

https://dspace.org/

Palaeontologia africana Volume 45

2010
Bernard Price Institute for Palaeontological Research
http://hdl.handle.net/10539/17295

Downloaded from a DSpace repository. https://dspace.org/

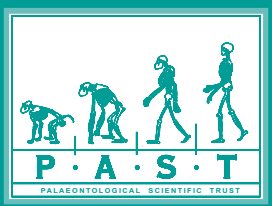
PALAEONTOLOGIA AFRICANA

Volume 45
December 2010

Annals of the
Bernard Price Institute
for
Palaeontological Research



Supported by
PALAEONTOLOGICAL SCIENTIFIC TRUST



ISSN 0078-8554

SCHOOL OF GEOSCIENCES

BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH

Academic Staff

Director and Chair of Palaeontology

B.S. Rubidge BSc (Hons), MSc (Stell), PhD (UPE)

Deputy Director

M.K. Bamford BSc (Hons), MSc, PhD (Witwatersrand)

Senior Research Officers

F. Abdala BSc, PhD (UNT, Argentina)

A.M. Yates, BSc (Adelaide), BSc (Hons), PhD (La Trobe)

Research Officer

L.R. Backwell BA (Hons), MSc, PhD (Witwatersrand)

Collections Curator

B. Zipfel NHD Pod., NHD PS Ed. (TWR), BSc (Hons) (Brighton), PhD (Witwatersrand)

Post Doctoral Fellow

F. Neumann BSc, MSc, PhD (Friedrich-Wilhelms-University, Bonn)

Editorial Panel

M.K. Bamford: Editor

L.R. Backwell: Associate Editor

B.S. Rubidge: Associate Editor

A.M. Yates: Associate Editor

Consulting Editors

Dr J.A. Clack (Museum of Zoology, University of Cambridge, Cambridge, U.K.)

Dr H.C. Klinger (South African Museum, Cape Town)

Dr K. Padian (University of California, Berkeley, California, U.S.A.)

Dr K.M. Pigg (Arizona State University, Arizona, U.S.A.)

Prof. L. Scott (University of the Free State, Bloemfontein)

Dr R.M.H. Smith (South African Museum, Cape Town)

Technical and Support Staff

Principal Technician

R. McRae-Samuel

W.P. Germishuizen (from September)

Senior Administrative Secretary

S.C. Tshishonga

W. King (from September)

Assistant Research Technician

C.B. Dube

Technicians/Fossil Preparators

P. Chakane

S. Jirah

P.R. Mukanela

G. Ndlovu

T. Nemavhundi

S. Tshabalala

Custodian, Makapansgat Sites

S. Maluleke

Honorary Staff

Honorary Research Associates

K. Angielczyk BSc (Univ. Michigan, Ann Arbor), PhD (Univ. California, Berkeley)

P.J. Hancox BSc(Hons), MSc, PhD (Witwatersrand)

R. Reisz BSc, MSc, PhD (McGill Univ., Montreal)

C.A. Sidor BSc (Trinity College) MSc, PhD (Univ. Chicago)

INSTITUTE FOR HUMAN EVOLUTION

Academic Staff

Director

J.F. Thackeray BSc (Hons), MSc (UCT), MPhil, PhD (Yale)

Reader

L.R. Berger BA (Hons) (GA Southern), PhD (Witwatersrand)

Research Officers

K. Carlson BSc (Michigan, Ann Arbor), MSc, PhD (Indiana, Bloomington)

J. Kibii BSc, (Nairobi), MSc, PhD (Witwatersrand)

B. Kuhn BSc (Washington State), MSc (UCL), PhD (UP)

Research Associates

C. Henshilwood BA (Hons) (UCT), PhD (Cambridge)

M. Lombard BA (Hons), MA (UNISA), PhD (Witwatersrand)

Administrative and Support Staff

Senior Administrative Secretary

Evlyn Ho

Preparators

T. Dingiswayo

T. Makhele

N. Molefe

A. Mollepolle

S. Motsumi

L. Sekowe

M. Seshoene

C. Yates

Honorary Staff

Honorary Research Associates

Dr Shaw Badenhorst, Transvaal Museum

Prof. Steve Churchill, Duke University, USA

Prof. Francesco d'Errico, BordeauxUniversity, France

Prof. Daryl de Ruiter, Texas A&M University, USA

Prof. Katerina Harvati, University of Tubingen, Germany

Prof. Jacopo Moggi-Cecchi, Laboratori di Antropologia, Dipartimento di Biologia Animale e Genetica, Università di Firenze, Italy

Prof. Peter Schmidt, Zurich, Switzerland

Prof. Himla Soodyall, Human Genomic Diversity and Disease Research Unit (HGDDRU), South African Medical Research Council in conjunction with the National Health Laboratory Service and University of the Witwatersrand

PALAEONTOLOGIA AFRICANA

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

ISSN 0078-8554

Volume 45, December 2010

CONTENTS

Articles

Van der Walt, M., Day, M., Rubidge, B., Cooper, A.K. & Netterberg, I. — A new GIS-based biozone map of the Beaufort Group (Karoo Supergroup), South Africa **1**

Yates, A.M. & Barrett, P.M. — *Massospondylus carinatus* Owen 1854 (Dinosauria: Sauropodomorpha) from the Lower Jurassic of South Africa: Proposed conservation of usage by designation of a neotype **7**

de Ruiter, D.J., Brophy, J.K., Lewis, P.J., Kennedy, A.M., Stidham, T.A., Carlson, K.B. & Hancox, P.J. — Preliminary investigation of Matjhabeng, a Pliocene fossil locality in the Free State of South Africa **11**

Bamford, M.K., Neumann, F.H., Pereira, L.M., Scott, L., Dirks, P.H.G.M. & Berger, L.R. — Botanical remains from a coprolite from the Pleistocene hominin site of Malapa, Sterkfontein Valley, South Africa **23**

Technical note

Zipfel, B., Yates, C. & Yates, A.M. — A case of vertebrate fossil forgery from Madagascar **29**

© 2010
BERNARD PRICE INSTITUTE
for
PALAEONTOLOGICAL RESEARCH
School of Geosciences
University of the Witwatersrand
Johannesburg

ACKNOWLEDGEMENTS

The Bernard Price Institute for Palaeontological Research gratefully acknowledges financial support for its programmes by

THE COUNCIL'S RESEARCH COMMITTEE, UNIVERSITY OF THE WITWATERSRAND

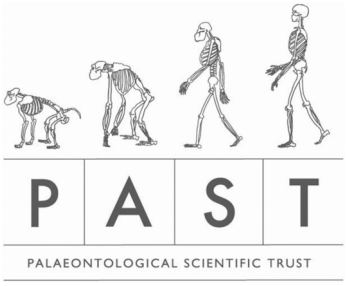
NATIONAL RESEARCH FOUNDATION (NRF)

DEPARTMENT OF SCIENCE AND TECHNOLOGY (DST)

and the

PALAEONTOLOGICAL SCIENTIFIC TRUST (PAST)

for publication of this journal







Pre-press production by Isteg Scientific Publications, Irene

Printed in South Africa by Ultra Litho (Pty) Ltd, Heriotdale, Johannesburg

A new GIS-based biozone map of the Beaufort Group (Karoo Supergroup), South Africa

Merrill van der Walt[1*], Michael Day[2], Bruce Rubidge[2], Antony K. Cooper[3] & Inge Netterberg[4]

[1]*Origins Centre, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa*

[2]*Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa*

[3]*Council for Scientific and Industrial Research (CSIR) Built Environment, P.O. Box 395, Pretoria, 0001 South Africa*

[4]*SAHA International, 39 Lytton Road, Observatory, Cape Town, 7925 South Africa*

Received 16 November 2010. Accepted 15 December 2010

The stratigraphic subdivision of the Karoo Supergroup of South Africa has been addressed for more than a century by various geoscience studies. A lack of good lithostratigraphic markers in the Beaufort Group and the fact that the succession preserves a rich diversity of therapsid fossils for which there is a robust taxonomic scheme, make biostratigraphy the best option for correlation. This is applicable both within the basin and when comparing the Karoo succession to other coeval depositional basins. Published biostratigraphic maps of the Beaufort Group were compiled based on rough estimates of the distribution of zone-defining tetrapod fossil genera throughout the basin. None of these simultaneously utilized all the databases of South African museum collections. The recent application of GIS technology to integrate the vertebrate fossil databases of all South African museums has resulted in a far more precise biozone map which can be continuously updated as new information is received. This digital map introduces an entirely new way of representing the geographical distribution of fossil data, and thus can potentially enhance basin development and tetrapod biogeographic studies.

Keywords: Karoo Supergroup, fossil tetrapods, biostratigraphy.

INTRODUCTION

Biostratigraphy

The rocks of the Beaufort Group (Adelaide and Tarkastad subgroups) of the Karoo Supergroup cover approximately 60% of the surface of South Africa and comprise an approximately 3000 m thick succession of predominantly sedimentary rocks that are richly fossiliferous. Absolute ages for the Beaufort Group are not well constrained, with current dates based mainly on faunal correlations. The oldest stratigraphic units are considered Middle Permian (Kazanian) (Rubidge 1995a) and the uppermost strata as Middle Triassic (Anisian) (Ochev & Shishkin 1989; Hancox *et al.* 1995; Hancox & Rubidge 1996; Hancox 1998).

The global importance of the Beaufort Group is largely due to its remarkable assemblage of tetrapod fossils representing one of the best preserved ecological assemblages of pre-mammalian (therapsid) terrestrial vertebrates in the world (Keyser & Smith 1979), and the succession is held by many to be the global biostratigraphic standard for the non-marine Permo-Triassic (e.g. Shishkin *et al.* 1995; Lucas 1998). Furthermore, the rocks of the Beaufort Group preserve one of the most complete and best-studied non-marine Permo-Triassic (PT) boundary sequences globally (Smith 1995; Ward *et al.* 2000; Smith & Botha 2005; Botha & Smith 2006). These boundary sections preserve the terrestrial record of the Permo-Triassic extinction event – the greatest mass extinction event experienced on Earth (Erwin 1993, 1994, 2006).

Tetrapod fossils (particularly therapsids) have long been used for biostratigraphic subdivision and correlation of the Group which is especially useful because of the scarcity of basin-wide lithostratigraphic marker beds (Broom 1907a, 1909; Haughton 1924, 1963, 1969; Kitching 1970, 1972, 1977, 1984; Keyser & Smith 1979; Keyser 1979; Rubidge 1995b; SACS 1980). The few major lithological boundaries that have been traced throughout the basin have been shown to be diachronous (Keyser 1979), whereas the biozones are considered to closely approximate time lines (Rubidge 2005). Dicynodonts, the dominant herbivores of the Permian and early Triassic, are the most abundant fossil tetrapod taxon in the Beaufort Group and for this reason they are used as index fossils for the majority (five of the eight) of the currently recognized vertebrate biozones (Hancox & Rubidge 1997). Moreover, due to their abundance, dicynodonts have great potential for global correlation and have therefore been used in a number of previous biogeographic studies and biochronological schemes (Cooper 1982; Cruickshank 1985, 1986; Lucas 1990, 1993, 1995, 1998; Shishkin & Ochev 1992; De Fauw 1993).

Following is a summary of the history of work on the biostratigraphy of the Beaufort Group (Table 1) since Seeley (1892) proposed the first biostratigraphic subdivision of the Karoo which included three zones. Broom (1907b, 1909) refined the biozonation of Seeley by recognizing six subdivisions. Watson (1914a) agreed with Broom's subdivision and was the first to indicate the distribution of these units (which he termed 'zones') on a map. Later he replaced the *Pareiasaurus* Zone with the *Tapinocephalus* Zone (Watson 1914b), and an updated biozone distribution map was published in 1940 by von Huene. Hotton & Kitching (1963) pointed out that *Procolophon* occurs throughout the *Lystrosaurus* Zone and suggested that a separate overlying *Procolophon* Zone was not valid. Kitching (1970, 1977) introduced the *Daptocephalus* Zone to encompass the strata between the level where *Cistecephalus* became

*Author for correspondence. E-mail: merrill@origins.org.za

Table 1. Table showing the historical progression of Beaufort Group biozonation.

Beds	Zones		Assemblage Zones		
Broom (1906)	Watson (1914 a, modified 1914b)	Kitching (1970, 1977)	Keyser & Smith (1979)	Keyser (1979) SACS (1980)	Current Biozonation Rubidge (1995b)
Cynognathus	*Cynognathus*	*Cynognathus*	*Kannemeyeria*	*Kannemeyeria Diademodon*	*Cynognathus*
Procolophon	*Procolophon*	*Lystrosaurus*	*Lystrosaurus*	*Lystrosaurus Thrinaxodon*	*Lystrosaurus*
Lystrosaurus	*Lystrosaurus*				
Kistecephalus	*Cistecephalus*	*Daptocephalus*	*Dicynodon lacerticeps*	*Dicynodon lacerticeps Whaitsia*	*Dicynodon*
		Cistecephalus	*Aulacephalodon baini*	*Aulacephalodon Cistecephalus*	*Cistecephalus*
Endothiodon	*Endothiodon*		*Tropidostoma microtrema*	*Tropidostoma Endothiodon*	*Tropidostoma*
Pareiasaurus	*Tapinocephalus*	*Tapinocephalus*	*Pristerognathus/Diictodon*	*Pristerognathus/Diictodon*	*Pristerognathus*
			Dinocephalian	*Dinocephalian*	*Tapinocephalus*
					Eodicynodon

extinct and the first appearance of *Lystrosaurus*, and discarded Broom's *Endothiodon* and *Procolophon* Zones. Kitching (1977) also produced a map showing zone-defining fossil localities. Keyser & Smith (1979) proposed a more refined vertebrate biozonation (and accompanying biozone map) for the Beaufort Group in the western part of the basin and linked their assemblage zones to the litho-stratigraphic scheme proposed by SACS (1980). The discovery of a tetrapod fauna from below the *Tapinocephalus* Assemblage Zone (Rubidge 1984; Rubidge *et al.* 1983; Rubidge *et al.* 1994) led to the erection of the *Eodicynodon* Assemblage Zone, which is currently the oldest vertebrate biozone of the Beaufort Group (Rubidge 1990, 1995a).

