol.

Stratigraphy

The standard nannoplankton zonation by Sissingh (1977) with additions by Perch-Nielsen (1985) and the zonal scheme by Burnett (1998) have been used for biostratigraphic sequencing of the Mzamba succession.

According to Perch-Nielsen (1985), the lower part of the section (samples 1/2–1/8 & 1–15; Beds 4–9) may be referred to the transitional Upper Santonian–Lower Campanian Zone CC17, which lower boundary is demarcated by the first occurrence of *Calculites obscurus* (Fig. 4.14). The first record of this species in the Mzamba section has been detected at the level of sample 1/4. This species is absent from samples 1/2 and 1/3, which, however, may be explained by the rarity of nannofossils in the section. Alternatively, the lowermost part of the section (prior to sample 1/4) can be assigned to Upper Santonian Zone CC16, but we refrain from doing so at this stage: although *C. obscurus* has not been found in this part of the section, *Arkhangelskiella cymbiformis,* which usually appears later, has been recorded in sample 1/2.

Beds 10–18 (samples 16–27) belong to the Lower Campanian Subzone CC18a due to the presence of *Broinsonia parca parca* (Figs 4.9, 4.10, 4.15), the first occurrence of which is recorded in sample 16.

According to Burnett (1998), the lower part of the section (samples 1/2–1/8 & 1–15; Beds 4–9) should be referred to the lower Lower Campanian Zone UC13 due to the presence of *Arkhangelskiella cymbiformis* (Figs 4.6, 4.7), the first appearance of which delineates the lower boundary of this zone. In the Boreal Province and Boreal-intermediate Province, Burnett subdivides this zone into two subzones and delineates their boundary by the consistent first occurrence of *Orastrum campanensis.* However, this species has not been found at low or high-southern palaeolatitudes (Burnett 1998; Lees 2002), and Burnett (1998) recognized no subzones in UC13 for the Tethyan-intermediate Province. We have detected *Orastrum campanensis* in samples 15 & 17 (Fig. 4.16), which is the first record of this species in southern hemisphere. Its first occurrence (sample 15) is situated below the level of the first occurrence of *Broinsonia parca parca,* which does not contradict Burnett's (1998) scheme for the Boreal and Boreal-intermediate provinces.

The upper part of the section (samples 16–27; Beds 10–18) refers to the Lower Campanian Subzone UC14a due to the first appearance of *Broinsonia parca parca* in sample 16.

Thus, according to available data from calcareous nannofossils the Santonian–Campanian boundary is either absent from the section at all, or situated within the interval between the visible base of the section and the base of Greyling's (1992) Bed 10. In both cases its position is lower than the boundary drawn by Greyling (1992) and considerably lower than the position of the boundary proposed on the basis of research done on ammonites (Klinger & Kennedy 1980) and foraminiferans (McMillan 2003, 2008).

Palaeoenvironments

Despite the species diversity and good preservation, nannofossils are extremely rare throughout the section, with 14 samples being entirely empty. This suggests that palaeoenvironmental conditions were generally unfavourable for the development of the calcareous nannoplankton. This assumption corroborates well with the hypothesis offered by McMillan (2008), who interprets the general setting at Mzamba to be within the mud belt and in proximity of active river systems.

Given the scarcity of the calcareous nannoplankton in the discussed deposits in general, noteworthy is its distribution within the type section. Species occur more frequently in the lower part of the section (samples 1/2–1/8 & 1–17, except for samples 13 & 14; Beds 4–10). This part is followed by a 'gap' with few nannofossils (samples 18–26; Beds 11–17). The reappearance of a rich assemblage has been detected in sample 27 (bottom part of Bed 18). This distributional pattern is intriguing, since it does not coincide with the detected zonal boundaries at the level of sample 16. It must have an explanation in the depositional environment or in diagenetic processes involved (Liu & Greyling 1996), and needs further investigation.

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Stratigraphic ranges of *Tapinocephalus* Assemblage Zone dicynodonts: implications for middle Permian continental biostratigraphy

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The rocks of the Karoo Supergroup of South Africa preserve the world's best record of continental Permian to Jurassic faunal biodiversity. The long temporal range of the rocks of the Supergroup, and their rich fossil record, has enabled studies of biodiversity over this extended time, particularly in relation to the Permo-Triassic mass extinction event (e.g. Smith & Ward 2001; Retallack *et al.* 2003), and enhanced understanding of the evolution of important tetrapod lineages, particularly reptiles and synapsids. A rich tetrapod record has allowed biostratigraphic subdivision of these rocks into seven Permian and two Triassic biozones (Rubidge 1995) which have served as the basis for global correlation of Permian–Triassic continental sedimentary deposits. In the absence of reliable radiometric dates for the Beaufort Group, recent enhanced basin development models for the Karoo have been reliant on biostratigraphic refinements.

While much recent research has been undertaken on refining the biostratigraphic ranges in the Middle (Botha & Smith 2006) and Upper (Hancox 2001; Neveling *et al.* 2005) Beaufort Group, biostratigraphic refinement of the Lower Beaufort has been more difficult. This is because of the relative paucity of tetrapod fossils in the lowermost Beaufort Group, the difficulty in extracting them from very hard matrix, and the complex nature of the folding of these rocks in the southern Karoo.

With the recognition of an extinction in the marine realm at the end of the Guadalupian, we aim to determine whether an equivalent occurred in the terrestrial realm. As the lower Beaufort Group is one of the few fossil-bearing terrestrial depositional basins which has the possibility of recording this event, an understanding of lithostratigraphy and the biostratigraphic ranges of tetrapods in this stratigraphic interval is critical. Lithostratigraphic subdivision of the lower Beaufort has been the subject of several publications (e.g. Stear 1980; Le Roux 1985; Jordaan 1990; Loock *et al.* 1994) but the complex nature of the folding as well as lateral facies changes have made lithostratigraphy difficult to apply. It is thus essential to develop a reliable biostratigraphic scheme.

Boonstra (1969) tabulated the relative numbers of lower Beaufort tetrapod families and their biostratigraphic ranges, suggesting that the *Tapinocephalus* Zone could be divided into a lower, middle and upper unit. He pointed out that the lower unit has a relative abundance of dinocephalians relative to dicynodonts, whereas the reverse applies to middle unit (corroborating the observation of Rossouw & De Villiers (1953)) and dinocephalians are completely absent in the uppermost unit. Keyser & Smith (1977/78) refined this by providing stratigraphic ranges of certain taxa. They also subdivided the *Tapinocephalus* Zone of Boonstra into a lower Dinocephalian Assemblage Zone, and an upper *Pristerognathus* Assemblage Zone and mapped out these units in the area West of longitude 26 degrees east. Loock *et al.* (1994), after extensive biostratigraphic and lithostratigraphic research in the Moordenaars Karoo, were able to corroborate the three units of Boonstra and correlated these with lithostratigraphic units. Rubidge (1990, 1995) recognized the presence of a new biozone, the *Eodicynodon* Assemblage Zone below the *Tapinocephalus* Assemblage Zone. Fossil collecting in the lowermost Beaufort over the past two decades with a view to biostratigraphic refinement has shown that the Beaufort–Ecca contact is diachronous (Rubidge 2005), with the earliest terrestrially deposited rocks of the Beaufort Group being limited to the area between Rietbron and Laingsburg in the southwestern part of the basin.

In the lower Beaufort, herbivorous dinocephalians, dicynodonts and pareiasaurs are the most abundant tetrapod fossils and offer the best possibility as biozone indicators. However, the large size of dinocephalians and pareiasaurs, and the fact that they are less abundant than dicynodonts, make the latter the best possibility. In addition recent taxonomic refinement of lower Beaufort dicynodonts (Cluver & Hotton 1981; Cluver & King 1983; Keyser 1993; King & Rubidge 1993) and the recent description of several new genera (Modesto *et al.* 2002, 2003) has facilitated use of dicynodonts as biostratigraphic indicator genera.

Ongoing stratigraphic collecting in the lower Beaufort and the inclusion of reliably identified dicynodonts on stratigraphic sections has led to the recognition of trends in the stratigraphic distribution of certain dicynodont genera. In addition, the recent production of a GIS database of all fossil tetrapods of the Beaufort Group (Nicolas 2007) has further facilitated understanding of the geographic distribution of different dicynodont genera.

The following distribution of dicynodonts has been observed immediately above the Ecca-Beaufort contact around the basin: *Eodicynodon* is geographically restricted to the southwestern part of the Beaufort Group; further northwards, five specimens of *Colobodectes* have been found between Sutherland and Carnavon, while still further northwards *Robertia* is present as far as Phillipolis. Following Walther's Law the same stratigraphic pattern would be expected in the southern Karoo where the most complete stratigraphic succession of the *Tapinocephalus* Assemblage Zone is present. *Eodicynodon* is restricted to the lower 1100 m of the Beaufort Group in the southern Karoo (Jinnah & Rubidge 2006), but so far no *Colobodectes* specimens have been reported from this area. *Robertia* first appears after the last occurrence of *Eodicynodon,* and occurs upwards into the *Pristerognathus* Assemblage Zone. The stratigraphic range of *Diictodon* begins about 1900 m from the base of the Beaufort, overlaps with the upper range of *Robertia* and continues up to the end of the *Dicynodon* Assemblage Zone.

ISSN 0078-8554 *Palaeont. afr.* (December 2009) **44**: 134–135

Our recent discovery of dateable volcanic ash layers in the lower Beaufort as well as the application of palaeomagnetic dating in these rocks offers additional opportunities for correlating fossils in the lower Beaufort and providing insight on the rate of evolution of the earliest therapsids as well as faunal turnover and diversity pulses in the Middle Permian.

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Continental displacement: early lines of evidence that deserve attention

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Palaeontologists, particularly those with Gondwanan distribution, are entitled to be irritated by the frequent dismissal of A. Wegener's Continental Drift (more correctly Continental Displacement), as an inadequate hypothesis which only came to maturity in the 1960s with the advent of 'Plate Tectonics'. The excuse is made that Plate Tectonics provided a mechanism missing from Wegener's concept. But, as has been pointed out (e.g. Rastall 1929), Fold Mountains and Ice Ages were accepted as real phenomena before mechanisms were postulated. Furthermore, sea-floor spreading, crucial to Plate Tectonics was not a new idea. Osmund Fisher in 1881, in his 'Physics of the Earth's Crust' had argued for convection in the mantle. O. Ampferer in 1906 introduced a 'subfluction' theory of the origin of folds. J. Joly had in 1923 pointed out that crustal radioactivity might provide subcrustal heat, so promoting crustal movement. G.A.F. Molengraaff in 1916 referred to the Mid Atlantic Ridge in connection with Wegener's Continental Displacement. In doing so, he initiated the concept of sea-floor spreading. In 1928 he recognized a 'Rift Valley' in the Mid Atlantic Ridge. In the same year O. Pratje analysed echo-sounding observations of the Atlantic sea floor, and referred to Wegener, while Arthur Holmes published on a convection concept which included subduction of edges distal to a hot plume. K. Wadati in 1928 published an extensive study of deep earthquakes at the margin of a continent, clearly associated with subduction; he referred to Wegener. O. Pratje's observations of the ruggedness of the Atlantic sea-floor, accorded with gravitational measurements made from submarines in several oceans from 1923 by F.A. Vening-Meinesz, using a precision double-pendulum he had invented. In 1959 H. Korn and H. Martin published a description of folds in southwestern Africa, where two series of folds, mostly detached from the original stratum in each case, were separated by a layer of dolomite without folds. They concluded that folding was caused by movement under gravity on a gentle slope. This suggests that gravity might be involved in sea-floor spreading and continental displacement. That Plate Tectonics itself is subject to revision is suggested by the title of A. Ribeiro's 2002 book '*Soft Plate and Impact Plate Tectonics*' and the use of the terms 'schizosphere' and 'plastosphere.'

Palaeontology provided most of the evidence for Continental Displacement. Between 1815 and 1841 the Geological Periods were recognized and named. Comparisons could be made between the palaeofloras and palaeofaunas of different regions. In 1843 C. Lyell compared the Carboniferous plant fossils of Europe and North America. E. Forbes in 1846 and 1859 noted contiguous faunas of littoral molluscs between the continents, and S.V. Wood, in 1862, noted distinct Miocene marine mollusca on either side of a land bridge between Europe and Northern America. In 1870 T.H. Huxley compared Miocene mammals of the two continents, and concluded that there had been a substantial land connection. He noted as probable that his Austro-Columbia (South and Central America plus southern parts of North America) was separated from North America during the Miocene.

A fossil flora, named the *Glossopteris* flora for characteristic leaves, was described for peninsular India in 1828 by A.T. Brongniart. That *Glossopteris* lived in a temperate region was indicated by their apparent deciduous habit, with an abscission zone at the base of the leaf, which cut off the supply of sap before the leaf was shed. Wood found in the same deposits showed annual rings, this despite the proximity of the site to the equator, unlike the distance from the equator of the floras studied by Lyell, which appeared to be at least subtropical, although only slightly older. In 1875 an article by H.F. Blandford was accompanied by discussion of whether the layers below the *Glossopteris* flora were glacial. The *Glossopteris* flora had been reported in Australia in 1847 by F. McCoy, in South Africa in 1867 by R. Tate, and in South America in 1869 by W. Carruthers. In 1885 E. Suess conceived Gondwana, a region which had in common a *Glossopteris* flora. As the parts of Gondwana all had glacial strata below the common flora, A. Wegener, who was a researcher on polar weather and climate, in 1912 conceived the idea of grouping the parts of Gondwana together around the South Pole. It might have been predicted that the *Glossopteris* flora would also have existed on Antarctica. Such a flora was reported for Antarctica by A. Seward in 1914. Any alternative to Continental Displacement would require explanation of the distribution of the *Glossopteris* flora sites between a southern polar region across the equator to a northern tropical region.

A.L. du Toit in 1921 studied the late Carboniferous glaciation in southern Africa. Rocky material in the flowing ice causes striations in the strata over which it passes, and features such as 'chatter marks' indicate the direction of movement. 'Glacial pavements' in the south-east indicated flow from the east. Since glaciers only form on land, there must have been land to the east of Africa. In 1974 M.R. Cooper and R. Oosthuizen, reported erratics in Dwyka tillite from near Prince Albert in the southern Cape of South Africa that contained pieces of coral-like *Archaeocyathia* apparently from Antarctica.

W.T. Blanford in 1890 discussed the question of the permanence of ocean-basins on the basis of palaeobiogeography.

P. Gervais in 1864 described a Lower Permian aquatic reptile from South Africa, and named it *Mesosaurus tenuidens,* from its numerous, slender, very long teeth. An obviously similar genus, *Stereosternum,* was described from Brazil by E.D. Cope in 1886, and a species of *Mesosaurus* from Brazil by J.H. McGregor in 1908. The moderate size of the animals suggested very strongly that they were not animals of the open sea. This was also suggested by associated sediments that indicated fossilization in anaerobic carbonaceous mud, probable in an

ISSN 0078-8554 *Palaeont. afr.* (December 2009) **44**: 136–138

embayment. The discovery of insect fossils in the same Formation, the Whitehill Formation, a few metres above the *Mesosaurus*, accords with proximity to land (mostly unpublished, but including Geertsema & van den Heever 1996).

F. Ameghino in 1891 described a fossil marsupial from Argentina, which he named *Prothylacynus patagonicus*, and which he compared to the living Tasmanian predator *Thylacynus*. No comparable fossils were known from the well-studied Palaearctic and Nearctic of North America, Europe and Asia, and none were later discovered. A direct connection between Patagonia and the Australian region was indicated. *Microbiotherium* Ameghino 1887 provided a valid taxon for such a study.

H. von Ihering from 1889 studied living and fossil freshwater molluscs, notably in South America. In 1890 and 1891 he distinguished old widespread taxa, young taxa common to Australasia and western South America, and still younger taxa which included some found also in North America. In 1891 he noted different flat worms (Temnocephala) on the molluscs on the two sides of the Andes and conceived the idea of using symbionts and parasites as biogeographic guides to dispersal. In 1904 F. Zschokke was able to place a tapeworm, from a South American marsupial, sent to him by von Ihering, in a genus known from an Australian marsupial. Harrison in 1928 reviewed applications of the technique in evaluating Wegener's hypothesis.

Palaeomagnetic data from strata of separate continents of different ages, can establish apparent pole-wandering curves, which can be used to locate and orientate the continents at various points in time. However, it was only after Holmes had shown in 1947 that absolute radiochronology coincided well with stratigraphy, that such curves could reliably be constructed, mainly from dateable igneous intrusions. P-L. Mercapton in 1926 referred to Wegener in his palaeomagnetic studies in Greenland and Australia. Data for pole-wandering for Europe and North America were available well before they were used.

A.L. du Toit in 1921 gave a public lecture which was published, in which he summarized much evidence of the Gondwanan relationships of South Africa, and in 1937 published a book dedicated to Wegener's memory.

G. Nelson and P.Y. Ladiges (2001) has a valuable discussion of opposition to acceptance of Continental Displacement as explanation of palaeobiogeography and biogeography.

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ABSTRACTS

Trends in metazoan body size, burrowing behaviour and ichnodiversity across the Precambrian–Cambrian boundary: ichnoassemblages from the Vanrhynsdorp Group of South Africa

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Rich assemblages of small-bodied metazoans with mineralized skeletons first appeared during the Early Cambrian, notably from the Tommotian Stage onwards (= 530 Ma). Several less diverse 'small shelly fossil' (SSF) assemblages have been recorded from the earliest Cambrian interval (Manykaian Stage). A very limited range of older shells are known from the latest Proterozoic or Ediacaran Period. They include calcified cone-in-cone and flask-shaped skeletons (*Cloudina, Namacalathus*), sandy agglutinated tubes (*Archaeichnium*), and colonial aggregations of tubules (*Namapoikia*), all of which were first recorded from limestones and siliciclastic sediments of the latest Ediacaran Nama Group of Namibia and the South Africa (key references in Frimmel *et al.* 1998; Grotzinger *et al.* 2000; Wood *et al.* 2002). Primitive sponge-like animals (*Otavia*) have been isolated from Otavi Group limestones in Namibia that are older than 720 Ma (Cryogenian Period) as well as from much younger Ediaracan horizons in the Nama Group (Brain *et al.* 2008, this volume, and references therein).

Molecular clock evidence suggests that bilaterally-symmetrical animals (bilaterian metazoans) had already evolved by 600–630 Ma, if not considerably earlier (Erwin 2001; Narbonne 2005; Peterson *et al.* 2005). Early bilaterians were probably very small and lacked mineralized skeletons, so their fossilization potential was extremely low. Trace fossils provide a useful proxy for mobile early bilaterians – or at least for sizeable, bottom-living animals – because the ability to penetrate and rework sediment implies a sophisticated nervous and muscular system as well as some sort of skeleton. Convincing trace fossils have not been recorded before 560 Ma (Ediacaran Period), although several tantalizing claims from older rocks have been made (Narbonne 2005; Jensen *et al.* 2006). Ediacaran trace fossil assemblages worldwide are typically sparse, very low in diversity and dominated by small, fairly simple horizontal burrows generated within shallow marine to offshore settings (Seilacher *et al.* 2005; Jensen *et al.* 2006). The variety, size, abundance, density, complexity and ecological range of trace fossils all increase markedly during the latest Precambrian/Early Cambrian time interval. There is a significant acceleration during the Early Cambrian in step with the explosive diversification of macroscopic body fossils of metazoans and the evolution of sophisticated foraging and other behaviours.

Seilacher & Pflüger (1994) have emphasized the pivotal role played by infaunal bioturbators in driving a profound 'agronomic revolution' on shallow marine bottoms during the Precambrian/Cambrian boundary interval. This entailed the widespread demise of well-laminated, poorly-oxygenated sea beds of the Proterozoic that were bound and sealed by cohesive microbial mats at the sediment-water interface. These archaic substrates supported shallow-tier horizontal burrowers feeding on or beneath the surface mats. With the advent of widespread vertical bioturbation in the Early Cambrian or shortly before, Precambrian 'matgrounds' were largely replaced by better-ventilated 'mixgrounds', especially in shallow marine settings. At the same time, the proliferation of macroscopic zooplankton and nekton may have substantially increased the supply of organic nutrients to bottom-living communities, fuelling the benthic substrate revolution. This was because faecal pellets generated by these floating and swimming animals were large enough to sink rapidly through the water column without being entirely consumed by microbial decomposers *en route* (Peterson *et al.* 2005). With an abundant supply of food and oxygen extending well beneath the sediment-water interface, and less cohesive sediments to penetrate and rework, an infaunal lifestyle became an attractive new option for a wide range of benthic invertebrates, especially in view of rapidly escalating predation pressures during the Cambrian explosion. Compared with their Ediacaran precursors, early Palaeozoic mixgrounds supported a much higher density and variety of infauna, including animals that hid, resided and foraged below the sediment surface, as shown by their far richer ichnoassemblages and higher bioturbation indices.

The thick, relatively undeformed Vanrhynsdorp Group of the Western and Northern Cape Provinces, South Africa, is emerging as a key succession for documenting important developments in ichnodiversity, ichnostratigraphy, body size and burrowing behaviour among infaunal metazoans across the Precambrian/Cambrian boundary (Seilacher *et al.* 2005; Buatois *et al.* 2007; Almond 2008 and references therein). Overall ichnodiversity is low, as is typical for marine sediments of Ediacaran/earliest Cambrian age, but preservation is good and trace fossils are often very abundant, especially in the upper parts of the succession.

So far the basal Flaminkberg Formation, characterized by coarse pebbly alluvial quartzites, has not yielded well-substantiated fossils of any kind. Within the Kwanous Subgroup, limestones of the Grootriet Formation – a probable correlative of the thick Huns Member of the Nama Group to the north – show abundant evidence for microbial binding of fine-grained carbonate (platy-clast limestone breccias, oncolites) but no discernible trace fossils. Narrow, straight to curved, horizontal burrows of the *Helminthopsis* ichnoguild are associated with wrinkly microbial mat textures within dark mudrocks of the overlying Hoedberg Formation. These traces typify inshore as well as deeper water settings in the Ediacaran Period and reflect shallow tier exploitation of superficial matgrounds by 'grazing' metazoans. Enigmatic tubular structures,

tentatively identified as decalcified, reworked *Cloudina,* occur within the lower Hoedberg. The heterolithic Arondegas Formation at the base of the Knersvlakte Subgroup also contains well-preserved horizontal burrows of the *Helminthopsis* ichnoguild (Fig. 1) associated with microbial mat textures and poorly preserved vendotaenids (cyanobacterial 'strings'). However, the stratigraphic position of these Ediacaran-type assemblages (also possibly uppermost Hoedberg) requires confirmation.

Large, one to 2.3 cm wide, horizontal burrows (Fig. 2) occur abundantly within the heterolithic upper Gannabos Formation, interpreted as an offshore, storm-influenced marine succession. The hypichnial wash-out burrows, which remain in taxonomic limbo, have a distinctive subrectangular cross-section and preserve occasional relicts of coarse meniscate back-fill. The gently to tightly curving burrows show frequent overlaps, but a crude meandering or 'scribbling' foraging pattern and even possible avoidance behaviour are also seen. The Gannabos Formation also yields microbial wrinkle marks, clusters of pyrite pseudomorphs, and comb-like tool marks that might have been generated by storm-entrained, finely-ribbed vendobiontans. An Ediacaran age for the Gannabos Formation is provisionally inferred from the notable absence of *Treptichnus* type probe burrows that characterize comparable storm-dominated shelf facies in the Early Cambrian. If correct, the Gannabos burrows would demonstrate that large-bodied (over 2 cm wide) infaunal metazoans appeared before the end of the Precambrian.

Further evidence for substantial infaunal animals, complex burrow infill and primitive meandering behaviour close to the Precambrian/Cambrian boundary is provided by as yet undescribed traces from the Nama Group in the Fish River Canyon, southern Namibia (Fig. 3). They come from thin-bedded micaceous sandstones within the carbonate-dominated upper Spitskop Member (Urusis Formation, Schwarzrand Subgroup). This stratigraphic unit has been radiometrically dated to 543 ± 1 Ma and has also yielded complex traces of the *Treptichnus*-like ichnogenus *Streptichnus* (Jensen & Runnegar 2005). The Fish River Canyon burrows, mostly preserved as positive, washed-out hypichnia, are up to 12 mm across and occasionally retain evidence for a crude meniscate backfill. They range from straight to strongly curved, show frequent internal overlap, and sometimes adopt tightly-coiled, 'pretzel-like' configurations that are unknown in Ediacaran ichnofossils described so far. Abundant comb-like tool marks, possible finely-pleated vendobiontans and a range of other problematic biogenic structures occur in the same beds.

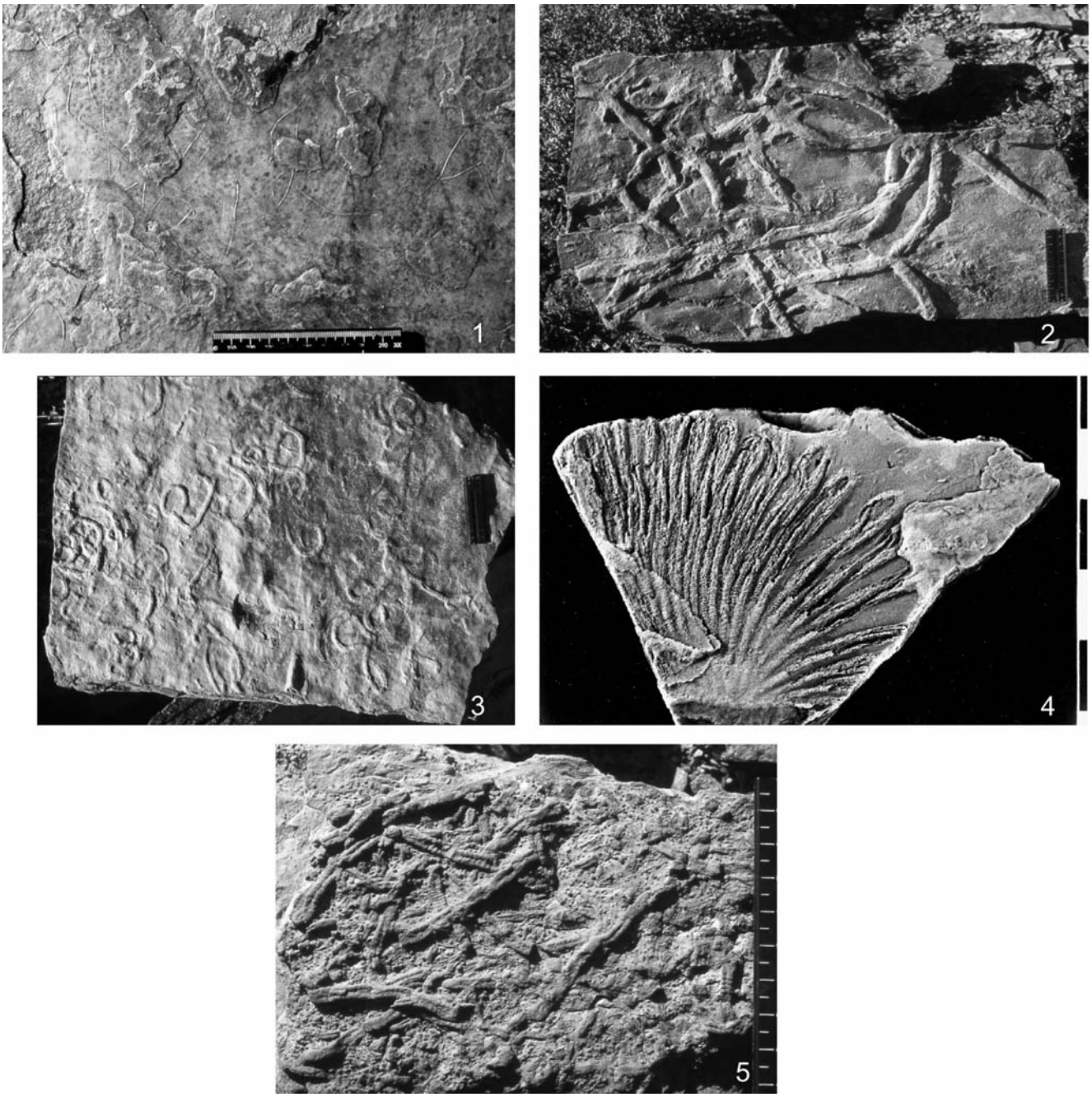
Returning to the Vanrhynsdorp succession of South Africa, complex subhorizontal burrow systems of the distinctive Cambrian ichnogenus *Oldhamia* are recorded from finely laminated mudrocks – probably distal turbidites – of the Besonderheid Formation in the Bokkeveld Escarpment. The Besonderheid specimens co-occur with microbial wrinkle textures and have been assigned to *O. geniculata,* also known from the Early Cambrian of Argentina (Seilacher *et al.* 2005). Well-preserved South African specimens clearly show complete, asymmetrical hair-pin loops at the terminations of closely paired radial burrow sections, demonstrating that these are not blind-ending tunnels (Fig. 4). Systematic centrifugal and centripetal movement of the trace-maker, alternately away from and towards the burrow axis, is also demonstrated by the finely-developed meniscate back-fill (*not* a cleavage artefact, as previously suggested). This sophisticated foraging behaviour may well be common to all *Oldhamia* burrow systems (a controversial point), but complete terminal loops and meniscate backfill are rarely observed so clearly. *Oldhamia* characterizes, but is not restricted to, the Early Cambrian and demonstrates the persistence of shallow tier mat-feeding in deeper water, offshore settings following the agronomic revolution.

Prolific but low-diversity trace assemblages within the younger formations of the Vanrhynsdorp Group (upper Knersvlakte Subgroup *plus* Brandkop Subgroup) are heavily dominated by intrastratal probe-burrows of the *Treptichnus* type. These have been tentatively attributed to priapulid worms (Jensen *et al.* 2006). Microbial wrinkle structures are also common. A spectrum of shallow marine, wave-dominated to tidal settings have been recognized here (Buatois *et al.* 2007). The Vanrhynsdorp treptichnids display considerable preservational, morphological and hence behavioural plasticity, with frequent intergradations between typical *T. pedum* and other *Treptichnus* ichnospecies within the same burrow system (Fig. 5). These systems range from strictly linear (perhaps indirectly current-orientated) to curved, coiled or irregular. The lower surface of individual burrow probes is variously smooth, bi- or tri-lobed, and/or transversely ridged. Transitions with *Curvolithus*-, *Saerichnites*-, *Arthrophycus*- and *Cruziana*-like morphs are observed, but with no discernible temporal succession. This plasticity and lack of stratigraphic pattern seriously undermine the utility of *Treptichnus* spp. for the biostratigraphic zonation of Ediacaran/Early Cambrian boundary successions (Buatois *et al.* 2007). The presence of *Treptichnus pedum* – often treated as a zone fossil for the basal Cambrian – as well as the absence of unequivocal arthropod scratch burrows such as *Rusophycus*/*Cruziana* strongly suggest an earliest Cambrian (Manykaian/Nemakit-Daldynian) age for the entire upper Vanrhynsdorp succession (*Monomorphichnus*-like comb marks are reported from the upper Brandkop Subgroup, but their identity and arthropod origin are controversial). A similar conclusion was reached by Geyer (2005) for the thick Fish River Subgroup (uppermost Nama Group) of Namibia and Gordonia. However, precise correlation of the Nama and Vanrhynsdorp successions remains elusive pending detailed sequence stratigraphic, sedimentological and palaeontological analysis of the South African successions in particular.

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Figures 1–4. **1**, *Helminthopsis* ichnoguild horizontal burrows, Arondegas Formation. Scale 10 cm. **2**, Large horizontal hypichnial burrows, Gannabos Formation. Scale 10 cm. **3**, Large horizontal scribbling traces, Spitskop Member. Scale 10 cm. **4**, *Oldhamia* looped burrow system, Besonderheid Formation. Scale units 0.5 cm. **5**, Treptichnids from the Knersvlakte Subgroup. Scale units 0.5 cm.

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Fossil woods from the early Pleistocene hominin site, Area 1A, Ileret, northern Kenya

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On the eastern side of Lake Turkana in northern Kenya are extensive Plio-Pleistocene deposits containing a rich diversity of fossil mammals, hominins and flora within the radiometrically dated tuffaceous, lacustrine and fluvial sequence. These sediments also contain stone artefacts and hominin-modified bone which greatly increases their interest as far as early hominin behaviour and landscape use are concerned. Reconstruction of this landscape and palaeoenvironment are part of an ongoing multinational and multidisciplinary human evolution project in the eastern Turkana Basin. Today there is a huge lake in the Rift but it has fluctuated from lake to various river systems and deltas of the Omo River, with associated flora and fauna, since the early Pliocene. Silicified wood is fairly common in some areas of the Koobi Fora Formation. One such site is FwJj14E alongside one of the tributaries of the Ileret River. Hominin hand and arm bones have been excavated from here in the Okote Member and dated at 1.52 Ma. The fossils are associated with hominin and bovid footprints. Thirty of the over 100 wood specimens collected have been sectioned and identified. In general the woods have large vessels and an average vulnerability index of 37 which implies a mesic environment with little or no water stress. Taxonomically the woods belong to large African families: Caesalpiniaceae (*Afzelia bipindensis, Didelitia* sp.), Euphorbiaceae (*Drypetes* sp.), Malvaceae (*cf. Sterculia* sp.), Rhamnaceae (*Ziziphus mauritiana*), Sapindaceae (*Blighia* sp.), and Palmae. Most of these taxa do not occur in the area today because now it is much drier and the local vegetation is predominantly *Acacia–Commiphora–Salvadora.* The reconstruction of the palaeovegetation supports the interpretation from the fauna, namely, a tall gallery forest and wooded grassland and more open bushland in the vicinity.

