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PAPERS

Gondwanan Middle Triassic cynodonts from Namibia

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Recent fossil findings exposed an amazingly abundant record of mammal-like cynodonts in the Namibian Upper Omingonde Formation. A re-evaluation of these fossils has revealed a much greater diversity for this group in the Namibian Middle Triassic than was previously known. Besides fossils of *Cynognathus*, *Diademodon* and *Trirachodon*, the new findings include the presence of *Luangwa*, *Aleodon* and *Chiniquodon*. The traversodontid *Luangwa* is represented in the Omingonde fauna by at least four skulls and associated postcranial remains. An isolated skull attributed to *Aleodon* has alveoli for three upper incisors, lingually expanded postcanines and an elongated palate, typical of this cynodont. *Chiniquodon* is represented by a skull with articulated lower jaw and unprepared postcranial remains. The particular combination of features that characterize this taxon include sectorial postcanines having a backward recurved main cusp, long secondary palate, extremely elongated pterygoid processes and the zygoma with a suborbital angulation between the maxilla and jugal. The newly enhanced record of Namibian cynodonts positions the assemblage as one of the most diverse cynodont faunas from Gondwanaland, and as the primary connection between Middle Triassic faunas from Antarctica, South Africa, Tanzania, Zambia, Argentina and Brazil. Prior to this record, the range of *Aleodon* was restricted to the Manda Formation in Tanzania, while *Luangwa* was known from the Ntawere Formation in Zambia, and more recently also documented from the Brazilian Santa Maria Formation. *Chiniquodon* has been described from the Middle Triassic Santa Maria Formation of Brazil, and the Middle and Upper Triassic Chañares and Ischigualasto Formations from Argentina. The record of *Chiniquodon* in Omingonde represents the third strand of evidence of faunal commonality among cynodonts from South America and Africa. The other two taxa common to these continents, *Cynognathus* and *Luangwa*, are moreover also represented in the Namibian fauna. More significantly, the Namibian record of *Chiniquodon* is a remarkable biostratigraphic enigma inasmuch as this carnivorous cynodont, previously known only from South America, represents the first Ladinian-Carnian aged taxon discovered from Middle Triassic faunas of continental Africa. The

presence of *Chiniquodon* in the Omingonde Formation suggests a younger age for the Namibian fauna, which can thus extend to the earliest Ladinian. The possible Ladinian age for this fauna is of great consequence as terrestrial ecosystems with vertebrate fossils of this period are poorly known in Gondwana sequences. In fact, the record of Middle Triassic vertebrates in continental south-central Africa is generally considered to be restricted to the Anisian.

The Late Triassic Molteno as World Heritage

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South Africa is remarkably richly endowed with palaeontological superlatives – from the earliest bacteria to early man – that put South Africa clearly on the global map. The case for the Late Triassic Molteno Fm., within this context of overabundance, being put forward for World Heritage status is made. In the history of terrestrial life on Earth since the colonization of the continents by vascular plants around 430 million years ago in the Silurian, the Molteno stands out in sharp focus.

If the Cape Floristic Region is seen as the biodiversity centre of the flowering plants (angiosperms) at their heyday, so the Molteno Fm. represents the known biodiversity hotspot of the cone-bearing plants (gymnosperms) at their heyday. And in the overall history of terrestrial life, the gymnosperms stand out much more significantly than do the angiosperms: they dominated global vegetation for close on 200 million years (Early Permian to Middle Cretaceous) while the latter, derived from them, have dominated for only half that time (Mid-Cretaceous to the present). Seen from a different perspective, that of overall biodiversity at all ranks, species to classes, the gymnosperms appear also to have attained a far greater range of basic morphology than did the angiosperms. Even in their relict extant 'old age', the gymnosperms are recognized as falling into four classes, the conifers, cycads, ginkgos and gnetaleans; while 225 million years back in their Late Triassic heyday, they possibly spread across as many as 10 classes (the collections from 100 sites around the outcrop of the Molteno demonstrate this diversity far more comprehensively than elsewhere globally). The wonderfully rich angiosperms of our time, from grasses to baobabs, nearing a quarter million species worldwide, are recognized in contrast as falling within a single class.

The Molteno, then, as currently understood, represents the continental biodiversity hotspot through geological time. It was essentially in the prolific ecosystems best

known in the Molteno – at the peak of the Triassic Explosion of life following the end-Permian Extinction – that both the dinosaurs and the mammals evolved. It was at this time also that the familiar spectrum of insect orders of today came into being, and that the spectacular diversity of beetles first appears. The origin of the flowering plants is very likely rooted at this time. The Molteno is the clearest window we have onto the dawn of the extant world.

Looking towards the next generation of palaeontologists in South Africa, the Molteno offers tremendous opportunity. With an outcrop extending c. 400 km north–south and 200 km east–west as a distorted rectangle around the outskirts of Lesotho, the potential for further collecting is almost limitless. Already our collection of some 30 000 slabs from 100 ‘localities’ (close on half also include insects) is the most extensive (taphocoenoses) and intensive (specimens) that we are aware of from any formation internationally. The scope for ecological studies, for statistics relating to biodiversity, for comparative morphology, for palynology, for palaeoentomology is open-ended.

With the Department of Science and Technology, through their African Origins Platforms, looking to the future, seeking ways of promoting our science holistically and placing it even more firmly on the global canvas, the Molteno has much to offer. With UN Global Heritage recognition it would draw ample funding and offer countless opportunities to many.

An integrative approach to distinguishing the dicynodont species *Oudenodon bainii* and *Tropidostoma microtrema*

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The dicynodonts *Oudenodon bainii* and *Tropidostoma microtrema* are remarkably similar in most aspects of their cranial and postcranial morphology. The most obvious distinguishing feature is the presence of tusks and postcanine teeth in *T. microtrema* and their absence in *O. bainii*. However, some specimens of *T. microtrema* lack tusks or postcanine teeth, and others display intermediate conditions such as possessing an erupted tusk on only one side of the skull. This variability raises the question of whether *O. bainii* and *T. microtrema* truly are distinct species, or simply endpoints on a morphological continuum. Resolution of this uncertainty is necessary because both species play important roles in Upper Permian terrestrial biostratigraphy. Here we address the issue using several types of data.

Our results show that variability in most discrete characters of the skull preclude them from being completely diagnostic of either species. However, both a geometric morphometric analysis of snout shape and a traditional morphometric analysis of skull dimensions can reliably differentiate tuskless specimens from those with tusks

and/or postcanine teeth. The histology of several *T. microtrema* limb bones was also examined. The primary bone tissue consists of moderately vascularized fibro-lamellar bone, which becomes parallel-fibred with annuli and/or LAGs towards the periphery. A free medullary cavity is usually absent or if present, is very small. These bone tissue characteristics are notably similar to those of *O. bainii*.

Stratigraphic range data and patterns of phylogenetic relationship suggest that the two morphotypes are best regarded as distinct species, not sexual dimorphs or other variants. Because *O. bainii* specimens have been collected at *Tropidostoma* Assemblage Zone localities in the Karoo Basin of South Africa, the first appearance of *O. bainii* can no longer be used to define the base of the *Cistecephalus* Assemblage Zone and *Oudenodon*-based correlations with other basins should be made with caution.

Large mammal mass death accumulation in the Holocene of South Africa

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Heelbo 1 is a palaeontological and archaeological site on the farm Spion Kop, near the town of Senekal in the eastern Free State. The grass-covered landscape is characterized by scenic flat-topped mountains of Karoo Supergroup rocks, with small alluvial fans draping many of the hill foot slopes and grading downslope into the floodplains of local rivulets. These fans are in turn dissected by large ‘dongas’ (gullies), revealing successions of silt-rich and gravelly palaeosols which represent repeated cycles of donga erosion and fill.

A remarkably dense and well-preserved fossil bone bed, extending over an area 35 × 13 m², has been discovered within one of the ancient donga floors. The bone accumulation is overlain by about 1.5 m of sediment, but is exposed in the wall of a donga near the foot of a fan. Preliminary investigations show that most of the remains belong to the black wildebeest (*Connochaetes gnou*). Several examples of articulated vertebral series, as well as bones showing little damage caused by sub-aerial weathering, indicate rapid burial before decomposition of the soft tissue. There appears to be no distinct orientation in the long bones, which together with a paucity of transport-induced abrasion of the bones, suggests deposition under relatively low-energy conditions, with little or no secondary movement by water once decomposed. While the exposed fossils do not appear to record percussion- or cut-marks, the occurrence of Later Stone Age tools at and around the site bear testament to human activity in the area, and the possibility that people were the accumulators of the bones. Different scenarios are explored to explain the mode of death and accumulation of the fossil deposit.

Comments on the Late Permian cynodonts (Synapsida, Therapsida) from South Africa

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During the two first thirds of the twentieth century, a number of genera and species of Late Permian cynodonts were described in South Africa. Most of them were attributed to the family Procynosuchidae Broom, 1948, whereas a few tiny forms were grouped by Haughton & Brink (1954) in the family Silphedestidae. Later, it became obvious that the number of real taxa had been overestimated. Indeed, earlier authors had sometimes created new taxa on the basis of inadequate, fragmentary material; post-mortem distortion had not always been taken into consideration; little attention had been paid to the fact that specimens of various sizes could have represented ontogenetic stages of only one species (see Anderson 1968). Then, to the time of 'splitters' succeeded the time of 'lumpers', which brought a welcome clarification to the classification of early cynodonts. It may however be asked whether the lumping process did not go sometimes too far. Two examples are given below.

The procynosuchids of south africa. According to Hopson & Kitching (1972), all the procynosuchids from South Africa belong to the species *Procynosuchus delaharpeae*. However, if we compare the complete skull of an adult specimen of *P. delaharpeae* and the skull of the type specimen of *Procynosuchus rubidgei*, it appears that both skulls have snouts of the same length, whereas the skull of *P. rubidgei* is much shorter and much narrower than that of *P. delaharpeae*. In my opinion, the differences in skull proportions are too big to fall within the range of individual variation, and the two species should be retained as valid (Battail 1991).

The 'silphedestids'. A few tiny Late Permian cynodonts were in the past placed in the now forgotten family Silphedestidae, created by Haughton & Brink in 1954. All these small forms are considered by Hopson & Kitching (1972) as juvenile specimens of *P. delaharpeae*. A careful examination of the 'silphedestids' reveals, however, many differences between them and *Procynosuchus*, especially in the tooth structure. At present, as the available material is rare and poorly preserved, it would perhaps not be wise to revive the family Silphedestidae. Doubts can be raised, however, regarding the attribution of the 'silphedestid' specimens to the procynosuchids.

Conclusions. Early cynodonts from the Upper Permian of South Africa were, in my opinion, more diversified than currently thought. A better fossil record, especially of small forms, could perhaps strengthen this hypothesis.