Following the recommendations of the International Stratigraphic Guide (ISSC 1976), the names of the assemblage zones that were accepted by SACS (1980) incorporated two genera. The most recent biostratigraphic scheme of the Beaufort Group which recognized eight biozones (Rubidge 1995b) follows the most recent nomenclatorial practice of the ISSC (1994) and uses only one taxon name in defining a biozone. This biozonation was represented in map form (Rubidge 1995b) and has since been the standard reference for the biozones of the Beaufort Group. The method used to create this map was manual drawing by enhancing the biozone maps of Kitching (1977) and Keyser & Smith (1979). This was essentially an exercise in outlining diagnostic fossil localities on an A3-sized map with a consequent low-level resolution. Over the past 15 years many more fossils from the Beaufort Group with quantifiable provenance data have been accessioned into museum collections and provide the impetus for a reassessment of biozone boundaries. In addition, since 2007 a GIS database has been built up incorporating data relating to all fossil specimens from the Beaufort Group which are curated in South African palaeontological collections (Nicolas 2007; Nicolas & Rubidge 2009) and is an excellent tool to produce an updated biozone map.

MATERIALS AND METHODS

To produce the refined biozonation map from the GIS locality data, each biozone had to be defined in terms of key or 'marker' genera. Filtering for key genera allowed for biozone boundaries from the database to be defined. Ideally the lowermost boundary of a biozone is marked by the first appearance datum (FAD) of a key taxon, but in practise this is not always practical in the Beaufort biozonation scheme, which is based on assemblage zones, as the stratigraphic range of some biozone defining fossils are not necessarily restricted to the Assemblage Zone named after them. The diagnostic taxa utilized to define the individual biozones were taken from data presented in Rubidge (1995b), but in order to circumscribe the lower boundary of each biozone on the map the criteria set out in Table 2 were used.

Although ArcGIS allows for complex spatial analyses, numerous obstacles relating to data quality were encountered that presented barriers to the generation of biozone boundaries. These were:

1) *Quality of the locality data*. For older collections this often constitutes a farm name only. These are represented on the GIS map as farm centroids (Nicolas 2007). A farm covering two or more biozones may thus group genera from different biozones at a single point. Problematic localities were checked and topography examined to deduce the cause and nature of such apparent overlaps.
2) *The relationship between geology and topography.* At localities of high relief, the surface area of each biozone represented on the map is much smaller than when

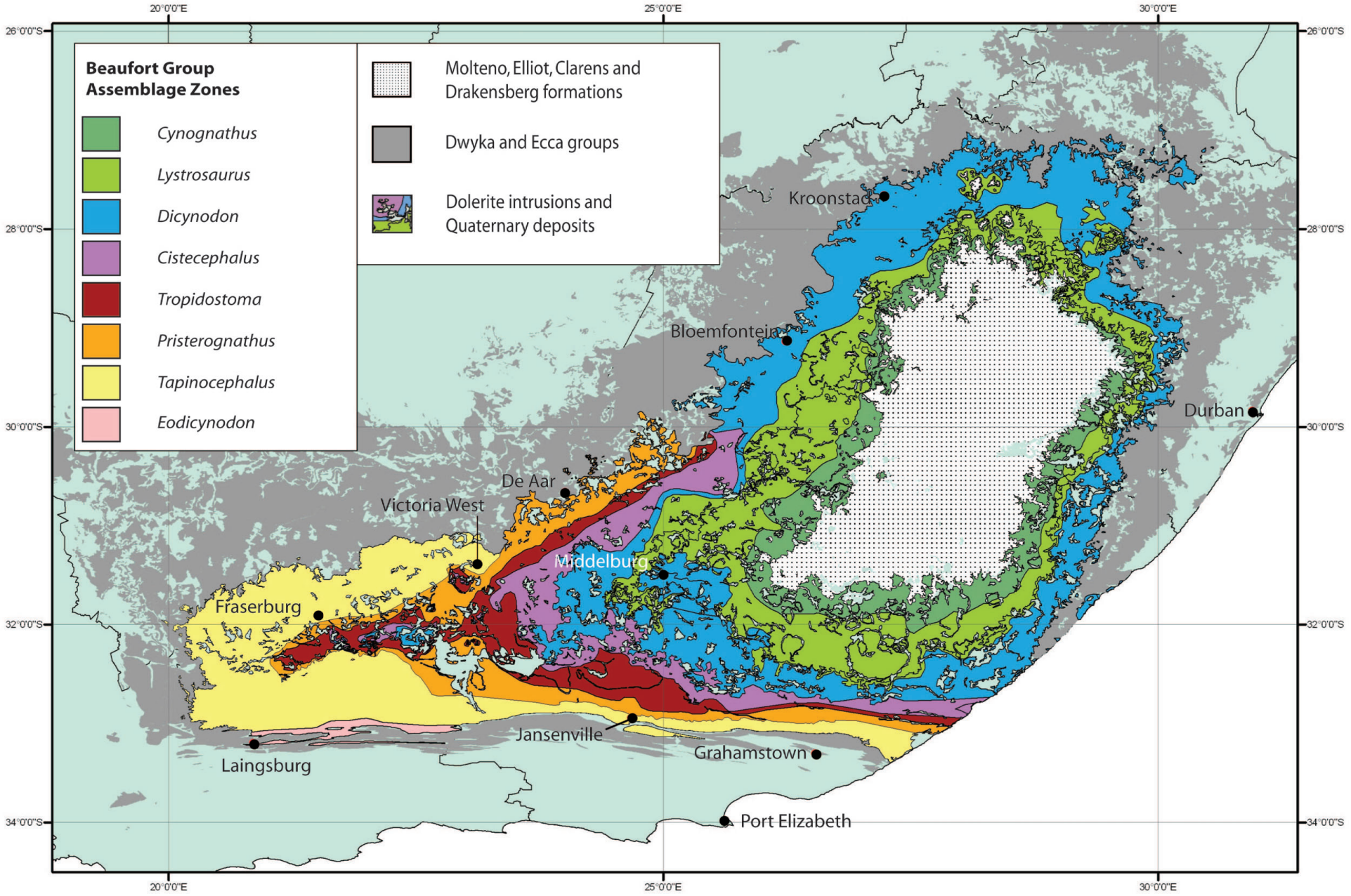


Figure 1. Geographic distribution of the vertebrate biozones of the Beaufort Group based on a GIS database.

Table 2. Criteria used to circumscribe lower boundaries of biozones shown on the map.

Assemblage Zone	Criteria used to circumscribe lower boundary
Eodicynodon	Ecca-Beaufort boundary
Tapinocephalus	Last appearance of *Eodicynodon, Australosyodon* and *Tapinocaninus*
Pristerognathus	Last appearance of dinocephalians, presence of *Pristerognathus*
Tropidostoma	First appearance of *Tropidostoma* with presence of *Endothiodon*
Cistecephalus	First appearance of *Aulacephalodon* with presence of *Cistecephalus*
Dicynodon	Presence of *Dicynodon, Daptocephalus* absence of *Cistecephalus*
Lystrosaurus	Last appearance of *Dicynodon, Daptocephalus*
Cynognathus	First appearance of *Trirachodon* and *Cynognathus*

exposed on flat ground. The orientation of topographic features, such as escarpments, relative to dip is also important as this defines whether the zone remains at a constant level or alters in height laterally. This meant that without sophisticated three-dimensional modelling the accurate mapping of biozone boundaries was not possible, even if all locality input data was exact. As a result, biozone boundaries were drawn digitally utilising overlays of fossil genus localities, as well topographic and geological maps. In areas of great fossil abundance accuracy is highest, but for many areas, particularly in the Free State and eastern portion of the Eastern Cape provinces, this could not be achieved as there is a dearth of collecting localities. In these places, where fortuitously the strata are relatively horizontal, biozone boundaries were established through extrapolation by following mapped contour lines from one locality to the next. In a few instances where fossil localities are separated by tens of kilometres and the topography is complex as a result of folding of the strata or dolerite intrusions, biozone boundaries were traced by assessing lithostratigraphic boundaries. It should be noted that neither topography nor geology are always reliable features to follow because of the dip of beds and the diachroneity of lithostratigraphic boundaries. However, in the absence of fossil data, this method provides the best approximation.

There are some spurious specimen localities in the database that are aberrant compared to surrounding data points and cannot be explained by the farm centroid effect. Possible causes include the presence of an outlier of another biozone, specimen misidentification, the specimen not being *in situ* or incorrect cataloguing. In areas without physical deformation and flat topography, the former could be ruled out with confidence. Specimens with apparently anomalous localities that could not be explained by relief or physical deformation had their provenance and description data checked. If they were incorrectly situated then they were either moved to the correct locality or, if their true provenance could not be determined, ignored. Any specimens that were correctly situated but the authors remained unconvinced of their identity, were ignored and listed to be reidentified at a later date.

DISCUSSION

The new, GIS-based biozone map (Fig. 1) shows relatively few large-scale changes compared to its published precursors (Rubidge 1995b). The termination of the *Tapinocephalus* AZ close to the town of De Aar is an educated estimation because of the absence of dinocephalian fossils further north. The exact position of the boundary here is unknown due to a lack of collecting and the Ecca-Beaufort boundary at the nearest site to the north at Somersfontein near Philippolis is known to be *Pristerognathus* AZ (Welman *et al.* 2001). Also, small biozone outliers which usually coincide with high hills, have been acknowledged where fossil evidence illuminates their position. Previously these occurrences were too small-scale to be mapped, but the far higher resolution of the new digital map now makes this possible.

Despite the caveats discussed above, it is clear that the use of GIS greatly increases the achievable accuracy and ultimately the utility of the resulting digital map. It can be viewed at both small-scale, for the observation of broad overall patterns, and at large-scale for the assessment of smaller areas. It will be useful to identify areas where collecting has been sparse and the need for further research is greatest, as well as those locations where the boundary is best visible. One of the foremost applications, at least in the early stages, will be to draw attention to misidentified specimens, or specimens identified long ago using outdated characters.

This is an ongoing project. The GIS database, which is housed and curated at the BPI Palaeontology (University of the Witwatersrand, Johannesburg), will be updated continuously to include nomenclatorial modifications of existing specimens as well as the inclusion of new acquisitions to collections. The map is available at http://web.wits.ac.za/Academic/Science/GeoSciences/BPI/ . Updating metadata will increase the accuracy of the map and provide an accessible record in 2D and ultimately in 3D. Use of this kind of spatial modelling will revolutionize the way biozones are mapped and will ensure that all new data are recorded in a systematic and centralized manner. The final product will serve as an up-to-date representation of the surface expression of vertebrate fossil assemblage zones of the main Karoo Basin in South Africa.

Setting up the Karoo fossil GIS database has been a long-term project which would not have been possible without the cooperation and enthusiasm of the curators of all the Karoo fossil collections in South Africa. We record our gratitude to Sheena Kaal and Roger Smith (Iziko South African Museum), Billy de Klerk (Albany Museum), Richard, Robert and Marion Rubidge (Rubidge Collection), Elize Butler and Jennifer Botha-Brink (National Museum), Bernhard Zipfel (BPI Palaeontology), Heidi Fourie (Transvaal Museum) and Johann Neveling and Ellen de Kock (Council for Geoscience). We are greatly indebted to Cynthia Kemp for the many hours she spent painstakingly editing and updating records. We also record our gratitude to the Palaeontological Scientific Trust (PAST), the Department of Science and Technology (DST), and the (National Research Foundation) NRF for providing funding. We are grateful to Jennifer Botha-Brink and an anonymous reviewer for improving the manuscript.

REFERENCES

BOTHA, J. & SMITH, R.M.H. 2006. Rapid recuperation in the Karoo Basin of South Africa following the End-Permian extinction. *Journal of African Earth Sciences* **45**, 502–514.

BROOM, R. 1906. On the Permian and Triassic faunas of South Africa. *Transactions of the Geological Society of London* **7**, 175–192.

BROOM, R. 1907a. On the geological horizons of the fossil vertebrates of the Karoo Formation. *Records of the Albany Museum* **2**, 156–163.

BROOM, R. 1907b. On some new fossil reptiles from the Karoo beds of Victoria West, South Africa. *Transactions of the South African Philospohical Society* **18**, 31–42.

BROOM, R. 1909. An attempt to determine the horizons of the fossil vertebrates of the Karoo. *Annals of the South African Museum* **7**, 285–289.

COOPER, M.R. 1982. A Mid-Permian to Earliest Jurassic tetrapod biostratigraphy and its significance. *Arnoldia Zimbabwe* **7**, 77–103.

CRUICKSHANK, A.R.I. 1985. Biostratigraphic significance of kanemeyeriid Evolution. *Terra Cognita* **5**, 136.

CRUICKSHANK, A.R.I. 1986. Biostratigraphic and classification of a new Triassic Dicynodont from East Africa. *Modern Geology* **10**, 121–131.