Reconstruction of the cervical vertebrae of *Massospondylus*: implications for neck movement and feeding envelope of the Prosauropoda

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Introduction

Massospondylus is a moderately derived prosauropod from the Early Jurassic, notable for its highly elongated neck of over a metre in length. The animal's dentition suggests a primarily herbivorous diet (Galton 1986), perhaps with opportunistic carnivory (Barrett 2000). Otherwise, little is known about its lifestyle. We attempted to deduce the type and range of movement for the neck of *Massospondylus.* Information on feeding behaviour, body posture and habitat was integrated with neck posture, in order to infer the ecological niche of the animal. No previous work had been done on the neck position of prosauropods. Conversely, recent studies have overturned the belief that the related clade, Sauropoda, possessed swan-like, vertically curved necks (e.g. Stevens & Parrish 2005; Christian & Dzemski 2007; Berman & Rothschild 2005). These researchers have concluded that the neck posture of most sauropods was actually closer to the horizontal, and while they possessed a good range of lateral and ventral movement, their dorsiflexion was limited. This has implications for prosauropods, which have also been conventionally reconstructed with swan-like necks. Many prosauropods were thought to be quadrupedal, but a new study has showed that *Massospondylus* was habitually bipedal (Senter & Bonnan 2007). Such discoveries ask for a revision of prosauropod body and neck posture.

Methods and research design

Plasticine models of each cervical vertebra were cast using a well-preserved, articulated specimen (BP/1/4934) as a template. Numerous dimensions were taken to ensure accuracy of the finished models, which were statistically re-evaluated against the original fossils to ensure that models and fossils were not significantly different. Models of nine cervicals (excluding the axis) and the first dorsal vertebra were fitted together in the neutral pose, according to the zygapophyseal alignment technique of Stevens & Parrish (2005). Models were then manipulated to determine the maximum ranges of dorsal, lateral and ventral movement.

Manipulation of models

Feeding envelope

The zygapophyseal alignment technique reconstructs the neutral posture as angled slightly upwards, with a curve in the posterior region (Fig. 1). It is clear that *Massospondylus* was limited in dorsal neck movements (Fig. 2), with the maximum dorsiflexion being only 45 cm higher than in the neutral pose. The vertebrae of *Massospondylus* are so elongate and flattened that only a small amount of dorsiflexion is possible without disarticulation. However, this design permits extensive lateral movement, which would have allowed for browsing from side to side on medium-height plants (Fig. 3). It also was capable of very good ventriflexion, aided in this regard by the distinctive downward curve of the axis and first dorsal vertebra (Fig. 4). This would have allowed it to reach ground vegetation. The habitually bipedal posture

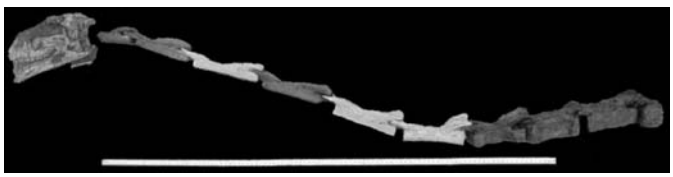


Figure 1. Neutral pose of *Massospondylus* reconstructed using the zygapophyseal alignment technique. Margins of the centra are parallel and centred, with the pre- and postzygapophyses superimposed. The skull is from the same specimen used to build the models of cervical vertebrae. Scale bar = 1 m.

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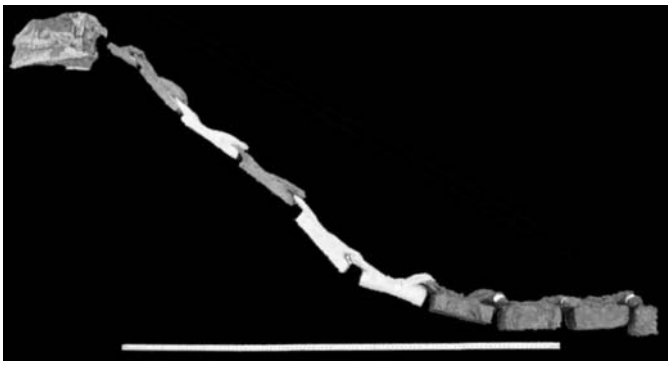


Figure 2. Maximum degree of dorsiflexion in *Massospondylus.* Zygapophyseal facets are overlapping by 50% in both the lateral plane and the plane parallel with the zygapophyses (the minimum degree of overlap before disarticulation occurs in extant birds and mammals). Scale bar = 1 m.

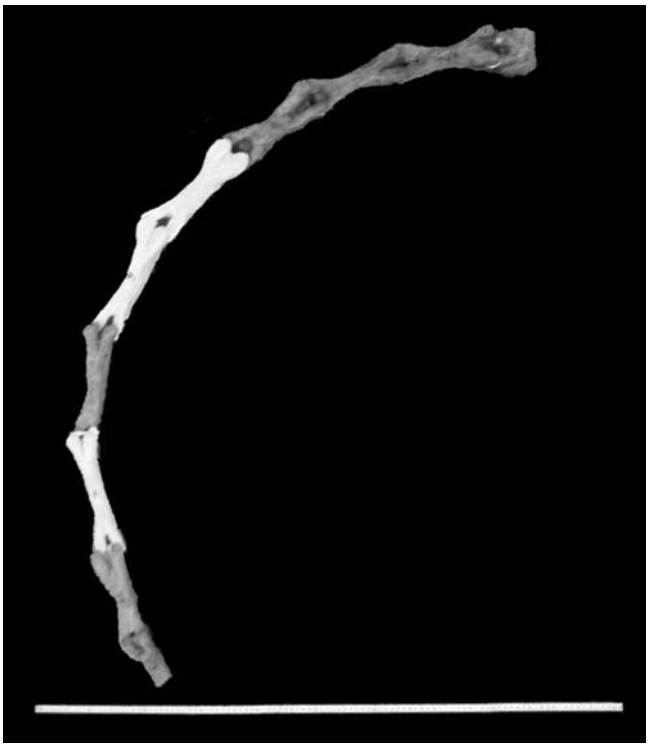


Figure 3. Maximum degree of lateral flexion in *Massospondylus*. Pre- and postzygapophyses rotate freely in the lateral plane, while still overlapping by 50% in both the lateral plane and the plane parallel with the zygapophyses. Axis is to the bottom left. Scale bar = 1 m.

of *Massospondylus* would have increased both its mobility and feeding envelope, especially aiding in dorsal movements. *Massospondylus* could also have adopted a tripodal position, permitting the animal to browse on taller vegetation that could have been present around local water sources (Parrish & Falcon-Lang 2007). The environment in which *Massospondylus* lived was strongly seasonal, and probably resource-limited for parts of the year. Thus, the animal could have adopted a variety of feeding behaviours depending on the nutritional value of the different types of plants, and whether or not they were available.

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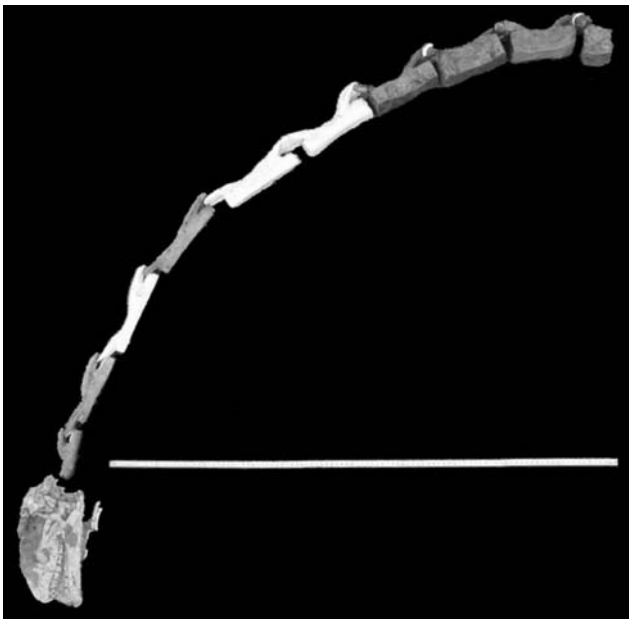


Figure 4. Maximum degree of ventriflexion in *Massospondylus*. Zygapophyseal facets are overlapping by 50% in both the lateral plane and the plane parallel with the zygapophyses. Scale bar = 1 m.

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Dicynodon from South Africa, '*Dicynodon*' from Russia and *Dicynodon*(?) from southeast Asia

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Introduction

The genus *Dicynodon* was erected in 1845 by Owen, with *Dicynodon lacerticeps*, from the Upper Permian of South Africa, as type species. Owing to the fact that *Dicynodon* lacks conspicuous specialized characters, and if we take into account that the genus was erected very long ago, it is

not surprising that many species were attributed to it. A certain number of species were ultimately transferred to other genera, mainly to *Diictodon* Broom 1913, and *Oudenodon* Owen, 1860 (see Keyser 1975, and Cluver & Hotton 1981). On the contrary, a few species were initially attributed to genera (*Daptocephalus,* for example) which are often nowadays regarded as synonyms of *Dicynodon.* On the list established by King 1988 (pp. 89–93), fifty-nine *Dicynodon* species are still found, but the author mentions that they are not necessarily all valid. Indeed, many are known only by incomplete and badly preserved specimens, making detailed comparisons impossible. Moreover, the genus *Lystrosaurus* might well be rooted in the genus *Dicynodon,* rendering the latter paraphyletic.

A rather detailed diagnosis of the genus *Dicynodon* was given by Cluver & Hotton (1981, pp. 106–107), and a slightly modified and expanded one by Cluver & King (1983): 'Medium-sized to large' dicynodonts (average skull length 100 mm to over 400 mm), single pair of maxillary tusks in upper jaw, lower jaw edentulous. Postorbitals tend to cover parietals behind parietal foramen. Septomaxilla merges smoothly with outer surface of snout, does not meet lacrimal. Low boss formed over external nares by nasals. Palatal rim sharp edged, uninterrupted by notch. Palatal portion of palatine large and flat, making short contact with premaxilla. Vomers form long, narrow septum in interpterygoidal fossa. Anterior border of interpterigoidal fossa formed by a crest that joins the vomerine septum. Ectopterygoid small, displaced laterally. Labial fossa present between maxilla, palatine and jugal. Pterygoid makes short contact with maxilla. Basioccipital tubera separated by intertuberal ridge. Fused dentaries carry narrow dentary tables. Dorsal edge of dentary carries deep sulcus behind dentary tables. Rear of dentary extended dorsally to form weak posterodorsally directed process. Mandibular fenestra large, bounded dorsally by lateral dentary shelf. Occipital surface of opisthotic carries depression above paroccipital process.' (Cluver & King 1983, pp. 234, 237).

The above mentioned diagnosis provides a frame which can accommodate all species traditionally attributed to *Dicynodon,* whether from South Africa or from Russia. But it is all too clear that many characters listed in that diagnosis are not restricted to *Dicynodon.* A dentition reduced to a pair of maxillary tusks, for example, is also observed in *Lystrosaurus,* in *Kannemeyeria* and in many other genera. And most characters are described in rather general terms, leaving room for a wide range of possible variations.

Dicynodon from South Africa, *'Dicynodon'* from Russia

Several recent authors reviewed the systematics and phylogeny of late Permian dicynodonts. Their works, undertaken from a cladistic perspective, deal with many more characters than earlier articles (see for example Angielczyk 2001; Maisch 2002; Angielczyk & Kurkin 2003a,b; Fröbisch 2007). However, some of the newly considered characters can seldom be observed, and others could easily have been altered by weathering or distortion, and their real value can therefore be questioned. Fröbisch (2007) established a list of 100 characters, most of which had been used in previous phylogenetic analyses, and particularly in that of Angielczyk & Kurkin 2003a. This list will be used hereafter as a basis for discussion.

The phylogenetic analyses by Angielczyk & Kurkin (2003a,b) and Fröbisch (2007) tend to consider *Dicynodon* as a paraphyletic genus, and to separate the South African form *Dicynodon lacerticeps* from the Russian forms, the latter being provisionally attributed to '*Dicynodon*' rather than to *Dicynodon* proper. The phylogenies presented by Angielczyk & Kurkin (2003a) and by Fröbisch (2007) differ slightly, but both consider *Dicynodon lacerticeps* as the sister-taxon of a clade containing *Lystrosaurus, Kannemeyeria* and the Russian *'Dicynodon*', and both keep two Russian species , *'Dicynodon' trautscholdi* and *'Dicynodon' amalitzkii.* Out of the hundred characters retained and coded by Fröbisch (2007), fourty-seven can be observed in both '*D.' trautscholdi* and *'D.' amalitzkii,* but only two are coded differently. The canine would be anterior to the level of the anterior margin of the orbit in *'D.'trautscholdi,* at the same level in *'D.' amalitzkii* ; this character is, in my opinion, debatable, because the way it is appreciated depends largely on the orientation given to the skull. And secondly, the interparietal would contribute to the intertemporal skull roof in *'D.' trautscholdi,* but not in *'D.' amalitzkii.* The difference, however, is extremely inconspicuous, and could easily be only the consequence of a slight distortion or weathering. Therefore I tend rather to consider *'D.' amalitzkii* as a junior synonym of *'D.' trautscholdi,* a position already expressed, in particular by Battail & Surkov (2000).

A few anatomical differences have been noted between *'D.' trautscholdi* and the South African *D. lacerticeps.* The septomaxilla is recessed within the naris in *'D.' trautscholdi,* it has a broad facial exposure in *D. lacerticeps.* The dorsal surface of the preparietal is relatively flat and flush with the skull roof in *D. lacerticeps,* it has a depressed dorsal surface relatively to the skull roof in *'D.' trautscholdi.* The postorbitals overlap the parietals nearly completely in *D. lacerticeps,* they are exposed on the skull roof between the postorbitals in *'D.' trautscholdi.* The palatal surface of the palatine is highly rugose in *'D.' trautscholdi,* moderately rugose in *D. lacerticeps.* On the basis of this set of characters, *D. lacerticeps* appears as significantly different from the Russian *'Dicynodon',* and Angielczyk & Kurkin (2003 a) could write: '…we consider it worth noting that in our personal observations of over 600 dicynodont specimens collected in Russia, South Africa, Tanzania, and Zambia, we have only observed the diagnostic suite of features that characterize *D. trautscholdi* and *D. amalitzkii* in specimens collected in Russia. We have not identified any Russian specimens that are referable to species of *Dicynodon* other than *D. trautscholdi* and *D. amalitzkii.* Likewise, we have only observed the diagnostic suite of features that characterizes *D. lacerticeps* in southern African specimens.' (Angielczyk & Kurkin 2003a, pp. 165–166).

Dicynodon(?) from southeast Asia

In southeast Asia, late Permian dicynodonts are known from limited outcrops of purple beds situated North of

Luang Prabang, Laos. The presence of dicynodonts in Laos was first reported more than one century ago by Counillon (1896). The only specimen collected at that time, the anterior half of a skull, was very briefly described by Repelin in 1923 as *Dicynodon incisivum* sp. nov. The attribution of the specimen to the genus *Dicynodon* was very convincingly confirmed by Piveteau (1938). Unfortunately, many authors referred it, without any anatomical (or stratigraphical) basis, to *Lystrosaurus* sp. (see Battail 1997); this specimen is now considered as lost.

In recent years, many specimens of dicynodonts were collected in the same beds of the same area during annual Franco-Lao expeditions led by Philippe Taquet (Muséum National d'Histoire Naturelle, Paris, France) (Battail *et al.* 1995). The collected dicynodont skulls are not all alike, and differ mainly in their proportions, in the shape of their tusks and in the shape of their occiput. However, all of them conform, in their observable characters, with the definition of *Dicynodon* as given by Cluver & Hotton (1981, pp. 106–107), or by Cluver & King (1983, pp. 234, 237). Indeed, a close examination of these specimens, now being described, rules out that they could belong to any other late Permian (or early Triassic) genus of dicynodonts whose dentition is reduced to a pair of upper tusks (*Aulacephalodon, Idelesaurus, Elph, Interpresosaurus, Delectosaurus, Lystrosaurus*). But a question arises: are they closer to the South African *Dicynodon lacerticeps* or to the Russian *'Dicynodon' trautscholdi*?

In fact, most specimens from Laos display some characters regarded as typical of the South African *Dicynodon,* and some regarded as typical of the Russian *'Dicynodon'*. A common association is that of a preparietal depressed relatively to the skull roof (as in *'D.' trautscholdi*), and postorbitals overlapping the parietals nearly completely (as in *D. lacerticeps*) (Fig. 1). Our knowledge of the anatomy of the dicynodonts of Laos remains unfortunately limited because, even in well-preserved specimens, the sutures are not clearly seen.

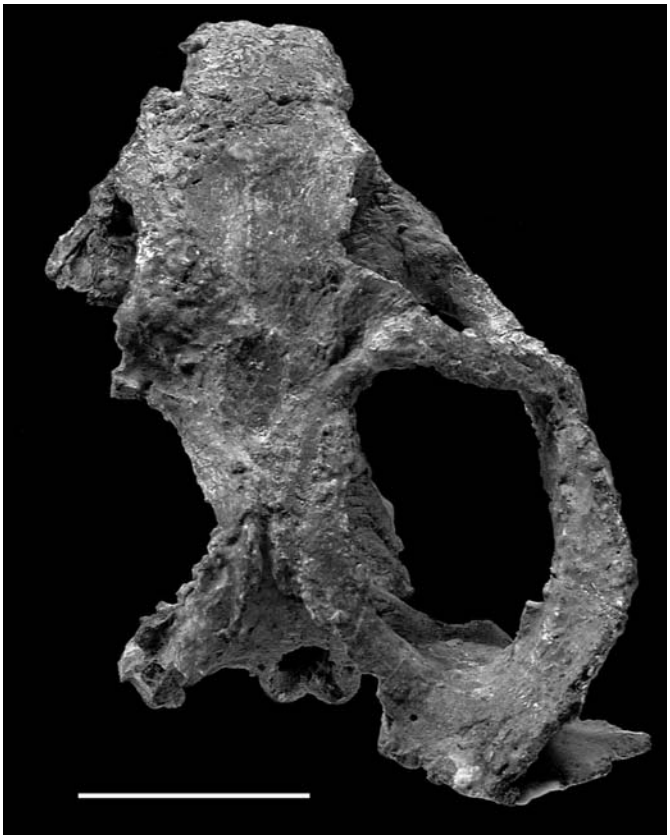


Figure 1. *Dicynodon* sp., skull, dorsal view. Late Permian, area of Luang Prabang, Laos. Musée de Savannakhet, Laos, specimen No. LPB 1993 – 2. Scale bar = 5 cm

Conclusions

The present paper is only a preliminary account of the difficulties encountered when dealing with the genus *Dicynodon* at a world level. No attempt has been made at this stage to establish a new phylogeny of *Dicynodon* and related genera that would include the forms from southeast Asia. It nevertheless appears that the relatively clear-cut distinction between Gondwanan forms (South African *Dicynodon*) and Laurasian forms (Russian *'Dicynodon'*), which could be expected on the basis of recent works, does not seem to be sustained by the analysis of *Dicynodon* material from southeast Asia.

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Taphonomy and taxonomy of the rare Triassic dinosaur *Eucnemesaurus* based on an articulated skeleton from the Eastern Cape

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The subject of this paper is based on a specimen found on the farm of Cannon Rock in the Eastern Cape and has been informally named the cannon rock dinosaur. The taphonomy of the cannon rock dinosaur BP/I/6234 has been undertaken.

The skeleton is completely articulated and associated, it was found lying on its left side with the right side exposed to weathering. The left side is in good condition as it has been protected and is therefore relatively unweathered compared to the right side. It shows a first stage of weathering in Behrensmeyers six-stage categorization of bone weathering (Behrensmeyer 1978). This site fits the channel fill mode proposed by Behrensmeyer (1988), which includes two taphonomic modes of attritional vertebrate accumulations in fluvial channels based on taphonomic features on bones and their sedimentary context. Some of the bones are deformed this is likely to have been largely due to sedimentary loading during final burial. The ontogenetic evidence of BP/I/6234 shows that the individual was mature. Specimen BP/I/6234 was located on the farm of Cannon Rock approximately 30 km south of Aliwal North in the Eastern Cape. This area is located within the *Euskelosaurus* range zone in the lower Elliot Formation (Kitching *et al.* 1984). The skeleton consists of the posterior end of the dinosaur and includes a number of thoracic vertebrae, the ilia, ischia and pubes, the hind limbs and caudal vertebrae (these are not in very good condition and have not been completely prepared) the anterior end is completely missing as the sandstone in which it was found had been partly eroded away. The lower Elliot Formation consists typically of multi-storeyed, asymmetrical channel fill sandstones. They are characterized by planar and trough cross-stratification and massive beds that are interpreted as perennial moderately meandering fluvial systems (Bordy *et al.* 2004). The sandstone in which BP/I/6234 was found is a typical lower Elliot Formation sandstone. A description of this rare dinosaur (previously known from a few highly fragmentary specimens) has been undertaken, using this information a re-examination and comparison has been done as to ascertain its position within dinosaur phylogeny. This dinosaur has a number of femoral synapomorphies which include a large round turbercle protruding from the proximal end of the femur, the fourth trochanter is rounded rather than sub-rectangular, and is separated from the from the femoral shaft by a rounded notch (Yates 2006). These synapomorphies are quite distinct and are seen within the Riojasuaridae. *Riojasaurus* is a sauropodomorph dinosaur from the late Triassic of Argentina (South America) and was discovered in the Los Colorados Formation (Galton *et al.* 2004). It is now apparent that *Euskelosaurus* is a 'wastebasket' name or nomen dubium that has been hiding a diversity of Triassic sauropodomorph dinosaurs.



Figure 1. The locality where the BP/I/6234 was discovered and excavated on the farm of Cannon Rock.



Figure 2. The prepared posterior end of BP/I/6234 on its left side showing a number of caudal vertebrae, the sacrum and some dorsal vertebrae.

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Variation in anomodont growth patterns across the Permo-Triassic boundary in South Africa

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The Anomodontia, which includes the dicynodonts, is a well-known group of non-mammalian synapsids that had a particularly long phylogenetic lineage from the middle Late Permian to the Late Triassic. The dicynodonts had remarkably specialized feeding modifications that allowed them to radiate globally to become one of the most diverse terrestrial vertebrates in Earth's history. Their worldwide distribution and abundance has allowed them to play a particularly significant role in global correlations (e.g. King 1992; Angielczyk & Kurkin 2003). They are important as biostratigraphic indicators (Rubidge 1995; Smith & Ward 2001) and they can be used in ecological studies where large sample sizes are required (e.g. Sullivan *et al.* 2003).

These and more traditional studies such as morphological descriptions have provided significant information about the palaeobiology and palaeoecology of this group. However, valuable information can also be gained by studying the bone microstructure or histology of these animals. Early studies, such as those of Enlow & Brown (1957), Ricqlès (1972, 1976) and Chinsamy 7 Rubidge (1993), and more recent, comprehensive works (e.g. *Oudenodon,* Botha 2003; *Diictodon,* Ray & Chinsamy 2004; *Lystrosaurus,* Ray *et al.* 2005; *Tropidostoma,* Botha & Angielczyk 2007), which included multi-element, detailed analyses, have provided important contributions to understanding the biology of dicynodonts. However, a broad overview of the changes in dicynodont bone histology (and hence biology) during their lineage is still lacking. This information is relevant because the dicynodonts were one of the few groups to survive the End-Permian extinction, the most catastrophic mass extinction in Earth's history, and they include the only genus that is known to have crossed the Permo-Triassic boundary, namely *Lystrosaurus*.

This study compares the bone histology of 12 South African anomodont taxa. It includes one non-dicynodont anomodont and 11 dicynodont anomodonts (including three species of *Lystrosaurus*), ranging from some of the earliest known forms, such as *Eodicynodon* from the middle Late Permian *Tapinocephalus* Assemblage Zone to some of the latest forms such as *Kannemeyeria* from the Middle Triassic *Cynognathus* Assemblage Zone.

The bone tissue of all the genera studied consists of fibro-lamellar bone interrupted by annuli and/or LAGs, indicating seasonal growth. However, the degree and pattern of vascularization varies between different genera, allowing some genera to be distinguished from others on the basis of bone histology alone. Enlarged erosion cavities in the peri-medullary region were observed in *L. murrayi,* as previously noted (Ray *et al.* 2005), but also in *L. declivis*, *L. maccaigi*, *Aulacephalodon* and *Dicynodon*. Many of the older individuals display poorly vascularized parallel-fibred tissue at the bone periphery, indicating a decrease in growth rate, but not a complete cessation, suggesting indeterminate growth.

Interestingly, all the genera studied exhibit a remarkably thick cortex, irrespective of the size of the taxon. Where possible, the relative bone wall thickness (RBT) of the bones was calculated, and apart from *Cistecephalus,* all the taxa studied had an average RBT of more than 30%. A free medullary region is absent in many of the genera and is instead filled with trabeculae even in the midshaft regions. These characteristics and their implications regarding lifestyle and phylogeny are discussed.

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Progress in the evaluation of sponge-like fossils from Neoproterozoic limestones of Namibia

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For the last ten years, one of the authors (C.K.B.) has been conducting a search for microfossils of ancestral animals (here defined as 'multicellular heterotrophs') in limestones and cherts of the Otavi and Nama Groups of Namibia. This has proved to be a very slow and labour-intensive occupation, involving the examination of thin-sections of the rocks, of which about 860 have been prepared thus far by Laura Brain, and the sorting of insoluble residues after samples of the limestone have been dissolved in acetic acid (about 350). A variety of interesting microfossils have been found, most of them preserved with calcium phosphate, as has been shown by analyses undertaken by A.J.B. The commonest of these microfossils appear to be ancestral sponges, referred to here by the informal name Otavia, which vary in overall length or breadth from 0.3 to 5 mm. However, there are various problems in the interpretation of these ancient fossils, as outlined by Brain *et al.* (2001).

When such fossils have been found in limestones from a particular locality by C.K.B., it is of course necessary to establish just where this outcrop fits into to the Neoproterozoic sequence of Namibia. All such outcrops have been examined in detail by A.R.P. and K-H.H. who have also taken samples for stable isotope analysis by A.E.F. Whenever ashbeds have been found, attempts have been made by D.C. to obtain absolute dates from zircon crystals that the samples might contain. We have now obtained *Otavia* fossils from a very long stratigraphic sequence, going back in time to limestones of the Ombambo Subgroup, in the Kaokoveld, which are below the older of the two 'Snowball Earth' glacial episodes, represented there by the Sturtian Chuos diamictite at about 720 million years, then through limestones of the Abenab Subgroup, up to the Marinoan Ghaub glacial deposits at 635 million years. Further to the south in the Nama Group, similar Otavia fossils have been found in a limestone of the Mara Formation at about 550 million years, indicating that these marine organisms survived the harsh climatic conditions associated with glacial episodes.

Although the shape of individual *Otavia* fossils varies, the overall structure of each remains similar, consisting of a hollow container, with several large openings to the outside, often on raised mounds, reminiscent of the exhalent oscula of later sponges. The outer walls of the organisms were also pierced by many smaller holes, similar to sponge ostia, leading into a 'peripheral labyrinth' that had many connections with the large internal cavity, which is reminiscent of a sponge's paragastric chamber. The smallest Otavia individuals may not have been particularly efficient at drawing nutrient-rich water into their bodies, but larger *Otavias* would have had no such difficulty.

When a formal description of *Otavia* species was recently drawn up and submitted for publication, comment from reviewers insisted that more detail of the internal structure should be provided. A complication in this regard is that, in thin petrographic sections, the phosphatized wall-structure appears opaque. For this reason we have established the current collaboration of specialists. Donald Herd, who runs the Electron Microscope Unit at St Andrews University has recently been obtaining exceptional back-scatter and cathode luminescence images of *Otavia* fossils, while at Abertay University in Dundee, Scotland, Iain Young and Craig Sturrock have used their High Resolution X-ray computer tomography (CT) apparatus to produce remarkable images of structural detail. We had the pleasure of showing some of these images to Rachel Wood, the fossil sponge expert, at Edinburgh University and she has generously agreed to be our adviser on this ongoing project.

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Morphological and trophic distinction in the dentitions of two early alcelaphine bovids from Langebaanweg (genus *Damalacra*)

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The early Pliocene fossil bovids from Langebaanweg are of interest, as they represent among the earliest well-defined members of modern tribes, such as Reduncini, Bovini and Alcelaphini (Gentry 1980; Vrba 1997). In these fossils typical tribal morphology appears to be in an early stage of evolution, which on the one hand hinders diagnosis, but on the other hand offers a unique opportunity to investigate ancestral morphological states and adaptations. We focus here on the two alcelaphine species from Langebaanweg, *Damalacra neanica* and *D. acalla.* They were of the size of the blesbok, *Damaliscus pygargus,* but their skulls and dental morphologies are underived, representing an early stage in the appearance of distinctive alcelaphine characteristics (Gentry 1980). The dentitions of the two species a very similar and difficult to distinguish, especially when dealing with individual teeth (Gentry 1980). The aim of this study was to define the morphological characters that differentiate the dentitions of the two species and to use this distinction as the basis for assessing their trophic niches.

The Alcelaphini and Caprini are thought to have evolved from an antilopine ancestry in the later Miocene (Gentry 2000). Pleistocene and modern alcelaphine species can be broadly classified into two morphological groupings; those with antilopine body proportions, such as hartebeest, blesbok and tsessebe (genera *Alcelaphus* and *Damaliscus*) and those with more advanced caprine-like body proportions, such as wildebeest (genera *Connochaetes* and *Megalotragus*), reflecting the common ancestry of the

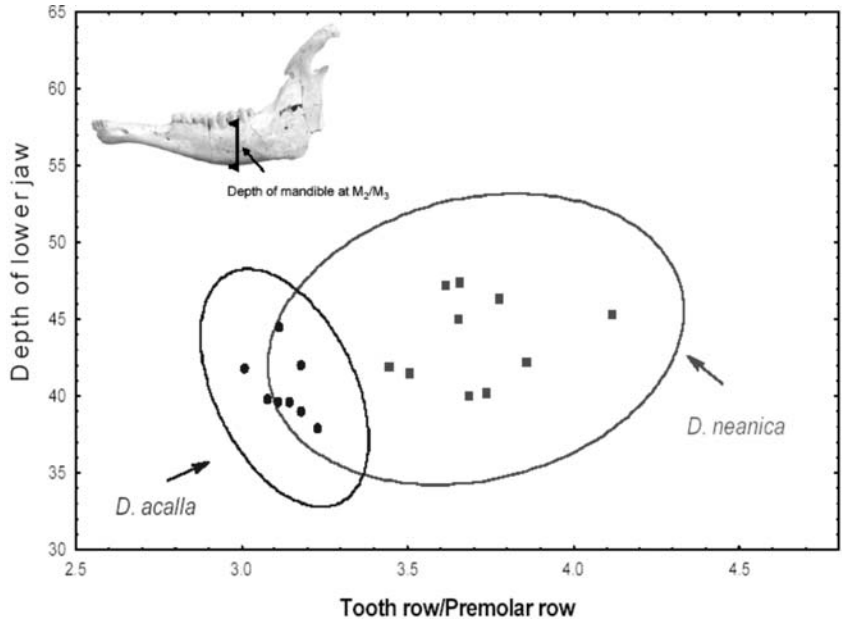


Figure 1. Plot of toothrow/premolar ratios against the depth of the lower jaw at the M_2–M_3 junction of *Damalcra neanica* and *D. acalla.*

Caprini and the Alcelaphini. This two-fold division is also evident in the dentitions of extant and Pleistocene Alcelaphini, where the genera *Damaliscus* and *Alcelaphus* tend to have less hypsodont tooth crowns, longer premolar rows and more complicated enamel folds in the molars. In spite of the underived nature of the alcelaphine dentitions from Langebaanweg, it was possible to classify the dentitions into two morphological groups. *D. neanica* has more derived and caprine-like dentitions, while the dentitions of *D. acalla* are more generalized, typical of what one might expect of an early alcelaphine. This is in accordance with Gentry's observation that the skulls of *D. acalla* are less derived than those of *D. neanica.* The dental characters distinguishing the two species of *Damalacra* can be summarized as follows:

The dentitions of *D. neanica* are generally slightly larger than those of *D. acalla* (Figs 1 & 2).

The premolar rows of *D. neanica* are shortened, the P_2 is absent and in the P_4 the tooth as a whole is distally shortened, giving it a very a caprine-like appearance (Fig. 1). In *D. acalla* the premolar row is longer, the P_2 is present and the P_4 is less squared off distally, more like in extant *Damaliscus* or *Alcelaphus.*

The lower jaws of *D. neanica* are deeper than in *D. acalla* (Fig. 1), suggesting greater hypsodonty. In both species there is a tendency for the metaconid-paraconid fusion to be incomplete, which is an underived character.