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Early Triassic vertebrate recovery following the end-Permian extinction event in South Africa

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The end-Permian extinction is widely accepted to be the most devastating mass extinction event in Earth's history (Erwin 1994). Until recently, most research on this extinction event has focused on the marine record because few fully preserved terrestrial Permo-Triassic boundary sequences were recognized. The main Karoo Basin of South Africa is now known to preserve several non-marine Permo-Triassic boundary sequences, which have become the focus of intensive research into the nature of the extinction and its possible causes (e.g. Ward *et al.* 2000; Smith & Ward 2001; Retallack *et al.* 2003; Smith & Botha 2005; Botha & Smith, in press). Detailed logging of multiple sections through the boundary sequence at several Karoo Basin sites reveals an extinction level of 54% of latest Permian vertebrate species, followed by the onset of a relatively rapid recovery, within an estimated 40–50 thousand years (based on the calculation of floodplain aggradation rates and compaction ratios), which included the origination of at least 12 new vertebrate species during the earliest Triassic. The Early Triassic recovery fauna comprises eosuchians, small temnospondyls, small procolophonoids, medium-sized dicynodonts, small therocephalians and non-mammalian cynodonts. The facies interpretation and taphonomic data allow us to propose that pronounced climatic warming and increased seasonality and storminess at the onset of an unreliable, monsoonal rainfall regime contributed to the mass extinction of terrestrial vertebrates in southern Gondwana.

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New developments in a search for fossils of ancestral animals in Neoproterozoic limestones of Namibia

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In recent years, one of us (C.K.B.) has been involved in

a search for micro-invertebrate fossils in Namibian Neoproterozoic limestones, initially in the Nama Group, but more recently in the Otavi Group further to the north. Many samples of limestone from the Otavi-Tsumeb-Grootfontein area were examined in thin-section and as acetic acid-treated residues, but recrystallization of these limestones from the folded Otavi Mountainland appeared to mitigate against the finding of fossils of well-preserved soft-bodied organisms there. But, to the north, on the flat calcrete-covered plain of the Etosha basin, several limestone hills make their appearance, well away from the metamorphic folded belt. When C.K.B. examined residues of some of these carbonates, he found numerous sponge-like objects that proved to have been phosphatized (Brain *et al.* 2001). Detailed geological mapping of these outcrops had not been done, but it was clearly important to establish just where in the Group's stratigraphy the sequence was positioned. The outcrops were therefore examined in detail in the field by K-H.H., A.R.P. and C.K.B. and samples were taken at close intervals for carbon isotope analysis and interpretation by A.E.F. and A.R.P. When a preliminary description of these sponge-like fossils was circulated for comment by specialists in the field, a number of pertinent issues were raised that needed to be considered when interpreting microfossils of such antiquity. These issues have now been addressed and a formal description of *Otavia antiqua* will be submitted for publication soon.

In the interim, the stratigraphic range of *Otavia* has been extended from a variety of new localities, such that it now spans the entire interval between the first of the 'Snowball Earth' glacials, the Sturtian Chuos diamictite at 720 million years, to the Marinoan Ghaub one at 635 million. C.K.B. has also recently recognized similar fossils from a limestone in the Mara Formation of the Nama Group in southern Namibia, considerably more recent than those in the Otavi Group. And now, more unexpected and exciting than ever, he has, in May 2006, found *Otavia* fossils in a limestone of the Ombambo Subgroup of the Otavi Group, considerably older than the Sturtian glacial and perhaps 750 million years in age. Thus we now have evidence that the calcareous sponge lineage is far older than had been thought, although molecular evidence predicted that this would be the case. The detective story continues!

We wish to thank Conrad Brain for drawing our attention to this particular Ombambo limestone outcrop as a likely source of microfossils similar to those in Etosha.

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Vicariance in coastal large ungulate populations during the Middle and Late Pleistocene in southern Africa

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In southern Africa there is a clear distinction between

coastal and inland environments. The interior of southern Africa includes the Nama Karoo and Grassland Biomes. From a large ungulate point of view these biomes can be seen as one biogeographic entity in that they share an open habitat structure, which is reflected in the distribution patterns of ungulates such as grazing bovids and plains zebra. This faunal composition is not found in the coastal environments beyond the Cape Fold Mountains, because of the lack of suitable open habitat. The Cape coastal areas are generally inhabited by closed habitat forms and not by plains ungulates. However, a surprising aspect of the Middle and Late Pleistocene large ungulate faunas from the Cape coastal zone is the periodic presence of a faunal component that resembles the interior faunas of today. This can be explained by open plains habitat becoming available during glacials, when lowered sea levels exposed the continental margin to produce habitat suitable for plains-living ungulates. In this study the appearance of biogeographic uniqueness in glacial populations of black wildebeest from the Cape coastal zone is demonstrated. In black wildebeest (*Connochaetes gnou*), as in the case of springbok (*Antidorcas marsupialis*), there appears to have been a decrease in body size compared to contemporary inland populations. This reflects genetic drift due to the reproductive isolation of populations on the eustatically exposed continental margin to the south of the Cape Fold Mountains. These populations, the descendants, or daughter populations, of ancestors from the interior became extinct in the Cape coastal zone when sea levels returned to their present levels after the Last Glacial. The exception to this extinction event is the bontebok (*Damaliscus pygargus pygargus*), a vicariant form of the blesbok, which survived as a glacial relict in the southern Cape.

Palaeobiological implications of the bone microstructure of early mammals

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Here we report on the first histological studies of early mammals. We examined the bone microstructure of *Morganucodon* from the Jurassic Pant Fissures of Wales, and multituberculates and eutherians, from the Late Cretaceous of the Gobi Desert. Our studies have provided significant insight into the biology and growth patterns of these five early mammals. We show that the two eutherian taxa (*Zalambdalestes* and *Barunlestes*) grew relatively slowly with periodic pauses in growth indicated by the presence of rest lines, while the multituberculates (*Kryptobaatar* and *Nemegtbaatar*) and *Morganucodon* had a faster rate of bone formation that suggests an overall rapid growth rate that slowed down later in ontogeny. The bone microstructure of these early mammals is also compared with that of non-mammalian cynodonts and traversodontids, extant monotremes, and placentals. Our findings suggest differences in the growth rate between the

multituberculates and the Mesozoic eutherians, and moreover, both groups appear to have slower growth rates compared with modern monotremes and placentals.

An osteo-histological assessment of *Pterodaustro guiniazui*

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Pterodaustro guiniazui is a medium-sized, filter-feeding pterodactyloid recovered from the Lower Cretaceous laminated shales of the Lagarcito Formation of Central Argentina (Sierra de Las Quijadas, San Luis Province). It is represented by hundreds of individuals – wing spans ranging from 300 mm to 2.5 m. This unique ontogenetic sample of pterosaurs has permitted deductions regarding allometric changes during postnatal development and has made significant contribution to our understanding of the palaeobiology of *Pterodaustro*. Here, we report on the preliminary results of our bone microstructure studies of *Pterodaustro*. Our sample included material to assess histological variability in single skeletons, as well as histological variation within the taxon. We also studied growth series of specific skeletal elements of different sized individuals to assess changes in bone microstructure during ontogeny. Our preliminary results highlight the contribution of bone microstructure in interpreting the biology and growth of this ctenochasmatid pterodactyloid.

A 'nycteroleter' parareptile in the Permian of South Africa

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The fossil was found on the farm Blaaukranz, Prince Albert District, Eastern Cape Province, in the lower *Tapinocephalus* Assemblage Zone (Permian: Guadalupian) (Gow & Rubidge 1997). It consists of a relatively small partial postcranium, including an almost complete vertebral column, partial pelvic girdle and right hind limb. The specimen has parareptilian features and it has been regarded as the earliest global record of a procolophonoid (Gow & Rubidge 1997). The previous oldest record of a procolophonoid was represented by *Owenetta rubidgei*, from the *Cistecephalus* Assemblage Zone (Permian: Lopingian). A reappraisal of this specimen, however, indicates that it is probably not a procolophonoid. The ventral surfaces of the thoracic pleurocentra are deeply concave and lack the laterally 'pinched' anteroposterior ridge that is characteristic of the Procolophonoidea. The specimen is also considerably larger than *Owenetta* or any Permian to lowermost Triassic procolophonoid.

Nevertheless, the anatomy of this fossil is entirely compatible with the group of parareptiles known as 'nycteroleters'. Nycteroleters are small- to medium-sized parareptiles, being notable for displaying a suite of characters that combine procolophonoid and pareiasaurid features. They are recorded in the Upper Kazanian and Early Tatarian (Permian: Guadalupian) of the Russian Cis-Urals (Ivachnenko *et al.* 1997). Apart from *Macroleter poezicus* (Tsuji, in press), the group is poorly known and its members have not been recently reviewed, nor have they been the subject of phylogenetic studies. Most nycteroleters are smaller than the Karoo specimen, but the genus *Macroleter* is equivalent in size. *Macroleter* is known from several articulated skeletons from the Mezen Fauna in the Cis-Urals. The vertebrae of *Macroleter* are in fact indistinguishable from that of the Karoo specimen, except for the absence of intercentra in the latter. This feature, however, is likely an artifact of taphonomy. Despite of the similarities with the genus *Macroleter*, we refrain from identifying our specimen to the genus level at this time, owing to the incompleteness of our material.

The presence of a taxon closely related to *Macroleter* in the lower *Tapinocephalus* Assemblage Zone is stratigraphically consistent with the age of the Mezen fauna of Russia, where *Macroleter* is found. *Macroleter* has been recently reported for the Chickasha Formation in the U.S.A. (Reisz & Laurin 2001), and it was employed by these authors to claim a Guadalupian age for that formation. The South African nycteroleter expands the geographic range of these parareptiles to Gondwana, a fact not surprising when considering that the closely related procolophonoids and pareiasaurids also possess trans-Pangaean distributions.

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Searching for signal in the early actinopterygian record

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The Actinopterygii (ray-finned fishes) is the largest and most diverse group of vertebrates, but little is agreed about the timing and branching pattern of its early evolution. Recent estimates based on mitochondrial genomic data suggest that the major actinopterygian clades are much older than previous age estimates indicate, based on available fossil data. This presentation will report the results of a multi-authored project (Hurley *et al.*, in press), combining morphological (Recent and fossil) with nuclear genetic data, to re-assess the time-scale of actinopterygian phylogeny.

Analyses of all data demonstrate that the age of the Neopterygii radiation, including teleosts, *Lepisosteus*, and

Amia, has been underestimated by at least 40 myr. The previous incongruity between molecular and morphological date-estimates was largely the result of missing and misinterpreted fossil data. Morphologically advanced stem-group neopterygians are present by the latest Lower Carboniferous, and the earliest crown-group example dates from the Early Permian.

These results imply that the early radiation of ray-finned fishes is under-determined, that groups associated with Mesozoic faunas have Palaeozoic roots, and that Upper Carboniferous and Permian collections of actinopterygians need to be re-examined for overlooked examples of early neopterygians. Finally, the results of this project allow reconciliation between Palaeozoic date estimates for the actinopterygian whole genome duplication event, and the hypothesis that this round of gene-duplication was specific to teleosts. However, there is no clear evidence that this event is tied to extinction event survivorship, or sudden episodes of morphological innovation.