DE FAUW, S.L. 1993. The Pangean dicynodont *Rechnisaurus* from the Triassic of Argentina. **In**: Lucas, S.G. & Morales, M. (eds), The nonmarine Triassic. *New Mexico Museum of Natural History and Science Bulletin* **3**: 101–105.

ERWIN, D.H. 1993. *The Great Paleozoic Crises: Life and Death in the Permian.* New York, Columbia University Press.

ERWIN, D.H. 1994. The Permo-Triassic extinction. *Nature* **367**, 231–236

ERWIN, D.H. 2006. *Extinction: How Life on Earth Nearly Ended 250 Million Years Ago.* Princeton, New Jersey, Princeton University Press

HANCOX, P.J. 1998. *A stratigraphic, sedimentological and palaeoenvironmental synthesis of the Beaufort-Molteno contact in the Karoo Basin.* Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.

HANCOX, P.J., SHISHKIN, M.A., RUBIDGE, B.S. & KITCHING, J.W. 1995. A threefold subdivision of the *Cynognathus* Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographical implications. *South African Journal of Science* **91**, 143–144.

HANCOX, P.J. & RUBIDGE, B.S. 1996. The first specimen of the Mid-Triassic Dicynodont *Angonisaurus* from the Karoo of South Africa: implications for the dating and biostratigraphy of the *Cynognathus* Assemblage Zone, Upper Beaufort Group. *South African Journal of Science* **92**, 391–392.

HANCOX, P.J. & RUBIDGE, B.S. 1997. The role of fossils in interpreting the development of the Karoo Basin. *Palaeontologia africana* **33**, 41–54.

HAUGHTON, S.H. 1924. A bibliographic list of Pre-Stormberg Karroo Reptilia, with a table of horizons. *Transactions of the Royal Society of South Africa* **12**(2), 51–104.

HAUGHTON, S.H. 1963. Note on the distribution of fossil reptiles of Karroo age. *Palaeontologia africana* **7**, 1–11.

HAUGHTON, S.H. 1969. *Geological History of Southern Africa,* 348–526. Johannesburg, Geological Society of South Africa.

HOTTON, N.& KITCHING, J.W. 1963. Speculations on upper Beaufort deposition. *South African Journal of Science* **59**, 254–258.

ISSC: International Subcommission on Stratigraphic Classification, 1976. Hedberg, H.D. (ed.), *International Stratigraphic Guide, 200.* New York, Wiley-Interscience.

ISSC: International Subcommission on Stratigraphic Classification, 1994. *International Stratigraphic Guide* (2nd edn). Trondheim, International Union of Geological Sciences, and Boulder, Geological Society of America.

KEYSER, A.W. 1979. A review of the biostratigraphy of the Beaufort Group in the Karoo basin of South Africa. Abstracts from Geocongress, Geological Society of South Africa **2**, 13–31.

KEYSER, A.W. & SMITH, R.M.H. 1979. Vertebrate biozonation of the Beaufort Group with special reference to the Western Karoo Basin. *Annals of the Geological Survey South Africa* **12**, 1–36.

KITCHING, J.W. 1970. A short review of the Beaufort Zoning in South Africa. **In**: *Second Gondwana Symposium – Proceedings and Papers,* 309–313. Pretoria, Council for Scientific and Industrial Research.

KITCHING, J.W. 1972. *On the distribution of the Karoo vertebrate fauna, with special reference to certain genera and the bearing of this distribution on the zoning of the Beaufort beds.* Unpublished Ph.D thesis, University of the Witwatersrand, Johannesburg.

KITCHING, J.W. 1977. The distribution of the Karoo vertebrate fauna, 131. *Memoirs of the Bernard Price Institute for Palaeontological Research, University Witswatersrand* **1**.

KITCHING, J.W. 1984. A reassessment of the biozonation of the Beaufort Group. *Palaeontology News* **4**(1), 12–13.

LUCAS, S.G., 1990. Toward a vertebrate biochronology of the Triassic. *Albertiana* **8**, 36–41.

LUCAS, S.G. 1993. The Shansiodon biochronology, Middle Triassic of Pangaea. *Albertiana* **11**, 40–42.

LUCAS, S.G. 1995. Towards dicynodont biochronology. *Albertiana* **16**, 33–40.

LUCAS, S.G. 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology* **143**(4), 347–384

NICOLAS, M.V. 2007. *Tetrapod biodiversity through the Permo-Triassic Beaufort Group (Karoo Supergroup) of South Africa.* Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.

NICOLAS, M.V. & RUBIDGE, B.S. 2009. Assessing content and bias in South African Permo-Triassic Karoo tetrapod fossil collections. *Palaeontologia africana* **44**, 13–20.

OCHEV, V.G. & SHISHKIN, M.A. 1989. On the principles of global correlation of the continental Triassic on the tetrapods. *Acta Palaeontologica Polonica* **34** 149–173.

RUBIDGE, B.S. 1984. The cranial morphology and palaeoenvironment of Eodicynodon Barry (Therapsida: Dicynodontia). *Navorsinge van die Nasionale Museum Bloemfontein, South Africa* **4**(14), 325–402.

RUBIDGE, B.S. 1990. A new vertebrate biozone at the base of the Beaufort Group, Karoo sequence (South Africa). *Palaeontologia africana* **27**, 17–20.

RUBIDGE, B.S. 1995a. Biostratigraphy of the *Eodicynodon* Assemblage Zone. **In**: Rubidge, B.S. (ed.), *Biostratigraphy of the Beaufort Group* (*Karoo Supergroup*), 3–7. South African Committee for Stratigraphy. *Biostratigraphic Series* **1**. Pretoria, Council for Geoscience.

RUBIDGE, B.S. (ed.) 1995b. *Biostratigraphy of the Beaufort Group* (*Karoo Supergroup*). South African Committee for Stratigraphy. *Biostratigraphic Series* **1**. Pretoria, Council for Geoscience.

RUBIDGE, B.S., KITCHING, J.W. & VAN DEN HEEVER, J.A. 1983. First record of a therocephalian (Therapsida: Pristerognathidae) from the Ecca of South Africa. *Navorsinge van die Nasionale Museum Bloemfontein,* South Africa **4**, 229–235.

RUBIDGE, B.S., KING, G. & HANCOX, P.J. 1994. The postcranial skeleton of the earliest dicynodont synapsid, *Eodicynodon* from the Upper Permian of South Africa. *Palaeontology* 37(2), 397–408.

RUBIDGE, B.S. 2005. Re-uniting lost continents – Fossil reptiles from the ancient Karoo and their wanderlust. *South African Journal of Geology* **108**(3), 135–172.

SACS: South African Committee for Stratigraphy, 1980. *Stratigraphy of South Africa. Part 1: Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia and the Republics of Boputhatswana, Transkei and Venda* (L.E. Kent, comp.), 690. Handbook of the Geological Survey, South Africa, 8.

SEELEY, H.G. 1892. Researches on the structure, organization and classification of the fossil Reptilia. **In**: *Further Observations on* Pareiasaurus, 311–370. *Philosophical Transactions of the Royal Society, London, B* **183**.

SHISHKIN, M.A. & OCHEV, V.G. 1992. On the problem of dating the Upper Beaufort vertebrate faunas. **In**: Abstracts, 24th Congress of the Geological Society South Africa, Bloemfontein, 366–368.

SHISHKIN, M.A., RUBIDGE, B.S. & HANCOX, P.J. 1995. Vertebrate biozonation of the Upper Beaufort Series of South Africa – a new look on correlation of the Triassic biotic events in Euamerica and southern Gondwana. **In**: Sun, A. & Wang, Y. (eds), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota.* Short papers, 39–41. Beijing: China Ocean Press.

SMITH, R.M.H. 1995. Changing fluvial environments across the Permian-Triassic boundary in the Karoo Basin, South Africa and the possible causes of tetrapod extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology* **117**, 81–104.

SMITH, R.M.H. & BOTHA, J. 2005. The recovery of terrestrial vertebrate diversity in the South African Karoo Basin after the end-Permian extinction. *Comptes Rendus Palévol* **4**, 555–568.

VON HUENE, F. 1940. Die Saurier de Karroo-, Gondwana- und verwandten Ablagerungen in faunistischer, biologischer und phylogonetischer Hinsicht. N*eues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abhandlungen* **83**, 275–303.

WARD, P.D., MONTGOMERY, D.R. & SMITH, R.M.H. 2000. Altered river morphology in South Africa related to the Permian-Triassic extinction. *Science* **289**, 1740–1743.

WATSON, D.M.S. 1914a. The zones of the Beaufort Beds of the Karoo System in South Africa. *Geological Magazine, New Series, Decade* **6**(1), 203–208.

WATSON, D.M.S. 1914b. On the nomenclature of the South African pareiasaurians. *Annals of the Magazine of Natural History* **8**(14), 98–102.

WELMAN, J., LOOCK, J.C. & RUBIDGE, B.S. 2001. New evidence for diachroneity of the Ecca-Beaufort contact (Karoo Supergroup, South Africa). *South African Journal of Science* **97**, 320–322.

Massospondylus carinatus Owen 1854 (Dinosauria: Sauropodomorpha) from the Lower Jurassic of South Africa: Proposed conservation of usage by designation of a neotype

Adam M. Yates[1*] & Paul M. Barrett[2]

[1]*Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3, WITS, 2050 Johannesburg, South Africa*

[2]*Department of Palaeontology, The Natural History Museum, Cromwell Road, London, SW7 5BD, U.K.*

Received 17 February 2010. Accepted 12 November 2010

The purpose of this article is to preserve the usage of the binomen *Massospondylus carinatus* by designating a neotype specimen. *Massospondylus* is the most abundant basal sauropodomorph dinosaur from the Early Jurassic strata of southern Africa. This taxon forms the basis for an extensive palaeobiological literature and is the eponym of Massospondylidae and the nominal taxon of a biostratigraphical unit in current usage, the '*Massospondylus* Range Zone'. The syntype series of *M. carinatus* (five disarticulated and broken vertebrae) was destroyed during World War II, but plaster casts and illustrations of the material survive. Nonetheless, these materials cannot act as type material for this taxon under the rules of the ICZN Code. In order to avoid nomenclatural instability, we hereby designate BP/1/4934 (a skull and largely complete postcranial skeleton) as the neotype of *Massospondylus carinatus*.

Keywords: Dinosauria, Sauropodomorpha, Massospondylidae, *Massospondylus*, *Massospondylus carinatus*, neotype, South Africa, upper Elliot Formation, Early Jurassic.

INTRODUCTION

Richard Owen described and named *Massospondylus carinatus* (1854, p. 97) with *carinatus* as the type species of the genus by monotypy. The original description lacked illustrations and was based on part of a collection of 56 disarticulated fossil reptile bones that were donated to the Hunterian Museum of the Royal College of Surgeons, London. These bones were collected from the farm Beauchef Abbey 215 in the Harrismith District of what is now the Free State Province, South Africa (Kitching & Raath 1984). Although the type stratum was not recorded only the upper member of the Elliot Formation is accessible at the type locality (Kitching & Raath 1984). Owen positively ascribed five vertebrae to *M. carinatus* (Owen 1854: catalogue numbers 331–335), although 13 others (336–337, 349–350, 352, 354, 358–364) were referred to this taxon with some reservations. No holotype was designated. Consequently specimens 331–335 form the syntype series of this taxon.

The syntype series was destroyed when the Hunterian Museum was hit during a bombing raid on 10 May 1941, but many of the bones were illustrated by Lydekker (1890), Seeley (1895) and von Huene (1906), and a series of casts of the syntypes still survive and are housed in the Iziko South African Museum, Cape Town, South Africa (SAM PKC 958–62), and the Natural History Museum, London (NHMUK R3027–8).

Owen (1854) proposed two additional binomials, based upon other bones from the same collection: *Pachyspondylus orpeni* (Owen 1854, p. 99) and *Leptospondylus capensis* (Owen 1854, p. 100). As noted by Seeley (1895), these taxa were based on caudal vertebrae that may represent the same taxon, possibly even the same individual, as at least some of the syntype series of *Massospondylus carinatus*. Their initial separation from *Massospondylus carinatus* was based on Owen's mistaken belief that the cervical vertebrae in the syntype series were caudals. Seeley (1895, pp. 103–104), acting as first reviser, affirmed the priority of *Massospondylus carinatus* and relegated *Pachyspondylus orpenii* and *Leptospondylus capensis* to the status of *nomina dubia* that may be junior synonyms of *Massospondylus carinatus*. All subsequent works that mention *P. orpenii* and *L. capensis* continue to treat these two taxa as *nomina dubia* that cannot be distinguished from *Massospondylus carinatus* (von Huene 1906; Broom 1911; Steel 1970; Cooper 1981; Galton 1990; Galton & Upchurch 2004; Sues *et al.* 2004).

Four other species in the genus *Massospondylus* (*M. browni* Seeley 1895; *M. harriesii* Broom 1911; *M. schwarzi* Haughton 1924; and *M. kaalae* Barrett 2009) have been named subsequently; the earlier three are based on fragmentary postcranial specimens from the upper part of the Elliot Formation. With the exception of *M. kaalae*, which is retained as a valid taxon, these taxa are currently regarded as either *nomina dubia* or junior subjective synonyms of *M. carinatus* Owen (e.g. Cooper 1981; Galton & Upchurch 2004). Numerous other taxa (*Hortalotarsus skirtopodus* Seeley 1894; *Aetonyx palustris* Broom 1911; *Aristosaurus erectus* Van Hoepen 1920a; *Dromicosaurus gracilis* Van Hoepen 1920b; *Gryponyx taylori* Haughton 1924; and *Thecodontosaurus dubius* Haughton 1924), also from the upper Elliot Formation or the overlying Clarens Formation, are similarly regarded as junior subjective synonyms of *M. carinatus* or *nomina dubia* that are indistinguishable from *M. carinatus*.