In comparison with *D. acalla,* the upper molars of *D. neanica* tend to have a more squared, blocky outline in occlusal view, they tend to expand more bucco-lingually towards the base of the crown, they have larger infundibulae, the styles are robust, ribs tend to be less well developed and basally on the M^3 the metastyle tends to flare distally. The general impression of the upper molars of

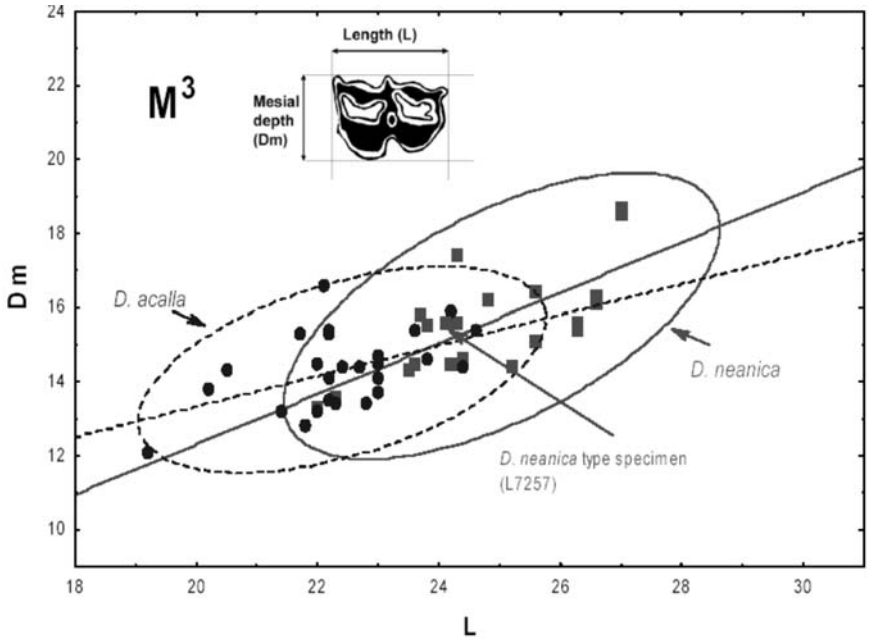


Figure 2. Plot of the occlusal length of the M3 against its bucco-lingual (mesial) depth of *Damalcra neanica* and *D. acalla.*

D. neanica, but in particular the last two characters mentioned, is caprine-like, whereas *D. acalla* has a less derived and more generalized alcelaphine appearance.

The dental characteristics of the two species of *Damalacra* agree broadly with Gentry's assessment of the skull morphologies. It appears that *D. neanica* was more derived and caprine-like in its morphology than *D. acalla.* If mandibular depth may be taken as a proxy for hypsodonty, then it appears that *D. acalla* (37.9–44.5 mm) is only marginal less hypsodont than *D. neanica* (40.0–47.4 mm) (Fig. 1), while both are very similar to the extant blesbok, *D. pygargus* (38.9–43.9 mm). This is somewhat unexpected, given the partly fused state of the metaconid and paraconid of the P_4, and suggests the need to test hypsodonty further by means of direct measurements on unworn M_3s.

If the mandibular depth data reflect hypsodonty then one would expect the trophic niches of both species of *Damalacra* to have tended towards grazing, as in the case of the blesbok. However, a mesowear analysis of the upper molars of *Damalacra* spp. suggests that this was not the case. *D. acalla* clusters with the sample of known mixed feeders and is closest to the bushbuck (*T. scriptus*) in mesowear pattern. *D. neanica,* on the other hand, clusters with the sample of known browsers and is closest to the mule deer (*O. hemionus*) in mesowear pattern. Unlike modern alcelaphines then, grass appears to have been a less important component in the diets of these two early alcelaphine species. The mesowear results are in good agreement with a microwear study of an undifferentiated sample of *Damalacra* teeth (Ungar *et al.* 2007), which suggested feeding niches ranging from browsers to mixed feeders. The apparent lack of agreement between the morphological analysis and the mesowear and microwear results is of interest and will be the focus of further research.

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Some factors leading to the good preservation of trilobite fossils within nodules of the lower Bokkeveld, Steytlerville district, Eastern Cape

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Introduction

Invertebrate fossils and fossiliferous nodules within the Bokkeveld Group (Cape Supergroup) were documented before the turn of last century, although their discovery is likely to have preceded this date considerably (Theron 1972). In general the preservation of fossils within the Bokkeveld is considered good.

Some nodules especially have been known to contain very well-preserved invertebrate fossils (Theron 1972; Oosthuizen 1984), many of which are described as type specimens. Preservation is usually in the form of impressions or hollow moulds with actual fossil material rarely preserved (Oosthuizen 1984). Fresh fossil samples often display pyritic encrustations (Theron 1999). However, very little attention has been paid to the nodular structures themselves and to the possible reasons for better preservation of fossils within them compared to within the surrounding shales. The following short note aims to highlight some macro-, micro-structural and mineralogical differences between trilobite material within shales and nodules. The lower Bokkeveld shales were deposited by prograding deltas bordering an epeiric sea at the margin of a shallow Devonian cratonic basin (Broquet 1992; Theron & Johnson 1991). These lithologies were subjected to advanced stages of diagenesis grading into low-grade metamorphism (de Swardt & Rowsell 1974). Nodular structures within them are considered to be early diagenetic in origin (Theron 1972).

Materials and methods

Some limitations of this study should be noted from the outset. In the absence of equipment needed for detailed chemical and isotope analysis, it was decided to adopt a different approach to nodule examination. Nodules were collected from the Gydo Formation within the Ceres Subgroup at various localities in the Cockscomb/Steytlerville area. Where possible, nodules were collected *in situ* and their GPS locations were recorded. Limited chemical analysis in the form of XRD (XRay diffraction) was carried out on both nodules and shale. However, the majority of the work entailed petrographic analysis of thin sections together with careful observations and photography of macrostructural features and field observations.

Results

Macro-structure

The preferential weathering of nodules indicates that they are more resistant than surrounding shales. Nodular cross-sections usually reveal a series of colouration zones which mimic their roughly circular to elliptical shape. The colouration of these zones varies from burnt orange to deep purple-maroon (Fig. 1). Fossil material within nodules varies but is usually dark grey in colour (Fig. 2). Fossil material within shales also varies but is typically burnt orange in colour and often associated with the growth of fine mica crystals.

Nodules contain a higher percentage of quartz, while the surrounding shale typically contains a higher mica percentage (Table 1). Feldspar is present within the shale. It was, however, not found within nodules (at least not within the detectable limit of the XRD equipment.

Petrography

The minerals replacing trilobite carapaces in shales and nodules differs. Within nodules the typical replacement

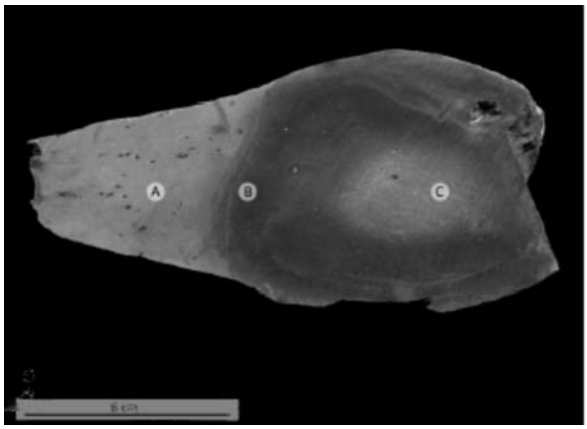


Figure 1. Macro-photograph of a sliced surface of a nodule and surrounding shale. Colouration varies from light grey in surrounding shale (A) through orange at the margin (B) to dark grey/purple in the centre.

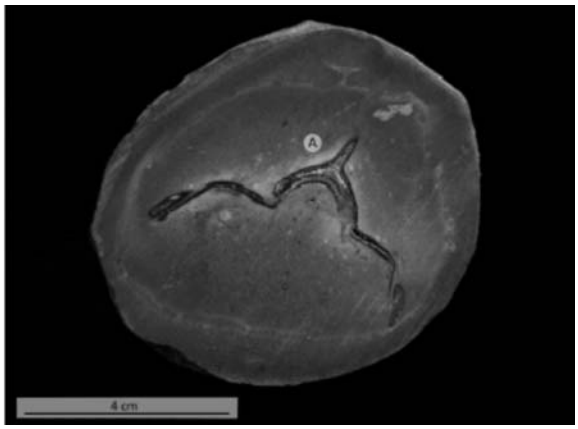


Figure 2. Macro-photograph of a sliced surface of a nodule containing a trilobite carapace (A).

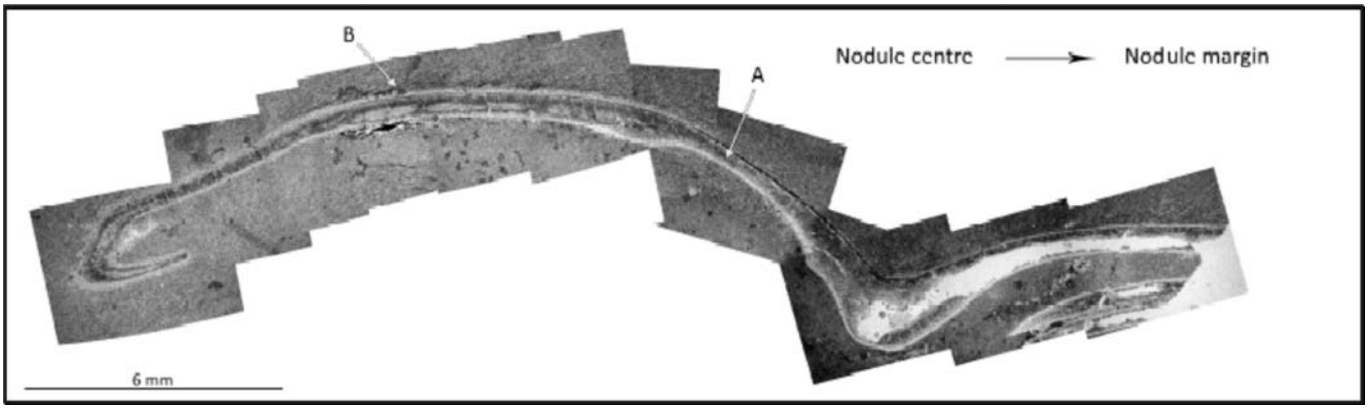


Figure 3. Photomicrograph composite composed of various images of a trilobite carapace within a nodule. Quartz is the dominant replacement mineral (A). The images were taken under PPL .Note the excellent preservation of the carapace and the formation of cleavage near the upper surface of the fossil (B).

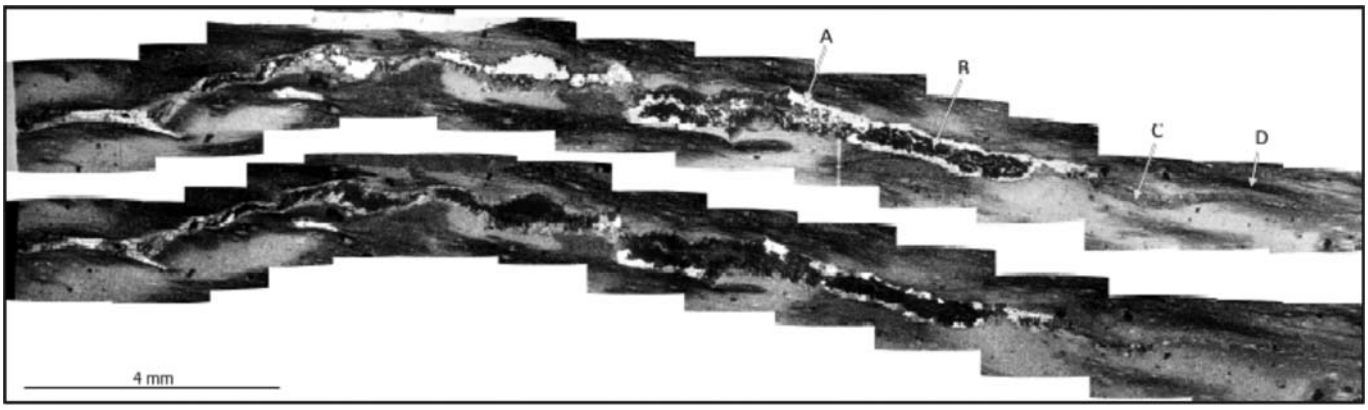


Figure 4. Photo-composite image composed of photomicrographs taken of a trilobite carapace within shale. The upper composite was taken under PPL while the lower one was taken under CPL. The general shape of the carapace can still be seen although deformation is evident. Replacement minerals include quartz (A), hematite (B) and biotite (C). Minor amounts of other white micas are found in association with biotite. Biotite seems to develop preferentially at the thinner margins of the fossil. Hematite is mostly found in the central portions of the carapace and generally shows a close association with quartz. Cleavage can clearly be seen in the shale matrix surrounding the carapace (D). Cleavage intensity varies as do colouration zones within the shale.

texture of aragonite by quartz is seen and quartz as well as some minor opaque minerals are the only replacement minerals (Fig. 3). Within shales the trilobite carapace material was composed to equal proportions of quartz, hematite and biotite (Fig. 4). Opaque minerals were also present as minor constituents. Hematite was found in the central portions of the carapace while quartz and biotite often replaced the thinner and outer portions of the

Table 1. XRD results showing the percentage of dominant minerals found within shales and nodules

	Nodule	Shale
Quartz %	62.6	28.31
Chlorite %	25.68	36.–7
Sericite %	11.72	30.29
Feldspar %	–	5.33

carapace. Deformation of fossil material is higher at the nodular margin than the centre.

Discussion

There are clearly differences in the nature of minerals which replace fossil material in the shales and within nodules. The colour zoning within nodules is probably as result of varying levels of oxidation of opaque and iron minerals within the nodule matrix. The fact that these minerals are often found in association with fossiliferous material supports this idea. It appears that the presence of quartz within both the nodule structure and as a replacement of the trilobite carapace within the nodule makes these structures more resistant to weathering than surrounding shales. These results could be clarified by the investigation of a wider variety of faunal groups as well as a more extensive chemical analysis of a range of nodules.

Conclusion

Although preservation of invertebrate fossiliferous material is better within nodular structures, material within the shales of the Bokkeveld are not as deformed and poorly preserved as would be expected for lithologies subjected to known levels of diagenesis and metamorphism. The reason for this appears to be mineralogical, with variations in both replacement minerals and overall nodule composition being the main contributing factors. These findings need to be clarified with more detailed analysis of general as well as isotope chemistry.

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Bone microstructure studies of southern African dinosaurs

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During life the bones of vertebrates record various aspects of the individual's life history. Soon after death, organic components of vertebrates decompose, but it is well documented that even after millions of years of fossilization, the microscopic structure of bone generally remains intact. Analyses of the texture and organization of the microstructure of fossilized bone, provides unparalleled insight into various aspects of the biology of extinct animals, particularly with regard to growth and development. This analysis provides a review of previous studies of the bone microstructure (osteohistology) of various Southern African dinosaurs.

Early studies of Southern African dinosaurs such as, *Euskelosaurus, Massospondylus carinatus* and *Syntarsus* (now referred to as *Megapnosaurus*) formed part of broader studies aimed at the documentation of types of bone tissue (histology) present among nonavian dinosaurs. Subsequently more focused and comprehensive studies of Southern African dinosaurs were conducted firstly on the Early Jurassic theropod, *Syntarsus* (*Megapnosaurus*) from Zimbabwe and South Africa, and later on the contemporaneous prosauropod, *Massospondylus* from South Africa. These landmark studies provided an analysis of the histological changes in bone microstructure during ontogeny and led to the deduction of the first growth curves for dinosaurs using bone microstructure.

More recent histological analyses were conducted on the coelurosaur, *Nqwebasaurus thwazi* from the Early Cretaceous, Kirkwood Formation of the Algoa Basin. The osteohistology of juvenile basal iguanodontians from the same deposits have also been analysed and new work is currently expanding our understanding of their biology. In addition, current studies, involves the assessment of the bone microstructure of a new prosauropod dinosaur from the Early Jurassic of South Africa.

Studies of the bone microstructure of southern African dinosaurs have made a significant contribution to understanding various aspects of the biology of the Dinosauria

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Introduction

The Rio do Rasto Formation of the Paraná Basin outcrops in the southern states of Brazil. This formation is currently interpreted as a sequence of fluvio-lacustrine deposits (Menezes 2000) and has produced continental vertebrates of Middle to Late Permian age, including paleoniscoid fishes, sharks, lungfishes, temnospondyles, dicynodonts, dinocephalians and pareiasaurids (Würdig-Maciel 1975; Barberena *et al.* 1985; Richter & Langer 1998; Langer 2000; Dias & Barberena 2001; Malabarba *et al.* 2003; Cisneros *et al.* 2005). In southern Brazil, fossil outcrops typically consist of very small exposures, usually human-made, isolated by dense vegetation. Stratigraphic correlations, even among sites that are separated by only a few hundreds of metres, are often impracticable. Here we present a preliminary report on new fossil finds at the Rio do Rasto Formation, including new fossil sites, that resulted from recent prospecting in the state of Rio Grande do Sul.



Figure 1. Map of the state of Rio Grande do Sul, in southern Brazil. 1, Posto Queimado site; 2, Aceguá site.

Aceguá

The municipality of Aceguá (Fig. 1) has produced two important sites, the type localities of the pareiasaurid *Provelosaurus americanus* and the temnospondyle *Bageherpeton longignathus* (Araújo 1995; Dias & Barberena 2001). The type specimen of *Provelosaurus americanus* was recovered from an exposure along RS 153 highway, less than three kilometres northeast from the border between Brazil and Uruguay. Fossils have not been recovered from this site for more than two decades, but during fieldwork in 2008 a new skull (Fig. 2A) and a scapula-coracoid of *Provelosaurus* were collected. In addition, a new fossil outcrop was discovered at the Farm Santo Antônio, in Aceguá, six kilometres east from the type locality of *Provelosaurus americanus.* The new site is characterized by a sequence of reddish siltstone interbedded by lenses of white fine-grained sandstones and intraformational conglomerate. Cranial (Fig. 2B,C) and postcranial elements of *Provelosaurus* were recovered, including previously unknown elements for this genus such as the first mandible, cervical vertebrae and interclavicle. Spiral coprolites referable to chondrichthyans, containing small bones and scales, were also recovered. Fossil gymnosperm wood was located *in situ* and a horsetail (Sphenopsida) was found in association with *Provelosaurus* bones.

São Gabriel (Posto Queimado)

A site in the municipality of São Gabriel, within the Posto Queimado geological sheet, has produced remains of lungfishes, sharks, temnospondyles, dinocephalians and the pareiasaurid *Provelosaurus americanus* (Langer 2000; Malabarba *et al.* 2003; Cisneros *et al.* 2005). A new fossil locality was located 7 km to the east, at the Farm Boqueirão. The outcrop is bent towards the southeast, being characterized by a sequence of siltstones interbedded by lenses of intraformational conglomerates and packages of sandstones. Fragmentary fossil vertebrates occur in high concentration within these conglomerates (Fig. 3). Preliminary investigation has allowed to recognize several labyrinthodont and shark teeth, paleoniscoid scales, and chondrichthyan spiral coprolites.

Discussion

The fossil content of the Rio do Rasto Formation in the State of Rio Grande do Sul at present supports the model

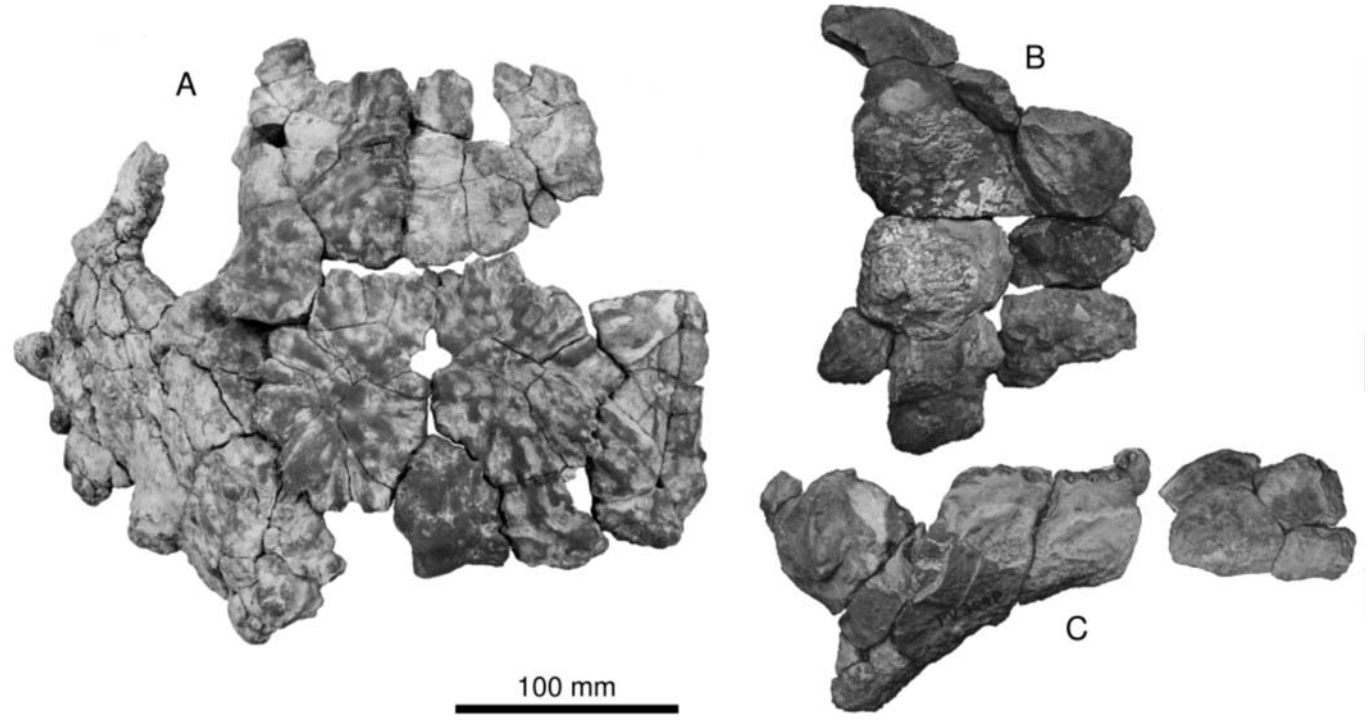


Figure 2. New specimens of the pareiasaurid *Provelosaurus americanus* from Aceguá. **A**, skull in dorsal view, from the type locality; **B**, right posterior portion of skull, in right lateral view, from Santo Antônio Farm; **C**, right mandible in lateral view, from Santo Antônio Farm.

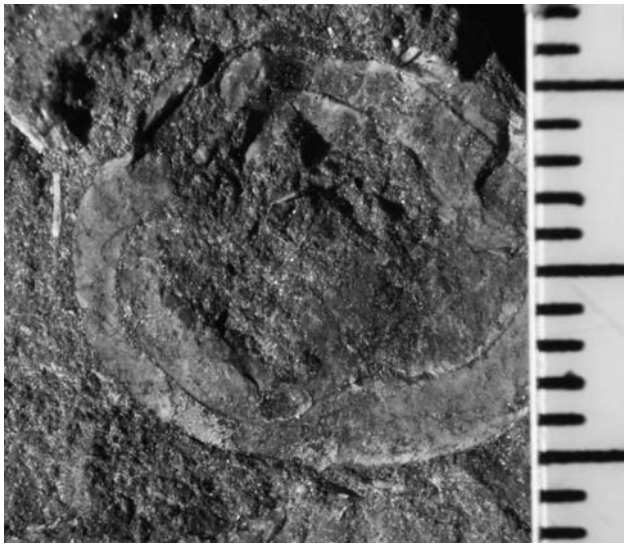


Figure 3. Chondrichthyan spiral coprolite in transverse section, within conglomerate, from Boqueirão Farm, Posto Queimado.

of a fluvio-lacustrine origin for the sedimentation of this stratigraphic unit. The local faunas of Aceguá and Posto Queimado share the presence of the pareiasaurid reptile *Provelosaurus* and are probably of Guadalupian (Middle Permian) age, due to the record of dinocephalians at Posto Queimado (Cisneros *et al.* 2005). Pareiasaurids and dinocephalians are known to co-occur elsewhere only in the *Tapinocephalus* Assemblage Zone of South Africa (Rubidge 1995). This biostratigraphic correlation, however, conflicts with preliminary data from radiometric dating of a bentonite layer from a *Provelosaurus* site in Aceguá (Rocha-Campos *et al.* 2006), which yielded an age of 275.1 ± Ma (Artinskian-Kungurian boundary, Cisuralian). This age is below Olson's Gap (Lucas 2004) and at least ten million years older than any known global record of a pareiasaurid.

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What's new in the world of Devonian tetrapods?

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The past 20 years has seen an exponential increase in the number of known Devonian tetrapod taxa, and a corresponding increase in geographical and environmental ranges that they are know to have inhabited. Recent finds of Late Devonian tetrapod-like fish and tetrapods with limbs are serving to close the morphological gap between finned and limbed tetrapodomorphs. Reviews of the climate during the mid and Late Devonian have suggested scenarios for the emergence of tetrapods, and new techniques are allowing fresh analyses and conclusions to be drawn from earlier collected material.

To date 11 genera of Devonian tetrapod have been named, with other material still awaiting description or publication. As recently as 1993 only three genera were known, two from Greenland and one from Russia. A record from Australia of a fourth remained controversial, though acknowledged tetrapod trackways were known. Since then tetrapods have been discovered in North America, Scotland, Latvia, China and Belgium, and the Australian record has been confirmed. Further finds from other Russian and other localities have also been recorded (Clack 2005, 2006). Thus they are known to have occurred in most of the major continental masses, including Gondwana, by the end of the Devonian. It is therefore not impossible that they will be discovered in other regions including southern Africa and South America. Southern Africa has already yielded an extensive fauna of Late Devonian fishes, some of which, such as a *Soderberghia*-like lungfish, accompanied the tetrapods in most of the other known tetrapod-yielding localities.

The environments that the tetrapods inhabited range from fully freshwater, to marginal marine, encompassing estuarine and lagoonal sites. The implication here is that the earliest tetrapods were euryhaline and could move around continents along their margins or through shallow interconnecting seas. The localities in which the tetrapod-like fish, *Elpistostege, Tiktaalik* and *Panderichthys* have been found are of this estuarine type (Daeschler *et al.* 2006), as well as that of the most primitive tetrapod with limbs, *Ventastega* (Ahlberg *et al.* 2008). The environment represented by the Late Devonian deposits around Grahamstown is also marginal marine/ estuarine (Gess *et al.* 2006). It has been considered that these localities may have been too far south and near to existing glaciated sites thus too cold to have suited tetrapods, but this is not certain.

During the mid- to Late-Devonian, the Earth apparently underwent a climate crisis in which oxgyen level dropped precipitously from over 25% to about 13%, much lower than today's (21%). At the same time, temperatures and carbon dioxide levels were both considerably higher than today. During this period, the area covered by terrestrial plants as well as their size and diversity also increased, resulting in increased organic matter content in the water. Its decay caused widespread anoxia in both marine and riverine systems, at a time of exceptionally low oxygen content in the atmosphere. This was the time during which the tetrapod stem group also diversified, and it is a notable fact that modifications to breathing, support and locomotory apparatuses took place also during this time. It may be that the climatic conditions of the time directly or indirectly affected or effected the emergence of tetrapods from the water (Clack 2007). Recently discovered or newly described taxa of tetrapod-like fish (*Panderichthys, Tiktaalik*) are beginning to show the sequence of character acquistion in the origin of limbed tetrapods (Shubin *et al.* 2004, 2006).

Recently recognized as the most primitive tetrapod known to have had limbs is *Ventastega*. Its skull bears close comparison with that of the tetrapod-like fish *Tiktaalik* from the Frasnian of Canada, especially in the posterior region, where both exhibit an enlarged spiracular notch. Although *Ventastega* is not known from limb material, its girdles are sufficiently similar to those of the better-known *Acanthostega* to infer the presence of limbs with digits. Its occurrence in Laurussia is consistent with a Laurussian origin for limbed tetrapods, although it is among the latest (late Famennian) of the known limbed forms (Ahlberg *et al.* 2008).

The iconic genus *Ichthyostega* has been reassessed in recent years. Three valid species are now recognized, occurring in separate geological formations in the same area in East Greenland (Blom 2005). Its ear region has been interpreted as adapted for underwater audition (Clack *et al.* 2003), whereas its postcranial skeleton shows a mixture of aquatic (paddle-like hind limb, finned tail) with terrestrial (robust shoulder and forelimb, differentiated axial skeleton with broad thoracic ribs) adaptations (Ahlberg *et al.* 2005).

Much of the latter information has been gathered by the use of the relatively new technique of computer-assisted tomography (CT scanning), which is allowing unprecedented access to previously intractable specimens (Callier, Clack and Ahlberg, work in progress). Application of such techniques at finer and finer resolutions will allow us to pose and answer questions that would have been considered impossible by earlier workers, such as the position and more importantly direction of muscle attachments.

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Stratigraphic correlation between the Karoo Supergroup and the Gondwana sequence of India

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The retroarc foreland Karoo Basin contains up to 12 km of sedimentary strata in the foredeep overlaid by at least 1.4 km of basaltic lava. The oldest strata are latest Carboniferous (312 Ma) and the lava Early Jurassic (184 Ma). In India, five basin belts are present, which are filled with up to 6 km of sedimentary strata overlaid by to 3 km of basaltic lava (Fig. 1). The strata are Permian (300 Ma) to middle Cretaceous (100 Ma) in age and the lavas (Deccan Traps) earliest Cenozoic (65 Ma). Only the correlation up to latest Jurassic (160 Ma) is described here.

Correlation is based upon Gondwanide-wide marine flooding events and other events such as the P-T extinction and widespread hiata. Seven sequences or time-slots have been recognized in South Africa and India (Fig. 2). Sequence 1 has a basal unconformable boundary and an upper conformable boundary at 290 Ma. The strata are glaciogenic and form the Dwyka Group in South Africa starting at 312 Ma and the Talchir Formation in India starting at 300 Ma. The upper boundary coincides with final rapid melting of ice sheets and an extensive marine transgression. Sequence 2 contains marine shale and in the northeast Karoo Basin, fluvio-deltaic sandstone of the lower Ecca Group in South Africa and wave-dominated deltaic sandstone and shale overlain by fluvio-deltaic sandstone of the Barakar Formation in India. The upper conformable boundary marks the start of another Gondwanide-wide marine flooding event at 271 Ma (Fig. 2). Sequence 3 begins with marine shale in both countries overlaid by a major regressive succession. Submarine fan sandstone is present in the Karoo foredeep. This is followed by a transition into deltaic shale and sandstone. These strata form the upper Ecca Group in South Africa and various formations in India (see Fig. 2). In South Africa, the regressive succession continued up into terrestrial mudstone and sandstone of the lower Beaufort Group. The upper conformable to disconformable



Figure 1. Reconstruction of central Gondwanaland during Permo-Triassic times showing distribution of basins investigated in South Africa and India.

boundary is placed at the Permian/Triassic contact (251 Ma), which is recognized by the appearance of the fossil mammal-like reptile *Lystrosaurus* and in most basins, the influx of prominent fluvial sandstone units (Fig. 2). Sequence 4 is characterized by terrestrial sandstone and predominant red mudstone indicative of semi-arid conditions. Fluvial sandstone is abundant in the lowermost part, but gives way to floodplain mudstone. The strata form the upper Beaufort Group in South Africa and various formations in India (see Fig. 2). Deposition ceased as a result of epeirogenic uplift and was followed by a widespread lacuna (Ladinian vacuity). The upper disconformable to unconformable boundary occurs at 228 Ma and marks the start of renewed accommodation space and deposition of Sequence 5 sediments (Fig. 2). Sequence 5 begins with fluvial sandstone that gives way to floodplain muds uplift and erosion. The strata form the lower Stormberg Group in South Afritone and minor fluvial sandstone. Several short hiata are present as a result of episodic tectonicca and the Supra-Panchet Formation in India. The upper conformable to disconformable boundary is placed at the base of a widespread hiatus (206 Ma), which was caused by epeirogenic uplift related to final coalescence of Pangea. In South Africa, it marks the break between the upper and lower Elliot Formation and a change in basin development from compressional tectonic processes to extensional tectonic processes (Fig. 2). In contrast, Indian basin development was entirely controlled by extensional tectonic processes. Sequence 6 was mostly a period of non-deposition in India apart from some terrestrial sandstone and mudstone and lacustrine shale of the Dhamarum Formation in the Wardha-Godavari Valley Basin (Fig. 1). In South Africa, floodplain mudstone and minor fluvial sandstone of the upper Elliot Formation were deposited after a short (6 million years) hiatus and these grade up into desert sandstone and minor mudstone of the Clarens Formation under an increasingly more arid climate (Fig. 2). The upper conformable boundary is drawn at the base of the extrusive lavas of the Drakensberg Group and the Letaba Formation dated at 184 Ma (Fig. 2). Sequence 7 is represented by basaltic lavas in South Africa, which terminated developments in all the basins at about 180 Ma. In India, few deposits of Sequence 7 are now preserved, as a result of subsequent erosion (Fig. 2), an exception being terrestrial sandstone and mudstone and lacustrine shale of the Kota Formation in the Wardha-Godavari Valley Basin (Fig. 1). The upper unconformable boundary is placed at 160 Ma, which marks the start of the separation between East and West Gondwanaland.