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Stable isotopes and palaeodiet: beyond the confines of C₃/C₄ barriers

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Ever since the discovery that the ¹³C/¹²C ratio of C₃ and C₄ photosynthesizing plants are consistently distinct, and that this distinction persists in the body tissues of animals feeding on these plants, stable carbon isotope ecology has been increasingly applied to study the diets of modern and fossil fauna. Linear mixing models allow researchers to quantify dietary inputs of C₃ (browse) and C₄ (grass) biomass in savanna herbivores from carbon isotope data. However, linear models cannot resolve diet beyond C₃/C₄ consumption, because resolution of more than two food sources from carbon isotope data alone yields more mathematical unknowns than equations. Dual-isotope mixing models based on combined evidence from more than one element, e.g. ¹³C/¹²C and ¹⁵N/¹⁴N ratios, can be used to resolve multiple source inputs into diet, but these have seldom been applied to mammal diet studies because mammalian ¹⁵N/¹⁴N ratios are influenced by numerous non-dietary parameters such as climate, protein uptake, ecophysiological adaptation, and water and nutritional stress. Thus, isotope-based diet studies have been limited largely to environments in which C₄ grasses predominate.

Here, I employ a novel approach using a multiple regression model to identify and control for non-dietary sources of variation on ¹⁵N-abundances in faeces of 19 ungulate species. Results are based on vegetation and faeces collected over three years across multiple spatial and seasonal scales from the Kruger National Park. I demonstrate that, after controlling for the effects of protein uptake, ecophysiology, and climate, ¹⁵N/¹⁴N and ¹³C/¹²C data from herbivore faeces lie within the distribu-

tion of available food sources when plotted as a mixing polygon in isotope space. I use a dual-isotope multiple-source mixing model (Isosource; Phillips and Gregg 2003) to resolve dietary inputs of multiple C₃ (foliage, fruit, reeds and sedges) and C₄ (NAD/PCK and NADP grass sub-types) food groups. Results show high consistency with expectations based on data derived from field observations. In addition, I demonstrate similar reliability for reconstruction of complex diets in mammalian carnivores. I propose that similar approaches can be applied to body tissues to resolve diet in palaeoecological settings, for specimens with intact biological proteins (up to ~10 000 years). Future studies of proxies less susceptible to diagenetic alteration, such as ¹⁸O/¹⁶O data, may also allow for improved dietary reconstructions of diet in deep time, even in pre-Miocene palaeoenvironments predating the origins of C₄ photosynthesis.

Phillips, D.L. & Gregg, J.W. 2003. *Oecologia*. **136**: 261–269.

The Devonian, Famennian, Witpoort Formation (Witteberg group) fauna of Grahamstown

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During the Devonian, plants evolved from small simple forms to a wide range of taxa, many the size of trees. With the exception of the angiosperms, all major divisions of the plant kingdom had evolved by the end of the period. Fish reached their broadest ordinal diversity during the Devonian as many ancient orders co-existed with emergent new ones.

At the Late Devonian Frasnian-Famennian boundary plants experienced a major extinction event, possibly precipitated by the movement of Gondwana into the Antarctic region – its consequent glaciation lowering global temperatures and sea levels. Alternately, lowered global temperatures may have resulted from reduced atmospheric CO₂ levels, resulting from the rapid spread of *Archaeopteris* forests during the Frasnian. This would have increased levels of fixed C entering drainage systems, perhaps accounting for the common precipitation of C-rich anaerobic sediments during the Famennian. A number of minor extinction events during the Famennian, culminated in a major extinction of marine organisms at the end. This resulted from widespread marine regression, or perhaps was triggered by the rapid spread of seed-bearing plants into relatively dry habitats.

The Bokkeveld Group contains a well-studied record of coastal marine invertebrate communities, as well as a small number of Early and Middle Devonian fish. Until recently, however, the Late Devonian rocks of the lower Witteberg Group had yielded very little record of life. Apart from the presence of '*Spirophyton*' trace fossils, and *Leptophloem australe* lycopod stem impressions, a few taxa had been erected on the basis of sparse plant fragments from a black shale of the (Upper Devonian, Famennian) Witpoort Formation at Howiesons Poort near Grahams-

town. The exposure of rich fossil-bearing Witpoort Formation black shale during roadworks at Waterloo Farm south of Grahamstown in 1985, however, opened a southern African window into the latest Devonian. The shale is interpreted as having been deposited as anaerobic mud in a palaeolagoon, on the protected side of a series of barrier islands and beaches cut by tidal inlets.

In addition to plant material similar to that from Howiesons Poort, but generally more complete, the new site provided a wealth of formally unrecorded algal and plant taxa, as well as fish and arthropod remains. A large sample of this material was collected during an excavation carried out at the locality between 1993 and 1995. Based on this material a number of phaeophyte and charophyte taxa, as well as a new species of progymnosperm, were formally diagnosed, and a large diversity of plant and algal material was recorded. Three species of placoderm fish were described, the antiarch *Bothriolepis africana*, in addition to two arthrodire placoderm species, *Groenlandaspis riniensis* and *Africanaspis doryssa*. A chondrichthyan specimen was described as *Plesioselachus macracanthus*. A large number of other fish fragments were tentatively identified as gyraacanthid acanthodian spines, small actinistian body impressions, elements of a large rhipidistian and a dipnoan, possible actinopterygian scales, isolated ptyctodontid placoderm plates and a range of problematic fragments. Remains of an unidentified eurypterid were also noted. These faunal elements could not be described due to the incomplete nature of the specimens available. Continued road works at Waterloo Farm have, however, allowed much new material to be collected. A large sample of shale has also been set aside for ongoing investigation. New material includes more complete specimens of recorded taxa, as well as remains of formally unrepresented species, including, Agnatha, Placodermi, Acanthodii, Chondrichthyes, Actinopterygii, and Arthropoda. Description of the new material will give unprecedented opportunities for biogeographic and biostratigraphic analyses, the Waterloo farm locality being the only one known in western Gondwana with a well represented fauna and flora from this important time period.

Two dicynodont postcranial morphotypes from the *Cynognathus* Assemblage Zone (subzone B) of South Africa and their taxonomic implications

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Kannemeyeria simocephalus is probably the best known Middle Triassic dicynodont from South Africa and has been the standard against which other Triassic dicynodonts are compared. In the past, studies have concentrated on the cranial morphology of *K. simocephalus* and how this affected Triassic dicynodont taxonomy and phylogeny. There has been little work on the postcranial anatomy of *K. simocephalus*, which remains poorly understood. A detailed descriptive analysis of the postcranial anatomy of

K. simocephalus has led to the identification of diagnostic characters of the postcranial skeleton. During the course of the analysis of the postcranial anatomy of *K. simocephalus* it was noted that material previously assigned to this taxon was significantly different from that recognized as *K. simocephalus*. Unfortunately, this material consists only of postcranial material and it is therefore referred to as Morphotype B rather than a new species of *Kannemeyeria* or as a new taxon from the *Cynognathus* Assemblage Zone (subzone B). A phylogenetic analysis was performed which included *K. simocephalus* and Morphotype B, and used cranial and postcranial characters. The preliminary phylogenetic results show that there are possibly two taxa of medium to large dicynodonts in the *Cynognathus* Assemblage Zone (subzone B); one a kannemeyeriid and the second a stahleckeriid. It has also become evident that more attention needs to be paid to the study of the postcranial anatomy of Triassic dicynodonts, especially those from Africa and Asia.

Why are species not all asexual? A simulation approach to an old problem in population biology.

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The two-fold advantage in growth rate of genetically similar populations of asexual and sexual populations should result in the sexual population rapidly going extinct if the two populations coexist sympatrically at a constant carrying capacity for the species, yet this seldom seems to occur in practice.

Populations of asexual and sexual individuals of defined genetic composition were generated in a computer program (ASPIC – Asexual and Sexual Populations In Competition). Mutations at diploid loci were generated at a defined rate. Other variables included population sizes, values of selection and dominance coefficients, and percentage of mutations that were advantageous. The two groups were allowed to evolve separately for a variable number of generations before being mixed in a single competing population, when one or other population would invariably become extinct. Neutral loci were an optional inclusion to monitor genetic diversity. The probability of an individual being able to breed was made a function of the average fitness across all loci under selection. By performing multiple iterations, accurate measures of extinction rates could be recorded under each set of conditions.

Results showed that the number of generations before mixing, mutation rate, percentage of advantageous mutations, value of selection coefficient, and value of dominance coefficient (expressivity) all affected the probability of one or other group going extinct. The key finding was that the sexual population would succeed only when the accumulation of mutations during separate evolution caused the ratio of sexual to asexual fitness levels to exceed 2, and has the general implication that provided the two

groups are not constrained geographically, or that niches are available which delay mixing, then an emergent asexual population, with its faster declining fitness, will not drive its sexual competitors to extinction.

New insights into therocephalian phylogeny (Amniota: Therapsida): a comparison of stratigraphy-free and stratocladistic methods

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Therocephalians constitute a diverse group of 'mammal-like' therapsids whose evolutionary radiation paralleled that of their sister taxon (cynodonts) in many respects. Within the Therocephalia, at least six major clades are currently recognized: Lycosuchidae, Scylacosauridae, Akidnognathidae (=Euchambersiidae), Hofmeyriidae, Whaitsiidae, and Baurioidea. Past systematic investigations have highlighted temporal trends in therocephalian evolution, emphasizing character evolution in the dentition and especially the secondary palate, yet high levels of homoplasy and inadequate descriptions in the literature have raised doubt over their higher-level relationships. Since previous systematic studies have failed to produce robust cladistic hypotheses, these investigations have lacked a well resolved phylogenetic context.

The phylogenetic relationships of therocephalian therapsids were studied based on a preliminary re-examination of poorly described holotypes and new specimens and utilizing multiple methods of computer-assisted phylogenetic analysis. Two key methods, traditional morphology-based cladistics and stratocladistics, were employed and the robustness of the phylogenetic hypotheses was tested against the stratigraphic record. The resulting tree topologies generally agreed on the monophyly and relative positions of the well-known clades, differing only in their placement of Akidnognathidae. Cladistic results placed Akidnognathidae at the base of Eutherocephalia, while stratocladistic results placed the group as the sister taxon to Hofmeyriidae + Whaitsiidae, supporting a monophyletic 'Whaitsioidea.' Results of the stratigraphy-free cladistic analysis showed relatively low statistical support due to high levels of homoplasy in Therocephalia. Furthermore, the stratocladistic trees appeared to be only slightly less optimal than cladistic trees with respect to morphology, yet are considerably more optimal with respect to the stratigraphic data. The consensus tree topology derived from the stratocladistic analysis is favoured because (1) the method can recruit operational taxonomic units (OTUs) that lack conspicuous autapomorphies as potential ancestors (whether direct or indirect); (2) the results generally show a higher level of stratigraphic congruence with less stratigraphic debt (whether or not the divergence models demonstrate budding cladogenesis or bifurcation); and (3) as a consequence, the method further minimizes the required

duration of ghost lineages to explain divergence times between closely related OTUs in possible instances of budding cladogenesis (since the divergence time for the descendant taxon need not be equal to the earliest stratigraphic appearance of the ancestral taxon). A systematic re-evaluation of basal akidnognathids, hofmeyriids, and enigmatic Eastern European whaitsiids is suggested in order to further test and refine the phylogenetic hypotheses offered here.