*Author for correspondence. E-mail: yatesam@gmail.com

THE NEED FOR A NEOTYPE

Examination of the surviving plaster casts indicates that the original syntype series is inadequate for diagnosing a genus and species of basal sauropodomorph. All of the diagnostic characteristics currently applied to *Massospondylus carinatus* are features of the skull (Sues *et al.* 2004) and the syntype series preserves no cranial material. A prominent muscle scar on the lateral surface of the midshaft of the fibula has also been proposed as an autapomorphy of this taxon (Galton & Upchurch 2004). However, this character is widespread amongst basal sauropodomorphs and cannot be determined in the syntype series, which includes only vertebrae. Indeed the syntypes are so inadequate that it is not possible to determine with confidence whether or not they belong to the more inclusive taxon Massospondylidae. This problem could be solved by designating *Massospondylus carinatus* a *nomen dubium* and re-instating the next available genus and species name based on diagnostic material. Unfortunately, only *M. kaalae* is based on a specimen that includes adequate skull material and this appears to be distinctive and unlike any of the other skulls referred to *M. carinatus* to date. None of the other named taxa displays any of the characters that are currently used to diagnose *Massospondylus carinatus.* Although it is likely that a relatively complete postcranium will display a unique combination of character states, none of the available names are based on sufficiently complete material. If *Massospondylus* is to be rendered a *nomen dubium* the only course left in strict accord with the code is to erect a new name for the set of specimens universally recognized as *M. carinatus* and to base this new name on one of several relatively complete specimens that include a well-preserved skull (e.g. BP/1/4779, BP/1/4923, BP/1/5241 or SAM-PK-K1314, for skulls see Gow *et al.* 1990; Sues *et al.* 2004; Barrett & Yates 2006).

Massospondylus carinatus has been regarded as the dominant vertebrate taxon of the upper Elliot Formation since its description. Due to its abundance, the biostratigraphical unit at the top of the Karoo succession in southern Africa has been designated the '*Massospondylus* Range Zone' (Kitching & Raath 1984), which is a term in general usage (e.g. Smith & Kitching 1997; Barrett 2004; Bordy *et al.* 2004; Sidor & Hancox 2006). Furthermore, the abundance of high quality material has enabled numerous palaeobiological studies that refer these specimens to the binomen *Massospondylus carinatus.* These include general anatomical studies (Cooper 1981; Gow 1990; Gow *et al.* 1990; Sues *et al.* 2004, Barrett & Yates 2006), detailed cranial anatomy based on CT-scanning (Sereno *et al.* 2007; Holliday & Witmer 2008), bone histology and growth trajectories (Chinsamy 1993), feeding ecology (Raath 1974; Cooper 1981; Crompton & Attridge 1986; Barrett 2000), nesting and possible parental behaviour (Reisz *et al.* 2005), eggshell microstructure (Zelenitzky & Modesto 2002) and embryological anatomy and growth allometry (Reisz *et al.* 2005). Lastly, *Massospondylus* has been a mainstay of numerical cladistic analyses of sauropodomorph dinosaur phylogeny (Upchurch 1995; Sereno 1999; Benton *et al.* 2000; Yates 2003, 2004, 2007; Yates & Kitching 2003; Galton & Upchurch 2004; Smith & Pol 2007; Upchurch *et al.* 2007; Martínez 2009). To rename the taxon would create widespread confusion by referring to a large set of material, widely known as *Massospondylus carinatus,* to a new unfamiliar binomen, with any new taxon name obscuring the relationship between these specimens and this large body of work.

Massospondylus is also the eponym of the family group name Massospondylidae (von Huene 1914, p. 13) which is in current use in dinosaur systematics (Galton 1990; Sereno 1999; Yates 2003, 2007; Smith & Pol 2007; Martínez 2009) and renaming *Massospondylus* would also necessitate destabilizing higher sauropodomorph taxonomy by requiring the replacement of Massospondylidae.

One might argue that if all basal sauropodomorphs from the upper Elliot Formation are referable to a single species, then the inadequacy of the syntypes is not an issue, since we can be confident that they belong to the same taxon that the name is being applied to. However, this is not the case. Although the recent literature treats the genus as monotypic, there are now indications that several basal sauropodomorph taxa are present in the upper Elliot Formation (Yates *et al.* 2007) and more than one species is present within the *Massospondylus* sample from the upper Elliot Formation (Barrett 2009). Without an adequate type specimen it is currently impossible to correctly decide which of these species might represent *M. carinatus* as based on its syntype series.

Sues *et al.* (2004, p. 240) suggested that it was advisable to designate a neotype specimen for *Massospondylus carinatus* but noted that this action would have to wait until a "comprehensive revision of all basal sauropodomorphs from the 'Stormberg Group' of South Africa". However, as we note in the preceding paragraph, the lack of a neotype is actually impeding the progress of this revision. Sues *et al.* (2004) suggested BP/1/4934 as a candidate neotype specimen, but it should be noted that this proposal does not qualify as a formal neotype designation as it does not fulfill all of the requirements of Article 75 of the ICZN Code (ICZN 1999).

The plaster casts of the syntype specimens cannot act as type specimens under the auspices of the ICZN code, which states clearly that type specimens must represent actual specimens, rather than copies or illustrations thereof (Article 72.5: ICZN 1999). As there is good documentary evidence that the syntype series of *Massospondylus carinatus* has been destroyed it is necessary and appropriate to designate a neotype for this taxon, under Article 75 of the Code (ICZN 1999). Such designations can be made without a formal ruling from the ICZN Commissioners (ICZN 1999; S. Nikolaeva, pers. comm. 2009).

SUGGESTED NEOTYPE

Here, we formalize the suggestion of Sues *et al.* (2004) and propose a neotype specimen for *Massospondylus carinatus.* BP/1/4934 is a well-preserved articulated skeleton, including a skull (Fig. 1). It is preserved in the collections of the Bernard Price Institute for Palaeontological Research, which maintains an active research collection, has adequate facilities for preserving type specimens and will make the

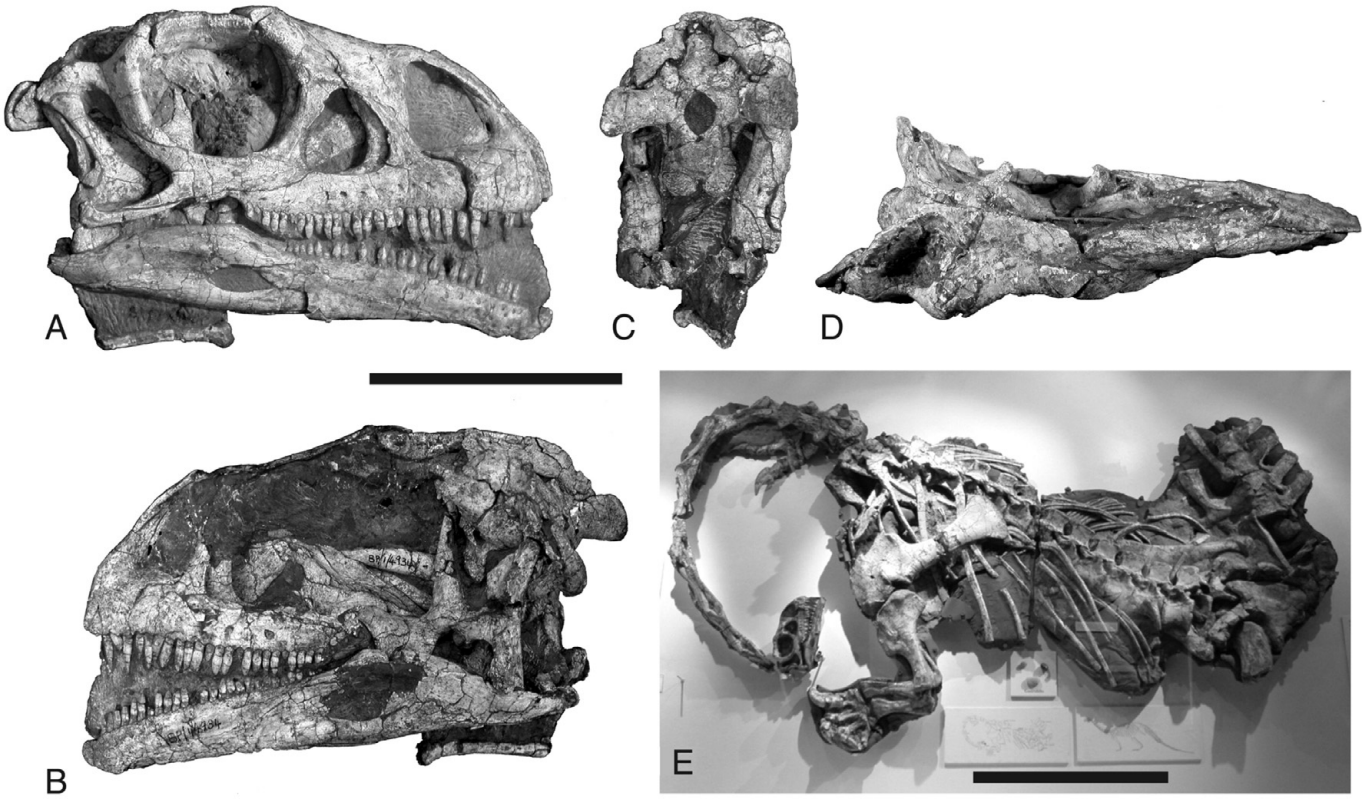


Figure 1. BP/1/4934 the proposed neotype of *Massospondylus carinatus* Owen. **A**, Skull in right lateral view; **B**, skull in left lateral view; **C**, skull in occipital view; **D**, skull in dorsal view; **E**, skull and postcranial skeleton as displayed at the Bernard Price Institute in 2001. Scale bar in A–D = 100 mm; scale bar in E = 500 mm.

proposed neotype accessible for study by other researchers. The skull of this individual has been figured and described in detail (e.g. Gow *et al.* 1990; Sues *et al.* 2004) and a figure of the postcranial skeleton has also been published (MacCrae 1999, p. 203). The specimen is widely acknowledged to be an individual of *Massospondylus carinatus* in the literature and possesses the characteristic features that have been proposed to distinguish this taxon from other basal sauropodomorph dinosaurs (e.g. Gow *et al.* 1990; Sues *et al.* 2004; Barrett 2009; see also references cited therein). Moreover, all features of BP/1/4934 are consistent with those that have been illustrated or described for the original syntype series of *M. carinatus.* No other binomen has ever been applied to this individual. The specimen was collected on the farm Bormansdrift, in the Clocolan District of the Free State Province from the upper part of the Elliot Formation and thus comes from the same stratum as the original syntypes. Fixation of BP/1/4934 as the neotype will solve the above-mentioned problems with no disruption to the existing usage of either the genus name *Massospondylus* or the binomen *Massospondylus carinatus.*

INSTITUTIONAL ABBREVIATIONS

BP	Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg
NHMUK	Natural History Museum, London
SAM	Iziko South African Museum, Cape Town

We thank Svetlana Nikolaeva of the ICZN for discussion and P.M.B. thanks Michael Raath (BP) and Sheena Kaal (SAM) for access to dinosaur material in their care.

REFERENCES

BARRETT, P.M. 2000. Prosauropod dinosaurs and iguanas: speculations on the diets of extinct reptiles. **In**: Sues, H-D. (ed.), *Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record,* 42–78. Cambridge, Cambridge University Press.

BARRETT, P.M. 2004. Sauropodomorph dinosaur diversity in the upper Elliot Formation (*Massospondylus* range zone: Lower Jurassic) of South Africa. *South African Journal of Science* **100**, 501–503.

BARRETT, P.M. 2009. A new basal sauropodomorph dinosaur from the upper Elliot Formation (Lower Jurassic) of South Africa. *Journal of Vertebrate Paleontology* **29**, 1032–1045.

BARRETT, P.M. & YATES, A.M. 2006. New information on the palate and lower jaw of *Massospondylus* (Dinosauria: Sauropodomorpha). *Palaeontologia africana* **41**, 123–130.

BENTON, M.J., JUUL, L., STORRS, G.W. & GALTON, P.M. 2000. Anatomy and systematics of the prosauropod dinosaur *Thecodontosaurus antiquus* from the Upper Triassic of southwest England. *Journal of Vertebrate Paleontology* **20**, 77–108.

BORDY, E.M., HANCOX, P.J. & RUBIDGE, B.S. 2004. Basin development during the deposition of the Elliot Formation (Late Triassic – Early Jurassic), Karoo Supergroup, South Africa. *South African Journal of Geology* **107**, 397–412.

BROOM, R. 1911. On the dinosaurs of the Stormberg, South Africa. *Annals of the South African Museum* **7**, 291–312.

CHINSAMY, A. 1993. Bone histology and growth trajectory of the prosauropod dinosaur *Massospondylus carinatus* Owen. *Modern Geology* **18**, 319–329.

COOPER, M.R. 1981. The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. *Occasional Papers of the National Museums and Monuments Rhodesia, Series B, Natural Sciences* **6**, 689–840.

CROMPTON, A.W. & ATTRIDGE, J. 1986. Masticatory apparatus of the larger herbivores during Late Triassic and Early Jurassic time. **In**: Padian, K. (ed.), *The Beginning of the Age of the Dinosaurs,* 223–236. Cambridge, Cambridge University Press.

GALTON, P.M. 1990. Basal Sauropodomorpha–Prosauropoda. **In**: Weishampel, D.B., Dodson, P. & Osmólska, H. (eds), *The Dinosauria,* 320–344. Berkeley, University of California Press.