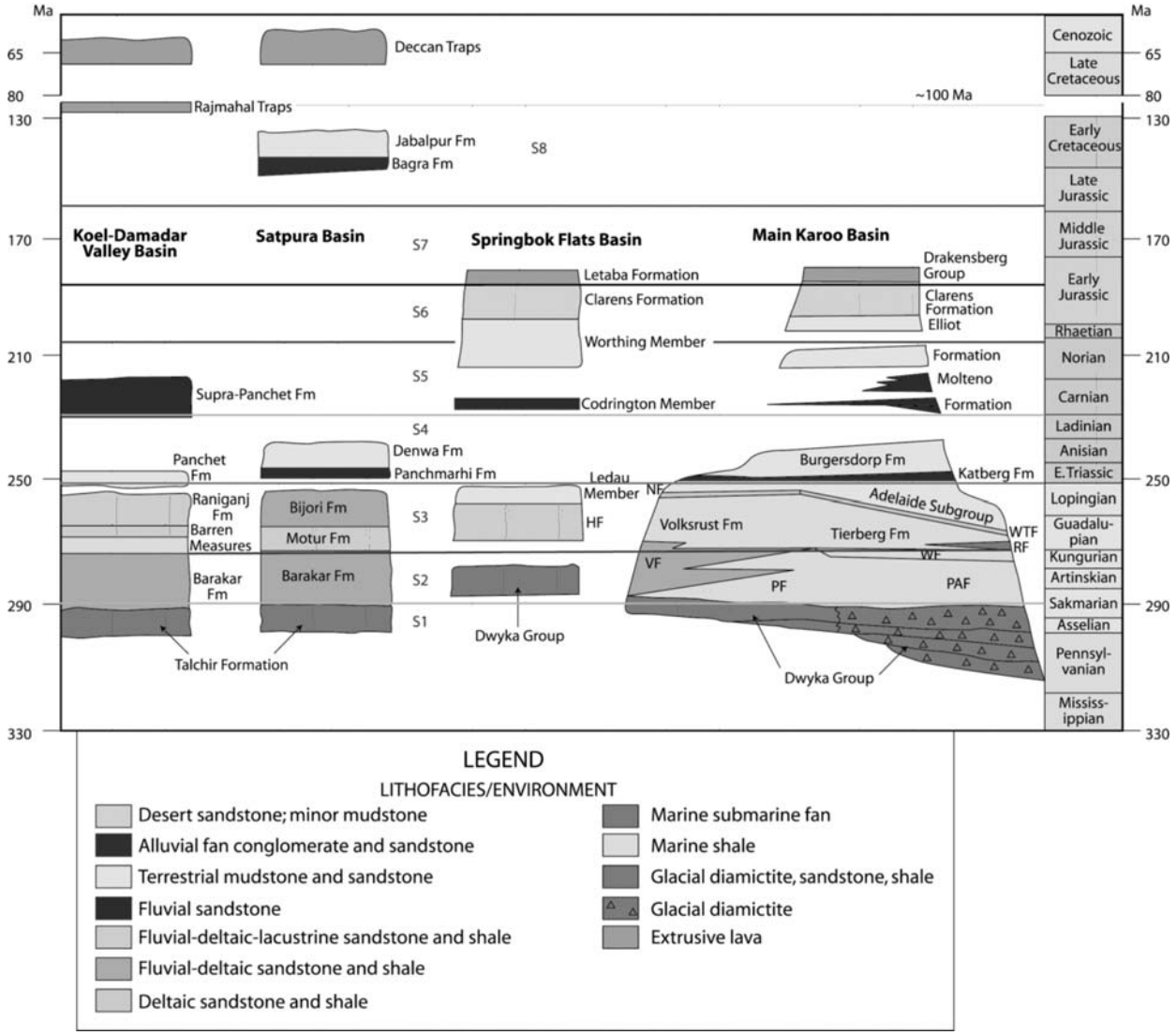


Figure 2. Time–space diagram of central Gondwanaland showing lithofacies/environment of stratigraphic units and their correlation in South Africa and India. S1 to S8 refer to the delineated stratigraphic sequences or time-slots.

Modern human origins and the Cave of Hearths Bed 3 mandible

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Introduction

The evolution of modern humans remains among the most important topics of hominin palaeontology. Most palaeoanthropologists consider Africa to have been the centre of origin for both *Homo sapiens* and later 'anatomically modern' members of this taxon (for a review of competing models see Curnoe 2007). Opinions differ about the details of fossil taxonomy and aspects of evolutionary history: ranging from a single, long-lived, slowly evolving and widely dispersed species (*H. sapiens*) containing three diachronic stages in the process of 'modernisation' (e.g. Bräuer 2008), through to five or six temporally shallow, rapidly appearing (speciating) and geographically narrowly distributed species (see reviews by Rightmire 1998; Stringer 2002; Bräuer 2008). Despite this diversity of opinions, the predominant view is that the human species began with the *H. sapiens-H. neanderthalensis* cladogenetic event (genetically clocked to ~370 thousand years ago (or ka): Noonan *et al.* 2006), while anatomically modern humans appeared in the fossil record about 170 ka later (i.e. at ~200 ka: see Stringer 2002).

The fossil-bearing deposits of southern Africa have provided some of the earliest examples of *H. sapiens* under a narrow definition of the species (see Stringer 2002). For example, the Florisbad cranium dated to around 260 ka is argued to be an example of the widely distributed although exclusively African early *H. sapiens*. Other examples include the Laetoli Hominid 18 fossil from Tanzania, Ileret (KNM-ER 3884) cranium from Kenya, Singa specimen from Sudan and Jebel Irhoud remains from Morocco. All of these fossils are thought to be from the period ~300 ka to ~170 ka (Bräuer 2008). Under the single-species model they all form part of the late archaic *H. sapiens* morphological-temporal grade (Bräuer 2008).

Less than a decade ago southern Africa was argued to provide some of the earliest evidence for anatomically modern humans at around 100 ka (Stringer 2002). Now, however, attention has shifted to East Africa where early

modern human fossils are now known to be almost 100 ka older than those in southern Africa. Fossils from the localities of Omo-Kibish and Herto in Ethiopia, Singa in Sudan and Mumba in Tanzania date to between ≤195 ka and ~110–130 ka (see a review in Trinkaus 2005). Thus, current dating evidence suggests that the appearance of early modern humans in southern Africa (i.e. Klasies River Mouth LBS ~100–120 ka: Trinkaus 2005) is broadly coincident with their earliest dispersal out of Africa and may form part of a broad exodus from East Africa.

The present author recently examined the Cave of Hearths (CoH) Bed 3 mandible (Fig. 1) as part of a broad investigation into the origins of *H. sapiens.* Although the precise age of this specimen is unknown, on geological, faunal and archaeological grounds it is generally considered to be >200 ka and perhaps within the range of ~250–350 ka (Bräuer 2008). Until now, studies of this fossil have emphasized its primitive morphology. Thus, it has mostly been considered to sample the same group as the Kabwe and Saldanha fossils (i.e. archaic *H. sapiens, H. heidelbergensis* or *H. rhodesiensis*: see Tobias 1971; Rightmire 1998; McBrearty & Brooks 2000; Stringer 2002; Bräuer 2008). However, investigations by the present author indicate the presence of a mosaic morphology in this specimen, combining many anatomical features diagnostic of early modern humans with a small number of primitive features. In light of this, there is a need to reassess its taxonomy and to reconsider its possible relevance to reconstructing the emergence of modern humans.

In the discussions that follow, the CoH specimen is compared to mandibular remains from late *H. erectus* and early anatomically modern humans from Africa and West Asia. As there are no mandibles from African archaic hominins (*H. heidelbergensis/H. rhodesiensis*) apart from the CoH specimen, a comparison will also be made with some Middle Pleistocene (non-Neandertal) fossils/samples from Europe. Comparative metric data for African/West Asian early modern humans, the Mauer mandible, a European Middle Pleistocene (non-Neandertal) sample and a late *H. erectus* sample were taken from: McCown & Keith (1939), Tobias (1971), Vandermeersch (1981), Singer & Wymer (1982), Wood & Van Noten (1986), Bräuer & Mehlman (1988), Bermúdez de Castro & Nicolas (1995), and Grine (2000).

It should also be noted that Tobias (1971) described the developmental age of the CoH specimen as juvenile; although, he had doubts about this diagnosis. However, comparisons with modern human dental eruption sequences and molar enamel wear made by the present author actually indicate that the specimen is likely to have been at least a late adolescent (+18 years old) and more probably an adult (+25 years old) (Curnoe, unpublished).

Morphological comparison

Table 1 lists some major anatomical features of the CoH mandible according to their polarity. The vast majority represent the modern morphological condition. Its body is short and thin, most closely resembling modern humans. As Fig. 2A shows, the symphysis thickness value in the CoH specimen is very small (thin) and well below

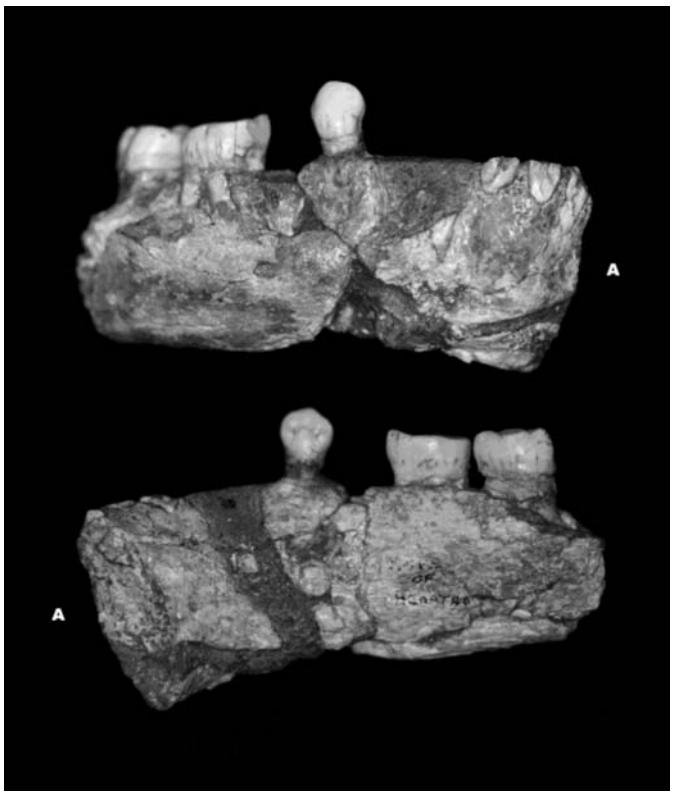


Figure 1. Cave of Hearths Bed 3 mandible in lateral (above) and medial (below) aspects (NB: 'A' denotes anterior).

the mean value for late *H. erectus* (difference being statistically highly significant), well below the value for the Mauer mandible (type specimen for *H. heidelbergensis*) and below the mean value for early modern humans. Interestingly, symphysis thickness in the Mauer mandible and the mean for modern humans are both significantly smaller than the mean for late *H. erectus.* This underscores the value of this measurement for systematics. At the level of M_1 (Fig. 2B), the body of the CoH mandible is thin, its value being almost identical to the mean for modern humans. Although the CoH datum is much smaller than the Mauer specimen and the mean for late *H. erectus,* the difference between them is not statistically significant.

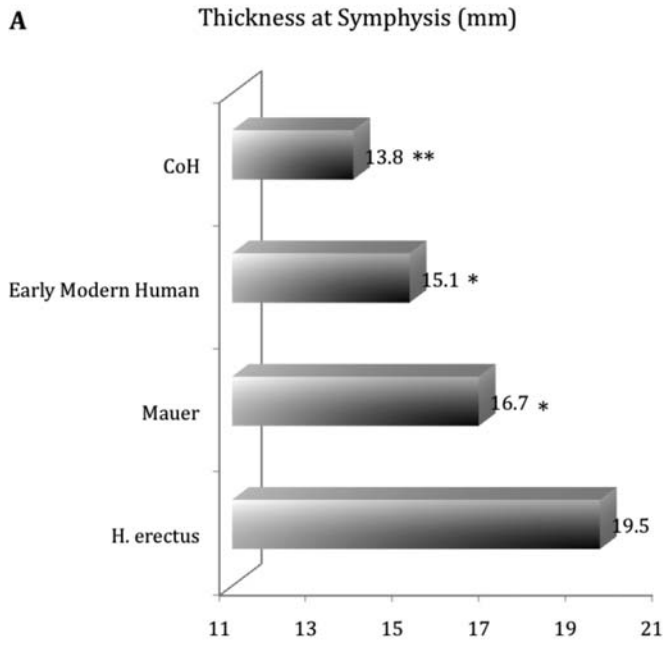
When viewed in lateral aspect, late *H. erectus* mandibles tend to maintain even body height anteroposteriorly so that their superior and inferior borders remain approximately parallel (Tobias 1971). However, the CoH body shows anteroposterior reduction in height (or tapering)

Table 1. The mosaic morphology of the Cave of Hearths Bed 3 mandible.

Modern features
1. Short and thin body
2. Body tapers (reduces in height) anteroposteriorly
3. Body thickens anteroposteriorly (absolutely and relative to height)
4. Mental foramen located anteriorly (inferior to premolars)
5. Mental eminence (?true chin)
6. Molar crown size reduction ($M_1 \rightarrow M_2$)
7. M_1 crown area more than double P_3 crown
8. Molar crown size reduces anteroposteriorly
9. M_3 agenesis

Primitive features
1. Marked prognathism
2. Taurodont molars

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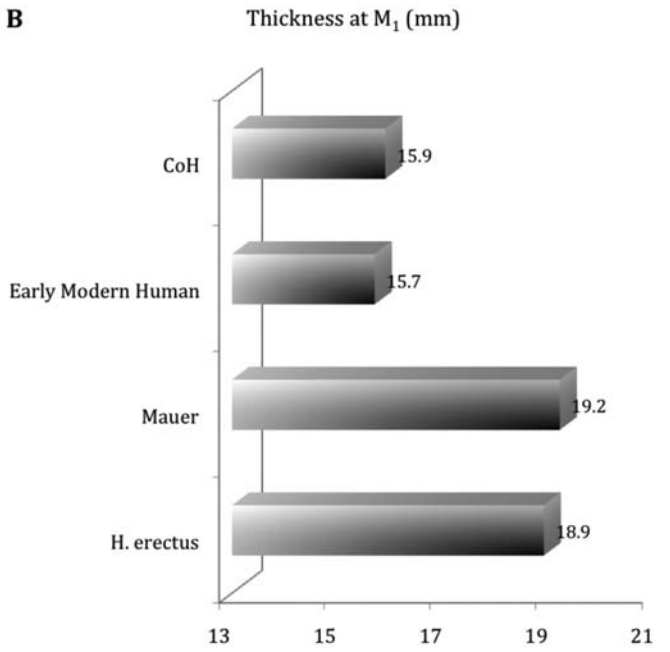
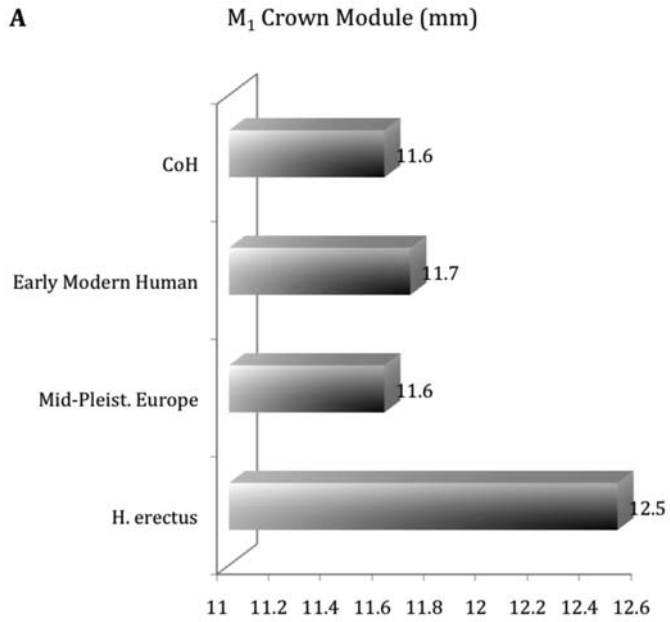


Figure 2. Comparison of mandibular body thickness. Asterisk denotes values as significantly different to the mean value of *H. erectus* using Student's *t*-test).



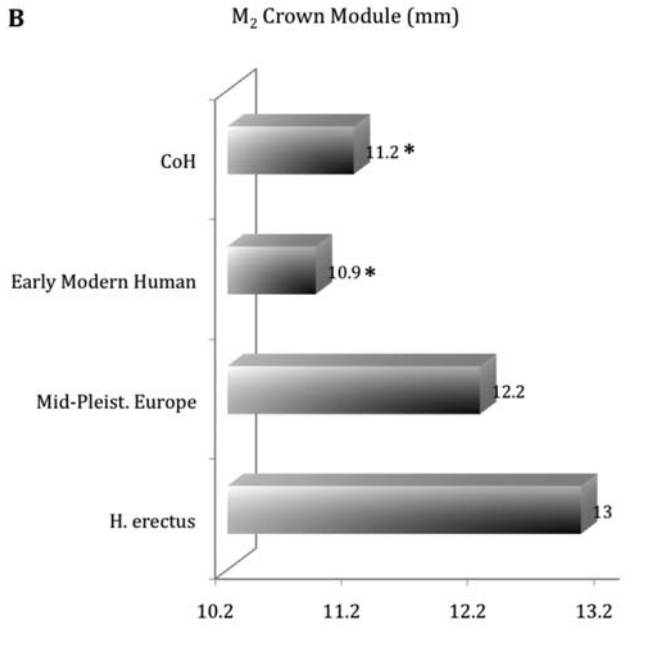


Figure 3. Comparison of molar crown size. Asterisk denotes values as significantly different to the mean value of H. erectus using Student's *t*-test).

the condition seen in early modern humans. Additionally, the body of the CoH specimen thickens anteroposteriorly, as seen in early modern humans, and contrasting with late *H. erectus,* in which it thins.

Another feature frequently cited as characteristic of anatomically modern humans is the anterior placement of the mental foramen. In early modern specimens, this foramen is located mostly inferior to the second premolar (P_4), but in archaic groups including late *H. erectus* and Neandertals it is mostly inferior to P_4/M_1 or M_1 (Lieberman 1995). In the CoH specimen, it is located inferior to P_4 (modern condition).

The presence of a chin is widely considered to be diagnostic of modern humans (e.g. Dobson & Trinkaus 2002; Trinkaus 2005, 2006). Criteria have been developed to distinguish 'true' chins from 'incipient' (developmentally non-homologous) chins (e.g. Lieberman 1995). According to Tobias (1971), the CoH mandible exhibits the components of a true chin (consistent with Lieberman's criteria). However, according to the approach of Dobson & Trinkaus (2002), the CoH chin would not be considered modern, as it lacks anterior projection in the median sagittal plane. Moreover, its very low symphysis angle (high prognathism), a primitive (*erectus*-like) feature, indicates the absence of a true chin.

The teeth of the CoH specimen are also very modern. Its molar crowns reduce in size anteroposteriorly ($M_1 \rightarrow M_2$), and its M_1 crown is more than double the size of its P_3

crown. Both features characterize early modern humans. Its third premolar (P_3) mesiodistal diameter (MD), buccolingual diameter (BL), crown module and crown area values lie outside of (below) the range of late *H. erectus* and sit close to the mean for early modern humans. Its M_1 MD, BL, crown module, crown area and shape index values are identical to or virtually indistinguishable from mean values for early modern humans. Thus, like modern humans, the CoH M_1 is small and characterized by BL narrowing. The CoH M_2 MD, BL, crown module and crown area values lie outside of (below) the range of late *H. erectus* and well within the range of early modern humans. Thus, its M_2 is much reduced in size compared to late *H. erectus* (dental reduction = modern).

As Fig. 3A shows, the CoH M_1 crown module (MD+BL/2) is identical to the mean value for a sample of Middle Pleistocene (non-Neandertal) European hominins; both values being virtually identical to the mean for early modern humans and indicating a common pattern of dental reduction. The mean value for late *H. erectus* is larger, but not significantly so. Figure 3B compares the M_2 crown module for the CoH mandible with comparative samples. Its value is very similar to the mean for early modern humans, but well below mean values for the European Middle Pleistocene sample and late *H. erectus.* When compared using Student's *t*-test the CoH value, early modern human sample mean and European Middle Pleistocene mean are significantly different to the mean for late *H. erectus.* This emphasizes the taxonomic utility of this feature.

The molars of the CoH specimen are characterized by taurodontism or an inferiorly extended pulp cavity. While this is the condition seen frequently in archaic hominins including Neandertals, it is found commonly among early modern specimens (McCown & Keith 1939) and occasionally among contemporary humans (Constant & Grine 2001).

In his description of the CoH mandible, Tobias (1971) argued that the specimen possessed several strong indicators of M_3 agenesis; although, one of them (anteroposterior molar crown size reduction) is suggested here to be a modern trait. Agenesis of the M3s is also a derived feature of later modern humans (Trinkaus 2006).

Discussion and conclusion

On the basis of the present reanalysis, the CoH mandible shows strong affinities to early anatomically modern humans from Africa and West Asia. This finding contrasts with previous studies which have emphasized its primitive morphology and mostly assigned it to *H. heidelbergensis* or *H. rhodesiensis.* However, while it presents as a morphological mosaic, the CoH specimen is overwhelmingly modern in its disposition. The CoH mandible should, therefore, be classified as belonging to *H. sapiens.*

Precisely which sub-group or grade of *H. sapiens* it belongs is a matter of opinion. At the minimum, it should be viewed as representing the 'archaic' grade described by Stringer (2002) or late 'archaic' grade according to Bräuer's (2008) scheme. In both instances, the CoH Bed 3 mandible would belong to the same broad group as the Florisbad cranium, as well as the Laetoli Hominid 18, Ileret, Singa and Jebel Irhoud remains, rather than the Kabwe-Saldanha population.

The alternate view, also consistent with its mosaic morphology, is to consider the CoH mandible to be part of an early anatomically modern group, such as represented by the Klasies River Mouth LBS sample. The lack of chin development in the CoH specimen is similar to the situation within both the later Klasies River Mouth sample (SAS: ~65–90 ka: Trinkaus 2005) and the Israeli Skhul and Qafzeh individuals (Lam *et al.* 1996). However, the CoH specimen is probably much older than these fossils, being either broadly contemporary with the oldest modern humans in East Africa (e.g. Omo-Kibish 1: ≥195 ka) or even pre-dating them by up to ~150 ka (estimated age ~250–350 ka: Bräuer 2008). The implications of such a view are considerable. It implies that modern humans emerged much earlier than is currently believed and that the earliest moderns had a wide distribution across sub-Saharan Africa. While it may be tempting to suggest that southern Africa was the centre of origin for modern humans, this would be unwise at present. First, the geological age of the CoH specimen remains poorly understood. Second, the CoH specimen is only one individual and from a statistical viewpoint a larger sample would be required to support such an argument. Finally, an early emergence for anatomically modern humans would be consistent with archaeologically views that the appearance of the Middle Stone Age marks the origins of modern behaviour (McBrearty & Brooks 2000).

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A study of small-bodied hominims from Palau, Micronesia

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Since the discovery of pygmy elephants in the early 1900s the concept of insular dwarfism has been one of great interest. This phenomenon, by which the size of animals isolated on an island shrinks dramatically over time, has been seen in large reptiles and mammals (Foster 1964). The potential of island effect on body size variation in the genus *Homo* was brought to light with the discovery of *Homo floresiensis.* Brown *et al.* (2004) announced the unearthing of a remarkably small hominid skeleton in Liang Bua cave on the island of Flores, southeastern Indonesia. The remains were dated to the late Pleistocene (95–12 ka) and were described as a new species, *H. floresiensis.* Since the discovery, *H. floresiensis* has been at the centre of a debate regarding its designation as a new hominin species. There are essentially three main arguments within this debate. Brown *et al.* (2004) and Fall *et al.* (2005) argue that *H. floresiensis* represents a case of insular dwarfism from an ancestral population of *Homo erectus.* The second argument by Weber *et al.* (2005) proposes that *H. floresiensis* is a microcephalic *H.* sapiens (i.e. they postulate a pathological condition). Lastly, Jacob *et al.* (2006) suggest that, due to features not unusual in modern pygmoid Australomelanesian *H. sapiens, H. floresiensis* is not a new species, rather a group of small *H. sapiens* that fall within the range of living pygmoid populations. Within the inter-populational variation of human body size polymorphism are a number of cases of 'pygmoid' or dwarfed populations. Typically these populations are known from mainland tropical forests in Africa and island settings in southeast Asia (Richards 2006), and these individuals are considered to be at the bottom of the range for human body size variation. Here we discuss preliminary results of our study of a recently discovered population of small-bodied humans on the island of Palau, Micronesia, which provides additional insight into the issue of dwarfism in human populations. This contribution represents an extension of the announcement paper of this new find (Berger *et al.* 2008), radiocarbon dated to between 1420 and 2890 BP.

Excavation and surface sampling of Ucheliung and Omedokel caves in 2006 and 2007 led to a substantial collection of human material ($n > 1000$). The remains are fragmented and very few associated skeletal elements were recovered due to secondary deposition and disturbance. Of the specimens collected from Palau, only 61 were measurable. Due to the fragmentary nature of the specimens, the measurements taken on individual elements varied. Measurements were taken following Martin (1928), and included for example, anterioposterior diameter of the femoral head, acetabular height and distal maximum breadth of the tibia. The same landmark measurements were taken on a large comparative collection of modern humans, of both 'normal' and small-bodied individuals, including both sexes of adult San from South Africa, pygmoid Andaman and Nicobar Islanders, and a Pygmy from the Democratic Republic of the Congo.

Measurements of the elements from the two Palauan caves indicate body sizes at the lower extreme of modern human variation, and in some cases the range of the small bodied *Homo floresiensis.* This could be seen in the mean estimate derived from the two Palauan femora, namely 43.065 kg, which did not differ significantly from the Andaman Island mean (43.765 kg, $n = 38$). Of the two measurable proximal tibia specimens recovered, one had a bicondylar breadth of 63.1 mm, which falls above, and is not significantly different from the mean of a pooled sex sample of Andaman Islanders (57.8–67.8 mm, $n = 29$). The other tibia specimen has a bicondylar breadth of 53 mm, which falls below the Andaman mean, but reflects an individual of similar size to *Homo floresiensis*, which has a bicondylar breadth of 51.5 mm. All postcranial elements are considered derived. A different observation was made for facial features which showed a combination of primitive and derived features. Primitive features of the Palauan fossils include an inflated glabellar region and the distinct development of a supraorbital torus. Derived features include a distinct maxillary canine fossa, moderate bossing of the frontal and parietal squama and a lateral prominence on the temporal mastoid process. For an extensive list see Berger *et al.* (2008).

The variation seen in the Palauan sample is unlike anything we have seen before. Among this sample are a number of individuals that are small even relative to other pygmy populations. While some individuals plot within the lower end of human variation, there are others that push this limit beyond what is typically considered small for *Homo sapiens.* Even though the Palauan remains exhibit features that are primitive for the genus *Homo,* they are clearly *H. sapiens* due to the craniofacial traits they possess. Colonization of Oceania is thought to have occurred around 4500 years ago by people from the Philippines, but remains of these settlers are rare. Palaeoenvironmental and palynological data support this date (Clarke *et al.* 2006), but archaeological evidence suggests at least one thousand years later (Fitzpatrick *et al.* 2003). Given the relatively recent age of the Palau population they may represent a case of rapid insular dwarfism.

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A review of the occurrence of disarticulated Early Cretaceous sauropod dinosaur fossils from the Kirkwood Formation of the Oudtshoorn and Algoa Basins, South Africa

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Dinosaur fossils, in the form of disarticulated bones and teeth from various taxa, have been recovered from Early Cretaceous Kirkwood Formation sediments in both the Oudtshoorn and Algoa basins over the past 163 years. During this time only two partly articulated dinosaur specimens have been recovered; the small coelurosaur theropod *Nqwebasaurus* (De Klerk *et al.* 2000) and the nominated holotype of the juvenile ornithopod (iguanodontian) from the Kirkwood Cliff locality (Forster & de Klerk, this volume). It was in 1845 that the first report of a dinosaur fossil discovery was made from South Africa when Mr Andrew Geddes Bain and Dr William Atherstone recovered disarticulated fossil 'bones bigger than those of an ox' from the Bushman's River valley between Grahamstown and Port Elizabeth from a locality that they named 'Iguanodon Hoek'. After a protracted history the material was eventually described by Galton & Combs (1981) as the stegosaur *Paranthodon africanus* (Broom).

Two instances of sauropod fossils material have been identified from the terrestrial Oudtshoorn Basin. In 1927 Broom sent a 3 cm long sauropod tooth that he had recovered from the 'grey-green sandstone' outcrops, to the north of Oudtshoorn, that he had misidentified as Sundays River Formation beds, to Von Heune (1932) for identification. The second report was made by Hoffman (1966) when he described a series of large vertebrae and bone fragments that had been recovered from the Carlitzdorp area in the western part of the Oudtshoorn basin – these fossils he ascribed to a 'gigantic pleisiosaur' which are accessioned at the National Museum Bloemfontein. On investigation of this occurrence in 1999 it was established that there is no evidence to support a marine origin for the Oudtshoorn basin sediments and the fossils are now considered to be from a large sauropod dinosaur.

Disarticulated sauropod fossils in the form of vertebra, partial long bones and numerous isolated teeth have been recovered from at least six localities in the Algoa Basin. The first fragmentary bones were reported by Broom (1904) from a brick quarry at Dispatch (near Port Elizabeth) that he named *Algoasaurus bauri.* Unfortunately the bones that were salvaged, before being made into bricks, were never accessioned into a museum collection and this dinosaur species now sadly languished in the realm of *nomina dubia.* By far the majority of sauropod fossils recovered from the Algoa Basin have come from the general stratotype locality of the Kirkwood Formation in the Sunday River valley 3 km south of Kirkwood village – the site now know as the Kirkwood Cliffs or 'Lookout'. Material recovered thus far includes:

- Large proximal heads of both the humerus and femur from a 'Brontosaurus' now on display at Bay World (Port Elizabeth Museum). The femur end measures 0.6 m across the top.
- Several sauropod teeth were reported by Rich *et al.* 1983) and more have been found since 1995 during successive field seasons, by the author and accompanying students and colleagues.

During the June 1995 field season a well-preserved single diplodocid caudal vertebra (centrum 26 cm) was recovered from the Kirkwood Cliffs. The specimen is now on display at the Albany Museum.

Two additional vertebrae, one a caudal (centrum 15 cm) and the other, thought to be a dorsal (centrum 12 cm) are very likely to have been collected from the Kirkwood Cliffs locality. These specimens were part of the Port Elizabeth Museum and Rhodes University Geology collections. These fossils had in the past been collected by students on field outings.

Recent discoveries of two (possibly three) sauropod vertebrae have been made at Umlilo Hunting Safari reserve some 17 km west of Kirkwood. The vertebra best preserved from this site has been tentatively identified as that of a cervicle from a titanosaurid while the other, displaying distinctive cancellous bone in cross-section is thought to be a dorsal. Both specimens are now nearing completion in their preparation. Several sauropod teeth have also been recovered from the Addo Elephant Park road cuttings since 1995. Within the broader expanse of the Bushmans River valley sauropod material has been recovered from the Shamwari Game Reserve (caudal vertebra and several teeth) and some teeth from the Amakhala Game Reserve ('Iguanodon Hoek' *Paranthodon* site). In summary the sauropod dinosaur taxa are indicated by the seven separate disarticulated vertebrae, a series of fragmentary long bones and numerous disarticulated teeth. Taxa represented by these fossils include diplodocids (possibly *Dicraeosaurid*) and titanosaurids. Diplodocids were previously unknown from the Cretaceous of southern Africa.

Re-evaluating the Jurassic structures identified as termite nests in the Clarens Formation in the Tuli Basin, Limpopo Province, South Africa

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Clusters of vertical structures discovered in the Clarens Formation sandstones in the Tuli Basin in the Limpopo Province have been identified as termite nests (Bumby *et al.* 2004). These structures have been described by Bumby *et al.* (2004) and Bumby & Bordy (2006) as tall pillar-like structures, some slightly ovoid in cross-section and with differing architecture depending on its level within the structure. They also mentioned fin-like vertical structures which buttressed the cylindrical central section, a basal section honeycombed with small filled-in tunnels and open central spaces. Some structures are described as having a north–south orientation which would have aided with thermoregulation of the assumed termitaria. To support their claim they compare these structures with those built by extant magnetic termites of Australia.

Darlington Munyikwa of the Natural History Museum in Bulawayo (1995) reported rock with a honeycomb-like structure from Zimbabwe similar to those reported by Bumby & Bordy (2006). The presence of enigmatic cylindrical objects in the sandstone was reported south of the Limpopo River, extending from the farms Pontdrift in the west to Schroda (De Villiers 1967; Van Eeden 1969). De Villiers believed that these structures were formed by the action of water and sand during the Jurassic while Van Eeden (1969) argued after revisiting the area and discovering a second site with similar structures on Pontdrift that they were formed by steam percolating through the unconsolidated sand after the deposition of sand on the still hot Drakensberg lavas.

After a study of the structures, microscope slides, mineralogy and comparison with extant termitaria we conclude that these structures were probably formed by means of sedimentary processes and agree in general with the findings of Van Eeden and De Villiers. An explanation for the formation and non-biogenic nature of the structures and a description of the palaeoenvironment are given.

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Large mammals and palaeoenvironmental reconstruction: lessons from a modern bone assemblage in southern Kenya

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The reconstruction of past environments from vertebrate fossil assemblages represents a fundamental goal of paleontology. Faunal analysts have developed numerous quantitative methods for reconstructing paleoenvironments from large mammal remains. These include examination of the presence/absence or relative abundances of particular taxa (Bobe & Behrensmeyer 2004; Klein 1972; Vrba 1980), species diversity indices (Avery 1982; Grayson *et al.* 2001), ecological structure analysis (Andrews *et al.* 1979; Reed 1998), and functional morphology (Kappelman *et al.* 1997; Plummer & Bishop 1994), among others. Paleoenvironmental interpretations are often made in reference to data from present-day faunal communities (Klein 1972; Reed 1997, 1998; Vrba 1980). This reasoning assumes that a death assemblage is a direct reflection of the living vertebrate populations. However, with the exception of Behrensmeyer's long-term taphonomic research in Amboseli Park, Kenya (Behrensmeyer & Dechant Boaz 1980; Behrensmeyer *et al.* 1979), the relationship between living animal communities and their death assemblages has received relatively little attention. Until this relationship is better understood, it will not be clear what exactly one is measuring when reconstructing environmental parameters from fossil assemblages.