Cranial mechanics of Dicynodontia using Finite Element Analysis and quantitative histology

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Dicynodonts were a diverse group of herbivorous non-mammalian therapsids known predominantly from the Permo-Triassic of South Africa and Russia. Unlike most dicynodont genera, *Lystrosaurus* crossed the Permo-Triassic extinction boundary, possibly due to its ability to exploit more resistant vegetation (King & Jenkins 1997). Although dicynodonts had a highly derived masticatory apparatus that allowed propaliny, it has been hypothesized that *Lystrosaurus* utilized more orthal jaw movements to crush tough vegetation. Several cranial specializations of *Lystrosaurus*, such as a patent premaxilla-nasal suture and a posteriorly deepened skull, may have increased the efficiency of its masticatory system relative to purely Permian dicynodonts such as *Oudenodon*.

This study quantitatively examines the biomechanical significance of cranial form of *Lystrosaurus* and *Oudenodon*, a generalized dicynodont, using Finite Element Analysis (FEA) and bone histology. FEA is a computational analysis that assesses the mechanical behavior of complex structures, thus it can be used to test whether the skull of *Lystrosaurus* was capable of withstanding high cranial stresses associated with the mastication of tougher vegetation. The concomitant histological analysis involved thin-sectioning of cranial bone at homologous points. Several features that may correlate with function will be quantified including: 1) density, size, and shape of secondary osteons; 2) orientation of channels in the bone; and 3) thickness of cortical bone.

In order to accurately model the distribution and magnitude of masticatory stresses in *Oudenodon* and *Lystrosaurus*, a three-dimensional skull model was created from CT data. Two bite directions were modelled: 1) a vertical and dorsally directed bite at the premaxilla-maxilla sutural junction to simulate the beak bite and 2) a horizontal and anteriorly directed bite at the palatine to represent shredding during propaliny. An average bite force was calculated by integrating adductor and temporal fossa dimensions and previous jaw muscle reconstructions. For the orthal biting model, the preliminary FEA

indicates that overall higher peak compressive stresses accumulate in the *Oudenodon* skull, suggesting that the *Lystrosaurus* skull could withstand higher compressive stresses; whereas the horizontal biting model suggests the opposite. Tensile stresses in *Oudenodon* and *Lystrosaurus* accumulated in the pterygoid-palatal region in both the orthal and horizontal biting models.

The preliminary FEA suggests that the *Lystrosaurus* skull could withstand higher stresses during a vertical bite, thus supporting the hypothesis that it was capable of a more powerful vertical bite necessary for feeding on resistant vegetation. Results of the histological analysis will be compared with the biomechanical results of FEA, thereby validating the results of this computational analysis.

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A double tusked dicynodont and its biostratigraphic significance

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As part of an ongoing project to determine the stratigraphic ranges of fossil taxa in the lowermost Beaufort Group in South Africa, the well-preserved skull and lower jaw of a small dicynodont with postcanine teeth was collected from the Abrahamskraal Formation north of Prince Albert Road. The specimen was found 1062 m above the Ecca-Beaufort contact and 498 m above the first maroon mudrocks of the Beaufort group.

The presence of large, laterally flared pterygoid processes, postcanine teeth that lie lateral to the lower jaw and laterally located post-temporal fossae allow the specimen to be identified as the most primitive dicynodont known. A remarkable feature is the presence of a double canine on the left side of the skull. While replacement canine teeth are well documented for theriodonts, a double canine on one side of the skull has been recorded in only three dicynodont specimens, despite the fact that dicynodonts comprise by far the largest proportion of therapsids which are known from the Beaufort Group. Apart from the specimen of reported here, the other two dicynodont specimens are and a specimen with affinity to . Explanations offered for the double tusked condition include tooth replacement, pathology and intraspecific variation. Examination of specimens of and suggest that the roots of their tusks are open-ended, and therefore, tusks presumably grew throughout the animals' lives. This suggests that the double tusk condition is pathological rather than representing canine replacement.

The distribution of is restricted to the southwestern part of the basin between the towns of Rietbron and Laingsburg, and so far all specimens have been found below the lowest maroon mudrocks of the Beaufort Group. This specimen is thus the first from above the lowest maroon mudrocks and occurs higher in the stratigraphy than any other yet

collected. Although the position of the lowest maroon mudrocks varies from place to place in the basin, they are possibly significant as indicators of environmental change, such as increasing subaerial exposure of sediments. The occurrence of Assemblage Zone fossils higher in the stratigraphic succession in the area around Prince Albert Road may have implications for Karoo basin development models.

A palaeobiological hypothesis for the origin of the Therapsida

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The replacement of the basal synapsid pelycosaur by the more 'mammal-like' therapsids in the Permian was an important event in the history of tetrapods because it involved changes in many characters, and effectively initiated the eventual transition to the mammals. It is also an example of taxon-replacement in the fossil record that is potentially amenable to explanation, based on a combination of analysis of the biological significance of the inferred character changes with the stratigraphic, palaeogeographic, and palaeoecological circumstances of the time. An hypothesis is presented in which the origin of the therapsids resulted from a correlated progression of character evolution leading to higher levels of metabolic activity and homeostatic regulation of the body. It was a response to the availability of a seasonally arid, savanna-like biome. The subsequent explosive radiation of therapsids was associated with the ecological opportunity for habitat expansion made possible by the Mid-Permian development of geographical continuity between that biome and temperate biomes. The final extinction of the few pelycosaur that lingered into the mid-Permian was probably a case of incumbent replacement by the new therapsid lineages.

Distribution of Tubulidentata species and their relationships with early hominids

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Currently, a single extant species represents the order Tubulidentata: *Orycteropus afer*, the armadillo. This mammal is very important in African ecology as many animals use the armadillo's deserted burrows. The occurrence of certain species even depends on the presence of the armadillo. They are also closely associated with modern humans in Africa. All over the continent, tribes are known to hunt the animal, consider it as a divinity, represent it in their art, use parts of its body as charms, or follow it when foraging termites. Plio-Pleistocene hominids also added termites to their diet. The study of the distribution of fossil armadillos with respect to early hominids is thus of great interest.

The extant aardvark is restricted to sub-Saharan Africa but the fossil record extends this distribution. The oldest unquestionable Tubulidentata come from the early Miocene of Kenya.

Slightly younger specimens have also been found in Namibia. By the late Miocene, Tubulidentata are found in central, eastern and southern Africa. Moreover, within the last seven million years in Africa, the co-occurrence of aardvarks and early hominids at many important sites (for example at Aramis, Koobi-Fora, Laetoli, Lukeino, Makapansgat, Olduvai, Swartkrans, and Toros-Menalla in Chad) is striking.

According to the fossil record, the first aardvarks reached Eurasia during the early middle Miocene. From the late Miocene to the early Pliocene, their European distribution spans Pakistan, Iran, Turkey, Greece, Italy, and France. The distribution of Tubulidentata has been restricted to Africa since the Plio-Pleistocene. Noticeably, within the same period, *H. erectus* dispersed out of Africa in regions that were more temperate and seasonal than eastern and southern Africa. At Swartkrans, Olduvai and East Turkana, *H. erectus* have been found in association with fossil aardvarks. Obviously, the dispersal pattern of those early hominids and the aardvarks deviated during this crucial period. It is important to try to understand the reasons for this divergence, as they might be linked to local environmental changes that did not affect both taxa to the same extent.

The Ecce–Beaufort contact in the Eastern Cape Province – reappraisal of litho- and biostratigraphy

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In contrast to the situation in the southern and western parts of the Karoo Basin, relatively little lithostratigraphic and biostratigraphic research has been performed on the Ecce–Beaufort contact in the south-eastern Karoo Basin. Thus the Ecce–Beaufort contact in this area has remained problematic. The Ecce–Beaufort contact in the southern and western Karoo Basin occurs between the Koonap/Abrahamskraal Formation (lower Beaufort) and the Waterford Formation (upper Ecce) (Johnson 1976; Rubidge 1988). The Koonap/Abrahamskraal Formation comprises fluvial facies and represents deposition in a subaerial lower delta plain environment. The Waterford Formation represents deposition in a subaqueous delta front environment and contains five unique facies (Facies A–E) (Rubidge 1988). Beneath the Waterford Formation lies the Fort Brown Formation that was deposited in a prodeltaic environment. Currently the Waterford formation is considered to be absent in the southeastern Karoo Basin and the Ecce–Beaufort contact in this area is mapped between the Koonap (subaerial fluvial) and Fort Brown (prodelta) Formation, an interpretation that is problematic.

Fieldwork conducted over the past three years has

shown that the five distinct lithofacies of the Waterford Formation do indeed occur in the southeastern Karoo Basin, albeit that this Formation is substantially thinner (65–202 m) than in the areas further west. The Ecce–Beaufort contact in this area thus occurs between the Koonap and Waterford formations and stratigraphically conforms to the situation in the rest of the southern Karoo Basin. The presence of dinocephalians and *Eumotosaurus* in the middle Koonap Formation indicates that the *Tapinocephalus* Assemblage Zone is present. This biostratigraphic interpretation supports the diachronous nature of the Ecce–Beaufort contact as previous workers have suggested (Welman *et al.* 2001).

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The palaeoecological and evolutionary implications of the micromammals from Langebaanweg (Mio-Pliocene, South Africa)

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The Mio-Pliocene site of Langebaanweg (LBW) represents one of the largest collections of Mio-Pliocene fossils in Africa, and contains an extremely rich and diverse range of over 230 vertebrate and invertebrate taxa. LBW is unique not only because of the richness of the fossil deposits, but because it is the only site in the Western Cape Province representing the Mio-Pliocene, a slice of time when modern micromammal genera were emerging. LBW is therefore a crucial site for our understanding of the evolution and dispersion of modern rodent taxa from southern Africa. Fossil micromammal (murid, chrysochlorid, macroselid and soricid) accumulations are frequently used in palaeoclimatic and palaeoecological research as micromammals are effective environmental indicators – they do not migrate long distances, they have small home ranges, and in many cases, they have precise ecological requirements. Micromammals were recovered from the two main fossil-bearing members of the Varswater Formation, that is the Langeberg Quartzose Sand Member (LQSM), and the Muishondfontein Pelletal Phosphate Member (MPPM).

The relationship between the LQSM and MPPM is complex and not very clearly understood, but the LQSM generally underlies the MPPM, and is thought to be the older member. Several of the large ungulate species in the MPPM show enamel hyperplasia on molars, and it has been postulated that the environment was becoming drier, and rainfall more unpredictable, at the time that the MPPM sediments were deposited. With this in view, the palaeoecological implications of the micromammal populations of the LQSM and MPPM are discussed. The micromammal population at LBW is placed within the context of other southern and East African fossil sites.