GALTON, P.M. & UPCHURCH, P. 2004. Prosauropoda. **In**: Weishampel,

D.B., Dodson, P. & Osmólska, H. (eds), *The Dinosauria* (2nd edn), 232–58. Berkeley, University of California Press.

GOW, C.E. 1990. Morphology and growth of the *Massospondylus* braincase (Dinosauria, Prosauropoda). *Palaeontologia africana* **27**, 59–75.

GOW, C.E., KITCHING, J.W. & RAATH, M.A. 1990. Skulls of the prosauropod dinosaur *Massospondylus carinatus* Owen in the collections of the Bernard Price Institute for Palaeontological Research. *Palaeontologia africana* **27**, 45–58.

HAUGHTON, S.H. 1924. The fauna and stratigraphy of the Stormberg Series. *Annals of the South African Museum* **12**, 323–497.

HOLLIDAY, C.M. & WITMER, L.M. 2008. Cranial kinesis in dinosaurs: intracranial joints, protractor muscles, and their significance for cranial evolution and function in diapsids. *Journal of Vertebrate Paleontology* **28**, 1073–1088.

HUENE, F. von. 1906. Uber die Dinosaurier der aussereuropaischen Trias. *Geologische und palaeontologische Abhandlungen* **8**, 97–156.

HUENE, F. von. 1914. *Saurischia et Ornithischia triadica ('Dinosauria' triadica). Fossilium Catalogus. 1. Animalia* **4**, 1–24.

KITCHING, J.W. & RAATH, M.A. 1984. Fossils from the Elliot and Clarens Formations (Karoo Sequence) of the North-eastern Cape, Orange Free State and Lesotho, and a suggested biozonation, based on tetrapods. *Palaeontologia africana* **25**, 111–125.

LYDEKKER, R. 1890. *Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History). Part IV (containing the orders Anomodontia, Ecaudata, Caudata and Labyrinthodontia; and Supplement).* British Museum (Natural History), London.

MACCRAE, C. 2009. *Life etched in Stone: Fossils of South Africa.* Johannesburg, The Geological Society of South Africa.

MARTÍNEZ, R.N. 2009. *Adeopapposaurus mognai,* gen. et sp. nov. (Dinosauria: Sauropodomorpha), with comments on adaptations of basal Sauropodomorpha. *Journal of Vertebrate Paleontology* **29**, 142–164.

OWEN, R. 1854. *Descriptive catalogue of the fossil organic remains of Reptilia and Pisces contained in the Museum of the Royal College of Surgeons.* London, Taylor and Francis.

RAATH, M.A. 1974. Fossil vertebrate studies in Rhodesia: further evidence of gastroliths in prosauropod dinosaurs. *Arnoldia* **7**(5), 1–7.

REISZ, R.R., SCOTT, D., SUES, H-D., EVANS, D.C. & RAATH, M.A. 2005. Embryos of an Early Jurassic prosauropod dinosaur and their evolutionary significance. *Science* **309**, 761–764.

SEELEY, H.G. 1894. On *Hortalotarsus skirtopodus,* a new saurischian fossil from Barkly East, Cape Colony. *Annals and Magazine of Natural History* (6)**13**, 411–419.

SEELEY, H.G. 1895. On the type of the genus *Massospondylus,* and on some vertebrae and limb-bones of *M.* (?) *browni. Annals and Magazine of Natural History* (6)**15**, 102–125.

SERENO, P.C. 1999. The evolution of dinosaurs. *Science* **284**, 2137–2147.

SERENO, P.C., WILSON, J.A., WITMER, L.M., WHITLOCK, J.A., MAGA, A., IDE, O. & ROWE, T.A. 2007. Structural extremes in a Cretaceous dinosaur. *PLoS One* **11**, e1230 (doi: 10.1371/journal.pone.0001230).

SIDOR, C.A. & HANCOX, P.J. 2006. *Elliotherium kersteni,* a new tritheledontid from the lower Elliot Formation (Upper Triassic) of South Africa. *Journal of Paleontology* **80**, 333–342.

SMITH, N.D & POL, D. 2007. Anatomy of a basal sauropodomorph dinosaur from the Early Jurassic Hanson Formation of Antarctica. *Acta Palaeontologica Polonica* **52**, 657–674.

SMITH, R.M.H. & KITCHING, J.W. 1997. Sedimentology and vertebrate taphonomy of the *Tritylodon* Acme Zone: a reworked palaeosol in the lower Jurassic Elliot Formation, Karoo Supergroup, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **131**, 29–50.

STEEL, R. 1970. *Saurischia. Handbuch der Paläoherpetologie,* **14**. Stuttgart, Gustav Fischer Verlag.

SUES, H-D., REISZ, R.R., HINIC, S. & RAATH, M.A. 2004. On the skull of *Massospondylus carinatus* Owen, 1854 (Dinosauria: Sauropodomorpha) from the Elliot and Clarens formations (Lower Jurassic) of South Africa. *Annals of the Carnegie Museum* **73**, 239–257.

UPCHURCH, P. 1995. The evolutionary history of the sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London B* **349**, 365–390.

UPCHURCH, P., BARRETT, P.M. & GALTON, P.M. 2007. A phylogenetic analysis of basal sauropodomorph relationships: implications for the origin of sauropod dinosaurs. **In**: Barrett, P.M. & Batten, D.J. (eds). - *Evolution and Palaeobiology of Early Sauropodomorph Dinosaurs,* 57–90. *Special Papers in Palaeontology* **77**.

VAN HOEPEN, E.C.N. 1920a. Contributions to the knowledge of the reptiles of the Karoo Formation. 5. A new dinosaur from the Stormberg Beds. *Annals of the Transvaal Museum* **7**, 77–92.

VAN HOEPEN, E.C.N. 1920b. Contributions to the knowledge of the reptiles of the Karoo Formation. 6. Further dinosaurian material in the Transvaal Museum. *Annals of the Transvaal Museum* **7**, 93–140.

YATES, A.M. 2003. A new species of the primitive dinosaur *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. *Journal of Systematic Palaeontology* **1**, 1–42.

YATES, A.M. 2004. *Anchisaurus polyzelus* (Hitchcock): the smallest known sauropod dinosaur and the evolution of gigantism among sauropodomorph dinosaurs. *Postilla* **230**, 1–57.

YATES, A.M. 2007. The first complete skull of the Triassic dinosaur *Melanorosaurus* Haughton (Sauropodomorpha: Anchisauria). **In**: Barrett, P.M. & Batten, D.J. (eds), *Evolution and Palaeobiology of Early Sauropodomorph Dinosaurs,* 9–55. *Special Papers in Palaeontology* **77**.

YATES, A.M. & KITCHING, J.W. 2003. The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. *Proceedings of the Royal Society of London B* **270**, 1753–1758.

YATES, A.M., BONNAN, M.F. & NEVELING, J. 2007. A new diverse dinosaur assemblage from the Early Jurassic of South Africa. *Journal of Vertebrate Paleontology* **27**(3-Suppl.), 169A.

ZELENITZKY, D.K. & MODESTO, S.P. 2002. Re-evaluation of the eggshell structure of eggs containing dinosaur embryos from the Lower Jurassic of South Africa. *South African Journal of Science* **98**, 407–408.

Preliminary investigation of Matjhabeng, a Pliocene fossil locality in the Free State of South Africa

Darryl J. de Ruiter[1,2*], Juliet K. Brophy[1], Patrick J. Lewis[3], Alicia M. Kennedy[3], Thomas A. Stidham[4], Keely B. Carlson[1] & P. John Hancox[2]

[1]*Department of Anthropology, Texas A&M University, College Station, TX, 77843-4352, U.S.A.*

[2]*Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3, WITS, 2050 Johannesburg, South Africa*

[3]*Department of Biological Sciences, Sam Houston State University, Huntsville, TX, 77341, U.S.A.*

[4]*Department of Biology, Texas A&M University, College Station, TX, 77843, U.S.A.*

Received 10 August 2010. Accepted 22 October 2010

The early Pliocene is a relatively poorly understood period in southern Africa. Fossil deposits such as Langebaanweg (*c.* 5.0 Ma) and Makapansgat (*c.* 2.5 Ma) have each produced large and well-documented faunal assemblages, and it is clear that a significant turnover of fauna occurred between the early and late Pliocene respectively. However, the temporal separation between Langebaanweg and Makapansgat represents a significant gap in our knowledge of faunal composition and evolution in the Pliocene of southern Africa. In 2007 we began a programme of excavation at an early Pliocene locality referred to as Matjhabeng (formerly Virginia) in the Free State of South Africa. With an estimated age of 4.0–3.5 Ma, this site represents a temporal and geographic intermediate between the better known sites to the north and south. It also represents the only well-documented, river-deposited Pliocene locality in the central interior of southern Africa. After three years of excavation, we have recovered a diverse fauna that includes fish, amphibians, reptiles, birds and mammals. Mammals range in size from rodents to mammoths, including an array of proboscideans, perissodactyls and artiodactyls, alongside rare carnivores. We report here on the macromammalian assemblage recovered to date. In total, we have recognized 29 taxa, including the oldest *Ancylotherium* and the oldest *Megalotragus* fossils in southern Africa. Some of the taxa from Matjhabeng are shared with Langebaanweg, and others with Makapansgat, confirming the intermediate status of this locality. Isotopic analysis reveals the earliest indication of extensive grasslands in South Africa, though these grasslands were part of an environmental mosaic that included significant woodland, and probable wetland, components.

Keywords: *Megalotragus, Mammuthus subplanifrons,* faunal assemblage, isotopes, earliest grasslands.

INTRODUCTION

The early Pliocene of Africa represents a crucial period in the evolutionary history of the Hominidae, and in East Africa, numerous fossil localities in Ethiopia, Kenya and Tanzania sample this time frame (Brunet *et al.* 2002; Haile-Selassie *et al.* 2004; Leakey *et al.* 1995, 1998; White *et al.* 1994, 1995, 2009). However, the same period in South Africa is relatively poorly known. The site of Langebaanweg in the Western Cape has produced a particularly rich, well-documented faunal assemblage dating to approximately 5.0 Ma (Hendey 1981a,b, 1982). However, the chronologically closest sites to Langebaanweg with significant faunal samples are the hominin-bearing caves of the former Transvaal, such as Makapansgat and Sterkfontein, both of which fall into the late Pliocene. With dates of less than 2.5 Ma for these latter sites (Berger *et al.* 2002; Latham *et al.* 2007; Pickering & Kramers 2010; Walker *et al.* 2006), the temporal separation between Langebaanweg and Makapansgat/Sterkfontein represents a significant gap in our knowledge of faunal composition and evolution in the earlier Pliocene of South Africa. What is therefore needed is a faunal sample from a locality within this time range.

In 1955, during the course of digging operations to open a new railway cutting near the town of Virginia in the Free State, workers uncovered several fossils of an extinct proboscidean, including a tusk, a molar, and a proximal ulnar fragment. The site is located on Farm Virginia 448 (reference map 2826BB; 28°06′39′S, 26°54′56′E), and was originally referred to as the Virginia Railway Cut Site, though to avoid confusion with sites outside of South Africa we have renamed the locality Matjhabeng in honor of the Municipality in which it resides (Fig. 1). Originally attributed to a new species, *Mammuthus scotti* (Meiring 1955), these first fossils were later referred to *M. subplanifrons* (Maglio 1973; Maglio & Hendey 1970). Although *M. subplanifrons* is currently poorly defined (Cooke & Maglio 1972; Maglio & Hendey 1970), there are nonetheless several cranio-dental features that can diagnose the taxon (Kalb & Mebrate 1993; Maglio 1973). In particular, the presence of a characteristically curved tusk in the Matjhabeng specimen renders it one of the most securely identified *Mammuthus* individuals in Africa (Coppens *et al.* 1978; Maglio 1973). Within the Free State, in fact within the central interior of southern Africa, the site of Matjhabeng affords the unique opportunity to examine the composition of an early Pliocene faunal assemblage recovered from a horizontally stratified, riverine deposit.