This study uses data from a modern landscape bone assemblage in the Shompole/Ol Kiramatian group ranch and conservation area (SOK) of southern Kenya to examine methods of paleoenvironmental reconstruction. Specifically this paper addresses the following questions: (1) Do environmental reconstructions obtained by different methods reflect local (microhabitat) or regional (macrohabitat) vegetational conditions? (2) What methods effectively distinguish habitats within the modern bone assemblage?

The Shompole/Ol Kiramatian group ranch (SOK) is located in southern Kenya along the Kenya–Tanzania border at the base of the Nguruman Escarpment, which marks the western edge of the East African Rift Valley. The semi-arid habitat (~500 mm annual rainfall) supports a rich faunal community that is typical of this region. The principal herbivores include wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), and Grant's gazelle (*Gazella granti*). Carnivores include lion (*Panthera leo*), leopard (*Panthera pardus*), and striped hyaena (*Hyaena hyaena*), among others.

The SOK bone assemblage was sampled following the taphonomic survey methods developed by Behrensmeyer (Behrensmeyer & Hill 1980; Behrensmeyer *et al.* 1979) in Amboseli Park, Kenya. Transects were surveyed for bones by a team of three individuals across the various habitats that characterize the SOK landscape. This study makes

Table 1. Summary of the results obtained in this study.

Method of environmental reconstruction	Local or regional environmental signal?	Are the reconstructions accurate?	Does the method distinguish SOK habitats?
Presence/absence	Regional	Yes	No
Taxonomic relative abundance	Regional	Yes	Yes
Ecological structure analysis	Regional	Yes	Yes
Diversity indices	–	–	Yes

use of data collected from the following habitats, listed in order of increasing vegetation cover: open grassland (OG), *Acacia tortilis* grassland (AG), *Salvadora* shrubland (SS), and gallery forest (GF). Following the broad habitat classifications described by Reed (1998), these samples within the SOK ecosystem would be classified as grassland (OG & AG), shrubland, and forest, respectively. The broader SOK ecosystem is appropriately classified as a shrubland, which also characterizes the nearby Amboseli and Tarangire (Tanzania) ecosystems (Reed 1998). The minimum number of individuals (MNI) sampled in a given habitat is used as the principal census data.

In a previous study, Reed (1998) compiled taxonomic and ecological data from a number of extant African faunal communities sampling a range of habitats and rainfall regimes (e.g. from the Congo Basin to the Namib Desert). These data are used to 'reconstruct' the vegetation of the four SOK death assemblages using presence/absence data, taxonomic relative abundances, and ecological structure analysis, which classifies faunal communities according to the proportion of species falling into certain locomotor and trophic ecovariables. Faunal similarity is assessed using the Dice/Sorenson coefficient for presence/absence data and Chord distance (converted to a similarity index) for relative abundances of taxa or ecovariables.

A comparison of the SOK death assemblages to extant African faunal communities by means of taxonomic presence/absence, taxonomic relative abundance, and ecological structure analysis consistently links the samples with grasslands (Serengeti Plains) or shrublands (Amboseli NP & Tarangire NP). This is an accurate assessment of the SOK ecosystem. Death assemblages from habitats characterized by extreme differences in vegetation cover (e.g. open grassland *vs* gallery forest) provide a faithful ecological signal of the broader environmental conditions. Because of this 'smearing' of ecological signals across habitats, however, these methods are limited in that they provide little insight into the immediate vegetation from which the death assemblages were sampled. For example, the heavily vegetated gallery forest provides a death assemblage that consistently allies with more open shrubland habitats.

Further exploration of the SOK data is undertaken to determine whether an ecological signal specific to each habitat can be recovered from the death assemblages. This analysis makes use of presence/absence data, taxonomic relative abundances, the relative abundance of individuals falling into various trophic and locomotor classes, and the Shannon diversity index.

Presence/absence data provides no clear signal that might differentiate faunal communities according to habitat. For example, zebra, wildebeest, warthog (*Phacochoerus aethiopicus*), Grant's gazelle, and giraffe (*Giraffa camelopardalis*) were recovered from all habitats. A contingency table analysis on the taxonomic abundances, however, indicates that relative abundances differ significantly across assemblages and in a manner that is expected given the habitat. For example, there is a clear decline in the abundance of wildebeest and an increase in the abundance of impala as vegetation cover increases. As expected, giraffe are particularly abundant in the *Acacia* grassland and rare in the open grassland. An analysis of trophic and locomotor variables provides similar results. For example, the proportion of grazers declines significantly as vegetation cover increases, whereas mixed feeders become increasingly abundant. Species practicing a mix of terrestrial and arboreal locomotion are particularly abundant in the gallery forest (purely arboreal species were not sampled at SOK). Finally, the Shannon index increases significantly as vegetation cover increases, perhaps hinting at the greater number of food resources that are available.

This study illustrates how taphonomic data from modern bone assemblages can be used to provide an enhanced understanding of paleoenvironmental reconstructions (Table 1). Analysis of the SOK faunal remains show that when comparing a death assemblage to extant faunal communities, one is most likely to recover a broad environmental signal that is characteristic of a particular region as opposed to the immediate habitat from which those bones were sampled. This is true whether one uses presence/absence, taxonomic abundance, or ecological structure analysis. Further analysis shows that different habitats can be reliably distinguished on the basis of relative abundances or the proportions of individuals classified into trophic or locomotor classes. Presence/absence data is of little value for distinguishing the SOK assemblages according to habitat.

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Preliminary report on a new basal iguanodontian dinosaur from the Early Cretaceous Kirkwood Formation, South Africa

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Over the past twelve years ongoing fieldwork in the Lower Cretaceous (Valanginian) Kirkwood Formation in the Algoa Basin, has produced a number of well-preserved vertebrate specimens. This material greatly increases our understanding of the Kirkwood fauna – particularly dinosaurs, known previously from scrappy, fragmentary material. This paper highlights a new taxon of ornithopod dinosaur (basal iguanodontian), consisting of numerous disarticulated elements from at least 20 individuals and a semi-articulated specimen. The first fossil specimens of this new dinosaur species were discovered in 1995 in a 'bone bed' concentration located on the Kirkwood Cliffs ('Lookout') some 3 km south of Kirkwood village. Systematic excavation over four successive field seasons (in 1996, 1997 and 1999) showed that the recovered specimens of this ornithopod are small in size (largest femur = 55 mm), and thus likely representative of juveniles. Several characters (e.g. hatchet-shaped sternal plate, absence of subsidiary ridges on teeth) indicate that this taxon is a derived iguanodontian. Sufficient fossil material from these juvenile ornithopods (hatchlings) has now been recovered and prepared and a new species of dinosaur is currently being described. From a taphonomic perspective the bone concentration appears to represent an accumulation of disarticulated skeletal elements produces by the natural mortality of hatchlings, of varying ages, found at communal nesting site. No eggshell material was found in association with the bones which suggests that the nests were located a short distance from the bone accumulation site.

Evidence for aggradational and degradational landscapes in the Karoo basin during the Early Triassic

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The Early Triassic Katberg Formation (Beaufort Group, Karoo Supergroup) in South Africa is an arenaceous unit that can be traced throughout the basin.

Exposures of its lowermost part at the Carlton Heights locality north of Middelburg provide an opportunity for a detailed sedimentological analysis and evaluation of the controls on its stratigraphy with implications for the paleontological record preserved therein.

Two distinct sandstone geometries co-occur in three thick, resistant benches characterizing the outcrop. Each bench is separated by greenish-grey siltstone. Medium-bedded, planar and/or ripple-laminated sheet sandstone conforms to the traditional description of the Katberg and these geometries are interpreted as ephemeral sheetflood deposits. The second architectural type consists of thick-bedded, cross-laminated sandstone organized into lenticular multi-lateral geometries that overlie deep erosional scours. Downstream accretionary macroforms and sandy barforms characterize these deposits and are interpreted as representing deeper, sand-bed braided systems. Sandstones of both types amalgamate laterally as the result of landscape degradation, thereby appearing as multi-storied sandstone architectures when exposed within resistant donga or roadcut sections. But, this feature is geographically restricted to distances of only several 100 metres. Intervening siltstones are burrowed heavily by the new ichnotaxon, *Katbergia carltonichnus* (Gastaldo & Rolerson 2008) which normally are restricted to the upper 0.5 m of this lithofacies.

Two distinct populations of pedogenic carbonate concretions occur in the stratigraphy. Pisolith-sized carbonate nodules of various shapes are aggregated within conglomerates that occur intermittently throughout the outcrop and often dominate lenses at the base of sandstone intervals. Larger, *in situ* carbonate nodules are restricted to horizons within thick siltstone intervals, and differ in terms of size, shape, surface texture, and stable isotopic signature. The $\delta^{13}C$ values of the pisolith-sized nodules, restricted to intraformational conglomerates, indicate that these precipitated in equilibrium with atmospheric CO_2. In contrast, the larger, *in situ* nodules indicate that cements were isolated from the influence of atmospheric CO_2 and formed below the water table in wetland paleosols (Tabor *et al.* 2007). Hence, a difference paleoclimatic signature exists for each suite of carbonate nodules. Intraformational conglomerates precipitated under seasonally dry conditions originally as components of aridosols. Seasonal, moist conditions are interpreted for the in situ nodules, a contention supported by the spatial relationship between the large pedogenic nodules and

Katbergia burrows (Hasiotis 2000; Gastaldo & Rolerson 2008).

To date, no physical evidence has been found for pisolithic nodules *in situ* within any paleosol interval of the Katberg Formation, at Carlton Heights or elsewhere. Hence, the only evidence that ardisols (calcisols) ever existed in the study area or other parts of the basin occur as remnants of these Early Triassic phreatic zones that had developed repeatedly across the landscape. Their restricted occurrence in channel-lag deposits indicates that these soils were scavenged during landscape degradation (Allen 1986).

We interpret variation in fluvial channel architectures and isotopic signatures of the carbonate nodules in terms of distinct periods of landscape aggradation, equilibrium, and degradation. Channel and overbank deposits represent deposition during aggradational stages with inceptisol and gleysol (wetland) interfluves dominating the landscape. When the landscape attained equilibrium, the character of interfluvial paleosols changed from seasonally wet gleysols to more seasonably arid calcisols. The latter were scavenged during landscape degradation and deposited within channel lags when there was a return to more seasonably wet conditions. The repetitive shifts between seasonally wet and seasonally arid conditions reflect the impact of strong oscillations of climate rather than pulses of orogenic activity or any ecosystem response to the end-Permian extinction.

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The Vertebrate Fauna of the Late Devonian, Famennian, Witpoort Formation, Waterloo Farm locality, near Grahamstown

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The Witpoort Formation of the Witteberg Group consists of mature quartz arenites, interpreted as having been deposited along a linear sandy, coastline with occasional thin black shales deposited in semi-enclosed lagoonal settings (Hiller & Taylor 1992). Cooper (1986) correlated South African sea level curves to determine the ages of units within the Cape Supergroup. He demonstrated an Upper Devonian (Famennian) age for the Witpoort Formation and a Frasnian age for the underlying Weltevrede subgroup. This is consistent with palaeontological evidence, such as the presence of Late Devonian type plants in the Weltevrede subgroup and lower Witpoort Formation (Plumstead 1967) and the occurrence of the Givetian to Frasnian articulate brachiopod, *Tropidolepis,* near the top of the Weltevrede subgroup (Boucot *et al.* 1983). Further palaeontological evidence comes from the extensive flora (Gess & Hiller 1995) (including the Late Devonian cosmopolitan, *Archaeopteris* (Anderson *et al.* 1995)) and fauna, discussed below, from the upper Witpoort Waterloo Farm locality. In addition, placoderm fish, which make up an important component of the Waterloo Farm fauna, are completely absent from overlying strata. The palaeoniscoid-dominated fauna recorded from the, upper Witteberg, Waaipoort Formation is consistent with an Early Carboniferous interpretation of its age. Cooper (1986) considered the Devonian–Carboniferous boundary to be at, or near, the contact between the clean white quartzites of the Witpoort Formation and the fine black sediments of the overlying Kweekvlei Formation, which he interpreted as a reflection of the Tournasian transgressive cycle.

At Waterloo Farm, a thick horizon of black shale lenses situated near to the top of the Witpoort Formation quartzites was exposed in road cuttings in 1985. It is interpreted as anaerobic sediment that was deposited in an estuarine lagoon, situated behind a sandy barrier bar (Hiller & Taylor 1992). It appears to be coeval with a series of quartzites to its east, interpreted as components of the barrier system. Abundant trace fossils, as well as plant fossils, similar to those found in the black shales, are preserved in the quartzites and in thin reddish shales that are interbedded with them. Fossil fish remains have been found in three lenses, close to the associated barrier-sand deposits. The uppermost of these three has been the richest source of fossils, and the subject of many years of excavation and study. The vast majority of the black shale horizon, stretching for hundreds of metres to the west of these lenses appears to be devoid of vertebrate and arthropod fossils though it contains, in places, large quantities of plant material, often comprised tangles of vascular plant branches. Substantial tree trunks have also been recorded, further suggesting the proximity of a wooded environment. It is likely that the lack of fish and arthropod fossils within these latter beds resulted from low oxygen levels caused by the large volumes of decaying plant matter. The relatively fish-fossil-rich upper lens is somewhat less carbonaceous, than many of the more westerly deposits, and contains isolated, more fragmentary plant remains. An abundance of diverse fish and probably arthropod derived trace fossils suggests that the water column, at this point, was less anaerobic because of its greater proximity to the marine ebb and flow.

Anoxic conditions, within the sediment accumulated below the aerated water, resulted in exceptionally good preservation of some small organisms. Its sulphurous, acidic nature caused poor preservation of large bony elements, generally represented by mineralized compres-

sions. Since exposure in 1985, the outcrop has provided evidence for a growing list of taxa.

Soft tissue compressions of a number of small, unarmoured jawless fish have been collected. These include the holotype of *Priscomyzon riniensis* (Gess *et al.* 2006), the oldest known lamprey, which already exhibited the oral specializations necessary for a parasitic lifestyle and much of the cranial anatomy seen in extant taxa.

The fauna was numerically dominated by groenlandaspid arthrodire placoderms, of which *Groenlandaspis riniensis* (Long *et al.* 1997), which reached a substantial size, was the most abundant. Two other species (including *Africanaspis doryssa* (Long *et al.* 1997)), characterized by extremely high median dorsal plates, were less abundant and more modest in size. Further arthrodire taxa were also present. Antiarch placoderms were represented by *Bothriolepis africana* (Long *et al.* 1997), which was also relatively large. A ptyctodont placoderm has been reported, on the basis of an isolated plate (Anderson *et al.* 1997).

Acanthodians ('spiny sharks') were fairly diverse, though not common, and included a large gyracanthid (Gess & Hiller 1995), at least one diplacanthid (*Diplanthus acus*) (Gess 2001) and an acanthodid. Chondrichthyans included *Antarctilamna,* elsewhere a mid Devonian Gondwanan taxon, *Plesioselachus macracantha* (Anderson *et al.* 1999), and two subadult forms, possibly representing further taxa, of uncertain affinities.

A small actinopterygian (ray-finned fish) was amongst the less common taxa. Sarcopterygian (lobe-finned fish) were more diverse and more numerous. The most abundant of these was a coelacanth (Gess & Hiller 1995), represented by numerous juvenile individuals, which may well have utilized the quiet estuarine environment as a nursary. Long-snouted dipnoans were present, as well as a large tristichopterid (Gess & Hiller 1995), which exhibits some similarities to *Hyneria.* The top predator, represented by fragments, including a large cleithrum, appears to have been a several-metre-long elpisthostegalid-like form.

Waterloo farm represents the only significant high latitude ecosystem known from the latest Devonian, a time when southern Africa formed part of western Gondwana. The palaeolagoon at Waterloo Farm drained into the high latitude, polar, Aghulas Sea, bounded by what is now southwestern South America, the southern Cape coast and West Antarctica. The south pole at the time (Scotese & Barrett 1990), was situated over southwestern Gondwana, most likely in the vicinity of Argentina, on the western shores of the Aghulas Sea. This placement would imply that the Waterloo Farm locality was within 10 to 15 degrees of the south pole.

The movement of Gondwana over the south pole during the Late Devonian and its consequent glaciation may have contributed to a series of global extinction events, that characterize the Famennian, by lowering sea levels and global temperatures. Alternately, or additionally, lowered global temperatures may have resulted from reduced CO_2 levels due to rapid global spread of the first (*Archaeopteris*) forests during the Frasnian, compounded by the colonization of dryer areas by the first seed-plants towards the end of the Famennian. This sudden increase in terrestrial biomass would have increased levels of fixed C entering drainage systems, perhaps helping to account for a series of C-rich anaerobic sediments deposited worldwide during the Famennian (Algeo *et al.* 2001). These sediments appear to be associated with a series of extinction events of variable severity. The most important and widespread two of these events are the Kellwasser extinction event, which approximately coincides with the Frasnian/Fammenian boundary (and mainly affected plant communities), and the Hangenberg extinction event, which coincided with the end of the Famennian and therefore the Devonian/Carboniferous boundary (Algeo *et al.* 2001). This latter extinction event was the finale of the Second Global Extinction Event. This was one of earths five 'major extinction events', and killed a large proportion of marine organisms, including whole groups of fish, such as the Placoderm fish. It may be no coincidence that black anaerobic shales are interspersed through the Witpoort Formation, the second most prominent of which is found near the base of the Witpoort Formation, the probable Frasnian/Famennian boundary at Howisons Poort. The most prominent is that at Waterloo Farm, near the top of the Witpoort Formation and, therefore, immediately preceding the end of the Devonian Period. What we may therefore see at Waterloo Farm, is a record of the protracted demise of the Devonian world in west Gondwana.

The massive explosion of advanced plant life during the Late Devonian, which may well have precipitated the staggered end-Devonian extinction of marine life, created new potential niches for animal life that, during the Early Carboniferous, would be inhabited by tetrapod vertebrates.

Recent studies show that the basic adaptations that permitted life on land were already established in aquatic tetrapods by the end of the Devonian (Clack & Coates 1995). Tetrapod stem group 'Tristichopterid' fish, known from the late Givetian to early Frasnian, coexisted with more crownward 'Elpisthostegalid' fish, from which 'Acanthostegid' tetrapods were probably derived during the Frasnian to Famennian (Clack 2002).

Fossil-bearing Late Devonian rocks are consequently of crucial interest in understanding the emergence of tetrapods and the drastic climatic and environmental changes that helped to drive the process. Waterloo Farm locality was near polar, while better known fossil vertebrate faunas of North America, Europe, China, Australia and Eastern Antarctica were all tropical. Elpisthostegalids and acanthostegids have, so far, only been recorded from Laurasia, (though tetrapod trackways are found in Australian Famennian rocks (Warren & Wakefield 1972)) – leading to the suggestion that tetrapods lived and evolved in the tropical, marginal marine environments of Laurussia before migrating to tropical parts of what is now Australia (Clack 2002). The discovery of an elpisthostegalid-like tetrapodomorph at Waterloo Farm suggests that taxa close to the Late Devonian tetrapod stem were not confined to the

warm tropical waters of Laurasia, but also included large cold-water Gondwanan forms.

The vertebrate fauna of Waterloo Farm is, in general, surprisingly diverse and cosmopolitan considering its high latitude position at a time of nearby glaciation and global cooling. Though retaining a relatively primitive (mid Devonian type) shark fauna, it includes many genera that are absent from mid-Devonian southern African fish faunas, such as the placoderm *Bothriolepis* that radiated out from China during the Devonian. The composition and phylogenetic relationships, of the described placoderm taxa of the Waterloo Farm locality, is most similar to that of East Gondwana (Long *et al.* 1997). Curiously its osteolepiform sarcopterygian fauna, comprising *Hyneria*-like and Elpisthostegalid-like forms, more closely recalls Late Devonian faunas of Laurasia than those of East Gondwanan Australia, which are characterized by more derived Tristichopterids and Rhizodontids. The influence of a warm, southwardly flowing current from the Laurussian tropics cannot be discountered as a mechanism of dispersal, as well as a means of explaining the lush wooded botanical environment adjacent to the lagoon.

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The impact of molecular systematics on palaeontology

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In the time before molecular data began to provide novel types of data for phylogeny constructions, morphological data was effectively the only data form available for construction of phylogenies. Molecular data currently consists almost exclusively of DNA sequences, with these sequences consisting of characters which can have any of four different states (A,G,C, or T). These differences allow for a variety of analytical approaches for constructing phylogenetic trees: whereas for morphological data, parsimony is generally the preferred method, since the data can come in many different forms, the simplicity of DNA sequence data, and mode of evolutionary changes over time, allow for a variety of newer and more powerful analytical approaches, with Maximum likelihood and Bayesian methods being popular, and allowing different types of confidence estimates to be calculated for branch points. The presence also of a molecular clock, albeit a stochastic clock, allows for time estimates to be attempted for branch points in the tree, estimates which, however, are only as good as the calibration of the rate of DNA changes over time. Since different genes change at different rates, gene sequences can be chosen to provide appropriate data sets for either closely or very distantly related taxa. The different genomes available for phylogenetic analysis – nuclear, mitochondrial, and (in plants) chloroplast, which follow different modes of inheritance, and differing rates of change, further expand the range of options available for the molecular systematist. Resolution of phylogenetic relationships where the fossil record is problematic (examples will be given for ordinal relationships in the mammalia (Arnason *et al*., in press), and at the genus/species level in the felidae (Driscoll *et al.* 2007) may be resolved by molecular means if extant taxa are available which are relevant to the question. Ancient but useable DNA can sometimes be extracted from tissues up to maybe 100 000 years old, and can address relationships such as those of recently extinct Proboscidea.

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Comparative feeding biomechanics of *Lystrosaurus* and the generalized dicynodont *Oudenodon*

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Dicynodonts were herbivorous therapsids best represented by fossils from the Permo-Triassic of South Africa. Differences in cranial morphology across Dicynodontia have been correlated with changes in masticatory function, and hence, dietary preference. Although the derived masticatory apparatus of dicynodonts allowed propaliny, it has been previously hypothesized that *Lystrosaurus* primarily utilized powerful orthal jaw movements to process fibrous vegetation. Cranial specializations of *Lystrosaurus*, such as shortened and deepened cranium and a patent premaxilla-nasal suture, have been hypothesized to have increased the efficiency of its masticatory system compared with generalized Permian dicynodonts.

Here we aim to test this assertion using biomechanical modelling techniques. We use finite element analysis (FEA) and a study of cranial functional morphology (including sutures and bone histology) to compare the biomechanical performance of the cranium of *Lystrosaurus* with *Oudenodon,* a generalized dicynodont, during orthal bite simulations. Muscle forces were estimated for each dicynodont using the dry skull method and applied to each cranium to produce a reaction force at a bite point. Patterns and average magnitude of Von Mises stress in each dicynodont cranium and in segmented regions of interest were assessed. During an orthal bite simulation, higher stress occurs throughout the *Oudenodon* cranium, indicating that the cranium of *Lystrosaurus* is more resistant to normal, static feeding loads. Despite this difference in stress magnitude, patterns of stress are similar within both taxa. The FE-stress results, along with mechanical advantage of adductor musculature, a broad symphyseal contact, and other cranial features suggest that *Lystrosaurus* may have employed a snapping bite for processing the tough fibrous vegetation it has been posited to feed on.

Speculations on buoyancy control and ecology in some heteromorph ammonites. 2. The ammonite family Nostoceratidae Hyatt, 1894

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In helically coiled ammonites of the subfamily Turrilitinae, buoyancy control is achieved by migration of the siphuncle towards the upper, adapapical edge of the whorls. This results in early decoupling of the cameral fluid, and probably negative or neutral buoyancy. This, in conjunction with apertural modifications, is suggestive of a vagile, benthonic mode of life. In contrast, helically coiled ammonites of the family Nostoceratidae Hyatt, 1894, with a single exception, retain a siphuncle situated at midflank. In addition, the body chamber in these forms is relatively larger than in the Turrilitinae, and the aperture remains simple. It is suggested that the different modes of coiling of the body chambers of helically coiled Nostoceratidae are adaptations to empty the phragmocones of cameral liquid through several stages of coupling and decoupling, and thus to achieve neutral buoyancy for a planktonic mode of life. This is probably an adaptation to a microphagous diet. A benthonic mode of life as suggested by several authors is rejected.

Large mammal butchering experiments using stone tools

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Due to the fact that numerous natural events and human practices modify bones, unequivocal interpretation of bone modifications is sometimes difficult. Further to this, mimics, which are a result of non-human activity, produce the same or qualitatively similar patterns that complicate positive identification of cut marks made by hominins. Reliable measures are required for interpretation of bone modifications, and actualistic experimentation can help towards this. A number of taphonomic processes, including bone modification by various animals and geological processes are recorded in comparative collections housed at institutions in Gauteng. These provide reference material for taphonomists attempting to identify agents responsible for the modification and accumulation of fossil bone assemblages, particularly from early hominin cave sites in the Sterkfontein Valley. However, no reference material exists for hominin modification of bone, and thus motivates for the collection of such traces. The primary goal of this research is to create a modern comparative collection of complete large bovid skeletons that record butchering marks made by stone tools. Four different raw materials commonly found in the southern African archaeological record, namely chert, quartzite, dolerite and hornfels were selected for flake production. Butchery was conducted on three cows by modern Bushmen subsistence hunters skilled in the processing of animals. They form part of a relatively isolated group of !Xo-speaking Bushmen resident in Kacgae village in the Ghanzi district of western Botswana. This study focuses on characterizing stone-generated butchering marks at a macro-and microscopic scale, and documenting their location, number, orientation, size and morphology. Future research will broaden the butchering experiments to include a range of indigenous people processing domestic and wild animals in order to address a number of faunal taphonomy questions. Here we present an account of progress to date.

The Saurichthyidae (Actinopterygii): origin, distribution and interrelationships

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Remains of saurichthyids were first mentioned nearly 300 years ago. The name *Saurichthys* was established by Agassiz in 1834 and refers to the plesiosaur-like appearance of these fish teeth. Three genera are currently accepted, and the validity of a fourth genus is equivocal. The oldest unambiguous member of the family is placed in the genus *Eosaurichthys* Liu & Wei, 1988 from the uppermost Permian of Meishan, China. The genus *Saurichthys* Agassiz 1834 occurs almost worldwide during the Triassic and at least 35 species are diagnosable within this genus. The youngest unequivocal and about coeval saurichthyid remains come from the Lower Jurassic of Canada, England and Germany and are assigned to the genus *Acidorhynchus* Stensiö, 1925. In southern Africa, saurichthyids are reported from various marin Early Triassic sites in Madagascar and Tanzania and from non-marine Middle Triassic sites in South Africa (Mutter *et al.* 2008).

With respect to their record in the southern hemisphere, recent review of saurichthyids revealed intriguing facts about this highly interesting group of primitive actinopterygians. While marine records outnumber non-marine records greatly worldwide and throughout their fossil record, the first unambiguous non-marine species come from the Hawkesbury Series in New South Wales – complete and articulated specimens of *Saurichthys gracilis* and *S. gigas* (Woodward 1890) – and are of Middle Triassic age. South African jaw fragments and isolated teeth, first described by Griffith (1978) were recently revisited by Bender & Hancox (2003) and may be slightly older (Mutter *et al.* 2008). Interestingly, saurichthyids have so far not been positively identified in any non-marine South American formations of Permo-Triassic age (Mutter *et al.* 2008). The apparent occurrence of certain species in non-marine waters have been interpreted as anadromous behaviour (Beltan & Tintori 1980) but preservation in most non-marine sites is fragmentary and remains are likely allochthonous. The South African saurichthyid remains from the Spathian–Ansian boundary of the Burgersdorp Formation are important, because they fill a blank spot on the palaeobiogeographic map, providing evidence for the oldest non-marine occurrence of any saurichthyid.

Patterns of distribution and early saurichthyid evolution are more complex than previously believed, and diversity was already high during the Early Triassic (Mutter *et al.* 2008). However, major traits during long-term saurichthyid evolution can be observed and include reductions of scale rows and skull roof bones, shortening or deepening of the elongate snout and development of various types of dentitions. The genus *Eosaurichthys*, originally confined to the Permian and completely covered by scales, leaped into the Early Triassic. The genus *Saurichthys*, showing various types of reductions in its squamation, existed probably throughout the Triassic and peaked in the Middle Triassic in diversity. A second Triassic genus possesses an extremely short snout, *Brevisaurichthys* Beltan, 1972. The latter genus may be valid but is currently poorly defined and only known from the late Middle Triassic of Europe. A stem group of *Saurichthys* must have given rise to the genus *Acidorhynchus* during latest Middle or in the Late Triassic, and both, *Saurichthys* and *Acidorhynchus* lingered into and coexisted in the Jurassic.

The phylogenetic origin of saurichthyids in the late Palaeozoic is unknown but all previously conducted phylogenetic analyses suspect monophyly and tacitly accept the most widely spread genus *Saurichthys* as the group's 'typical' representative. Early attempts at resolving this issue pointed at a pholidopleurid origin but these studies were based on evaluation of primitive features only (Wade 1935; Nielsen 1935, 1936). Using cladistics, the genus *Saurichthys* is usually non-conclusively classified as an unresolved trichotomy with *Acipenser* and *Birgeria* or with neopterygians and acipenseriforms + *Birgeria* (Gardiner 1984; Rieppel 1992; Grande & Bemis 1996; Bemis *et al.* 1997). Gardiner & Schaeffer (1989) resolved their '*Saurichthys* group' as the sister group of acipenseriforms ('chondrostean group') supported by six apomorphies. A consensus tree using the same matrix, however, left *Saurichthys* as a sister group to *Birgeria* and more advanced actinopterygians (Coates 1999). Coates (1999) presented also three hypotheses with *Saurichthys* in differing phylogenetic positions, overall in a more derived position (unrelated to chondrostean ancestry) than suggested by Gardiner & Schaeffer (1989). The most recent review (Gardiner *et al.* 2005) emphasized the 'old' phylogenetic position for *Saurichthys* – as a sister group to acipenseriforms. Following the latter hypothesis, *Birgeria* + (*Saurichthys* + acipenseriforms) form the sister group of all other more derived actinopterygians.

A single study focusing on intrageneric relationships of *Saurichthys* has so far been conducted (Rieppel 1992). Nine well-known species were chosen and coded using eight well-defined characters. The resulting groups basically mirror the gaps of the fossil record in time and space and support a general but weak evolutionary trend that has recently been even more counterbalanced by the discovery of well-preserved Lower Triassic specimens in the northern hemisphere (Mutter & Cartanyà 2005; Mutter *et al.* 2008).

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Beaufort Group GIS initiative: creating and maintaining an interactive fossil database for palaeontological research

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For more than a century, large collections of fossils from the Beaufort Group have been built up in South Africa. Records of these collections have been maintained as separate databases by each of the seven museums which curate them (Kitching 1977; Keyser & Smith 1979; Nicolas 2007). The databases contain a unique time-extensive record of continental vertebrate biodiversity – represented by the fossils of the Karoo Supergroup (Rubidge 1995). As an initiating project, a dataset of records of fossil tetrapods collected from Permo-Triassic Beaufort Group rocks of South Africa was compiled from the seven museum catalogues, and this was linked to a newly created database within the Geographical Information System (GIS). The process required rigorous evaluation of both the quality of the original records, and the degree of collecting bias that may have existed in the different collections. Assessment of quality endorsed the establishment of the two databases and no significant degree of collecting bias was encountered. Thus this new dataset makes possible the determination of terrestrial tetrapod ecological representation from the Middle Permian to Middle Triassic Beaufort Group of South Africa (Nicolas 2007).

GIS offers a spatial map which allows access to more than one map layer simultaneously, giving a multifaceted view of data that shows trends more clearly than tabulated data (Cooper & Netterberg 2004). Thus GIS provides the user with not only data concerning the taxonomy of any record, but also identifies the museum collection and specimen number, as well as giving specimen locality details. For the first time, fossil-collection data can now be viewed on a map of southern Africa which demarcates farm boundaries and shows the topographic and geological signature of farms.

The first five years of the GIS project (2003–2007) was the foundation phase during which all viable tetrapod fossil data from the Beaufort Group was converted to a reputable GIS system, ESRI® ArcInfo® being the system of choice. Suitable map layers were obtained in order to facilitate research relating to distribution patterns of fossil taxa. These map layers include a geological map, farm and farm boundaries, magisterial districts, provincial data, grid-references, and map and satellite imagery for southern Africa. Accessing and importing the data sets took four years (Nicolas 2007).

The second phase (January–December 2008) is current and is a secondary setting-up stage which when complete will provide a streamlined and user-friendly product. It involves rigorous editing and standardization of the seven museum databases. All fields of data content are now identical for each museum: data fields include museum collection name; museum collection number; genus; taxon; province; district; farm name; farm number; commonly used farm name; *x–y* coordinates and assemblage zone. Font and font size are standardized, spelling errors are eliminated, as are records with insufficient or inaccurate data (the latter affect the integrity of the GIS database).