A new genus of the cockroach family Umenocoleidea from Cretaceous deposits at Orapa, Botswana

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The Cretaceous kimberlite deposits from Orapa, Botswana have revealed a diverse assemblage of fossil plants and insects. Many of the insects show a similarity to modern forms. However, the deposit also includes extinct Cretaceous forms. One of these is the archaic cockroach family Umenocoleidea, a group of cockroaches distinguished from modern forms by a pair of sclerotized tegmina and a short ovipositor. The umenocolids are known from the Early Cretaceous of Siberia, China, Brazil and Lebanon, as well as the Late Cretaceous of New Jersey. The Orapa forms, which probably represent two species, are unique, not only amongst umenocolids, but also in the insect world because they have tiny reduced tegmina with a similar pitted pattern to that of a golf ball. The only other insects with similarly reduced and pitted tegmina are the earwigs (Dermaptera) and staphylinid beetles (Coleoptera). The presence of the Umenocoleidea from Orapa confirms the Cretaceous age of the deposits and suggests that many more intriguing archaic forms remain to be discovered in the collections.

Palaeontology and evolutionary thought in South African schools: providing a fresh context to promote palaeontology and launch a new network of museums – the Kitching Fossil Gallery, the Wits Origins Centre and the Kitching Fossil Exploration Centre

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Although South Africa's school curriculum has been changing since 1998, the first matriculants that are wholly steeped in the new system will only graduate in 2008. Senior school teachers are, therefore, presently facing the serious challenge of preparing their students for an unknown examination, with some completely new subject and skills areas. New subject areas in the Grade 12 Biology curriculum include 'fundamental aspects of fossil studies', 'cradle of mankind – South Africa', and 'popular theories of mass-extinction'. In addition, teachers are also expected to cover the basics of evolutionary theory with their students.

These developments suggest that there is a strong new role for palaeontological museums to support life science teachers as they grapple with the new topics in the curriculum. Museums provide a venue that schools can visit to see real fossils and allow teachers and learners access to the actual evidence for evolution, including 'extinction', 'macro evolution', 'missing links' and 'living fossils'.

This revival of interest in palaeontology will also

provide renewed demand for palaeontology museums. This is good news for established museums and suggests a role for new initiatives. Two interconnected initiatives are described here. The first is the Kitching Fossil Exploration Centre (KFEC), an initiative of the Albany Museum, Bernard Price Institute of Palaeontology, the Owl House Foundation, the Department of Science and Technology and a Private Donor. Essentially, the KFEC, located at Nieu Bethesda, consists of a small exhibition centre and fossil trail in the Gats River bed. The exhibition, which utilises specially adapted displays from a number of institutions, draws attention to the incredible diversity of fossils in the area, the nearby Permo-Triassic extinction boundary, and James Kitching who grew up in Nieu Bethesda. Five guides from Nieu Bethesda have been trained and are available seven days a week to take tours.

The second initiative is the Origins Centre at the University of the Witwatersrand. Phase one of this project is devoted to Rock Art and was opened at the beginning of this year. Phase 2 will be devoted to palaeontology and should achieve fruition in two years' time. However, the education outreach programmes of the rock art museum and the School of Geosciences are already merging to make maximum use of the Wits university facilities.

It is hoped these initiatives, which draw on the resources of the public, private and tertiary education sectors, will make a significant and sustainable impact on Palaeontology Outreach in South Africa.

Taphonomy of the fauna from the Plover's Lake cave flowstone bounded unit

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Recent excavations at Plover's Lake cave, a site located in the Cradle of Humankind World Heritage area, South Africa, have yielded rich archaeological and palaeontological assemblages from a flowstone-bounded stratigraphic horizon dated by Uranium series and Electron Spin Resonance to between 62 000 and 88 000 years ago. This cave represents one of the few inland Middle Stone Age (MSA) sites in Sub-Saharan Africa, and the studied horizon contains human remains bearing possible cut- and impact-like marks, suggesting that perior postmortem treatment of the human body took place at the site. Analysis of the associated fauna, numbering 874 pieces, was conducted to identify the agent of accumulation and substantiate arguments in favour of cannibalism. This was done by comparing and quantifying the modifications recorded on the human and non-human fossils. Microscopic examination of the fauna from this layer revealed no diagnostic cut marks, relatively few traces made by carnivores in the form of tooth scores and pits, and an abundance of marks made by rodents. Some of these marks bear features identifying porcupines as the agent of modification and probably accumulation, while others are attributed to smaller unidentified rodents. A number of tiny star-like traces were noted, reminiscent of

those observed on the Plio-Pleistocene-aged fauna from Laetoli, interpreted by different authors as insect damage, caused by ant and termite gnawing. In sum our results show little, if any, involvement of humans in the modification of the faunal remains from the flowstone bounded unit, thus providing no evidence for an interpretation of the modifications recorded on the human remains as the result of cannibalism. It is widely accepted that such an interpretation requires identifying the same treatment of human and non-human remains from the same deposit.

Sedimentological perspectives on a unique Upper Elliot fossil locality in the northeastern Free State

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For a long time the vertebrate fossil fauna of the Late Triassic to Early Jurassic Elliot Formation has received comparatively little research attention in Karoo palaeontological studies. This has resulted in an unsatisfactory knowledge of the taxonomic composition of this important interval spanning the Triassic-Jurassic boundary. The two biozones currently recognized within the Elliot Formation, the '*Euskelosaurus*' Range Zone (equated with the lower Elliot Formation) and *Massospondylus* Range Zone (equated with the upper Elliot Formation), are characterized by relatively depauperate vertebrate faunas, generally represented by isolated fossils, with rare complete or semi-complete skeletal remains.

Given this situation, research conducted on the farm Spioen Kop (Senekal district, northeastern Free State) over the last three years represents a very important contribution to this palaeontological dataset. At this locality the entire Elliot Formation is exposed on the slopes of a series of low hills, and over the last decade numerous fossils have been discovered from these rocks. Several field crews have visited this locality during the study period to excavate dinosaur fossils, with the primary focus on two partially complete skeletons from the upper Elliot Formation (or *Massospondylus* Range Zone). Early results indicate that these specimens are significant not only for representing as yet undescribed dinosaur taxa, but also for the semi-complete nature of the skeletons and excellent surface preservation exhibited by individual bones.

In order to ascertain the local palaeo-environment of the fossil-bearing rocks, we undertook a detailed sedimentological and taphonomic investigation of the site. Fossil material from upper Elliot Formation is largely confined to the red siltstones of the Elliot Formation, but detailed facies analysis has shown that they are often found at the base of muddy channel fills. Both arenaceous and argillaceous channels deposits are more common in the study area than expected, raising the possibility that the locality may have served as a channel locus area. At this stage research is continuing to determine whether the

presence of well-preserved fossils should be attributed to collecting and preservational agents only, or whether unusual local palaeo-environmental conditions also played a role.

Analysis and application of Beaufort Group data

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For more than a century large collections of fossils have been built up at various museums in South Africa. With the cooperation of all the South African museums that house collections of Karoo fossils, a single standardized database has been put together for the fossils collected from the Beaufort Group.

The incorporation of the datasets from the various museums required rigorous standardization, quality testing and manipulation. In particular, locality information had to be entered onto the database so that it would be useful for qualitative evaluation. This unique dataset now, for the first time, provides a record of fossil vertebrate continental biodiversity from the Middle Permian to Middle Triassic, and provides accurate numbers of specimens of the various taxa that have been collected.

The methodology used to set up this database will be presented and analysed, and preliminary findings on Permian-Triassic biodiversity and palaeontological patterns will be addressed.

Preliminary report on restoring identity to mummified human remains from South Africa: uncovering hidden information

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The majority of ancient human remains reported in the literature are skeletonized, leaving only the bone available for observation. Mummified remains in southern Africa are rare and potentially contain a wealth of information on such diverse topics as sex, stature, genetic affiliation, palaeo-diet, mobility patterns, pathology, ancient disease, cultural practices and processes of decomposition.

In the 1930's the remains of a single mummified individual were donated to the Transvaal Museum and subsequently relocated to the National Cultural History Museum (NCHM) in Pretoria. In the past, the remains were displayed with cultural artefacts; however, their association as well as provenance data were not clearly recorded in the early museum catalogues.

Multi-disciplinary techniques and collaborative work using for example, anthropometrics, entomology, geology, botany, ethnography, stable light isotopes, genealogy and DNA, are being applied in the study in order to recover the context and cultural affinity of the remains, as well as pathology, disease and reasons for preservation. The likely area of origin of the remains has been established as spanning from the Rustenburg area north of Pretoria to

the Bronkhorstspuit area east of Pretoria. The remains are of those of a woman in her early twenties from the Iron Age. Results of the research to date are presented.

Current research into uranium–lead dating of Sterkfontein Cave, South Africa

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The absolute dating of the South African hominid-bearing caves is an outstanding issue in palaeoanthropology. Without an extensive and precise chronostratigraphic framework, the South African hominid-bearing deposits can only be compared in broad terms to the deposits found elsewhere in Africa. Recent advances in the understanding of global climate shifts during the last ~5 Ma and how these changes are reflected in the climate of Africa, have revealed that climate may have played an important role in the emergence and evolution of hominids. Quite how and why changing climates affect landscape and organism evolution is an ongoing debate, one in which a secure chronology is essential. Recent advances in isotopic dating techniques have provided new opportunities to date the South African caves by cosmogenic isotopes of ¹⁰Be–¹⁶Al on quartz in breccias (Partridge *et al.* 2003) and the radiogenic decay of U to Pb in speleothem layers (Walker 2005).

U–Pb dating is not a simple task; problems with contamination of common lead persist and ages have to be calculated using isochrons, increasing the number of measurements needed to produce an age. We have adapted the method used in the pioneering work of Walker (2005). Without modelled or measured initial 234/238 ratios only maximum ages can be obtained. We model initial conditions, i.e. excess initial 234U and depleted 230Th. Samples are pre-screened using β -scanner imaging to identify U-rich layers. Initial MC-ICP-MS results indicate that relatively U-rich layers can exist near the base of flowstones, with U concentrations of between 0.1 and 2.4 ppm. Strong initial (234U/238U) disequilibrium is found for samples younger than 2.5 Ma. Both high U and large initial 234U excess may result from slow weathering of bedrock, without leaching, in the arid phase preceding conditions conducive to flowstone formation. [Pb] ranges between 20–200 ppb and is highly heterogeneous. Small scale (~cm spaced) sampling of U-rich speleothem layers provides a range of U–Pb ratios, and isochron ages can be calculated.

A number of problems remain: discrepancies between ages obtained by different dating methods, poor stratigraphic control of the breccias at Sterkfontein and estimates of initial 234U/238U values for samples >3 Ma. Efforts to constrain the latter using O and C isotopes as proxies are under way.

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New Cretaceous and Palaeogene vertebrates from the East African Rift, Tanzania: stratigraphic, tectonic and palaeobiogeographic implications

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The Rukwa Rift is located in southwestern Tanzania and forms part of the western branch of the East African Rift System. Late Neogene tectonics and sedimentation are superimposed on a complicated sequence of earlier rift-filling events, ranging from Carboniferous–Palaeogene in age, associated with repeated tectonic reactivation of Precambrian basement lineaments.