PLIOCENE FAUNAS OF SOUTHERN AFRICA

The remarkable fauna recovered from the site of Langebaanweg stands in stark contrast to the faunas recovered from such late Pliocene South African localities as Makapansgat and Sterkfontein. Langebaanweg is generally considered to be earliest Pliocene in age at *c.* 5.0 Ma (Hendey 1981a,b, 1982), though some have suggested an even older date of 6.0 Ma (Gentry 1980). The

*Author for correspondence. E-mail: deruiter@tamu.edu

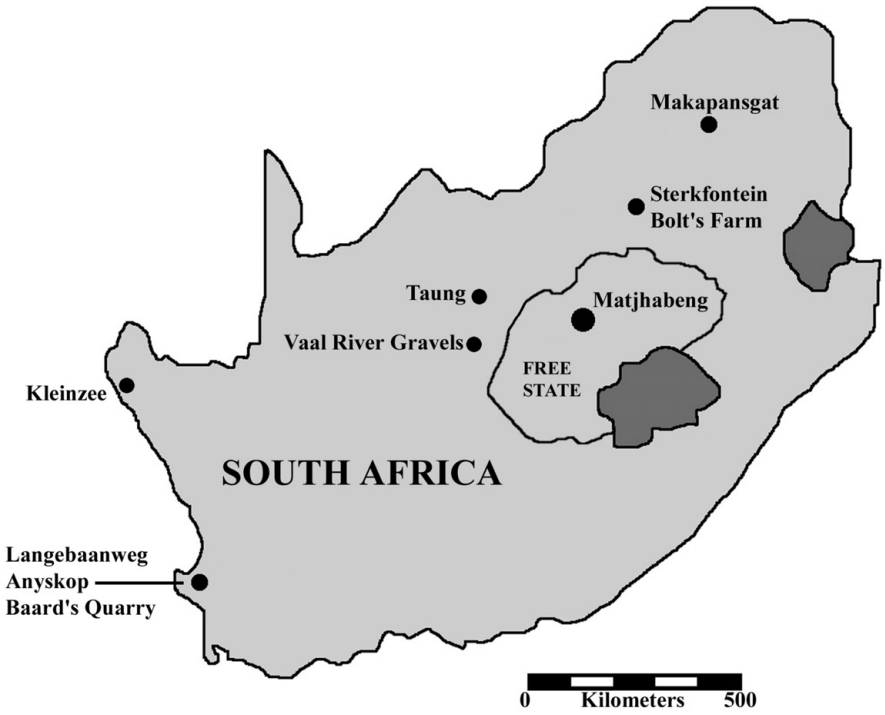


Figure 1. Map of South Africa showing the main fossil localities mentioned in the text.

faunal assemblage itself exhibits a number of taxa not known from elsewhere in southern Africa (Hendey 1976a,b, 1982), and represents a particularly rich and diverse animal community (Bone & Singer 1965; Gentry 1974, 1980; Hendey 1970, 1972, 1973, 1976a,b, 1978a,b, 1981a). The majority of Langebaanweg species are extinct, and include such exceptional taxa as the only ursid (*Agriotherium africanum*), okapi (Palaeotragine) and peccary (*Pecarichoerus africanus*) known in southern Africa (Hendey 1976a,b, 1982). Approximately 2 km east of Langebaanweg is the fossiliferous Bredasdorp Formation, which includes two separate deposits, Anyskop and Baard's Quarry (Hendey, 1978c, 1982). Anyskop appears to be later Pliocene in age, and comprises mainly land snail and tortoise shells with rare mammalian fossils (Hendey 1982). Baard's Quarry contains highly fragmented terrestrial vertebrate fossils that are considered to be either late Pliocene or early Pleistocene (Gentry 1980; Hendey 1978c). The first fossil specimen recovered from Baard's Quarry was a proboscidean molar fragment that was referred to *M. subplanifrons* (Hendey 1978c; Maglio & Hendey, 1970; Singer & Hooijer 1958). Unfortunately the specimen has since gone missing, and its identification as *M. subplanifrons* is inconclusive (e.g. Maglio 1973). Hendey (1978c) documented some level of mixing in the Baard's Quarry fauna, further complicating age estimation of the deposit.

The 'Older Gravels' of the Vaal River Gravels have produced a series of haphazardly collected fossils, some of which possibly exceed 4.0 Ma in age (Butzer *et al.* 1973; Helgren 1977, 1979). The majority of the fossils were collected in the early half of the last century by amateurs thus only minimal provenance information is available. Today virtually all of the Vaal River Gravels have been disturbed or destroyed by more than a century of active diamond mining. Although there is no clear relationship between fossils attributed to the 'Older Gravels', several important specimens have been described in the past, including the type specimen of *M. subplanifrons* (Osborn 1928). On the west coast of South Africa, Kleinzee is a little known fossil locality located approximately 400 km north of Langebaanweg in Namaqualand, at the mouth of the Buffels River. Originally thought to be 'middle Pliocene' (Stromer 1931), the site is now considered to be late Pliocene or early Pleistocene (Hendey 1970).

The site of Taung in the Northwest Province revealed the first ever recovered australopith fossil (Dart 1925). Although the initial consignment of breccia sent to Dart in 1924 included a selection of non-hominin fossils, the association between these fossils and the Taung Child itself is uncertain owing to the blasting operations that originally revealed the hominin skull (de Ruiter *et al.* 2010). Subsequent exploration in the 1920s (Hrdlička 1925) and again in the 1980s and 1990s (McKee & Tobias 1990) failed to recover additional hominin remains and the composition of the animal paleocommunity to which the Taung fossil belonged remains unknown. The age of the site is estimated at 2.8–2.4 Ma (McKee 1993), though uncertainty over the actual make-up of the Taung faunal assemblage makes an accurate age estimate difficult.

Bolt's Farm is located approximately 2 km southwest of Sterkfontein, and consists of a series of irregularly excavated gravel pits that have been unsystematically sampled over the past several decades. The majority of the fossil deposits have been destroyed by gravel mining activities, and the relationship between recovered fossils is uncertain. Age estimates range from 4.0–2.0 Ma for different components of the site, and it is clear that the Bolt's Farm complex does not represent a single depositional unit (Cooke 1991; Senegas & Avery 1998).

Sterkfontein was intermittently excavated between the 1930s and the 1950s (Broom 1951). Beginning in 1966, exca-

vations that continue to this day have revealed an extensive collection of hominin fossils (Clarke 1998; Lockwood & Tobias 1999, 2002; Moggi-Cecchi *et al.* 2006). In addition, large and diverse faunal assemblages have been recovered from the various members of Sterkfontein (Brain 1981; Kibii 2007; Pickering 1999; Pickering *et al.* 2004; Turner 1987, 1997; Vrba 1976). Member 2 has been dated to approximately 3.3 Ma using magnetostratigraphy (Partridge *et al.* 1999, 2000) and 4.1 Ma using cosmogenic nuclides (Partridge *et al.* 2003). However, more recent estimates based on U-Pb indicate an age of 2.2 Ma (Pickering & Kramers 2010; Walker *et al.* 2006), a date that is more consistent with the fauna recovered from the site (Berger *et al.* 2002). Member 4 is estimated to be between 2.0–2.5 Ma (Berger *et al.* 2002; Delson, 1984, 1988; White & Harris 1977), with an ESR date of 2.1 Ma falling well within this temporal range (Schwarcz *et al.* 1994). The most recent U-Pb age estimate of 2.6–2.0 Ma for Member 4, with a probable rapid accumulation of most fossils around 2.2 Ma, supports these latter dates (Pickering & Kramers 2010). A series of infills once collectively referred to as Member 5, but now separated into 3 discrete deposits within this Member, are considered Plio-Pleistocene, aged between approximately 1.4–2.0 Ma respectively (Kuman & Clarke 2000).

Makapansgat has produced a very large and well-documented faunal assemblage (Ewer 1956, 1958; Reed 1996; Vrba 1987; Wells & Cooke 1956). Of the four fossil-bearing Members, only two have produced hominins (Members 3 and 4). With the exception of the younger and less completely excavated Member 5, the Makapansgat deposits can be dated to approximately 2.5 Ma (Delson 1984, 1988; Latham *et al.* 2007; White & Harris 1977). Although Makapansgat and Sterkfontein have themselves produced several extinct taxa (Reed 1996; Wells & Cooke 1956), it is clear that a significant turnover of fauna occurred between the early and the late Pliocene. At the same time, while primates tend to be relatively abundant in the Transvaal caves, to date only a single individual primate has been recovered from Langebaanweg (Grine & Hendey 1981).

THE MATJHABENG FAUNAL ASSEMBLAGE

In 2007 we began the first systematic excavations at the site of Matjhabeng, and have now conducted three excavation seasons. We have concentrated our activities in two principal areas: a 14 ×14 m pit on the Farm Virginia 448, and the erosional faces of the railway cutting itself. To date we have recovered 903 individually numbered specimens, representing a diverse assemblage that includes 14 orders, 21 families, and at least 29 discrete taxa (Table 1). At present the majority of taxa are not identifiable to the level of the species, though additional materials recovered continue to refine our taxonomic diagnoses. In this paper we describe the macromammalian assemblage, while the micromammalian and non-mammalian assemblages will be described elsewhere.

Excavations at Matjhabeng follow a complete collection strategy, as every bone, tooth, or fragment encountered is retained. Excavation proceeds in 1 × 1 metre squares along 10–20 cm depths depending on the sediment being excavated. Trowels are employed in softer sediments, while the more heavily cemented gravels require hammers and small probes to remove matrix. All fossils are point-provenanced when recognized *in situ,* and are provenanced to grid squares during sieving. Apart from overburden sediments, all materials are sieved using ¼-inch screens. A sample of these sieved sediments is rescreened using 0.4 mm fine-mesh screens to search for microfossils. Fossils are cleaned with small brushes, accessioned, and stored at the National Museum, Bloemfontein. Dental measurements are recorded for complete dental specimens using digital callipers, to the nearest 0.1 cm.

Order **PROBOSCIDEA** Illiger, 1811

Family **ELEPHANTIDAE** Gray, 1821

Mammuthus subplanifrons (Osborn), 1928

The original fossils recovered from Matjhabeng in 1955 were attributed to *M. subplanifrons* (Maglio 1973; Meiring 1955). The majority of mammoth fossils that we have recovered are isolated enamel fragments, though a complete molar tooth was retrieved in 2007 (MRC 138, Fig. 2). Although individual mammoth teeth are difficult to identify, the small size of this specimen suggests it represents a deciduous tooth, and several features of this tooth align it with *M. subplanifrons.* The tooth is broad, with 6 plates. The plates are relatively thick, with wide intervening cementum intervals. The enamel averages 3.2 cm thick, and is relatively unfolded. Each crown is divided into 6–9 apical digitations, with a prominent median cleft on the first plate. Additional mammoth tooth fragments, including several relatively complete enamel plates, support this diagnosis. The recovery of additional *M. subplanifrons* material is important in that it confirms we are indeed sampling the same area from which the original Matjhabeng (= Virginia Railway Cut) fossils were recovered.

Order **CARNIVORA** Bowdich, 1821

Family **HYAENIDAE** Gray, 1869

Three tooth fragments were recovered that are similar to hyaenid specimens from Langebaanweg, including half of a mandibular incisor (MRC 152), a canine enamel fragment (MRC 137) and a partial P^4 (MRC 210). These remains are too fragmentary to identify beyond the family level, nonetheless demonstrate the existence of at least one form of hyaenid at the site.

Family **CANIDAE** Gray, 1821

cf. *Vulpes* (A. Smith, 1833)

Two mandible fragments are identifiable as belonging to a small canid. One fragment is edentulous (MRC 734), while the other retains a slightly eroded premolar tooth

Table 1. List of taxa recovered during systematic excavations at Matjhabeng between 2007 and 2009.

Class	Order	Family	Tribe	Genus and species
Actinopterygii	Order indet.			
Amphibia	Anura	Family indet.		
Reptilia	Squamata	Agamidae		Gen. indet.
		Varanidae		*Varanus* sp.
		Gerrhosauridae		*Gerrhosaurus* sp.
		Elapidae		Gen. indet.
	Testudinata	Testudinidae		Gen. indet.
	Crocodylia	Crocodylidae		Gen. indet.
Aves	Podicipediformes	Podicipedidae		Gen. indet.
	Ciconiiformes	Threskiornithidae		Gen. indet.
Mammalia	Rodentia	Bathyergidae		cf. *Cryptomys*
		Muridae		Gen. indet.
		Gerbillinae		cf. *Tatera*
		Murinae		cf. *Aethomys*
				cf. *Euryotomys*
		Pedetidae		*Pedetes* sp.
	Insectivora	Soricidae		Gen. indet.
	Lagomorpha	Leporidae		Gen. indet.
	Proboscidea	Elephantidae		*Mammuthus subplanifrons*
	Carnivora	Hyaenidae		Gen. indet.
		Canidae		Gen. indet.
	Perissodactyla	Equidae		*Eurygnathohippus* sp.
		Chalicotheriidae		*Ancylotherium* sp.
	Artiodactyla	Giraffidae		*Sivatherium* sp.
		Hippopotamidae		*Hippopotamus* sp.
		Bovidae	Alcelaphini	*Megalotragus* sp.
				cf. *Damalacra* sp.
			Reduncini	Gen. indet.
			Antilopini	Gen. indet.
			Neotragini	Gen. indet.

(MRC 390, Fig. 3). Although the small size of the mandibles and tooth overlap with some larger viverrids, the premolar root is robust, rounded, and straight like that seen in canids. MRC 390 also compares favourably with the small canids from Langebaanweg that are equivalent in size to *Vulpes* (Hendey 1974).

Order **PERISSODACTYLA** Owen, 1848

Family **EQUIDAE** Gray, 1821

Eurygnathohippus van Hoepen, 1930

Numerous equid tooth fragments have been recovered, alongside a complete LP_4 (MRC 1), a complete RM_1 (MRC 845) and an isolated incisor (MRC 496) (Fig. 4). The premolars are hypsodont, with clearly delineated ectostylids, and both arms of the preflexids are short and directed perpendicular to the mesiodistal axes of the teeth. The incisor is large and cement filled, with an open infundibulum. Based on these characters, all three of these teeth can be attributed to the genus *Eurygnathohippus,* though a specific diagnosis is not yet possible.

Family **CHALICOTHERIIDAE** Andrews, 1923

Ancylotherium (Dietrich, 1942)

Two specimens have been attributed to the Chalicotheriidae, a right calcaneum (MRC 613) and an isolated tooth cusp (MRC 619). The only chalicothere taxon recognized in the Pliocene of Africa is *Ancylotherium hennigi* (Butler 1978). However, given the fragmentary nature of most African chalicothere fossils, and our imperfect grasp of morphological variability in this taxon, we refrain from assigning our fossils to the species level at present. That being said, the calcaneum does appear particularly diagnostic, as it compares favourably with calcanei assigned to *A. hennigi* from Makapansgat (Butler 1978; Webb 1965). Although it is approximately the same overall size as other large perissodactyls, such as white (*Ceratotherium simum*) and black (*Diceros bicornis*) rhinoceroses, it is less robustly built with a relatively slender neck (Fig. 5). Chalicothere fossils are quite rare in Africa, and Matjhabeng represents the earliest record of this taxon in South Africa.