The *x–y* coordinates are important for this phase of product development. Because many older records lacked accurate grid-references, it has been necessary to establish them – for each and every farm in the Beaufort Group where fossils have been discovered. In the past, confusion resulted from farm names being repeated within a given district, but by assigning *x-y* coordinates to farm names and listing the registered farm number, the arbitrary use of popular nicknames is eliminated. Old farm names are not discarded, however, affording researchers as much past-naming information as possible. In the end, all viable fossil records will be identified by a coordinate set which correlates with modern GPS usage.

Maintenance of the database in this new standardized state requires that contributing museums provide updates of new records which comply with the set format. To this end, a manual of procedure for future fossil collection recording is being created. It is anticipated that new contributions to this database will be added on an annual basis. While the pilot project has concentrated on only Beaufort Group data, the concept should be expanded to

incorporate databases of fossils from different stratigraphic successions – and include not only southern African but also international specimens.

Applications of this database are extremely wide and it is hoped that the palaeontological community will make full use of them. For example, it will afford assessment of geographic and stratigraphic distribution of selected taxa, determination of the number of specimens of individual taxa, relative numbers of specimens of different taxa, co-occurrence of taxa in both a stratigraphic and geographic context, and refining of biozone boundaries. The information will have significant application in basin development studies, environmental impact analyses, as well as in research on ecological and population distribution and biodiversity changes through time.

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Shape variability in the skull of *Aelurognathus* (Therapsida: Gorgonopsia)

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The infraorder Gorgonopsia Seeley 1894 was initially created to isolate the specimen of *Gorgonops* from other members of the order Therosuchia, on the basis that the, 'temporal vacuities [of the skull were 'roofed over,' (p. 1014). Broom (1910a) recognized that the specimen of *Gorgonops* was damaged and shared cranial features with *Titanosuchus,* and he later (1910b) placed *Gorgonops* in the suborder Dinocephalia. Broom (1913a) reduced the Gorgonopsia to the rank of family, but later (1913b) re-established it as a distinct suborder of the Therapsida, after the discovery of additional specimens.

Between 1913 and 1958 a large number of gorgonopsian specimens were discovered, and many new taxa described, often from poorly preserved and fragmentary material. In 1970 Sigogneau provided an extensive taxonomic revision of the Gorgonopsia synonymizing many of the genera and discarding some taxa based on fragmentary specimens. In her revision, Sigogneau recognized three subfamilies; the Gorgonopsinae, Rubidgeinae and Inostranceviinae.

The Gorgonopsinae as defined by Sigogneau-Russell (1989), contained 18 genera that were grouped together on the basis of sharing several characters, including a narrow interorbital and intertemporal width relative to the total length of the skull, and slender cranial arches. In contrast, the Rubidgeinae, comprising six genera (Sigogneau-Russell 1989), were characterized as having a broad interorbital and intertemporal width relative to the total skull length, and thickened cranial arches. Finally the Inostranceviinae, which contains two Russian genera, has a skull width and length ratio intermediate to that seen in the other two subfamilies.

Gebauer (2007) further revised the taxa of the Gorgonopsia, reducing the number of recognized genera from 26 to 15. Gebauer also performed a phylogenetic analysis on the group, the results of which provided support for only one of the subfamilies proposed by Sigogneau (1970) and Sigogneau-Russell (1989), the Rubidgeinae. The 'Inostranceviinae,' now represented by only a single genus, fell as the sister taxon to the Rubidgeinae, while other taxa are represented as 'evolutionary stages' leading up to the monophyletic group formed by the four genera of the Rubidgeinae: *Rubidgea, Sycosaurus, Clelandina* and *Aelurognathus.*

In this study we are focussing on *Aelurognathus* as it contains the largest number of formally described specimens, 16 in total. This genus is mostly confined to localities of the *Dicynodon* and *Cistecephalus* Assemblage Zones of South Africa, except for one specimen which comes from deposits of a similar age in Malawi. These 16 specimens are currently assigned to six species (Gebauer 2007): *A. tigriceps* (5 specimens), *A. kingwilli* (1 specimen), *A. ferox* (5 specimens), *A. maccabei* (1 specimen), *A. alticeps* (2 specimens) and *A. broodiei* (2 specimens). *Aelurognathus* is a medium- to large-sized gorgonopsians, with a heavy skull and a convex dorsal profile of the snout. The orbits are generally small and temporal opening high. Cranial arches are thick and strong and the posterior of the zygomatic arch has a ventral extension. All these materials are housed in South African collections and most of them were examined first hand by the senior author. Specimens examined so far, vary between 18 to 30 cm in skull length. Approximately 70 cranial measurements will be used to explore changes in skull shape in relation to the size variations of specimens (allometry). This analysis will allow us to determine if there are any major shape variations between different sized individuals and highlight differences that can be attributed to sexual dimorphism in this morphologically conservative genus.

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Expanding the modern reference collection of phytoliths from an *Acacia–Commiphora* grassland in northern Kenya

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The site complex of FwJj14 is located in the Okote Member of the Koobi Fora Formation in the Lake Turkana Basin of northern Kenya and dates to *c.* 1.5 million years ago (mya). FwJj14 has yielded faunal remains which include postcranial hominin bones as well as three footprint layers (including a set of hominin footprints), stone tool artifacts and fossil wood. The aim of the current project is to contextualize the remains and behavioural signatures found in the lithological units at FwJj14 within their climatic and vegetational settings through phytolith analysis.

Phytoliths (literally 'plant-stones') are three-dimensional micrometric hydrated opal-A particles that precipitate in cells and/or between cells of the living tissues of certain plants. They are composed of amorphous biogenic silica (opal) and form due to the uptake of dissolved monosilicic acid ($Si(OH)_4$) in ground water during plant growth. Living plants do not make use of the silica in their metabolic processes and the silica is deposited within cavities in the cell lumen or the intercellular space resulting in partial mineralization of some tissues. Not all plants produce phytoliths. However, opal phytoliths have been reported for pteridophyts (Piperno 1988), gymnosperms (Klein & Geist 1978; Sangster *et al.* 1997), Mono- and dicotyledons (for example Twiss 1992; Kealhoffer & Piperno 1998; Rovner 1983). Phytoliths have been observed in different parts of plants such as the leaves, Angiosperm reproductive organs, woody tissues, culms and roots. Their morphologies vary according to the plant organ and plant type.

After the death and decay of plant tissue, opal phytoliths are released into the environment. Phytolith specimens have been identified in sediments dating as far back as the Miocene (Thomassen 1980).

For palaeo-ecologists, phytoliths both supplement and complement palaeoenvironmental information gleaned from other sources and form a useful tool in the reconstruction of past vegetational histories. Several phytolith indices have been developed as aids to environmental reconstructions. These make use of phytolith morphotypes and abundance to discriminate short- and tall- grass abundance, closed or open vegetation community structure, tree cover, the relative abundance of C_3 and C_4 grasses and identify drought stress (Diester-Haas *et al.* 1973; Alexandre *et al.* 1997; Barboni *et al.* 1999).

In order to provide a robust interpretation of past vegetation composition at FwJj14 using phytolith assemblages in palaeo-sediments, a detailed local to regional modern reference collection is required for comparison. In this study, modern vegetation samples were collected from an *Acacia–Commiphora* grassland in northern Kenya and processed using a dry-ashing technique. Observed distinct morphologies where noted and recorded following the International Code for Phytolith Nomenclature (Madella *et al.* 2005). In addition samples of modern sediment in the region were collected and processed to extract phytoliths. This to test whether the sediment samples did indeed reflect the observed modern vegetation. The test and modern reference collection database forms the initial phase of the project which aims ultimately to analyse the phytolith assemblages across all the lithological units at FwJj14. The results of this project are presented.

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The Swartkrans Paleoanthropological Research Project: progress report for 2005–2008

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Swartkrans Cave (Gauteng, South Africa) is one of the most important paleoanthropological sites in the world. Robert Broom and John Robinson's early research at Swartkrans provided large samples of the Pleistocene

hominid *Australopithecus robustus* and demonstrated that the species was synchronous and sympatric with *Homo erectus*, the direct ancestor of modern humans. C.K. Brain's subsequent work at the site resulted in the recovery of large fossil and archaeological samples that, because they were collected with acute regard for stratigraphy and taphonomy, provide essential context for these extinct hominids. In addition, Brain analysed these samples within a robust actualistic framework, allowing him to draw novel inferences about early hominid behavior at Swartkrans between *c.* 1.8 and 1.0 million years (Myr) ago. Included among Brain's most important results were: (1) the recognition that many of the hominid fossils were collected in the cave as the prey of large carnivores; (2) the identification of a hominid bone tool culture; (3) the identification of burned bones from Member 3, indicating the earliest known control of fire by hominids at *c.* 1.0 Myr ago.

Building on this foundation, we initiated the Swartkrans Paleoanthropological Research Project in 2005. Our current excavations are focused in the northeastern portion of the cave. It is here that the Lower Bank, the site's oldest known deposit (*c.* 1.8 Myr old), is in close spatial proximity to Member 4, a Middle Stone Age (MSA) unit and one of the site's most recent deposits. Not only are we interested in defining the contact between these two depositional units, but each contains important archaeological materials in need of better understanding.

Prior to our work, the sample of stone tools from the Lower Bank was very small and less informative behaviorally than the larger assemblages from the more recent Pleistocene units of Swartkrans Members 2 and 3. Our expanded lithic sample from the Lower Bank will allow us to determine if this assemblage belongs to the Oldowan Industrial Complex, the first known stone tool industry in the world or the more technologically advanced Early Acheulean Complex. In addition, the Lower Bank contains a rich, and previously unrecognized, zooarchaeological record – evidence (in the form of stone tool cut- and percussion marks) of the earliest known systematic butchery by hominids in southern Africa.

The MSA is a critical phase in human evolution that heralded the emergence of anatomically modern humans. It is, however, debatable whether these first *Homo sapiens* were cognitively and culturally modern. Technological analysis of artifacts figures prominently in testing the hypothesis that modernity was a complete and simultaneous 'package' of physical and cultural change that appeared first in Africa, at or near the beginning of the MSA. Thus, the Member 4 lithics from Swartkrans are vitally important, especially considering our finding that it is the largest and most complete assemblage from the important Cradle of Humankind area.

Finally, our excavations to determine the geomorphological relationship between the Lower Bank and Member 4 and the vertical extent of the latter yielded unexpected and exciting results. Two stratified layers underlie the MSA level: (1) a large volume of brecciated talus infill that contains an abundance of early Pleistocene fossils (including *A. robustus*); (2) a lower deposit that appears to be a previously unknown extension of the fossil- and archaeology-rich Lower Bank infill. We report here on these findings.

A preliminary assessment of the *Glossopteris*-dominated fossil plant assemblages of the Emakwezini Formation (lower Beaufort, Karoo Supergroup, South Africa) and their palaeoenvironmental setting

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The Emakwezini Formation crops out in a narrow strip just inland of the eastern coast of South Africa in northern KwaZulu-Natal. The formation is of economic interest as several of its coal seams are being actively exploited at the new Somkhele mine near St Lucia. Although it has been long considered a temporal equivalent of the Normandien Formation (lower Beaufort Group) in the main Karoo Basin, this inference has been based mainly on sparse palaeobotanical evidence and the stratigraphic position of the formation within the Karoo Supergroup. Previously only *Glossopteris* leaves, *Phyllotheca australis* and organs erroneously attributed to *Dictyopteridium* had been described from this formation, on the basis of a few very small, scattered and poorly provenanced collections.

Recent regional-scale investigations of the geology and palaeobotany of the Emakwezini Formation have facilitated a more in-depth interpretation of the floras and depositional environments that persisted in this part of the Karoo Basin during the Late Permian. The formation is characterized by fining-upward successions of medium- to fine-grained sandstones and mudstones that were rapidly deposited in moist, fluvio-lacustrine settings.

Investigations of archived material, several newly discovered and other known plant fossil localities, notably those at KwaYaya railway siding (west of Empangeni) and Emakwezini Station, have led to the recognition of a well-preserved and diverse palaeofloral assemblage. The recovered suite of plant taxa strongly supports a Late Permian age for at least the upper parts of the Emakwezini Formation based on correlation with floras from Upper Permian units in the main Karoo Basin. Key discoveries include the first conclusive occurrences in the region of *Dictyopteridium flabellatum, Rigbya arberioides, Lidgettonia* spp. and *Trizygia speciosa.*

Exploration of the excavations in the open cast mine at Somkhele led to the discovery of a new flora of an as yet undetermined age. The presence of both *Ottokaria* glossopterid fructifications (typical of the Lower Permian in South Africa) and the sphenopsid *Schizoneura gondwanensis* (an index fossil for the Upper Permian in South Africa) in the same stratum may indicate that these deposits are not temporal equivalents of the exclusively Upper Permian strata at KwaYaya and Emakwezini. Alternatively, the prolonged existence of moist fluvio-lacustrine habitats in the region may have promoted the growth and

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preservation of plants atypical of floras commonly associated with the Upper Permian in the main Karoo Basin.

In pursuit of Paradise Lost: a call to rekindle palaeontology in Zimbabwe

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The first report of fossils in what was then called Rhodesia (now Zimbabwe) was in 1901, when one of the first geologists in the newly settled country, A.J.C. Molyneux, reported fossil plants, bivalves and fish from 16 localities in the northwestern parts of the country bordering on the Zambezi Valley (Bond 1969). The fish, a palaeoniscid actinopterygian originally described as *Acrolepis molyneuxi* but now referred to the genus *Namaichthys,* indicated a Late Permian age for those beds.

More than a decade passed before the next significant reports of fossils came in – scrappy dinosaur remains, found in 1914 by H.B. Maufe of the Geological Survey on farms in the Nyamandhlovu District near Bulawayo, and described by S.H. Haughton (Maufe & Haughton 1916). At almost the same time, Ben Lightfoot, also of the fledgling Rhodesian Geological Survey, recovered fossil plants of Ecca age from the shales above and below the just-discovered coal seams at Wankie (Lightfoot 1914).

Little else of palaeontological interest came to light until that other indefatigable pioneer of Rhodesian geology, A.M. Macgregor, appeared on the scene in the 1930s. He soon made his mark, finding Precambrian stromatolites in a limestone quarry near Bulawayo (Macgregor 1941) and a re-visit to Molyneux's Sebungwe localities netted more fish, plants and bivalves, but also some unmistakable tapinocephalid dinocephalian remains (Macgregor 1946). These helped to fix a Lower Beaufort age for Molyneux's locality, specifically the *Tapinocephalus* Zone.

The arrival in 1941 of Geoffrey Bond, as part of a Royal Air Force training group stationed at Heany, near Bulawayo, during the Second World War, soon heralded a new spike in palaeontological activity. Working mainly on his own but sometimes with a few collaborators and colleagues, Bond greatly extended knowledge of Rhodesia's palaeontology and the sedimentology of its largely neglected sedimentary sequences – Rhodesia was, after all, a country occupied and settled mainly for its mineral riches, especially gold, so 'hard rocks' were what all the geologists were after; the sedimentary 'soft rocks' were dismissed as worthless 'overburden'. When the War ended, Bond stayed on and joined the National Museum of Rhodesia as its Keeper of Geology – the quaint almost Dickensian British terminology for curatorial positions in the museums of the colonial outposts – based in Bulawayo, and there he began to assemble an impressive collection of fossils, vertebrate, invertebrate and plant. He was particularly interested in the sedimentology and flora of the extensive coal deposits at Wankie, in the far northwest of the country, and of the associated equivalents of the Lower Karoo in those parts, but his field work extended well beyond that to many other parts of the rest of the country. But one man can do only so much, and despite Bond's efforts (summarized in Bond 1973), large parts of the country remained unstudied or only rather superficially picked over – distances were huge, and infrastructure in the way of roads and availability of supplies were virtually non-existent, not to mention the ever-present threats of the Big Five wild animals and a variety of deadly insect-borne diseases like malaria and sleeping sickness, to name just two.

Just over a decade later, when the University College of Rhodesia and Nyasaland opened in what was then Salisbury (now Harare), Bond became its inaugural Professor and Head of the Department of Geology. This inevitably meant that his work in the field would be severely cut back.

Bond's palaeontological work culminated in his having two fossils named after him, the graceful, gazelle-like extinct springbok *Antidorcas bondi,* and a cockroach, *Rhodesiomylacris bondi*; characteristically, he was especially proud of the latter!

I joined the staff of the National Museums of Rhodesia in 1965, based in Salisbury, and tried to do what little I could to fill the very considerable void left by Bond's departure to the academic world. My main focus was on the dinosaurs and other fauna of the Forest Sandstone Formation, an equivalent of the Upper Elliot Formation of the main Karoo Basin in South Africa, but discoveries of younger fauna in other strata broadened my focus to the overall vertebrate fauna of the Mesozoic beds of Rhodesia.

The Chimurenga War of the 1970s brought all of this to an abrupt end. When I left the country to come to South Africa in 1978, Mike Cooper took over the museum post and continued with the dinosaur work that Bond had started and I had continued. But when Cooper himself emigrated to South Africa, palaeontological work in what is now Zimbabwe virtually came to a full-stop.

Little has been done since then, other than what Tim Broderick, together with his wife, Patricia and colleagues like Phil Oesterlen and Solly Lingham-Soliar, have done, mainly during mapping and exploration in the Zambezi Valley (Ahmed *et al.* 2004). Oesterlen's work for the Geological Survey, mostly conducted while mapping and searching for exploitable hydrocarbon deposits in the Zambezi Valley, produced some surprises, including the first Late Triassic rhynchosaurs in southern Africa which co-existed with the earliest dinosaurs during late Molteno times (Raath *et al.* 1992).

Although the National Museums and Monuments of Zimbabwe have retained a post of Palaeontologist on their staff establishment, filled for several years by Darlington Munyikwa at the Zimbabwe Natural History Museum in Bulawayo – Bond's old department – Munyikwa's ability to make a meaningful contribution was frustrated by an almost total lack of resources in a country whose economy has been in free-fall for almost a decade. Indeed, its decline seems to have been accelerating even beyond the theoretical limit of 'terminal velocity'. The worthless Zimbabwean currency is now the laughing stock of the world, and the people of that country are facing personal hardships undreamed of in the colonial era. So the

chances of rekindling any sort of palaeontological work in Zimbabwe right now seem utterly fatuous and hopeless.

But literally as we speak, talks are under way between the rival political groupings in Zimbabwe aimed at ending the disastrous rule of Robert Mugabe and his ZANU-PF party. Whether or not those talks succeed, one way or another the rot must end in Zimbabwe, and peace and sense must ultimately return, sooner rather than later – it simply cannot continue indefinitely on its current path.

The people of Zimbabwe rose up, stood against, and ultimately defeated, the vastly superior colonial regime of Ian Smith and his Rhodesian Front party in the 1970s; there is no reason why they should not do the same again against their new oppressors. And when the dawn of the new era does finally break, my call is for the members of the PSSA to be ready to grasp the opportunities that are there, ready and waiting. There is huge potential for ground-breaking palaeontological work in Zimbabwe, and our Association is perfectly placed not only to take the lead in exploiting those opportunities, but also to play its part in rebuilding and expanding capacity in our neighbour to the north. We should be actively recruiting and training Zimbabwean students, to work with our own researchers, to reveal the riches that lie hidden beneath the surface of the vast, still almost untapped, Zimbabwean palaeontological treasure-house.

This is the 'Paradise Lost' that I call on us to pursue, before all is indeed forever lost to the grinding finality of erosion.

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Last interglacial fossil trackways in coastal aeolianites at Still Bay

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The impressive Pleistocene coastal aeolianite exposures in sea cliffs east of Still Bay on the west-southern coast of South Africa host a rich archive of fossil mammalian trackways, including the African elephant (*Loxodonta africana*). A new optically stimulated luminescence (OSL) and amino acid racemization (AAR) chronology, the first joint application of OSL/AAR dating in South Africa provides a temporal framework for assessing the palaeoenvironmental significance of dune sedimentation patterns, pedogenesis and ichnology (Roberts *et al.* 2008).

The Pleistocene aeolianite exposures at Still Bay represent the recently wave-eroded remnants of a dune cordon, mainly built by coalesced parabolic dune systems. Sedimentary facies are dominated by large-scale planar cross-stratification formed by foreset progradation in the nose and trailing arms of the dunes and low angle bedding, chiefly representing sedimentation in low relief interdune terrain. The main dune-building wind regime was westerly, associated with cyclonic polar frontal systems (as at the present time). The OSL and AAR dating demonstrate ages ranging from Marine Isotope Stages (MIS) 5e to 5b and termination of Pleistocene aeolian sedimentation at ~90 ka, coinciding with late MIS 5 shoreline regression. The Pleistocene aeolianite is separated from the overlying Holocene dunes (dated to ~8 ka), by a major hiatus recorded by a zone of intense pedogenesis (Roberts *et al.* 2008).

Mammalian footprints were seen in profile, as casts on the underside of beds and as natural impressions. They provide further insights into the Last Interglacial faunas and hence contemporary floras and climate (Roberts *et al.* 2008). The taphonomic processes controlling the morphology and preservation of these unique ichnofossils were found to be complex. The presence of *L. africana* at Still Bay represents the southernmost occurrence of this species recorded to date and possibly, a closer proximity of woodland during MIS 5. This and other observations may indicate a higher moisture regime than at present. There is no available evidence that the elephants were predated by contemporary Middle Stone Age people.

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Biostratigraphic evidence from the central Free State enables a new perspective on Beaufort basin development

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The Karoo basin was formed as a retroarc foreland basin in front of the Cape Fold Belt in southwestern Gondwana during the Late Carboniferous to mid Jurassic (Catuneanu *et al.* 1998). The highly asymmetrical basin fill is thickest towards its southern provenance area whilst thinning rapidly to the distal north. Loading and unloading produced by the Cape Fold Belt allowed for the depocentre, foresag and forebulge to advance and retreat (distal to proximal) through time. This in turn created simultaneous areas of deposition, erosion and hiatus and a reciprocal or out of phase stratigraphy relative to stratigraphic hinge lines (Catuneanu *et al.* 1998). Accordingly the area in the vicinity of these stratigraphic hinge lines

would have a truncated and relatively rapid changing stratigraphy. This makes regional correlation of local stratigraphic units difficult. Stratigraphic hinge lines relating to the Karoo basin occur largely within the central Free State Province (Catuneanu *et al.* 1998)

Three groups (Dwyka, Ecca and Beaufort) and three additional formations (Molteno, Elliot and Clarens) make up the Karoo sedimentary infill (SACS 1980). Lithological boundaries between these groups and formations manifest changes in depositional style over time. The Beaufort Group has been subdivided into the Adelaide and Tarkastad Subgroups. While the lower Adelaide Subgoup is present only in the proximal sector of the basin the uppermost formations of the Beaufort Group (Balfour, Katberg and Burgersdorp formations), have been correlated across the basin (Groenewald 1989; Neveling 2002).

The Beaufort Group contains a rich tetrapod fossil fauna which has allowed for the Group to be subdivided into eight biostratigraphic assemblage zones (Rubidge 1995). The subdivision of the Beaufort Group into these biostratigraphic units has helped in producing a detailed description of the development of the basin and the regional lithostratigraphy within which they are contained (Catuneanu *et al.* 1998; Hancox 1998; Hancox & Rubidge 2001; Neveling 2002; Rubidge 2005; Botha & Smith 2007). Recent work has allowed for the further sub division of some of the assemblage zones, in particular the *Cynognathus* AZ into A, B and C subzones and the addition of a *Procolophon* biozone within the *Lystrosaurus* Assemblage Zone (Hancox & Rubidge 2001). In addition the change in species of *Lystrosaurus* across time has allowed for a much more finely detailed biostratigraphy for this assemblage zone (Botha & Smith 2007).

It has been argued that the distribution, both geographically and stratigraphically, of the assemblage zones supports the idea that the depocenter, forebulge and foresag advanced and retreated through time (Rubidge 2005). The theory has been shown to hold in both proximal and the distal sectors of the basin (Neveling 2002). However, until now the idea has not been tested in that portion of the basin outcropping in the central Free State and which lies in close proximity to the stratigraphic hinge lines.

In an attempt to understand the effect of the changing depocenter field work was undertaken in the vicinity of the town of Thaba Nchu in the central Free State. Numerous fossils were collected and their lithostratigraphic and geographic position carefully noted. In addition existing fossil collections from the area were accessed and utilized. Most of the fossils collected by previous workers could not be accurately placed within the local stratigraphy as the collection records contained inaccurate coordinates or general localities but they do point to the presence of particular biozones in the area.

Fossils from the *Dicynodon*, *Lystrosaurus* and *Cynognathus* Assemblage Zones were recorded. Three different species of *Lystrosaurus* (*L. murrayi, maccaigi, curvatus*) have been collected from the Thaba Nchu area. The presence of *Procolophon* and taxa belonging to subzones A and B of the *Cynognathus* Assemblage Zone demonstrate the presence of these biozones as well as the proposed *Procolophon* Zone. No taxa from the *Cynognathus* subzone C were recorded.

The combined use of bio- and lithostartigraphy has refined current understanding of the stratigraphy and pointed to great attenuation of the Beaufort Group in the study area.

Stratigraphic gaps have been highlighted, thus supporting the idea of reciprocal infilling of the Beaufort Basin as the forebulge and foresag shifted with time.

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Macroscelidea from the Miocene of the Sperrgebiet, Namibia

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The diamond exploitation in the Sperrgebiet (Southern Namibia) led to the discovery of several Miocene deposits which have yielded a diverse and rich mammalian fauna in different settings. These deposits occur in the fossil loops of the Oranje river (Arrisdrift and Auchas Mine) in the South and in fluviatile and flood plain deposits in the North (Langental, Grillental and Elisabethfeld). Among the mammals, the Macroscelididae (elephant-shrews) are very well represented. The first ones from the area was described by Stromer in the early 1920s.

Oranje River

The first Macroscelideans were discovered at Arrisdrift in the mid-1970s by Corvinus (Corvinus & Hendey 1978) which were later referred (Hendey 1978) to the East African genus *Myohyrax oswaldi*, a very hypsodont species which occurs at Songhor, Rusinga and Karungu in Kenya and at Napak in Uganda (Andrews 1914; Hopwood 1929; Whitworth 1954; Patterson 1965; Butler 1984). New exca-

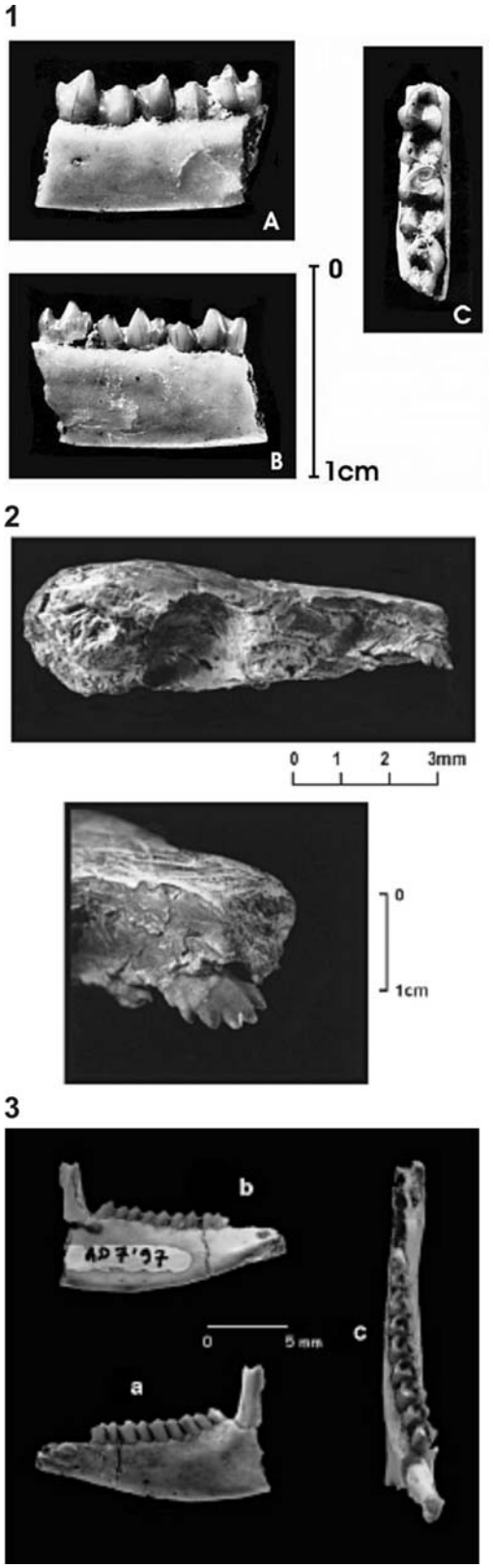


Figure 1. **1**, Mandibular fragment of *Miorhynchocyon gariepensis* (A, labial view; B, lingual view; C, occlusal view); **2**, skull of cf. *Miorhynchocyon gariepensis* (above: lateral view; below: detail of the upper I1); **3**, Mandible of *Myohyrax oswaldi* (a, labial view; b, lingual view; c, occlusal view).

vations were made in the Orange River deposits by the Namibia Palaeontology Expedition and fossils have been unearthed at two sites: Auchas Mine from the Lower Miocene and Arrisdrift from the Middle Miocene (Pickford & Senut 1999, 2003). Two taxa have been described: the

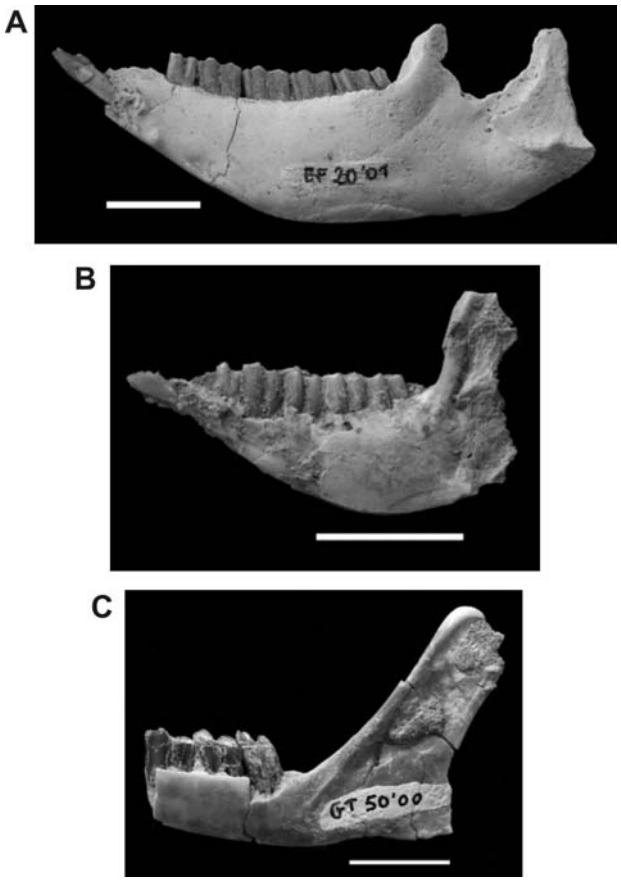


Figure 2. **A**, Left mandible of *Protypotheroides beetz*; **B**, left mandible of *Myohyrax* oswaldi; **C**, left mandible of the large brachyodont species.

abundant hypsodont *Myohyrax oswaldi* (more than 400 specimens) and the poorly represented (3 specimens) brachyodont *Miorhynchocyon gariepensis* (Senut 2003) which recalls the East African miorhynchocyonines described by Butler in 1984, but differs from them by the talonid which is much lower than the trigonid and by the fact that the paraconid is not separated from the protoconid by a deep groove (Fig. 1.1). A large skull and three upper incisors with six main digitations have been tentatively referred to this latter taxon.

However, new discoveries at the Lower Miocene site of Grillental and Langental in the Northern Sperrgebiet suggest that these specimens might belong to a new taxon (Fig. 1.2).

Northern Sperrgebiet

In the Northern Sperrgebiet, the Lower Miocene infillings of Oligocene valleys such as Langental and Grillental or flood plain deposits such as Elisabethfeld yielded abundant macroscelidids remains. The macroscelidids are known by two hypsodont species, a small one which is the same as that occurs at Arrisdrift, *Myohyrax oswaldi* (Fig. 1.3) and a large one, *Protypotheroides beetzi* described by Stromer in 1922 and 1926 from Lüderitzbucht in the Sperrgebiet. The 2 taxa are represented at the three main sites by mandibular, dental, cranial and postcranial remains. At Elisabethfeld, a mandible of a Miorhynchocyoninae is present but is bigger than than the one from Arrisdrift. At Grillental and Langental, a few specimens (a mandible and a few upper incisors with several digita-

tions) of a very large brachyodont species have been found and probably belong to a new taxon.

In terms of numbers of individuals, the macroscelidean fauna is largely dominated by hypsodont species which suggest that these animals were adapted to herbivory, eating grass or seeds. We note a strong imbalance between the frequency of hyposodont and brachyodont species, the latter being very rare; as is also the case in the Middle Miocene sites of the Southern Sperrgebiet. At this stage, it is difficult to suggest any explanation; was there any competition between the species? It seems that the brachyodont ones were slightly more diverse in the Lower Miocene sites than in the Middle Miocene ones. A study of Oligocene macroscelidids might shed some light on the matter.

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Vertebrate taphonomy and ichnology of a Permian 'wet desert' in central Pangea

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Paleogeographic models position the vertebrate fauna of the Upper Permian Moradi Formation, northern Niger, approximately 20 °S of the paleoequator in central Pangea (Fig. 1). This basin lies east of the Tethys sea within a 5000 km wide 'corridor' between Gondwana and Laurasia (Gibbs *et al.* 2002; Ziegler *et al.* 1997). Recent field investigations have confirmed that climate was warm, arid with seasonal monsoonal rainfall (Kutzbach & Gallimore 1989; Kiehl *et al.* 2005) and, possibly as a result of these unique physioclimatic conditions, the tetrapod fauna shows a high degree of endemism (Sidor *et al.* 2005).