Based on reports of fossiliferous strata in the southwestern Tanzania and the extreme paucity of fossiliferous Cretaceous and Paleogene strata in sub-Saharan Africa, a research project was initiated in 2002 to explore the palaeontology and stratigraphy the Red Sandstone Group in the Rukwa Rift Basin. Four field seasons of work have resulted in the discovery of diverse new vertebrate faunas of both Cretaceous and Paleogene ages. Over 40 new vertebrate fossil localities have been discovered, with specimens ranging from heavily abraded, isolated elements to exquisite, nearly complete articulated skeletons. Cretaceous vertebrate remains include osteoglossomorph and ceratodontid fish, turtles, crocodyliforms, mammals, and at least four taxa of dinosaurs, including theropods and lithostrotian sauropods. Palaeogene vertebrate discoveries include phiomorph rodents, elephant shrews, anthropoid primates, birds, fish, and crocodyliforms. A range of other non-vertebrate fossils have also been recovered from these Cretaceous and Palaeogene sequences, including plant macrofossils, pollen, gastropods, bivalves, and crustaceans.

Stratigraphic and sedimentological investigations, conducted in tandem with palaeontological investigations, have helped to resolve the much disputed age of the Red Sandstone Group. This work demonstrates a more complex tectonic and depositional history for East Africa than has previously been recognized. Based on detailed mapping and stratigraphy, the Red Sandstone Group has been subdivided into three new informal members: Unit I (Cretaceous), Unit II (Oligocene), and Unit III (late Miocene–Pliocene?). Conventional and unconventional methods have been utilized to determine the age of each of these temporally distinct units, including: biostratigraphy, radiometric dating, detrital zircon geochronology, and heavy mineral provenance. Tied to improved stratigraphic control, these new fossil discoveries hold promise for testing and refining a myriad of phylogenetic and palaeobiogeographic hypotheses relating to the origin

and diversification of Southern hemisphere vertebrate groups.

Only Albany dinocephalian reveals new toothy information

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Dinocephalians are a diverse group of basal therapsids known primarily from Middle Permian rocks of South Africa and Russia (Chudinov 1983, Boonstra 1969), although new finds have been reported from Zimbabwe (Lepper *et al.* 2000), Brazil (Langer 2000) and China (Li *et al.* 1996). They were the first large tetrapods to live on land and a wide diversity of taxa were present right from their earliest appearance. Despite their early success, however, they soon became extinct (Boonstra 1971), probably by the end of the Middle Permian. Of the five main groups of dinocephalians, the anteosaurids, titanosuchids and tapinocephalids are most abundantly represented in South Africa.

This paper reports the discovery of the only dinocephalian from the Albany area, and is also most easterly record of a dinocephalian in South Africa. The presence of heels on the incisors, reduced canine, and all teeth interdigitating, identifies the specimen as a tapinocephalid dinocephalian, despite the fact that it lacks great pachyostotic thickening of the skull roof which is a characteristic of all tapinocephalids (Rubidge 1991). The presence of intermeshing incisors distinguishes dinocephalians from other therapsids and was a mechanism of dental occlusion which was not utilized by other therapsids. In all South African dinocephalians the teeth are poorly known, especially in tapinocephalids where the teeth tended to fall out of the alveoli before fossilization (Boonstra 1962). The new specimen is the first tapinocephalid dinocephalian which has all its teeth well preserved so that it is possible now, for the first time, to provide an accurate dental formula for a tapinocephalid and to study dental occlusal patterns.

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Quest for African dinosaurs

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Despite the vast area encompassed by Africa, greatly

exceeding that of any other southern continent, we still know relatively little about the Mesozoic world of African dinosaurs. Nevertheless, the past two decades have witnessed a plethora of dinosaur discoveries in such countries as South Africa, Kenya, Tanzania, Niger, Morocco, and Egypt, as well as the nearby island of Madagascar. These finds, when combined with work on other southern landmasses—including South America, India, and Antarctica—have begun to fill major gaps in our knowledge, relating to such topics as diversity, phylogeny, biogeography, and terrestrial ecosystems. Of particular interest, has been the integration of dinosaur biogeography and Gondwanan fragmentation, with great potential for reciprocal illumination. Most notable and surprising has been recognition of several derived clades of Late Cretaceous dinosaurs and other terrestrial vertebrates in both South America and Indo-Madagascar, suggesting a degree of cosmopolitanism that was previously unsuspected. These findings, combined with new geophysical data, have resulted in the formulation of a pair of rival hypotheses. The 'pan-Gondwana' hypothesis postulates that the observed biogeographic patterns are the result of origination and dispersal of these clades throughout Gondwana prior to its fragmentation into isolated landmasses. By contrast, the 'Africa-first' model posits that Africa broke away and persisted as an island continent for millions of years during the Cretaceous while faunal exchange was occurring between and among other southern landmasses. Although imbalanced sampling across Gondwanan landmasses currently prevents rigorous testing of these ideas, observed patterns are arguably most consistent with the Africa-first model.

Reconstructing palaeoclimates: an exploratory study using the technique of xylem analysis

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A digitizer/computer-based approach to the quantitative analysis of areas of wood sectioned in the transverse plane is applied in the analysis of nine charcoal assemblages from Boomplaas Cave, Congo Valley, southern Cape. Values for a range of wood anatomical variables are used to reconstruct eight climatic periods. The data are examined as (1) the mean values for wood anatomical variables for each assemblage; (2) the mean values for wood anatomical variables for individual morphological types per assemblage; (3) the distribution of dimensions in the trachea system for selected taxa; (4) the distribution of dimensions in the trachea system of a constructed 'typical' area of xylem tissue for each assemblage.

The results indicate that: from c. 60 000 to 11 000 BP the climate was generally harsh, cold and dry; for a period around 32 000 BP, winter rainfall probably prevailed while around 22 000 BP summer rainfall is indicated; a major change toward more mesic conditions occurred between 11 000 and 14 000 B.P.; the climate was optimum, mesic and equable, for a period during the end Pleistocene, c. 14 000 to 12 000 BP, and that subsequently, temperatures

were higher and xeric conditions were experienced during the mid-Holocene, 1000 to 5000 BP; there is again evidence for summer rainfall during the late Holocene.

The xylem analytical approach is briefly contrasted with the established discipline of dendroclimatology in order to highlight the limitations and potential of the former.

Drought conditions in the South African Karoo Basin at the Permo-Triassic Boundary

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Isotope and palaeomagnetic stratigraphy have been used to position Permo-Triassic boundary (PTB) in the main Karoo Basin of South Africa and correlate the study sections with terrestrial PTB sequences in other parts of the world (Ward *et al.* 2005). The Karoo PTB coincides with a major extinction episode recorded in the fossil record of the *Glossopteris* flora (Retallack *et al.* 2004) and the therapsid-dominated tetrapod fauna (Smith and Ward 2001). This study uses field observations of the sedimentary facies, and taphonomy of *in situ* fossils of two well-exposed PTB sequences in the southern Karoo Basin to provide evidence of environmental aridification that may have brought about the breakdown of the Late Permian terrestrial ecosystems in southern Gondwana.

Pattern of tetrapod extinction. The End-Permian extinction in the central Karoo basin lasted some 100 000 years (Smith and Ward 2001) during which time there was a gradual extinction of small herbivorous dicynodonts and their gorgonopsian predators before the main pulse of extinction that involved medium and large herbivores and carnivores. This pattern suggests that the smaller ground foraging animals, feeding on the undergrowth of ferns and clubmosses, disappeared before larger browsing fauna feeding on *Glossopteris* shrubs and trees. This is in keeping with the interpreted onset of drought conditions. The fact that the medium- and large-sized *Lystrosaurus* arrived in the basin and seemingly flourished as the *Dicynodon* fauna began to fade, indicates that it was somehow pre-adapted to survive the worsening drought conditions. The characteristic spade-shaped maxilla with shock-resistant sutures was most likely the key to the survival of *Lystrosaurus* (Botha and Smith, submitted). It had the ability to continue grazing throughout the drought, probably on the tough equisetalian 'reeds' that remained growing in the moist areas around ponds and along the increasingly ephemeral floodplain channels. It appears that *Dicynodon* and associated herbivores were unable to digest the fibrous stems and leaf whorls of the horsetails efficiently enough to ensure their survival.

Karoo PTB palaeoenvironments. The Karoo PTB facies sequence is interpreted as a relatively rapid change in fluvial landscape from an alluvial plain traversed by a few large highly meandering rivers with expansive lowland floodplains (*massive dark grey mudrock*) through a transitional stage when the rivers straightened and widened

and branched into a distributary channel network that scoured the now abandoned floodplains (*massive maroon siltstone*). As the sediment load increased these channels continued to widen and formed in-channel bars that eventually separated the flow into a braidplain of interconnected sand-dominated ephemeral channels (*conglomeratic sandstone*). During deposition of the massive maroon siltstone facies there was an apparently synchronous depositional event that coincided with the extinction of *Dicynodon* – the last of the Permian dicynodonts to disappear from the Karoo basin. This resulted in the accumulation of up to five metres of red laminated mudrocks (*maroon laminites*) that show evidence of shallow standing water with periodic sub-aerial exposure and desiccation. This is interpreted as an interval when soil formation almost ceased over large parts of the Karoo floodplains. Periodic flooding deposited sand/mud couplets that show little post depositional colonization by either animal or plant life except for a calliannassid-like burrowing arthropod.

Evidence for drought. The calcic palaeosols reflect not only a change in rainfall regime but also an increase in mean annual temperature in the early Triassic resulting in widespread reddening of the floodplain mudrocks. The conclusion drawn from sedimentological and taphonomic evidence of waterhole bone accumulations is that for a period following the disappearance of *Dicynodon*, the central Karoo basin was subject to an increasingly more unreliable and stormy rainfall regime combined with an increase in mean annual temperature which effectively allowed only drought-tolerant flora, and their dependent fauna, to survive into the Early Triassic.

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Palaeoenvironments and indenter mechanics of an Early Jurassic tracksite in southern Lesotho

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In Moyeni, southern Lesotho, abundant ornithopod, theropod and sauropod tracks are preserved on a sandstone surface 15 m above the base of the Upper Elliot Formation, a contact that is widely cited as the Triassic/Jurassic boundary. This study is a re-investigation of the site with particular emphasis on the environmental setting of the tracksite and the sequence of colonization during emergence and desiccation of the surface. A new 'cheirotheroid' trackway at the site questions the use of this ichnotaxon as a Triassic indicator.

The tracks are preserved on several convex scroll bar

surfaces, showing evidence of shallow falling water levels, emergence and early stages of desiccation. The surfaces dip approximately 20 degrees toward the inferred palaeochannel. Numerous rib-and-furrow palaeocurrent readings indicate they were formed on the inner bank of a channel meander.