Order **ARTIODACTYLA** Owen, 1848

Family **GIRAFFIDAE** Gray, 1821

Sivatherium Falconer & Cautley, 1835

Exploration of the eroding banks of the railway cutting revealed two giraffid specimens, a large ossicone fragment (MRC 650, found by J.S. Brink) and a partial tibia (MRC 3). Given their close proximity it is possible that they are derived from the same individual. The large ossicone fragment is well preserved (Fig. 6), and can be attributed to the extinct short-necked giraffe *Sivatherium.* Since ossicones are generally absent in *Sivatherium* females this is likely to be a male individual. Furthermore,



Figure 2. *Mammuthus subplanifrons* deciduous molar tooth (MRC 138). Scale bar = 50 mm.

given the relative lack of adornment of the ossicone, it is probable that this was a relatively young individual (see Churcher 1978: 525). The tibia is highly fragmented but appears relatively stout and long.

Family **HIPPOPOTAMIDAE** Gray, 1821

A single hippopotamus tooth fragment was recovered (MRC 647), likely representing a premolar. Given the fragmentary nature of the find, identifying the genus to which this tooth belongs is difficult. The genus *Hippopotamus* has been recognized at Langebaanweg (Hendey 1976a), while *Hexaprotodon* is unknown in the earlier Pliocene of South Africa. On this limited evidence we anticipate that future, more complete discoveries will confirm a diagnosis of *Hippopotamus* sp., though at present we assign this specimen only to the family Hippopotamidae.

Family **BOVIDAE** Gray, 1821

Tribe **Alcelaphini** Rochebrune, 1883

Megalotragus van Hoepen, 1932.

Bovid fossils in the form of isolated teeth are relatively common, though they tend to be badly fragmented and eroded from water rolling, rendering identification difficult. However, one specimen in particular is well preserved, a hemi-mandible with RM_{1-3} attributable to

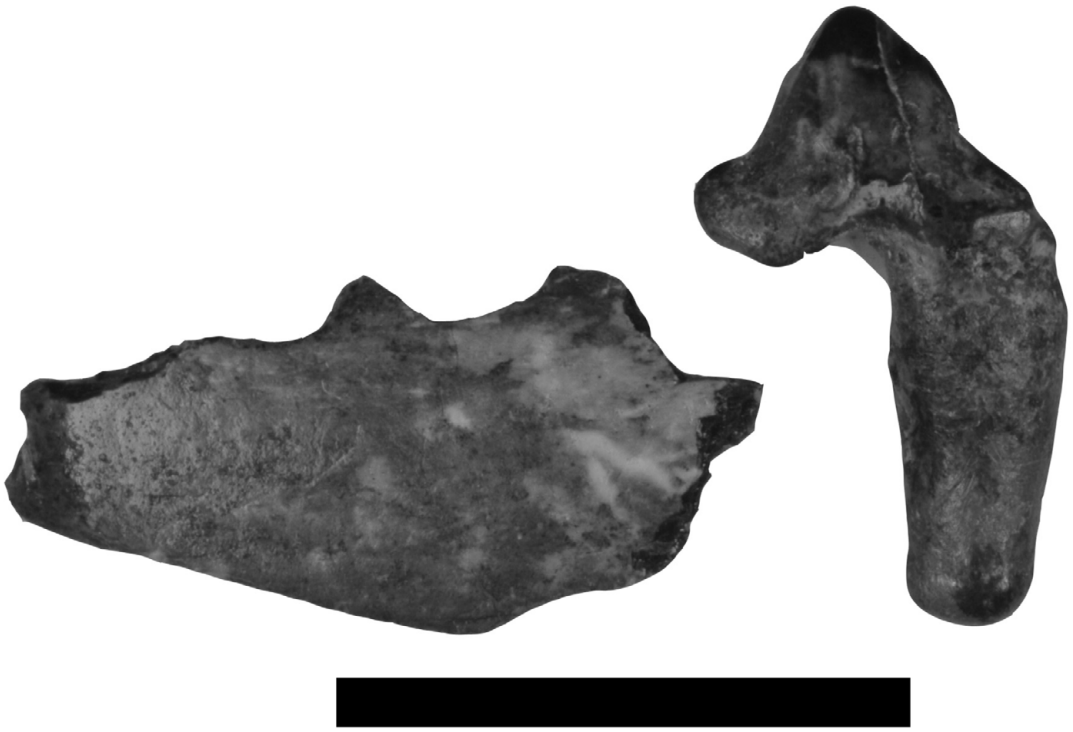


Figure 3. Mandible fragment and associated tooth of a small canid, probably *Vulpes* (MRC 390). Scale bar = 10 mm.

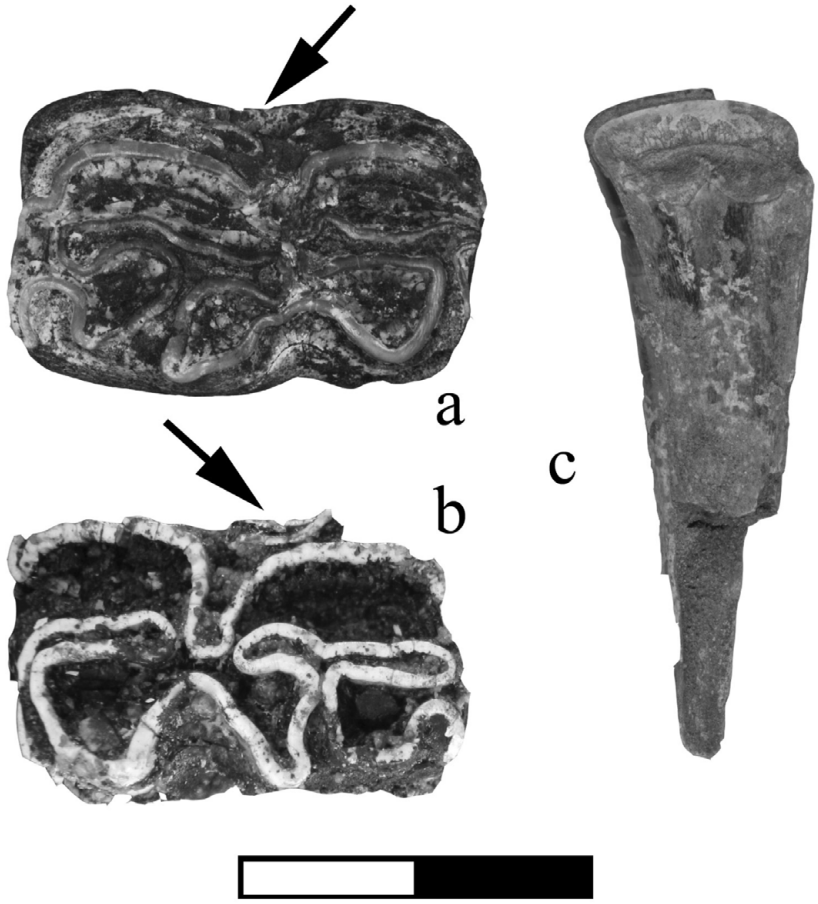


Figure 4. Isolated teeth of *Hipparion* sp.: **a**, LP_4 (MRC 1); **b**, RM_1 (MRC 845); **c**, isolated incisor (MRC 496). Arrows point to clearly separated ectostylids. Scale bar = 20 mm.

Megalotragus (MRC 605; Fig. 7). The lobes of the mandibular teeth of alcelaphines from Langebaanweg are more pointed, with more pronounced styles, confirming that this Matjhabeng specimen is not a late representative of the Langebaanweg fauna. Although small relative to later Pleistocene specimens from the Free State (Fig. 8), the teeth of MRC 605 nonetheless fall within the range of *Megalotragus* molar measurements recorded elsewhere in Africa. In addition, the corpus of the mandible is notably elongated and the angle of the ramus relative

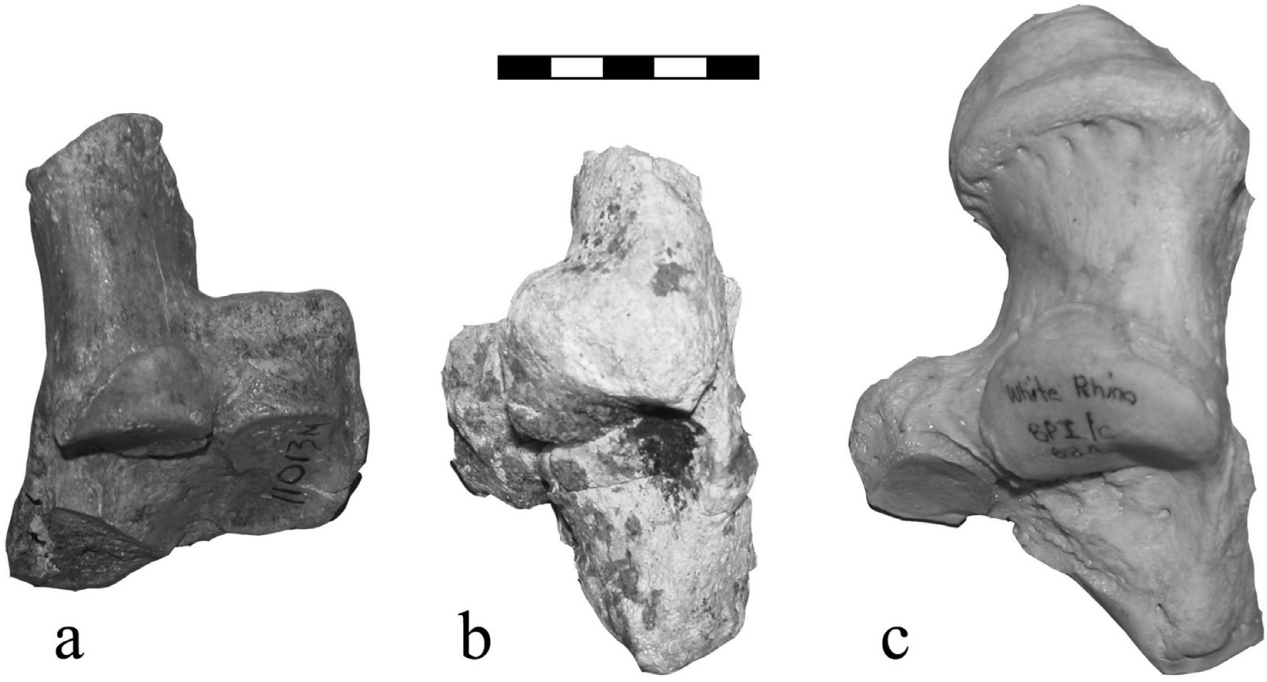


Figure 5. Perissodactyl calcanei attributable to *Ancylotherium*: **a**, 11013M from Makapansgat; **b** MRC 613 from Matjhabeng; compared to a calcaneum of *Ceratotherium simum*: **c**, BPI/C 684. Scale bar = 50 mm.



Figure 6. Large ossicone fragment of a probable young male *Sivatherium* (MRC 650). Scale bar = 50 mm.

to the corpus approaches 135°, similar to Mahemspan specimens (Brink 2005). Alongside the relatively uncomplicated occlusal pattern of the molars this posteriorly inclined ramus implies an elongated cranium such as that characterizing *Megalotragus.* Most species described in the genus *Megalotragus* are diagnosed on horn cores making comparison of MRC 605 difficult. As a result, until additional cranial material is recovered, we can only identify this specimen to the genus level. Notwithstanding, this mandible likely represents the oldest recorded appearance of *Megalotragus* in South Africa (see below).

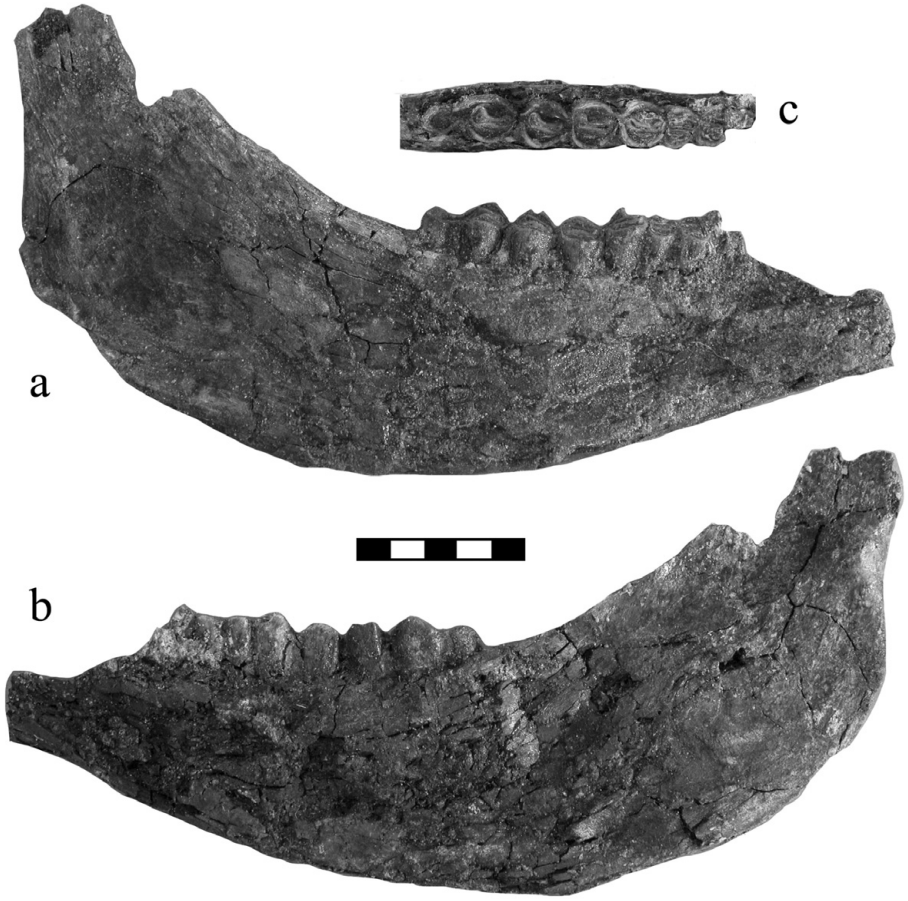


Figure 7. Relatively complete hemi-mandible of *Megalotragus* sp. (MRC 605) in (**a**) lateral, (**b**) medial and (**c**) occlusal views. Scale bar = 50 mm.