The Moradi Formation of northern Niger has yielded the only substantial tetrapod fauna from the Upper Permian of central Pangea (de Ricqlès & Taquet 1982)The body fossil record presently consists of two large temnospondyls *Nigerpeton* and *Saharastega*, the pareiasaur *Bunostegos,* the captorhinid *Moradisaurus,* and a possible therapsid (Taquet 1967). This endemic fauna, which is strikingly different in composition from others of the Upper Permian, suggests that the high-latitude southern African and Russian faunas have yielded an oversimplified picture of the distribution of terrestrial faunas in Pangea.

The Moradi sediments accumulated on a flat, semi-arid to arid alluvial plain with large, low angle gravelly alluvial fans prograding from the tectonically active Aïr Massif to the east, which at times impinged on a large stable meandering channel system flowing generally northwards along the axis of the basin.

Taphonomy of 'pareiasaur cemetery' site

Fossil-rich intervals are characterized by wide shallow anastomosing channels conformably filled with a conglomerate of reworked pedogenic carbonate nodules, rhizocretions, and claystone clods overlain by massive sandy siltstone. At Ibadanane 20 km west of Arlit, an area measuring 280 × 50 m was found to contain at least 15 concentrations of dissociated bones comprising ribs, vertebrae and long bones of pareiasaurians (Fig. 3).

Preliminary quarrying revealed disarticulated, but still associated, skeletons of *Bunostegos* as well as amphibians such as *Nigerpeton* and the captorhinid *Moradisaurus.* These 'bone on bone' bonebed occurrences are generally elongated and dip gently towards the channel axis (Figs 4 & 5). The preliminary interpretation of the depositional setting of the pareiasaur 'cemetery' site is of a distal alluvial fan where ephemeral flash-flood streams swept across a silt-dominated loessic plain, scouring through the sparsely vegetated soils to the more resistant calcrete horizons, reworking previously buried bones and burying desiccated drought-stricken cadavers.

Sedimentology and ichnology of Moradi end-point playa deposits

Localized depressions filled with brecciated limestone overlain by finely-laminated calcic siltstone are interpreted as end-point playa deposits (Fig. 6). They clearly demonstrate that this 'wet desert' hosted standing water bodies and preserve a range of insect, arthropod, amphibian and reptile tracks not previously recorded from the Moradi Formation.

The trackway horizons contain an exquisite tetrapod ichnofauna that is preserved within a local, 1.2 to 1.5 m-thick deposit of thinly bedded calcareous siltstone, with polygonal desiccation cracks upon the upper surfaces. The ichnofauna consists of beautifully preserved trackways and isolated footprints made by at least three

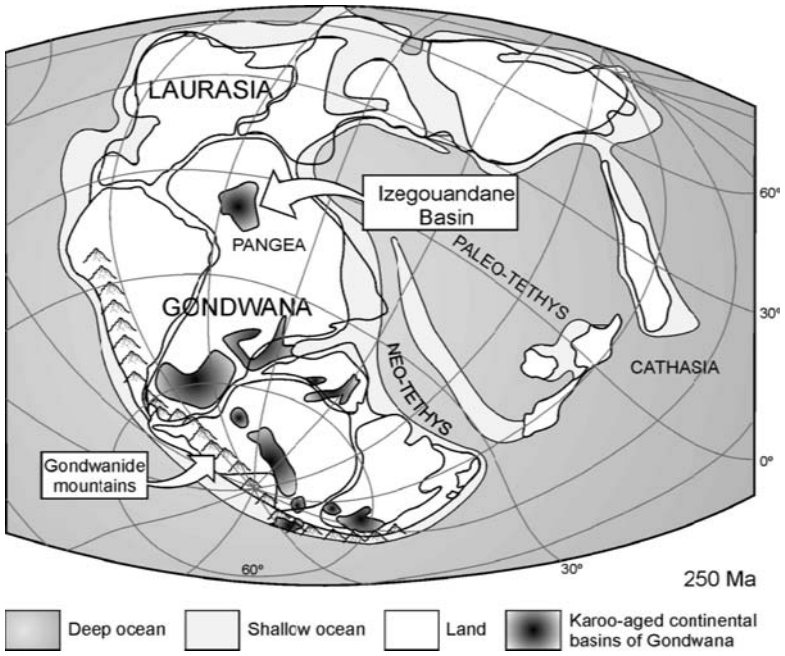


Figure 1. Palaeogeographic setting of the Izigouandane Basin in the latest Permian (after Ziegler *et al.* 1997).

types of amphibians and reptiles, which can be distinguished by their digit number and shape, as well as attributes of their trackways.

The footprints and trackways are preliminary referred to the ichnotaxa *Hylopus* herminatus or *Hyloidichnus* (ascribed to captorhinomorphs or bolosaurs), *Dromopus* or *Rhynchosauroides* (ascribed to lacertoids), and ?*Paradoxichnium* (with parallel digits – possibly therapsid). Interestingly, all of these records suggest Euramerican rather than Gondwanian affinity, as is the case of the associated body fossils outlined above. Importantly, the ichnofauna documents small-bodied tetrapods that have

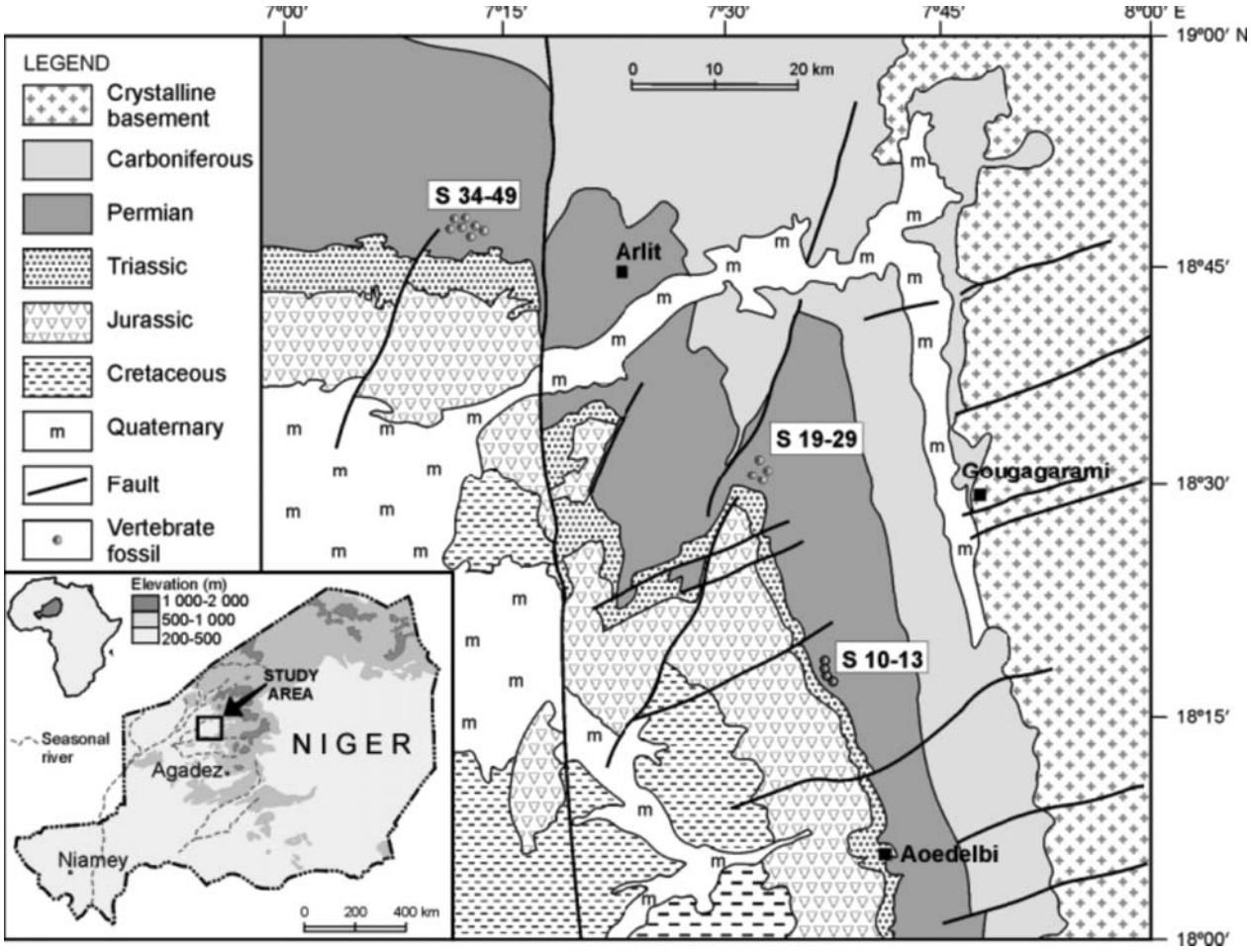


Figure 2. Geology of the study area around Arlit in northern Niger.

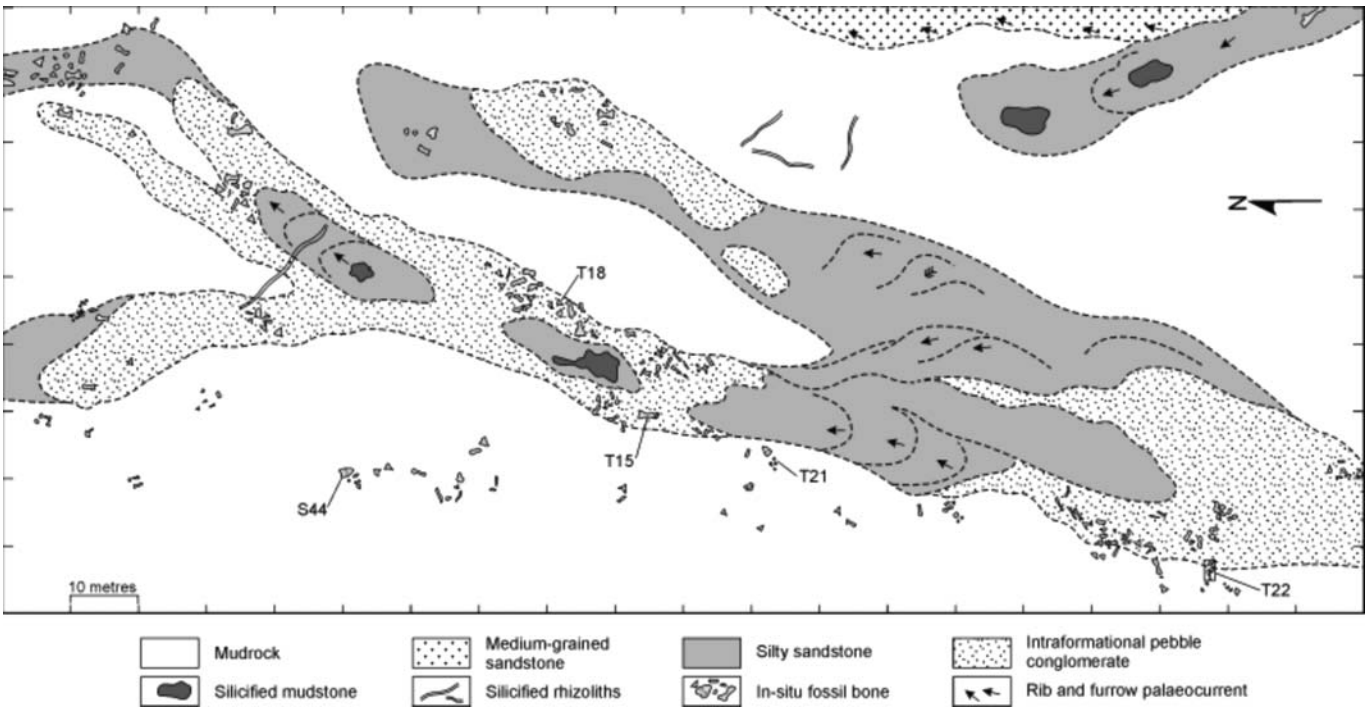


Figure 3. Map of channel-hosted pareiasaur skeletons in the Moradi Fm.

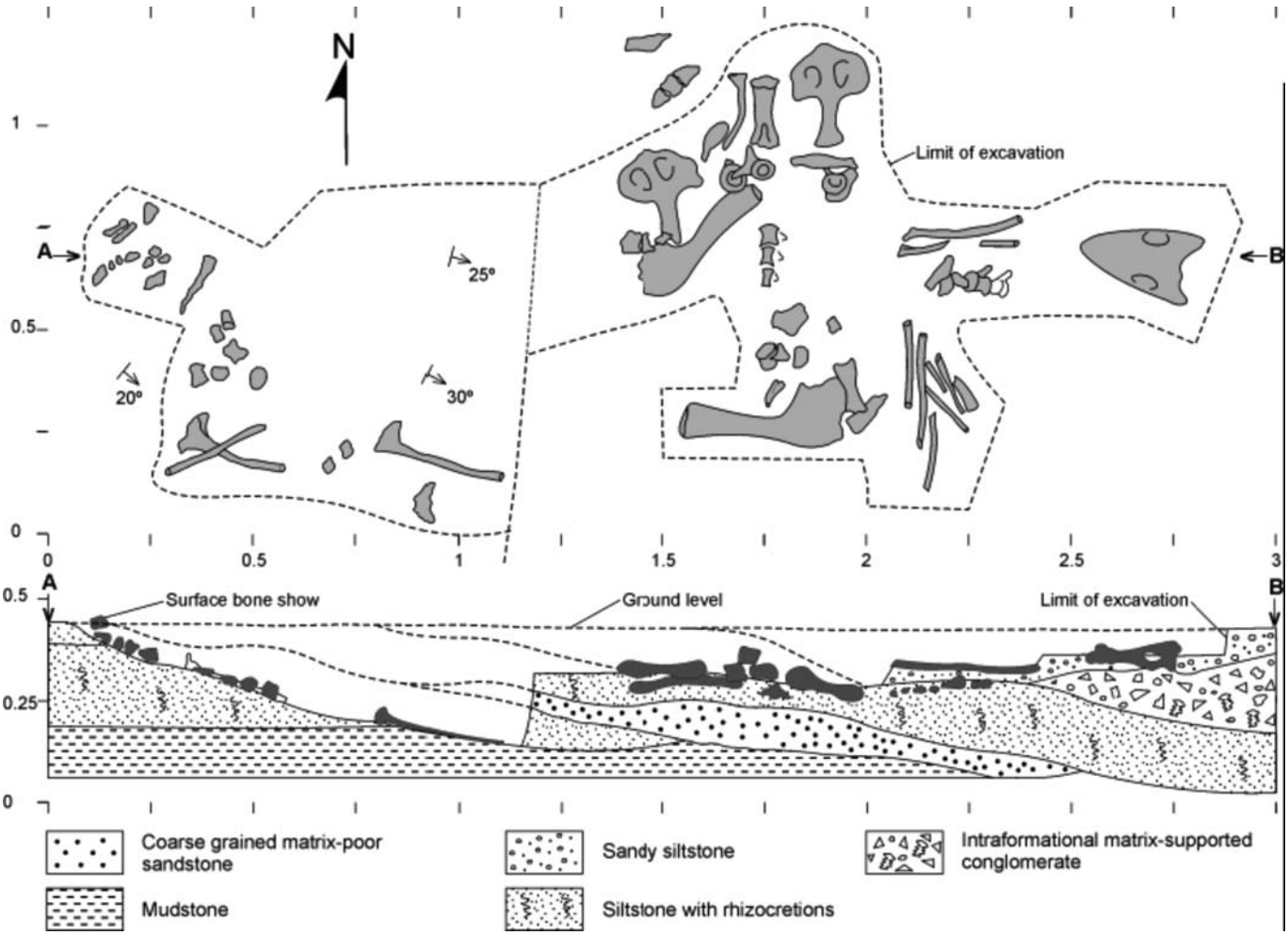


Figure 4. Quarry plan and vertical section through T22 in Fig 3, a scattered *Bunostegos* skeleton in the Moradi Fm.



Figure 5. *Bunostegos* skeleton T22 (Chris Sidor working on the skull).

not yet been recovered from the Moradi Formation as body fossils possibly because of preservational bias but more likely due to lack of sustained and systematic collecting.

The ichnofauna consists of beautifully preserved trackways and isolated footprints made by at least three types of amphibians and reptiles, which can be distinguished by their digit number and shape, as well as attributes of their trackways. The footprints and trackways are preliminary referred to the ichnotaxa *Hylopus herminatus* or *Hyloidichnus* (ascribed to captorhinomorphs or bolosaurs), *Dromopus*or , *Rhynchosauroides* (lacertoids in shape, see Fig. 7), and ?*Paradoxichnium* (with parallel digits). Interestingly, all of these records suggest Euramerican rather than Gondwanian affinity, as is the case of the associated body fossils outlined above.

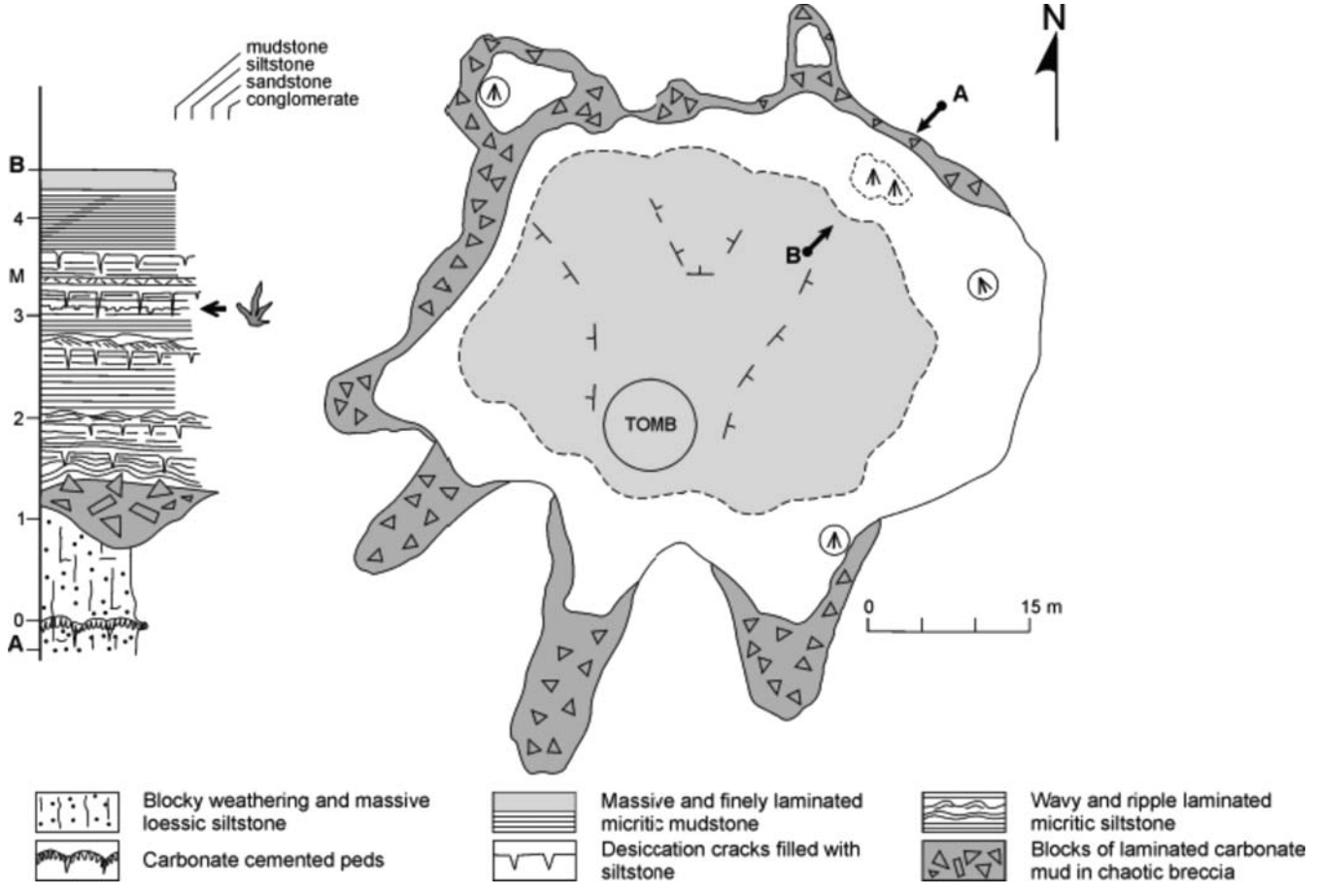


Figure 6. Map and section through a playa-hosted trackway site in the upper Moradi Fm.

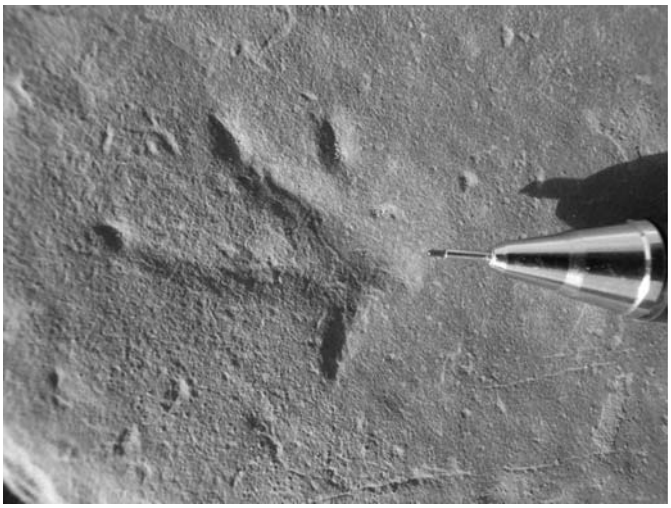


Figure 7. Small trackway with lacertoid affinities tentatively ascribed to *Dromopusor* or *Rhycosauroides*.

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Are bovid dietary preferences integral in understanding past ecosystems?

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As primary feeders, bovids have varied diets and occupy a diverse range of ecological niches. They are abundant in modern African ecosystems and prolific in the fossil record. Dietary strategies of modern and fossil bovids are often put into broad categories along the browser/grazer continuum: grazer, mixed feeder and browser. Often reconstructions of ecosystems rely heavily on information about diet at these broad scales. However, are bovid dietary preferences integral in understanding past ecosystems? There has been substantial debate regarding whether these categories are sufficient to explain the full extent of dietary diversity among bovids. Testing dietary hypotheses has often been limited by these broad trophic categories which require arbitrary boundaries. A more informative interpretation of dietary behaviour can only be accomplished by eliminating the circularity of these subjective trophic categories, and examining the full extent of diet variability or flexibility amongst bovid species. The most informative data are not always what the average behaviour of a particular bovid species reflects, but rather what the outliers of the group may imply. Dietary variability or flexibility may be an essential adaptive strategy especially during times of vegetation shifts due to climatic fluctuations. In this regard, intraspecific variations in diet can reveal trends about bovid dietary strategies, and changes in those trends can provide insight into how bovids respond to local climatic change.

This research tests whether the dietary strategy of fossil bovids remained constant at two spatio-temporally similar Plio-Pleistocene South African hominin sites. Dental remains from various fossil bovid species were selected from Swartkrans and Cooper's Caves. Using a multi-proxy approach, stable carbon isotope, dental microwear texture analysis, and mesowear techniques were applied to provide a comprehensive interpretation of the dietary strategies of the bovids. The study was guided by the following research aims: (1) identify the dietary strategies of fossil bovids from two contemporaneous sites, (2) determine the variation or flexibility of dietary strategies, (3) using the data from 1 and 2, compare the dietary strategies of fossil bovids between the different Swartkrans Members (1–3) and Cooper's Cave D locality; and (4) if possible, infer ecological stability or heterogeneity using the dietary strategies of fossil bovids from these various deposits.

To understand the dietary complexity of fossil bovids and their relevance to addressing palaeoecological questions, a multi-proxy approach applied at multiple spatio-temporally similar fossil sites is required. While different techniques have their strengths and weaknesses, when applied together, they are able to result in a solid palaeodietary reconstruction.

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RoA mesowear perspective on the diets of ungulate from the middle Pleistocene levels of Elandsfontein, Western Cape, South Africa

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The dietary regimes of 15 ungulate species from the middle Pleistocene levels of the hominid-bearing locality

of Elandsfontein, South Africa, are investigated using the mesowear technique. Previous studies, using taxonomic analogy, classified 12 of the studied species as grazers (*Redunca arundinum, Hippotragus gigas, Hippotragus leucophaeus, Antidorcas recki, Homoiceras antiquus, Damaliscus* aff. *lunatis, Connochaetes gnou laticornutus, Rabaticerus arambourgi, Damaliscus niro, Damaliscus* sp. nov., an unnamed 'spiral-horn' antelope and *Equus capensis*), one as a mixed feeder (*Taurotragus oryx*) and two as browsers (*Tragelaphus strepsiceros* and *Raphicerus melanotis*). While results from mesowear analysis sustain previous dietary classifications in the majority of cases, five species were reclassified. Three species previously classified as grazers, were reclassified as mixed feeders (*Hippotragus gigas, Damaliscus* aff. *lunatus* and *Rabaticerus arambourgi*), one previously classified as a grazer, was reclassified as a browser (the 'spiral-horn' antelope), and one previously classified as a mixed feeder, was reclassified as a browser (*Taurotragus oryx*). While present results broadly support previous reconstructions of the Elandsfontein middle Pleistocene environment as one which included a substantial C_3 grassy component, the reclassifications suggest that trees, broad-leaved bush and fynbos were probably more prominent than initially thought.

A study of tooth crown form to elucidate niche partitioning in late Miocene/early Pliocene hyaenas from 'E' Quarry, Langebaanweg, South Africa

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The late Miocene/early Pliocene 'E' quarry deposits at Langebaanweg, South Africa, have yielded fossil material of at least four hyaena species *(Ikelohyaena abronia, Hyaenictitherium namaquensis, Chasmaporthetes australis, Hyaenictis hendeyi*). The co-occurrence of four closely related hyaenids at this site raises interesting questions about niche partitioning which have not been sufficiently addressed. In the only previous systematic attempt to tackle this issue, an analysis of M1 lengths, M1 trigonid lengths and P3 widths found evidence for character displacement in the first two variables. While this study suggests that morphological character displacement was a factor in niche partitioning among the 'E' Quarry hyaenas, it was only based on two teeth and three metric variables. In the current study, a geometric morphometric approach is used to compare P2, P3, P4 and M1 (carnassial) crown form to better understand feeding niche partitioning among the four Langebaanweg hyaena species. While results indicate that the four species are very similar in crown shape, *I. abronia* and *H. namaquensis* tend to have slightly shorter, broader cheek teeth than *C. australis* and *H. hendeyi*. This suggests that *I. abronia* and *H. namaquensis* may have been less carnivorous than *C. australis* and *H. hendeyi.* The biggest difference between the species, however, relates to crown size. The four species are evenly spaced with respect to median crown size in all teeth except the P4. These results support a previous suggestion that size-related character displacement was in operation among the 'E' Quarry hyaenas and probably played a major role in reducing inter-specific competition.

Dental size and frequency of pathologies in the teeth of a small-bodied population of mid–late Holocene Micronesians, Palau Micronesia

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Introduction

The study of the size and shape of teeth has generated more literature than any other aspect of dental anthropology (Wolpoff 1971). The notion of a linear or exponential relationship between crown size and body size is recurrent in the dental and paleontological literature. For some human groups, low but positive correlations between tooth size and body measures have been noted, and some of the correlations are significant (Garn *et al.* 1968), demonstrating that teeth remain in proportion to body size, whatever the body size of a mammal.

However, a recently discovered small-bodied population of hominins from Palau, Micronesia, has been shown to exhibit a number of unusual traits, including extremely small body size, facial size reduction and high degrees of robusticity. They also appear to possess very large teeth and high frequency of certain tooth forms. The presences and absences of these tooth forms are normally observed at very low frequencies in modern human population.

This study intended to compare the size and shape of the teeth of the Palauan population to living humans and fossil hominids, as well as examine the frequency of four apparent pathologies noted in the Palauan samples.

Materials and methods

Four different population groups – namely namely Zulus, Tswanas, Khoisan and Europeans were examined in this study. The teeth of 100 specimens were measured from each population – 50 males and 50 females. Standard measurements of the teeth were obtained using the dimension described by Shaw (1931). In addition, the entire sample of humans from the Dart collection, comprising approximately 2500 specimens, will be used to record the presence and absence of the four pathologies. These pathologies are congenital absence of the third molar, incisiform canines, caniniform premolars and rotated premolars. Degree of expression, orientation and other characters were noted for observed pathologies. Photographs of the pathologies were also taken. Both the measurements and observations were then compared to the Palau sample using statistical analysis. Univariate and bivariate analysis of the Stat view program were used.

Results

The teeth of the Palauens were larger than those of the four population groups, despite having very small stature, and skull, and absence of cheeks. The Khoisan had the smallest teeth of all the groups studied, supporting the fact that they have microdont dentition (Drennen 1925; Haeussler *et al.* 1989). They were followed by the Europeans, in some instances having the same dimensions as the Zulus, and Tswanas, which have mesodont dentition. Megadontia as observed in the Palauen sample could be due to the diet they consumed, or a lag phase in the reduction of the teeth (Berger *et al.* 2008).

Frequencies of pathologies were low in the human sample compared to the Palauen sample, and this is mostly due to the less space available for the teeth to develop in. Teeth erupting so close together tend to look more like the teeth next to them (Greenfield 1993).

Estimating body size from tooth size is something that needs to be done carefully, since it is possible that the linear relationship between the two can be lost, as have been demonstrated by the Palauen Micronesians. There is no optimum tooth size that would meet the requirements for all populations. Rather tooth size must be viewed in relationship to other factors, such as diet.

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The identification of fossil herpetological remains from selected Plio-Pleistocene aged fossil-bearing sites in South Africa

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Introduction

The abundant southern African animal fossil assemblages have long been recognized as important as a record of ancient life (Lee-Thorp *et al.* 2003). In particular, the Plio-Pleistocene aged fossil deposits are among the most important record of animal evolution during this period on the African continent (Vrba *et al.* 1995). These sites, largely confined to cave breccias in dolomitic regions, have proven particularly important in revealing information about the mode and tempo of human evolution (Hilton-Barber & Berger 2002), as well as the evolution of non-hominin macro- and micro-mammals (Vrba *et al.* 1995). These sites have also been recognized as being important for understanding the recent evolutionary history of other groups including avians (Avery 2001).

Given the intensive research conducted on these fossil assemblages, it is surprising to note that little attention has been given to the herpetological remains that are known to be present in these assemblages. This is even more surprising given the fact that extant herpe-fauna are recognized as being particularly sensitive in their adaptation to specific environments and are often found in very constrained geological environments, plant communities and temperature ranges (Goin & Goin 1971). Thus, the identification of specific forms of fossil herpetofauna at a variety of taxonomic levels could lead to a greater understanding of both the evolution of specific forms of herpe-fauna as well as be a benefit to increased understanding of the palaeoenvironments of these Plio-Pleistocene aged sites. This in turn could lead to insight into changes in environment that affected the mode and tempo of evolution in mammal species.

This study helps in redressing the lack of understanding of the herpe-fauna of selected southern African sites through a detailed study of the fossil herpe-fauna hypothesized to exist in the fossil collections.

The main purpose of this project was to assess the variety and abundance of herpe-fauna (herpetiles) contained in Plio-Pleistocene fossil record of South Africa with the intent of identifying where possible families, genera and species that may give insight into ecology of sites during different temporal periods.

Materials and methods

Examination of the known herpe-fauna and the search for additional material will be conducted in the fossil assemblages of Makapansgat, Swartkrans, Coopers, Gladysvale and Taung. Several of these sites have already been recognized as containing herpe-fauna in varying degrees of abundance, indicating that the condition within these deposits was suitable at the time of accumulation for preserving herpe-fauna. Herpe-fauna was identified through a visual search of the existing material and comparison with modern herpetological material.

Once identified, herpe-fauna was sorted into the highest taxonomic category possible based on the condition and quality of material recovered. Once this material has been sorted, it was then described in detail and compared and contrasted with known extant species where possible.

A broad community of herpe-fauna was then constructed for each of the assemblages. At this point, this study attempts to find meaningful patterns in these communities and examine whether the ancient herpe-faunal communities can give insight into broad palaeo-environments. This is done through comparisons with extant communities of herpe-fauna from known environments.

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An evolutionary explanation why the facial nerve in birds passes lateral to the polar cartilage while in crocodiles it passes medial to the homologous structure

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One of the classical problems in anatomy is represented by the different path of the facial nerve (palatine ramus) from its exit from the endocranium to its entry into the 'vidian canal' in crocodiles and birds. It seems clear that both the polar cartilages and the palatine rami of the facial nerve are homologous structures and yet, in crocodiles, the nerve pass medial to the polar cartilage but in birds and lizards, it passes lateral to it. Study of crocodile and bird ontogeny confirms the problem but the resolution of recapitulation is inadequate to suggest what happened in the phylogeny. It was the objective to investigate this problem at the hand of direct palaeontological evidence.

Well-preserved, carefully prepared braincases of a phylogenetic series of fossil reptiles linking birds and crocodiles to their reptilian ancestors were studied to obtain direct evidence of what happened in natural history. The path of the palatine ramus relative to the position of the polar cartilage and the dermal basitemporal covering its ventral surface on the basicranium was reconstructed and compared in the various fossil forms.