The majority of the vertebrate tracks were made higher on the bar, into a firmer substrate covered in adhesion warts. Smaller tridactyl trackways are mostly confined to the bar top and clearly run up and down the long axis parallel to the inferred strandline. Larger three- and five-toed trackways follow the same trend, but lower down on the bar surface and, judging from toe scrapes, were probably made beneath shallow, gently flowing water.

Regularly spaced skip marks associated with large tridactyl bipedal trackways have been interpreted as tail drag marks. However, detailed analysis of the cross-cutting relationships with the prints and the direction of movement of the indenter both appear contrary to conventional tail drag dynamics.

Scratches and pits: the usefulness of dental microwear for interpreting palaeo-diets

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Palaeoenvironmental reconstruction has increasingly gained support in the past two decades. Morphology, behaviour and the migration of mammals including hominids is directly linked to the environment which they inhabit.

The time between 2.5 and 1.5 Ma is of particular interest as species of *Paranthropus* and *Homo* coexisted. Over time *Paranthropus* became extinct while *Homo* thrived and dispersed into other regions of Africa and out of Africa. What was the environment like for these major evolutionary transformations to have taken place? Was our adaptation to a cooler and more seasonal environment the key to the survival of our genus *Homo* and to the detriment of *Paranthropus*?

To better answer these questions about the habitat occupied by hominins, we look towards a particular group of mammals – the Artiodactyla. They are often used as palaeoenvironmental indicators because of their abundance in most fossil assemblages, and importantly, because they can easily be separated into general dietary categories that reflect habitat preferences.

Study of dental microwear represents one of the most effective techniques from which to infer palaeo-diets. Microwear is the result of abrasion and attrition during the process of mastication, providing a record of what the animal ate during its life. Different types of foods have different material properties and shapes, and will require different strategies of mastication. A grazer must process grass using a lateral cyclical motion. The combination of this movement and the phytoliths found in grass results in abrasion across the occlusal surface of the tooth. Under

a high magnification microscope, the abrasions appear as linear scratches. Conversely, browsers that prefer leaves, seeds, nuts or fruit use vertical pressure for breaking these brittle food items. An animal that is a predominate browser will have a higher percentage of pits on the occlusal tooth surface than one which grazes.

Dental microwear thus reflects dietary preference directly, and this in turn can be used to interpret palaeoenvironments. One of the strengths of microwear study that is not offered by other techniques is that it can reveal dietary patterns such as seasonal variation and uses of fall-back foods when the animal is under dietary stress due to environmental change or competition for resources.

Microwear analysis on its own is effective in determining dietary preferences, and is therefore useful as a proxy for broad-brush palaeoenvironmental reconstruction, but in combination with other techniques such as stable isotope analysis and ecomorphological studies, it promises a much more comprehensive and reliable interpretation of past environments.

A new dinosaur fauna from the Early Jurassic of South Africa

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The upper Elliot Formation (UEF) of South Africa has a well-known fauna, dominated by a single species of basal sauropodomorph dinosaur *Massospondylus carinatus*. Sedimentological evidence suggests that the environment of deposition was a semiarid to arid floodplain with sediment supplied by small, ephemeral streams with intermittent flashy discharge. Calcareous pedogenic horizons are common, as are pedogenic nodule conglomerates in channel lags. A distinctive, reworked palaeosol, called the *Tritylodon* acme zone, is widespread near the base of this unit. The section of the upper Elliot formation at Spioenkop (Heelbo Farms), Rosendal District, northern Free State is sedimentologically atypical. Palaeosols are only represented at the base of the UEF and the bulk of the unit is formed by stacked channel sands, some laid down in large, possibly permanent, streams. The *Tritylodon* acme zone is not present. Several bonebeds are present in the UEF at Spioenkop. Our team has systematically excavated two of these bonebeds over three field seasons between 2004 and 2006. These have revealed that the fauna is also atypical. *Massospondylus*, which is so common elsewhere, is apparently absent. Instead there is a diverse sauropodomorph fauna consisting of three new species: a basal sauropodomorph similar to *Thecodontosaurus*; a riojasaurid; and a basal sauropod more derived than *Antetonitrus ingenipes*. The basal sauropodomorph can be distinguished from other UEF sauropodomorph taxa by its plesiomorphic dentary, which lacks a ventrally curved rostral tip and any trace of a buccal emargination. Its teeth are also plesiomorphic in having a smooth enamel surface

and extensively denticulated carinae on the mesial and distal margins. The riojasaurid is an unusual, strongly autapomorphic taxon that can be diagnosed by: a highly pitted and foraminate band around the dentigerous margins of the maxilla and dentary; low, triangular cervical neural spines; and stout pedal elements including phalanges that are wider than long in all cases. The third taxon can be referred to Sauropoda on the basis of: the lingual concavities of the tooth crowns; extensively rugose enamel surfaces of the tooth crowns; dorsal neural spines that are much higher than long; hypospheneal ridges in the caudal vertebrae; and transversely compressed and laterally canted pedal unguals. It can be diagnosed by the autapomorphic anteroventral inclination of the anterior face of the cervical centra. The quarry that produced the sauropod bones was rich in small, irregular rounded bones that are interpreted as osteoderms. This would be the first record of ossified armour in a non-titanosaurian sauropod. Other elements of the fauna include an *Allosaurus*-sized theropod, known only from teeth. The only typical UEF faunal elements found at Spioenkop are the small carnivores *Protosuchus haughtoni* and *Coelophysis rhodesiensis*. The unusual fauna, with its diverse fauna of large herbivores, is interpreted as inhabiting a well-vegetated microenvironment on the upper Elliot floodplain. Given the absence of the typical palaeosols and the dominance of channel sands we suggest that this microenvironment was a riparian gallery forest alongside one of the larger, more permanent streams crossing the floodplain.

POSTERS

The taphonomy of an Early Jurassic dinosaur bone-bed in the northern Free State

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The taphonomy of a bone-bed in the upper Elliot Formation (Early Jurassic) on the farm Spioenkop (Rosendal District, Free State) is described and discussed. The bone bed was excavated, gridded and mapped by a team from the Bernard Price Institute during the 2006 field season. All bones were numbered and collected. Well over 95% of the bones in this bed can be attributed to a new taxon of large (juvenile femur length = 700 mm) basal sauropodomorph. The minimum number of individuals of the sauropodomorph is two (based on ribs). The only other taxa present are two theropods, one very large and represented by isolated tooth crowns, the other is small (femur length = 146 mm long) and is represented by a femur and a sacrum. The latter can be referred to *Coelophysis rhodesiensis*, which is known from other sites in the upper Elliot Formation.

The bones are buried in an upwardly-fining lens of sand and are of limited lateral extent (6 m in outcrop). This package is interpreted as the fill of a small-scale channel

on the floodplain. The bones are densely packed with 160 bones having been recovered from an area of less than 5 m². The bones are often found lying on top of one another, but with no sign of articulation, or association. The lack of articulation indicates some degree of transport by water and this is supported by a preferred orientation of the long bones (strike: 301–121°, dip: 007°S). Nevertheless, transport of the bones is likely to have been minimal, as the bones (including several delicate skull bones) have pristine surfaces that show no sign of abrasion due to extended water transport. The pristine bone surfaces (on both upper and lower surfaces), also indicate that exposure at the surface was limited. Nevertheless there is some evidence of *in situ* modification before final burial. A few fully buried bones were cleanly broken and ended abruptly, despite not having been exposed to recent erosion. The dorsal process of a maxilla was found to have been folded through 150° from its original vertical position. The base of the process shows that the bone deformed plastically up to 90°, after which brittle failure occurred. No other bones show such signs of deformation, indicating that the force involved was highly localized and happened while the bone was fresh enough to bend. We believe the cause of this damage was trampling by another dinosaur, possibly the large theropod. Another source of evidence that a theropod visited the site before final burial, is a possible coprolite buried amongst the bones. The coprolite is a flattened, irregular mass of bone chips dispersed through a hematitic groundmass, surrounded by small, closely spaced stringers of hematite and bone chips spread over an area with an approximate diameter of 30 cm. The flattened irregular shape is also thought to be the result of trampling.

The sauropodomorph bones show several signs of belonging to juveniles, including the striated texture of many bone surfaces and the lack of sutural closure between the braincase elements, as well as the neural arches and their centra. The agent that killed the juvenile sauropodomorphs remains unknown.

Ichnological Problematica from the Lower Jurassic Clarens Formation, southern Africa

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The ichnological record of the Lower Jurassic Clarens Formation in southern Africa contains a number of unique trace fossils unlike any other known modern or ancient biostructures. Here some enigmatic horizontal, regularly-oriented biogenic sedimentary structures (Fig. 1) are described that occur in association with features that were previously interpreted as Early Jurassic termite nests. These spectacular, but rather puzzling trace fossils are exposed in enormous profusion as straight, ~0.5 cm cylinders in parallel alignment to one another and to ancient horizontal bedding planes. The structures, which occur in both epirelief and full relief, and which show no evidence of overlapping or crosscutting, are filled with material identical to the rest of the host rock: a compo-

sitionally and texturally uniform, very fine to fine-grained, massive quartzarenite. In cross-sections, each structure is defined by a subtle, ~0.1 mm thin, concentric gap.

Spatiotemporal distribution patterns of the oriented structures and associated back-filled trace fossils, as well as other sedimentological and palaeontological lines of evidence, collectively imply recurrence of favourable ecological parameters (e.g. increased moisture content of the substrate) related to periodic climate fluctuations in the Early Jurassic of Gondwana. The limited stratigraphic resolution of the Clarens Formation hampers correlation of the study sites, and thus the question as to whether or not the preserved biotic communities were secluded in time and space, flourishing only in certain favourable landscape mosaics of the more arid Clarens palaeoclimate, remains open for future research.

Without comparable modern biogenic structures of similar dimensions and spatial arrangement, the evidence for organic origin of these enigmatic structures remains equivocal. Furthermore, the function these structures served is also rather perplexing. Hopefully, this morphological description and hypothesis put forward regarding their origin will stimulate further investigations, leading to the recognition of similar ancient and modern structures, and eventually revealing their true genesis.

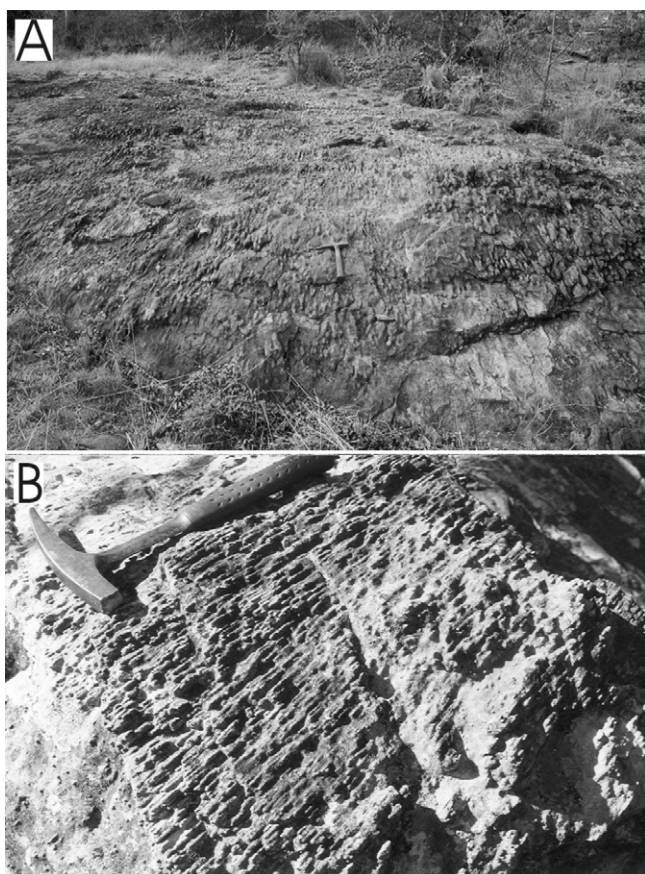


Figure 1. Field occurrences of the enigmatic horizontal, regularly-oriented structures from the Lower Jurassic Clarens Formation of southern Africa (30 cm long hammer for scale). The structures often occur in great profusion, *en masse* on weathered, horizontal surfaces up to 100 m² (A) as well as in localized, smaller (eroded) patches (B). Note that these unbranched, smooth, straight, cylindrical structures of ~0.5 cm diameter show no evidence of overlapping or crosscutting.

Analysis of microfauna-bearing breccia from Kromdraai-A in the Cradle of Humankind World Heritage Site

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Kromdraai-A is situated 1.75 km east of Sterkfontein in the Cradle of Humankind World Heritage Site. It is rich in mammalian microfauna, largely deposited by owls (Brain 1981). Calcified breccia from the Kromdraai-A dump, as well as stratigraphically constrained, *in situ* samples, were chemically analysed using X-Ray Fluorescence. Correlation of the samples was attempted, with the aim of determining the original host matrix, and hence stratigraphic location, of each dump-site sample.

There appear to be two specific types of breccia present at the site, representing two separate periods, or modes of deposition. The distinction between the two breccias is based on differences in colour, faunal density, faunal preservation and chemistry.

Detailed analysis of the breccia, before and after preparation in dilute acetic acid, serves to address the question as to whether it is possible to reassign context to ex-situ breccia, as well as whether bone density is correlated with chemical differences that relate to environmental factors. It is clear that two different sets of conditions prevailed during deposition. Taxonomic investigation is underway to further clarify these conditions.

The latest dirt on acid preparation

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Acid preparation remains the only reliable means of preparing certain fossils, such as microfaunal specimens, which are too delicate to undergo mechanical preparation. In fact, the Transvaal Museum and Hope experimental laboratory prepares all Plio-Pleistocene material in this manner. Advances in materials and techniques have minimized the influence of the chemicals upon the faunal remains. Consequently, this means of preparation deserves renewed investigation. The quest for new methods that will not compromise the fossils' integrity has led to an experimental approach in order to test new techniques in dealing with traditionally problematic tasks, including bulk and localized preparation.

Cranial bone (Sts 5 (i)) adhering to calcified matrix associated with 'Mrs Ples'

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When Robert Broom prepared Sts 5 ('Mrs Ples') mechan-

ically with hammer and chisel in 1947, after discovery of the fossil at Sterkfontein on 18 April of that year, he removed six blocks of breccia, each of which had a thin veneer of bone representing the outermost layers of the cranium of this specimen of *Australopithecus africanus*. One of these pieces has been catalogued as Sts 5 (i). This block of breccia is being carefully prepared with the intention of exposing potential evidence of temporal lines and other external features on the cranium. The surface of 'Mrs Ples' as prepared by Broom does not represent the outer table of cranial bone. This accounts for the fact that temporal lines have not been recognized previously. Current work in preparation expects to address this problem. The identification of temporal bones is relevant to issues relating to the developmental age of Sts 5, believed to have been adolescent at the time of death, 2.1 million years ago.

Palaeontology in the Digital Age: the future of electronic publication

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Palaeontologia Electronica (PE) is an open access publication, primarily sponsored by the Palaeontological Association, Society for Vertebrate Paleontology and the Paleontological Society. Not only is it free to authors and subscribers, it is a journal to be taken seriously. PE is now ISI listed, and is also fully compliant with both the International Code for Zoological Nomenclature (ICZN) and the International Code for Botanical Nomenclature (ICBN). This has opened the door for the electronic publication of all types of palaeontological papers, and will allow palaeontologists to fully embrace the age of burgeoning digital scientific communication.

At the forefront of electronic publication of palaeontological articles, PE has had to overcome many challenges in its pioneering nine-year history. Not the least of these, has been achieving compliance with the ICZN and ICBN. Both codes express a reluctance to entrust posterity to digital media, and insist that certain minimum requirements be met for the valid electronic publication of new names and nomenclatural modifications, including deposition of web, CD-Rom and paper versions of each PE issue at a specified number of archive libraries.

The concerns regarding electronic publication of botanical and zoological taxonomy no doubt stem from a mistrust of digital media as a long-term storage option. Such concerns are not entirely unfounded, with issues such as rapidly changing software, hardware and data-storage technology, and the limited lifespan of data storage media, providing ample reason for concern. However, systems are currently being developed to combat these problems. Library administrators are deeply invested in their role as custodians of world knowledge in the

digital age, and many are taking a proactive stance toward finding effective long-term methods of electronic data storage and preservation. For instance, one of the most successful and widely supported initiatives is the LOCKSS (Lots of Copies Keeps Stuff Safe) Program, developed by Stanford University Libraries. LOCKSS provides a means for libraries to collect, protect and provide access to web-based journals. Long-term preservation of archived data on hard disk is effected through a self-regulating, cooperative, peer-to-peer process of damage detection and repair across a global network of computers.

Despite lingering fears surrounding the permanence of digital information, the benefits of on-line publication overwhelmingly outweigh the potential hazards. Open access journals such as PE provide a venue for taxonomic work that is cost-free, rapidly published, universally distributed, and where unlimited pages, illustrations and colour images are available to describe a new species accurately. Open-access publication takes us one step closer to creating a synergistic community of palaeontologists able to freely exchange ideas, without discriminating against those unable to afford costly subscriptions or access limited distribution documents.

The freedom provided to palaeobotanists and botanists alike by an electronic journal format is limited only by the imaginations of the author and editor, and the available technology. A publication need not only contain text and photographs, but video clips, interactive images, and 3D models—all in full colour. We are already fully immersed within a new culture of digital freedom, and we should be prepared to exploit it to the full.

A non-size-dependent metrical and non-metrical study of the pelvic complexes of *Australopithecus africanus* and *Australopithecus afarensis*

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There is ongoing debate amongst palaeoanthropologists regarding the limb and body proportions of two of the best represented early hominin species, *Australopithecus africanus* and *Australopithecus afarensis*. The greatest area of difference is argued to be in joint areas associated with habitual bipedalism, namely the knee, pelvis and lumbar sacral complex. This research compares the pelvic complexes of the two fossil hominin species to establish the extent of variation, independent of size. Original fossil specimens Stw 431 and Sts 14, as well as a high-quality cast of AL 288, will be used. Modern human pelvic complexes will be used as a control for sex. It is hypothesized that no significant difference exists between the morphology of these two pelvic complexes.

This study should shed light on the debate concerning differences and similarities in early hominin pelvic complexes and add to the debate of the mode and tempo of the bipedal evolution of early hominins, their body proportions and phylogeny.

Breaking down barriers: the use of Venn diagrams to illustrate that *Australopithecus*, *Paranthropus* and *Homo* are not necessarily three discrete taxa

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African hominins dated between 1.5 and 2.5 mya are significant in relation to questions concerning the origin and diversification of species within the genus *Homo*, relative to penecontemporaneous species attributed to the genera *Australopithecus* and *Paranthropus*. It is generally considered that hominin species within the past 2.5 mya can be assigned to one or other discrete genus. However, boundaries between genera are not necessarily clearly expressed. Venn diagrams are used here as an example whereby relationships between African hominin species can be re-assessed, without assuming distinct boundaries between genera.

For example, a hominin temporal bone from Chemeron in the Baringo area, catalogued as KNM-BC 1, has previously been claimed to be the earliest representative of the genus *Homo* in Africa, dated c. 2.4 mya. Pairwise comparisons between KNM-BC 1 and temporal bones of other African hominins, using geometric morphometric (Procrustes) analyses, indicate that the Chemeron specimen displays a striking morphological similarity with specimen TM 1517, the type specimen of *Paranthropus robustus* from Kromdraai in South Africa. In fact the degree of similarity reflects a high probability of conspecificity, using extant hominoids as a frame of reference. The minimum date for the TM 1517 cranium, based on faunal associations and magnetostratigraphy, is 1.95 mya (Thackeray *et al.* 2002). KNM-BC 1 is also morphologically similar to AL 444-2, a Pliocene hominin attributed to *Australopithecus afarensis* from Ethiopia. In terms of a Venn diagram, the Chemeron fossil is placed at the intersection of three sets A, P and H, respectively representing *Australopithecus*, *Paranthropus* and *Homo*.

Excavations at Kromdraai A and B

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Excavations have been undertaken at Kromdraai since

1938, beginning with the discovery of the type specimen of *Paranthropus robustus* (TM 1517) described by Robert Broom. Since then, excavations have been undertaken at Kromdraai under the direction of Bob Brain, Elizabeth Vrba and Francis Thackeray of the Transvaal Museum. We present a summary of results obtained from recent research and fieldwork. Of particular interest is the discovery of a hominid humerus shaft, which probably originated from the same individual as specimen TM 1517 (the type of *P. robustus*). A minimum date of 1.95 million years has been obtained for TM 1517, based on palaeomagnetic and biostratigraphic data. It is evident that hominids were probably scavenging for bones from carcasses of animals such as wildebeest, which were preyed upon by predators such as *Dinofelis*. Kromdraai A was probably a *Dinofelis* lair. However, Kromdraai A was also visited at least temporarily by hominids, as indicated by the presence of stone artefacts. X-ray diffraction analyses have indicated traces of bone apatite on stone artefacts (polyhedral cores), suggesting that hominids may have been occasionally breaking long-bones of ungulates for marrow.

Hybridization and osteology: the case of bontebok and blesbok

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Damaliscus pygargus is one of three species found within this genus of Alcelaphinae. It has two subspecies: *Damaliscus pygargus pygargus* and *Damaliscus pygargus phillipsi*, which show hybridization since the introduction of the former in the Free State during the 1960s. The aim of the study is to investigate discrimination of the two subspecies by means of an osteological approach using specimens from the National Museum, Bloemfontein, and the Iziko South African Museum, Cape Town. It is hypothesized that bone measurement will serve to differentiate between the subspecies, which are adapted to different environments, and thus experience different stresses. This research project can be envisaged as a proxy for studying speciation events in southern African bovid populations, and will contribute to our knowledge of bovid evolution as it represents the first exploration of this methodology on *Damaliscus* subspecies.