The path of the palatine ramus of the facial nerve can be reconstructed with some confidence according to foramina and grooves that indicate the path of the nerve in the different fossils. We found that the polar cartilage and the basitemporal shortened over a period of 50 million years and that this opened up a fissure between these elements and the basioccipital about 200 million years ago. The path of the facial nerve coincided with this fissure and the nerve slipped into this crack in some early dinosaurs. When the polar cartilage and basitemporal subsequently expanded again, the nerve became trapped, now following a route medial to the polar cartilage.

This landmark development is documented in the anatomy of all dinosaurs and the earliest crocodilomorphs that made their appearance slightly later in time. On the one hand it strongly suggests that modern crocodiles are true dinosaurs and on the other hand, it confirms that birds are neither closely related to crocodiles nor to dinosaurs.

Evolution of the lateral column of the hominin foot – evidence from the StW 114/115 fifth metatarsal (Sterkfontein)

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Introduction

A complete, undistorted right fifth metatarsal, StW 114/115 was recovered in August 1982 by the Sterkfontein excavation team under A.R. Hughes. Deloison (2003), in describing early hominin foot bones from South Africa, interpreted the anatomical features of StW 114/115 as being consistent with those of an australopithecine from Member 5. Given the proximity of StW 114/115 to dental remains from Member 4 (Moggi-Cecchi *et al.* 2006), it is reasonable to hypothesize that the metatarsal belongs to *Australopithecus africanus,* though we caution that given the complex stratigraphy of Sterkfontein, there remains the possibility that StW 114/115 is from early *Homo* or from *Paranthropus robustus.*

The hominoid foot consists of a lateral column (that leads to the fourth and fifth digits) and a medial column (that leads to the hallux and the second and third digits) (Aiello & Dean 1990). The medial column of the anterior elements of the foot, best represented by the first metatarsal, has been studied to some extent (e.g. Lewis 1980; Susman & Brain 1988; Deloison 2003; Susman & de Ruiter 2004; Zipfel & Kidd 2006). The lateral column of the anterior foot, however, has received less attention due to the paucity of complete fourth and fifth metatarsals in the fossil record. The StW 114/115 fifth metatarsal, therefore, being the earliest complete hominin fifth metatarsal to date, provides a unique opportunity to further investigate the lateral column of the hominin foot and its evolution.

Materials and methods

The fossil was compared to human and great ape counterparts. Morphological comparisons were made on fifth metatarsals from Victorian British humans (11 females and 16 males). Also included in comparisons were wild-shot great ape individuals comprising chimpanzees (20 females and 19 males), gorillas (20 females and 19 males) and orang-utans (16 females and 11 males). In addition to extant apes and humans, StW 114/115 was compared to the partial fifth metatarsals SKX 33380 from Member 3 of Swartkrans, South Africa (Susman 2004), OH 8 from Bed I, Olduvai Gorge, Tanzania (Day & Napier 1964; Leakey *et al.* 1964; Susman & Stern 1982), AL 333-13 and AL 333-78 from the Afar Locality, Ethiopia (Wood 1974; Grausz *et al.* 1988; Gebo & Swartz 2006) and KNM ER-803f from Koobi Fora, Kenya (Latimer *et al.* 1982).

Morphometric analyses of StW 114/115 are based on the four extant species and females and males were treated as separate groups. Eight variables were chosen so as to reflect the broad morphology of the bone and its functional attributes. The comparative fossils are excluded in the morphometric analysis because of their fragmentary nature. The linear dimensions are based loosely on the definitions by Martin & Saller (1957).

The multivariate objective of the study was to establish patterns of morphological discrimination within and between the groups, initially using principal components analysis (PCA) (Blackith & Reyment 1971; Bryant & Yarnold 2001) and subsequently using canonical variates analysis (CVA) (Reyment *et al.* 1984; Albrecht 1980, 1992). Computations for both analyses were undertaken using PC *SAS*® 9.1.

Non-metric observations of StW 114/115 are the torsion angle of the metatarsal head relative to the base and qualitative assessments of the sagittal and transverse curvatures of the shaft. In addition, plain film radiographs were examined for cortical thickness and pathology.

Results

The general morphology of the bone appears to be very human-like and of an adult. The shaft curves in the transverse plane with the concavity on the lateral side. There is a medial (internal) torsion of the head of approximately 10° measured as the deviation from the vertical axis of the metatarsal head relative to the vertical axis of the base. The shaft is short and stout with a distinct sagittal curvature plane producing a plantar concavity. In profile the shaft has approximately the same dorsoplantar height from just distal to the base, to just proximal to the head giving it a parallel-sided appearance. The base is expanded and the lateral border traces a gentle curve as it passes from the proximal end to the shaft. In profile, the distal articular surface extends well onto the dorsum of the bone and is flanked by prominent epicondyles. On the dorsum there is a shallow sulcus, or depression, between the head and the shaft.

The East African fossils have in common with the Sterkfontein fifth metatarsal an expanded base with the lateral border tracing a gentle curve as it passes from the base to the shaft. In profile, the distal articular surface of StW 114/115 extends onto the dorsum of the bone as in modern humans. The head of StW 114/115 displays an axial torsion which is medial or internal and similar to that of modern humans. In contrast, the apes have a torsion of the metatarsal that is laterally or externally rotated so that the head faces the other metatarsals (Morton 1922; Lewis 1980; Aiello & Dean 1990). The basal articulations for the cuboid and fourth metatarsals are human-like in the acute angle of the articulation with the cuboid with respect to the shaft. The dorsoplantar shape of the proximal articular surface of StW 114/115 is similar to all of the other known hominin metatarsals in being flatter than modern African ape metatarsal facets and falling in the distribution of modern human fifth metatarsal-cuboid facet curvature (DeSilva 2008). The ape proximal articulation with the cuboid is 'elongated' in the mediolateral direction (Susman 1983) and appears also to be more mediolaterally concave than in humans, StW 114/115, OH 8, AL 333-78 and KNM ER-803; this is therefore a distinct feature discriminating the apes from hominins. AL 333-13 has a slightly concave articulation for the cuboid in the mediolateral direction.

Principal components analysis of the eight linear measurements reveals that the majority of the variation lies within the first two principal components, together accounting for just over 76 % of the total variance. The fossil, StW 114/115 lies centrally on the first principal component within the spread of humans. On the second principal component, containing 17.86 % of the total variation, the fossil lies negatively to all the apes, centrally within the humans.

In the CVA of the fossil together with the extant species, the majority of the discrimination lies within the first two variates, together accounting for over 92 % of the total discrimination. Subsequent variates contain considerably less variation, the third, 11.12 % and the fourth, 3.70 % of the total discrimination. Along the first canonical variate, the fossil lies between the human males and chimpanzee females. On the second canonical variate there is a clear discrimination between the fossil, the apes and humans. The fossil is thus of distinct form but has the greatest affinity for humans and chimpanzees. On the third canonical variate the fossil lies broadly between the humans on the one hand, and the apes on the other closest to the human females, gorilla males and orang-utan females.

Discussion

The principal features that distinguish human from ape fifth metatarsals are the sagittal and lateral curvatures of the metatarsal shaft, the torsion of the metatarsal head, and the extension of the distal articular surface onto the dorsum of the head. The dorsal extension of the distal articular surface of StW 114/115 would allow for a human-like metatarsophalangeal dorsiflexion which is essential for successful toe-off during the propulsive phase of bipedal gait (Bojsen-Møller 1979; Bojsen-Møller & Lamoreux 1979). A distinctive feature of the human metatarsal shaft is that it is relatively straight in the sagittal (dorsoplantar plane) and has a slight concavity on the lateral side. In contrast, the ape fifth metatarsal has a sagittal plane curvature with the concavity on the plantar side and a straighter lateral border than in humans. StW 114/115 has a mosaic of these features.

Another compelling feature suggesting a bipedal gait in the StW 114/115 specimen is the internal (medial) torsion of the metatarsal head (Morton 1922; Lewis 1980; Aiello & Dean 1990). This torsion of the metatarsal head in the StW 114/115 individual, which is the same as that of humans, strongly suggests that this hominin had both transverse and longitudinal arches.

The derived (human-like) features in StW 114/115 are therefore: 1) a short robust bone, 2) an internal torsion of the head, 3) a distal articular surface extending onto the dorsum of the metatarsal head with a sulcus or depression between the head and shaft, 4) a transverse plane curvature (lateral concavity) tracing a gentle curve as it passes to

the expanded base and, 5) a dorsoplantar flattened proximal articular surface. Primitive (ape-like) features in StW 114/115 are: 1) a sagittal plane curvature (plantar concavity) of the shaft and 2) a lack of posterior expansion of the plantar shaft at the base.

In the CVA of the morphometric analysis, morphological information is interpreted not only on any single variate, but is jointly held between variates. On a plot of variates one and two, StW 114/115 lies on the line discriminating humans and African apes from orang-utans. This could be interpreted as a broad geographic discrimination between the Homininae of African origin, and the Ponginae of Asian origin.

On a plot of variate one against variate three, the fossil lies on a line discriminating the humans on the one hand and the apes on the other. As the plots of the apes and humans possibly suggest discrimination in terms of locomotion, being quadrupedal terrestrial and arboreal for the apes and habitual bipedalism for the humans, the position of the fossil suggests a unique morphology and perhaps associated function. The isolated fossil does, however, lie closest to the humans and chimpanzees, located in a unique position of the group means along the first two variates.

Skeletal correlates of midfoot stability can be found in both humans and the StW 114/115, which have a mediolaterally 'shortened', dorsoplantarly flat proximal fifth metatarsal articular surface that appears to have evolved for maintaining a stable joint during mid-stance. This morphology results in the midfoot becoming a rigid lever, shifting motion to the metatarsophalangeal joint during the push-off phase of gait. A skeletal correlate of this metatarsophalangeal motion is a dorsally extended articular surface on the distal head of human metatarsals. In contrast, the dorsal-most portion of the metatarsal head of apes appears flat in profile (Susman 1988; Latimer & Lovejoy 1990; Aiello & Dean 1990). The fossil, StW 114/115, displays a very human-like dorsally extended articular surface. Additionally, in the human lesser metatarsals, there is also a depression between the head and shaft (Aiello & Dean 1990). This also relates to an increased potential for dorsiflexion at the metatarsophalangeal joints. This is essential to a bipedal gait where the metatarsophalangeal joint acts as a fulcrum so that the posterior part of the foot can 'roll' over during the toe off phase of gait. This feature is present, though not as well developed in the Sterkfontein specimen as in modern humans.

The human-like functional affinities of this fifth metatarsal, however, do not necessarily indicate that the remainder of the foot would have the same degree of human-like function. In fact, it is unlikely that the gait of the StW 114/115 individual was exactly the same as that of modern humans as the comparatively thicker cortex suggests greater pressure on the lateral column of the foot more closely resembling that of apes (Vereecke *et al.* 2003). Furthermore, the lateral side of the hominin foot may not have evolved in concert with the medial side of the foot (Kidd *et al.* 1996). It would appear that formation of the lateral longitudinal arch, together with increased calcaneocuboid stability was an early evolutionary event in the history of terrestrial bipedalism in hominins. The equivalent modifications to the medial side of the foot, as seen in modern humans, seem to have occurred subsequently, as evidenced in the OH 8 assemblage, and so-called 'Little Foot' assemblage StW 573 (Clarke & Tobias 1995; Kidd *et al.* 1996; Kidd & Oxnard 2005).

Clearly, the StW 114/115 fifth metatarsal is very human-like and the available evidence suggests that the function of this element may not have been much different (if different at all) from that of modern humans. It should, however, be noted that StW 114/115 is only an isolated element of the foot and mixed affinities have been noted in hominin feet suggesting that the medial and lateral columns have not necessarily evolved in concert.

Our grateful thanks go to the University of the Witwatersrand for permission to study StW 114/115 and Jaymati Limbachia of the Helen Joseph Hospital for help with radiography. We thank Stephanie Potze and Lazarus Kgasi of the Transvaal Museum for their help. Thank you to Emma Mbua and Amandus Kwekason. Paul Msemwa, Yohannes Haile-Selassie, David Pilbeam and Michele Morgan for assisting with access to the East-African fossils and casts. We thank the staff of the Smithsonian Institution, Powell-Cotton Museum and British Museum of Natural History for access to human and ape comparative skeletal specimens.

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POSTER ABSTRACTS

The postcranial skeleton of *Galesaurus planiceps*: implications for biology and lifestyle

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Galesaurus planiceps is a basal non-mammalian cynodont from the Lower Triassic, *Lystrosaurus* Assemblage Zone (LAZ) of South Africa. The stratigraphic range of *G. planiceps* is relatively short, extending from just above the Permo-Triassic boundary to approximately one third of the way into the LAZ. The range is notably shorter than that of *Thrinaxodon liorhinus*, the better-known sister taxon of *Galesaurus*, whose range extends all the way through the LAZ (Botha & Smith 2006). Both these taxa appeared very quickly after the End-Permian mass extinction event in the Karoo Basin and can be regarded as disaster taxa. The difference in the ranges of these taxa is not fully understood and may be related to lifestyle preferences. Although the postcranial skeletons of *Galesaurus* and *Thrinaxodon* are traditionally considered to be indistinguishable from one another (apart from the ribs) (e.g. Jenkins 1971), newly discovered *Galesaurus* material (associated with positively identified skulls) has come to light allowing this assumption to be tested. Several almost complete skeletons and numerous postcranial elements of *Galesaurus* are currently under study. Preliminary results indicate that the forelimb and pectoral girdle of *Galesaurus* is relatively similar to that of *Thrinaxodon*, particularly where the interclavicle, humerus, radius and ulna are concerned. However, some differences in the scapula-procoracoid-coracoid-complex, the clavicle and manus have been observed. These preliminary results have facilitated in distinguishing these genera using elements other than the ribs or skull. Further study will include examining the rest of the appendiculer skeleton as well as the axial skeleton. The bone histology of *Galesaurus* will also be assessed and compared with that of *Thrinaxodon*.

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An African Origins Platform/West Coast Fossil Park Project

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The West Coast Fossil Park has been granted three years funding from the African Origins Platform (Department of Science and Technology) to maximize the research, educational and tourism potential of the Fossil Park. The project aims to integrate palaeontological and geological investigations of environmental change over the past 20 million years on the Cape West Coast, focusing on the site of Langebaanweg. Research will be used to develop curriculum based education programmes for schools, foster palaeotourism and create employment opportunities in and around the West Coast Fossil Park at Langebaanweg. A Research Director has been appointed to coordinate a number of on-site research programmes which aim to:

1. Survey and map the extent of the fossil deposits at Langebaanweg
2. Determine the stratigraphy, palaeogeography and age determination of Cenozoic deposits of the Cape West Coast
3. Study the taphonomy and depositional history of the Early Pliocene sivathere-dominated bonebed deposit at Langebaanweg
4. Reconstruct the paleoecology of Langebaanweg using an ecomorphological approach on a number of the taxa (e.g. a study of morphology, isotopes, microwear and mesowear)
5. Reconstruct the Early Pliocene ecosystem of the Cape West Coast using a morphological and taxonomic approach to the fossil micromammals from Langebaanweg

Under the auspices of this programme a number of bursaries have been made available for Honours, Masters and post-doctoral students to work on the geology, geochemistry, palaeoecology and fauna of Langebaanweg. An educational consultant has been appointed to develop and implement a curriculum-based educational programme at the Park, using the unique and exciting fossil and ecological experiences that the West Coast Fossil Park provides.

A comparative study of Late Holocene- and Plio-Pleistocene-aged micromammalian owl accumulations from South Africa

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South African Plio-Pleistocene-aged cave deposits often contain well-preserved macro- and micro-mammalian fossil fauna. This is largely due to the taphonomic environment of dolomitic caves, which allow the preservation of fine detail in fossils not found in most other depositional environments (Brain 1981). Microfossils have not received the same attention afforded to macrofossils. Micro-faunal remains are typically intact and well preserved. This is assumed to be due to the way in which the majority of micro-mammalian remains find their way into the fossilization environment, through the introduction of owl pellets into the system (Sparks & Soper 1970; Bunn *et al.* 1982). Owl pellets are essentially neatly packaged death assemblages allowing insight into a particular feed-

ing event (Tarboton & Erasmus 1998). Although, preliminary studies have indicated that it is probable that accumulations of discrete owl pellets can be identified within the consolidated breccias, it has never been given much attention. Despite the abundance and preservation of these micro-mammalian remains, studies of this material have largely been confined to the cranial elements with little regard given to postcranial remains. This leaves open the possibility that fossil taxa have different postcranial morphology to their extant counterparts that has been missed.

If it is possible to recognize discrete owl pellets within fossilized microfaunal deposits, then it is likely that the skeletal elements are associated and the postcrania may therefore legitimately be analysed alongside the cranial remains.

Analysis of modern pellets from both wild and captive owls is expected to contribute to our understanding of taphonomic processes involved in the accumulation of micro- and macro-faunal remains within the dolomitic caves of southern Africa.

An actualistic feeding study conducted on captive owls sheds light on differences in individual and skeletal element representation, as well as the degree of skeletal element association within pellets. This also provides a good mechanism to further understand digestive damage to various skeletal elements.

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A palynological investigation of the mid-Cretaceous Orapa kimberlite pipe in Botswana

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Introduction

The Orapa diamond mine is situated within a large kimberlite pipe approximately 220 km west of Francistown in north-central Botswana.Younger fossilferous sediments filled the resultant craters and have been dated as middle to Upper Cretaceous (Mckay & Rayner 2001), during the time that angiosperms radiated in South Africa.

Previous palynological studies at Orapa suggested that a number of the individual palynomorph assemblages were dominated by *Ephedripites* forms and the occurrence of the genus *Classopollis* which is considered to be mid to Upper Cretaceous in age (Scholtz 1984). Some of these palynomorphs are thin-walled and inaperturate and they may have affinities with the coniferous families Araucariaceae or Cupressaceae. According to Scholtz (1984), they are not useful for precise dating but range from mid to Late Cretaceous. Goldblatt (1978) postulated a warm humid climate for Africa during the mid- to Late Cretaceous, and that tropical forest flora was present over the continent.

Materials and methods

Collection of material

Macroplant samples from Orapa that were collected by staff and students are housed in the BPI herbarium were used. Twenty samples were removed from the blocks from different lithologies. Both reduced and oxidized samples were used to compare numbers of palynomophs in each lithotype.

Pollen extraction

Sediments were crushed with a mortar and pestle to approximately 2 mm fragments and 60 g of each sample was treated. In the fume cupboard carbonates are

dissolved by adding 10% HCl to beakers in a water bath for 2 hours. Washing was carried out by adding distilled water and centrifuging at 3000 rpm for 5 minutes, decanting the supernatant, and repeating the procedure. Organic material was removed by boiling the sample together with 10% KOH and washing as above. Once the pellet was neutral, HF was added to remove silicates and washed again. A saturated solution of zinc chloride was added for density separation and centrifuged at 1800 rpm for 25 minutes.

Some of the supernatant was transferred to the small centrifuge tubes and followed a dehydration series with the increase in alcohol concentration to absolute alcohol and centrifuged at 90 rpm for 3 minutes. The solution was transferred to the cover slip on the Petri dish to dry. After drying the cover slip was mounted on the slide using DPX. Acetone was used to clean the slide.

Pollen slides were studies under a Zeiss petrographic microscope with ×400–1000 magnification. Pollen and spores were identified using the literature. Size, shape, surface texture, number, position of colpi and pores are important features which were used to make the identification in conjuction with reference material.

Results

Palynomorphs found included trilete spores, monolete and tricolpate pollen. Trilete polynomophs are from lower plants, monoletes are from gymnosperm and tricolpates are angiospermous. Angiosperms were the most numerous forms followed by gymnosperms and a few lower plants. According to Bamford (1990) fern macrofossils are numerous and comprise five taxa. The gymnosperm /angiosperm dominance shows that the surrounding environment during deposition was either a fringing forest or shrubland. The pollen yield was too low to allow a reliable interpretation of the past vegetation and climate but the macroplants indicate a small leaved dry and/or cool climate.

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Further light on cranial bone adhering to matrix surrounding Mrs Ples as prepared by Robert Broom

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In 1947, Robert Broom and John Robinson of the Transvaal Museum discovered the most complete cranium of *Australopithecus africanus*, nicknamed Mrs Ples (Sts 5). Unfortunately the skull was broken into two pieces due to the fact that dynamite had been used by lime miners. Broom and Robinson mechanically broke the surrounding breccia at the cave, and subsequently used hammer and chisel at the Transvaal Museum to extract the cranium from the surrounding matrix. However, in the process six pieces of matrix were removed that retained the outermost layer of cranial bone. These six pieces were placed in a store at the museum were they remained for about 50 years.

In 1997, Francis Thackeray reported the discovery of these six pieces in the store and was able to demonstrate that they could be refitted back onto the skull of Mrs Ples. These pieces have been labelled Sts 5 (i) – (vi). Sts 5 (ii) was of particular interest because it included a layer of calcite that could be matched with a horizontal band of calcite visible in a photograph of the *in situ* matrix near the wall of the cave, as photographed on the day of the discovery on 18 April 1947. Thackery and Kirschvink have undertaken palaeoamagnetic analyses of the matrix associated with Sts 5 (ii) and demonstrated normal polarity. In the context of other data, it has been suggested that Mrs Ples dates to the time of the Réunion event, 2.15 million years ago.

Sts 5 (i) was a large block of breccia associated with nucchal bone of Mrs Ples. The matrix has been prepared after very careful dissolution in acetic acid. Of great interest is the exposure of temporal lines which had never been seen before. An additional block of breccia Sts 5 (iii) is currently being prepared and is expected to demonstrate how close the temporal line on the left side of the cranium approached bregma. The evidence currently available suggests that the temporal lines on the right and left sides did not meet at bregma, but were relatively close. It is probable that Mrs Ples may have developed a sagittal crest if the individual, a presumed male, had lived into adulthood. The CT scans undertaken by Thackeray and Braga have shown conclusively that Sts 5 was an adolescent at the time of death. The cranial sutures exposed on cranial bone, recently prepared in acid, are distinctly open. This confirms the fact that Mrs Ples was adolescent rather than an adult, as had been suggested by Robert Broom.

Temperature indices based on relative abundances of rodent taxa represented in South African Plio-Pleistocene assemblages from the Cradle of Humankind World Heritage Site: a preliminary study

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Rodents are among the most common mammals represented in Plio-Pleistocene faunal assemblages excavated from cave deposits in the Cradle of Humankind World Heritage Site and other localities in South Africa. We present temperature indices based on multivariate analyses, using a method previously applied to Late Quaternary microfaunal samples from southern Africa (Thackeray 1987). The indices are calibrated in terms of

temperature expressed in degrees Celsius. The results suggest that assemblages from Kromdraai A, Swartkrans, Bolts Farm, Gladysvale, Haasgat and Drimolen relate to interglacial episodes within the Plio-Pleistocene. The coolest episode represented by samples included in this study is associated with Plovers Lake, dated at about 1 million years ago.

A statistical (probabilistic) definition of a species in palaeontological contexts, based on morphometric analyses of a diversity of modern fauna, using hominid (australopithecine) and therapsid (dicynodont) examples

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A major problem in palaeontology is the definition of a species in the fossil record. An approach has been developed whereby probabilities of conspecificity can be assessed, when pairs of specimens are compared (Thackeray *et al.* 1997). As a frame of reference, pair-wise comparisons have been made between measurements of extant vertebrate and invertebrate taxa, using least-squares regression analyses associated with regression equations of the form $y = mx + c$. Of particular interest is the degree of scatter around a regression line, quantified in terms of the standard error of the m-coefficient (s.e.$_m$) associated with the slope of the regression line. Pair-wise comparisons of conspecific pairs of extant taxa show a log-normal distribution of the standard error of the m-coefficient. The mean log s.e.$_m$ value (T) is –1.61, with a standard deviation of 0.23, based on 1424 specimens of extant species. This essentially provides a definition of a species. 1.61 is an approximation of the Golden Ratio. Pairs of hominid fossil crania can be compared using this approach, and assessed in terms of probabilities of conspecificity. For example, when Sts 5 ('Mrs Ples') and Sts 71 (also from Sterkfontein) are compared, a log s.e.$_m$ value of –1.538 is obtained. This is within the 95 % confidence limits of log sem values obtained for conspecific pairs of extant taxa. It is concluded that Sts 5 and Sts 71 are conspecific, contrary to the view expressed by R.J. Clarke. Similarly, when two specimens of *Lystrosaurus* are compared against each other (TM 18 and TM 20), a log sem value of –1.50 indicates a high probability of conspecificity although Brink (1982) thought that they were distinct species (*L. murrayi* and *L. declivis*). It is probable that both TM 18 and TM 20 can be attributed to *L. murrayi* since the latter nomen (described by Huxley in 1859) has precedence over *L. declivis.* (described by Owen in 1860). At least some specimens attributed to *L. murrayi* are probably females and at least some specimens attributed to the larger *L. declivis* are probably males of *L. murrayi* which is also recognized in India as a sexually dimorphic taxon (S. Ray 2005).

Bolt's Farm in the Cradle of Humankind

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The Bolt's Farm area includes about 20 sites. Some were excavated in 1947 and 1948 by members of the University of California African Expedition. These sites have yielded primates, sabre-tooth cats, pigs, bovids, equids and rodents. Since 2001, the HOPE team has surveyed the area and collected breccia from several sites on Bolt's Farm. Waypoint 160 is about 4.5 million years old. It is the oldest site in the Cradle of Humankind. It was discovered in 1996 by B. Senut, M. Pickford and J. Michaux. The breccia of Waypoint 160 contains a rich microfauna, including extinct rodents. The discovery of *Parapapio* at Waypoint 160 is of particular interest because this extinct primate has been found with hominids at other sites such as Lothagam in East Africa and Sterkfontein, Taung and Makapansgat in South Africa. As yet, Waypoint 160 has not yielded hominids, but it has great potential.

STYLE GUIDE FOR AUTHORS — REVISED 2009

GENERAL

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Submission of a manuscript for publication will be taken to indicate that the material is original and has not been submitted for publication elsewhere.

Authors wishing to reserve copyright to themselves should stipulate this at the time of submission of a manuscript.

PREPARATION AND SUBMISSION OF MANUSCRIPTS

Manuscripts

Manuscripts should be typewritten in English on one side of A4 size paper in double spacing throughout and with margins at least 25 mm wide all round. All pages must be numbered consecutively in the top margin (central), beginning with page 1 on the title page.

One hard copy of each manuscript plus illustrations and an electronic copy by e-mail and/or on CD are required by the Editor. The text should be composed in 'MS Word' or 'WordPerfect', or saved in 'Rich Text Format'). We are unable to accept files on disks formatted for MAC-OS.

Layout

Except in the case of short communications, manuscripts should normally be divided into appropriate conventional sections set out in the following order: title, abstract, introduction, body of text (subdivided as appropriate), acknowledgements, references.

Title

The title should be concise and should reflect the contents clearly. Names of new biological taxa proposed in the manuscript should not be included in the title. If the title is long a suitable abbreviated running title must be provided.

The title must be followed on a separate line by the authors' name/s and institutional address/es (the e-mail address of the first-named author should also be included if possible). In multi-authored contributions, the institutional address of each individual must be linked to the relevant name using superscript numbers.

Abstract

An informative abstract not exceeding 300 words must be provided.

Keywords

At least three keywords should be provided immediately after the abstract.

Introduction and main text

The manuscript should be divided as appropriate into conventional sections (e.g. Introduction, Materials and Methods, Results, Discussion, References, etc).

Acknowledgements

Authors should include only those acknowledgements that are truly warranted.

References

References are listed at the end of the manuscript, beginning on a new page. Under this heading, authors must list only published works that have been cited in the text.

Unpublished works, even those that are 'in press', must not be included unless full bibliographic details can be provided, including pagination. However, formal theses and dissertations, even though unpublished, may be listed provided full details are supplied; this must include reference to the institution where the master copy is lodged. Work that is 'in preparation' and 'personal communications' may be referred to in the text, but must not be included in the list of references.

The list of references must be arranged alphabetically, then chronologically, according to the layout of the examples below. Leave one blank line between each reference, and do not indent or otherwise format each entry. The layout sequence is:

(i) Author's name(s) and initials (in uppercase only). In the case of multi-authored manuscripts, successive authors' names should be separated by commas, with an ampersand (&) between the penultimate and last name;
(ii) Year of publication (not in brackets). If more than one paper by the same author is listed for the same year, successive entries must be designated by placing the letters a, b, c, etc., after the year of publication;
(iii) Full title of paper. Use capitals only for the first letter and for proper names. Generic and specific names must be italicized, unless such names themselves fall within an italicized title, in which case the names should be in regular (non-italic) script. If your equipment is unable to produce italics, please underline those words that should be italicized;
(iv) Full (*unabbreviated)* title of journal, book or other source, in italics. Book titles should be followed by the edition (if other than the first), the place of publication and the name of the publisher.
(v) Volume specification of journal: i.e. series (if applicable), volume number (in bold), part number (if any) in brackets, pagination (first and last page).

Examples of reference citations (to save space, the blank line between successive entries has been omitted):

ANDERSON, H.M. 1976. *A revision of the genus* Dicroidium *from the Molteno Formation.* Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.

ANDERSON, H.M. & ANDERSON, J.M. 1970. A preliminary review of the biostratigraphy of the uppermost Permian, Triassic and lowermost Jurassic of Gondwanaland. *Palaeontologia africana* **13**, 1–22.

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.

ROMER, A.S. 1966. *Vertebrate Palaeontology* (3rd edn). Chicago, University of Chicago Press.

ROMER, A.S. 1973. Permian reptiles. **In**: Hallam, A. (ed.), *Atlas of Palaeobiogeography,* 159–168. Amsterdam, Elsevier.

VAN DER MERWE, N.J., LEE-THORP, J.A., THACKERAY, J.F., HALL-MARTIN, A., KRUGER, F.J., COETZEE, H., BELL, R.H.V. & LINDEQUE, M. 1990. Source-area determination of elephant ivory by isotopic analysis. *Nature* **346**, 744–746.

Reference citations in the text should give the name of the author and the date on each occasion, and substitutes such as *op. cit., loc. cit.* should not be used, e.g. 'Smith & Jones (1943) suggested that ...', '... extinction rates (Smith & Jones 1972) and other factors ...'. In the text, successive references by the same author should be separated by commas, and those of different authors by semi-colons: (Brain 1990, 1991; Hughes 1961; Smith & Jones 1972).

Headings

Three orders of headings are used.
FIRST ORDER, printed in bold capitals and left-aligned.
Second order, printed in bold upper and lower case and left-aligned.
Third order, printed in upper and lower case italics and left-aligned.

Headed sections and paragraphs should not otherwise be numbered or lettered in the manuscript.

Tables

Tables must be set out on separate sheets, with their headings in lower case. They are numbered consecutively in arabic numerals. Please indicate the position of each table by appropriate pencil notation in the margin of the text.

When referring to Tables in the text the word 'Table' is spelt out in full and given a capital initial letter, e.g. Table 2.

Illustrations

All illustrations are termed Figures (the word is to be spelt out in full with a capital initial letter), and they are numbered consecutively with arabic numerals. Each illustration must bear in pencil on the reverse side the author's name, a key word(s) from the title, the figure number and the word 'top' in the appropriate position to indicate orientation.

Please mark the position of figures by pencil notation in the margin of the text. When referring to figures in the text the word is abbreviated with a capital initial letter, e.g. Fig. 23.

All artwork should be submitted as camera-ready originals. The use of computer-generated lettering (high-quality laser or ink-jet) or dry transfer lettering is preferred for labelling, and stencil or hand-lettering is to be avoided.

Drawings, maps and diagrams should be in black drawing ink on high quality tracing paper or good quality white card. If drawings are submitted on translucent draughting film, labels and other lettering should *not* be stuck onto the original. Instead they should be clearly written on a submitted photocopy of the original, showing their correct positions clearly, for typesetting by the printers. All illustrations should be designed for same-size printing or slight reduction (by no more than 1/3) in the final form. The maximum acceptable size for illustrations on the printed page is 245 × 175 mm. Tip-ins and fold-outs are not accepted except under very special circumstances, and generally any additional costs will be for the account of the author.

Photographs should be high quality glossy b/w prints of good contrast made from critically focused negatives, and similar constraints on size apply as in the case of drawings.

Good quality digital images in TIF and EPS format (at least 350 dpi for photographs and 1200 dpi for line drawings) may also be accepted. They may be submitted on PC-format disks or CD-ROM.

Scale should be represented by suitably labelled scale bars of appropriate size, with the units of measurement specified in the caption; avoid reference to magnification in captions.

Authors must submit the original of each figure plus two copies, which may be photocopies provided the quality is good and all details are clear.

Numerical data

The metric system (SI units) is to be used throughout for all numerical data. If there is good reason for using units other than metric, the SI metric equivalents must be given in brackets. Authors should familiarize themselves with the standard abbreviations of SI metric units; non-standard abbreviations are not acceptable.

ACCEPTANCE OF PAPERS

All manuscripts offered to the Editor are submitted to two or more referees for critical appraisal, and the substance of the referees' comments is forwarded to the author in the event that the manuscript is rejected or requires revision. The Editor will advise the author whether or not the manuscript is accepted for publication.

If the manuscript is accepted, one set of proofs (usually page proofs) will be submitted to the author for careful checking and these must be returned as soon as possible. The cost of any additions or major alterations to the text at proof stage may be charged to the author. Further proofs may be submitted to the author if the Editor considers it to be necessary or desirable, but at this stage any postal charges will be for the account of the author.