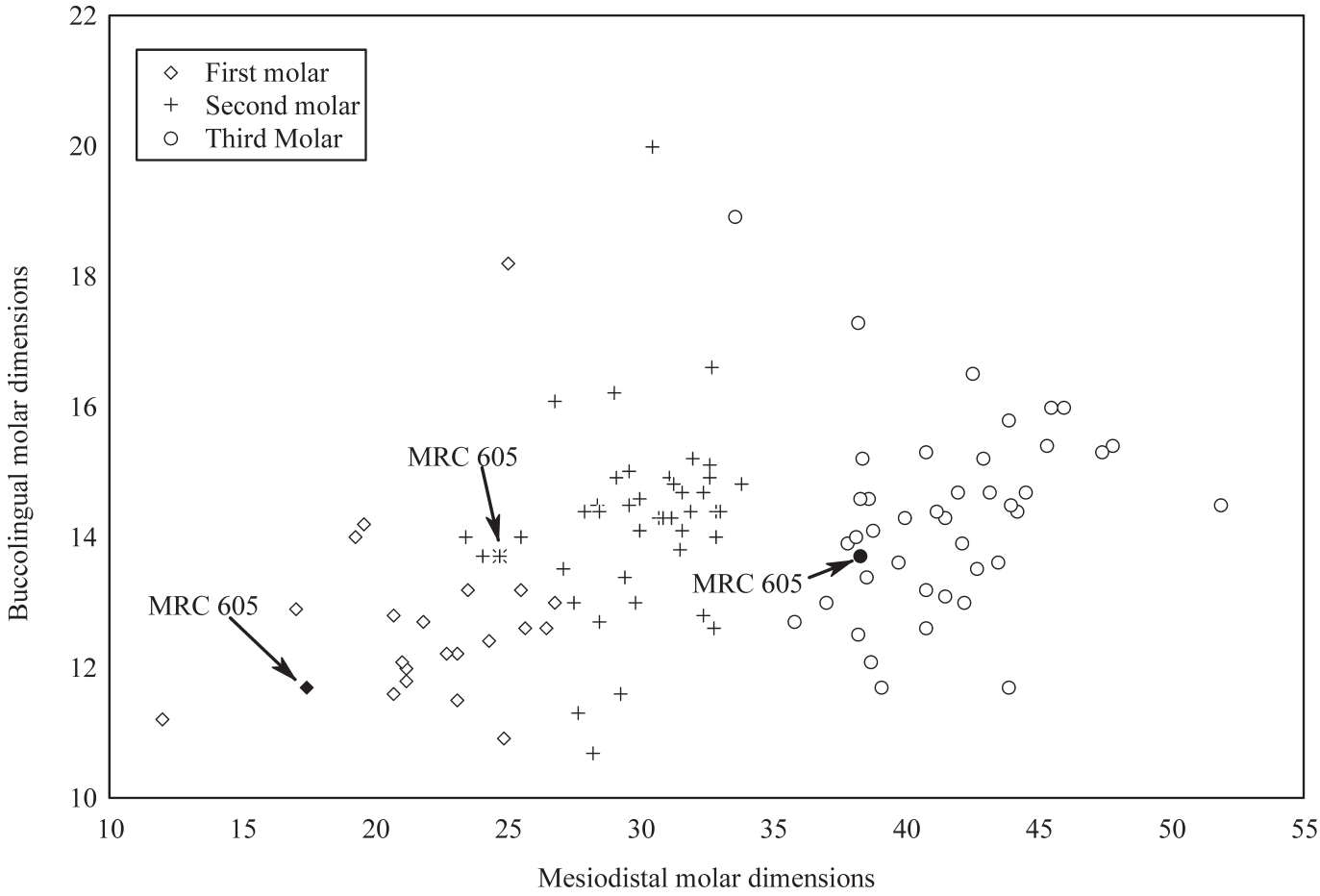


Figure 8. Scatter plot of mandibular molar measures of *Megalotragus* from Matjhabeng (MRC 605) compared to a selection of specimens from East and South Africa (measurements by D.J.D. for South African specimens, and from Harris (1991) for East African specimens). Although the Matjhabeng specimen is small, it falls within the ranges of molar teeth of *Megalotragus* from elsewhere in Africa.

cf. *Damalacra* Gentry, 1980

Several tooth fragments and a badly fragmented mandible (MRC 96) of alcelaphines were recovered, all of which compare favourably in size and morphology with *Damalacra* specimens from Langebaanweg. However, given that none of these fragments preserve complete teeth, the identification of *Damalacra* is only tentative at present.

Additional Bovidae specimens

A single tooth of a small Reduncini was recovered (MRC 795) and although little detail beyond a tribal level diagnosis is available we nonetheless record the presence of this tribe at Matjhabeng. The Antilopini are represented by a single tooth fragment (MRC 820) that is approximately the same size as a modern springbok. The Neotragini are represented by two post-cranial elements, an external cuneiform (MRC 804) and a magnum (MRC 824), both of which are consistent with being from a single individual. These neotragine fossils are considerably smaller than springbok (Antilopini) and are approximately similar in size to steenbok (*Raphicerus*) though they do not conform to this latter taxon. In fact their closest comparison is *Ourebia,* a taxon with a poorly documented fossil record. Post-cranial remains attributable to the Bovidae are also known with several relatively complete elements such as radii and cervical vertebrae present. These relatively rare post-cranial elements illustrate the potential for good preservation since the cervical vertebra, for instance, is almost complete including much of the otherwise delicate zygapophyses.

STRATIGRAPHIC ANALYSIS OF MATJHABENG

In addition to fossil recoveries our excavations have allowed for a comprehensive stratigraphic analysis to be completed. Results revealed a slightly more complex sedimentological sequence than was recognized by Butzer (1973) with 9 facies in 3 discrete facies associations. The site represents a good aggradational sequence that is unique in the central interior of southern Africa. Of particular interest is facies association 1 at the base of the sequence, which contains the fossiliferous sediments (referred to by Butzer as Horizon 2). This predominantly graveliferous unit includes genetically identical interbedded silty-sand units that together comprise between 1.0 to 3.0 m of fossiliferous deposition. The gravel component represents a high-energy river discharge while the silty-sand units represent abandoned-channel equivalents formed when the paleo-river periodically changed its course. Fossils have been recovered from both units and tend to be concentrated near the interface between these components. Fossil density is low relative to cave infills such as Makapansgat and Sterkfontein. Fossils recovered from the gravels tend to be more eroded though some

display excellent preservation while those recovered from the abandoned-channel, silty-sand deposits tend to be relatively well preserved.

AGE OF THE DEPOSIT

Mammuthus subplanifrons was first named for an isolated tooth recovered from Sydney-on-Vaal (Osborn 1928), a fossiliferous unit of the 'Older Gravels' of the Vaal River Gravels in South Africa (Helgren 1979). The oldest specimens of *M. subplanifrons* are from Langebaanweg and are thus dated to approximately 5.0 Ma (Hendey 1981a,b, 1982; Maglio & Hendey 1970). Maglio (1973) suggested that the original Matjhabeng *M. subplanifrons* material described by Meiring (1955) was more derived than specimens known from Langebaanweg (Maglio & Hendey 1970), indicating a probable age near 4.0 Ma for Matjhabeng. In his examination of the geomorphology of the deposit, Butzer (1973) agreed with an estimate of 4.0 Ma for the site. Elsewhere in Africa, *M. subplanifrons* is recorded from the lower Kaiso Formation, Kanam, Chemeron locality J.M. 511, the Sinda Beds of Zaire, and the older Stratigraphic Unit 2 of the Chiwondo Beds, all of which are considered to be early Pliocene (>4.0 Ma) (Bromage *et al.* 1995; Cooke & Maglio 1972; Coppens *et al.* 1978; Howell 1972; Maglio 1973; Maglio & Hendey 1970; Yasui *et al.* 1992). Specimens consistent with *M. subplanifrons* are also known from the Wee-ee Dora in the Aramis Member of the Sagantole Formation (4.1–3.8 Ma) and the Kuseralee Dora in the Kuseralee Member of the Adu-Asa Formation (>4.4 Ma) in the Middle Awash sequence of Ethiopia (Kalb & Mebrate 1993). There do not appear to be any *M. subplanifrons* specimens in sediments younger than 4.0–3.5 Ma in East Africa, thus this taxon can best be ascribed an age of approximately 5.5–3.5 Ma (Maglio 1973).

Megalotragus has been recovered from both Pliocene and Pleistocene sediments throughout Africa. In East Africa the earliest occurrence of *Megalotragus* is in the Lokochot Member of the Koobi Fora Formation, with a maximum age estimate of 3.5 Ma (Harris 1991). Additionally *Megalotragus* fossils have been recovered from elsewhere in the Koobi Fora Formation, in the Nachukui Formation of west Lake Turkana, throughout the Shungura sequence, and in all four Beds of Olduvai Gorge. In South Africa *Megalotragus* fossils are known from Sterkfontein, Makapansgat, Swartkrans, Kromdraai, Coopers, Drimolen, Bolt's Farm, Haasgat, Gladysvale and Plovers Lake in the former Transvaal, as well as numerous sites in the Free State such as Florisbad, Vlakkraal and Mahemspan, among others. As a result, the age of *Megalotragus* appears to span from 3.5–0.009 Ma.

With an age estimate of 5.0–3.5 Ma for *M. subplanifrons,* and 3.5–0.009 Ma for *Megalotragus,* we can presently constrain the probable dates for Matjhabeng to 4.0–3.5 Ma. This range is consistent with earlier reports of 4.0 Ma for the site (Butzer 1973; Maglio 1973), though Matjhabeng is likely to fall nearer the younger end of this range. Recognizing the circularity of the argument (i.e. the age of Matjhabeng is partially established based on the presence of *Megalotragus*), the *Megalotragus* material from Matjhabeng nonetheless represents the oldest occurrence of this taxon yet recorded in South Africa.

ISOTOPIC ANALYSIS OF MATJHABENG FOSSILS

Carbon isotopes derived from enamel hydroxyapatite provide a reliable source of information relating to the dietary behaviour of Cenozoic herbivores (Lee-Thorp & van der Merwe 1991; Quade *et al.* 1992; Sponheimer *et al.* 2006). Variations observed in the $\delta^{13}C$ of carbonate hydroxyapatite of enamel reflect differences in the relative proportions of grass (C_4) and browse (C_3) vegetation consumed by the animal throughout its life. Because of the great potential for ecological information, we selected several samples for destructive analysis to determine their isotopic composition. Approximately 5.0 mg of powder was extracted per dental sample, and the samples were pretreated with sodium hypochlorite (NaOCl) and acetic acid (CH_3COOH). The samples were then combusted and analysed using a GasBench II system in combination with the DeltaPlusXP isotope ratio mass spectrometer to obtain $\delta^{13}C$ values. The results are reported against PDB (Pee Dee belemnite), and the standard NBS-19 (National Bureau of Standards) was used for calibration with a precision of 0.06‰. The results of this isotopic analysis are presented in Fig. 9.

Cerling *et al.* (1997) hypothesized an early emergence of C_4 grasslands in equatorial Africa during the late Miocene, suggesting that these grasslands gradually expanded both north and south over time. Sponheimer *et al.* (2005, 2006a,b) demonstrated considerable dietary flexibility in the early hominins of South Africa, and hypothesized that the ability to consume significant quantities of grassland-based C_4 resources was a fundamental hominin characteristic lacking in other African apes. The location and age of Matjhabeng allows us to test the Cerling *et al.* (1997) C_4 expansion model, to document if grasslands had already become a significant component of the Free State environment in the middle Pliocene. Carbon isotope analysis of a sample of Matjhabeng fossils (Fig. 9) reveals that most of the animals fall into a mixed feeder category, with a distinct preference for grazing. Interestingly, this includes a fragmented tooth of *Ancylotherium,* which is typically considered to have been a dedicated browser. Comparing these data to a series of average isotope values from sites elsewhere in Africa (Sponheimer & Lee-Thorp 2009), Matjhabeng differs from the predominantly browsing fauna of Langebaanweg (Franz-Odendaal *et al.* 2002), and indicates more extensive C_4 grasslands even than later sites such as Makapansgat and Sterkfontein. It thus appears that the Free State was dominated by grasslands from at least the later–early Pliocene. These data represent the earliest isotopic evidence for significant C_4 grasslands in South Africa, and are consistent with a relatively late grassland expansion into southern Africa (Cerling 1992; Segalen *et al.* 2007).

DISCUSSION AND CONCLUSIONS

The Matjhabeng faunal assemblage is predominated by animals considered to be largely grassland-preferring, including mammoths, equids, hippos and ancestral

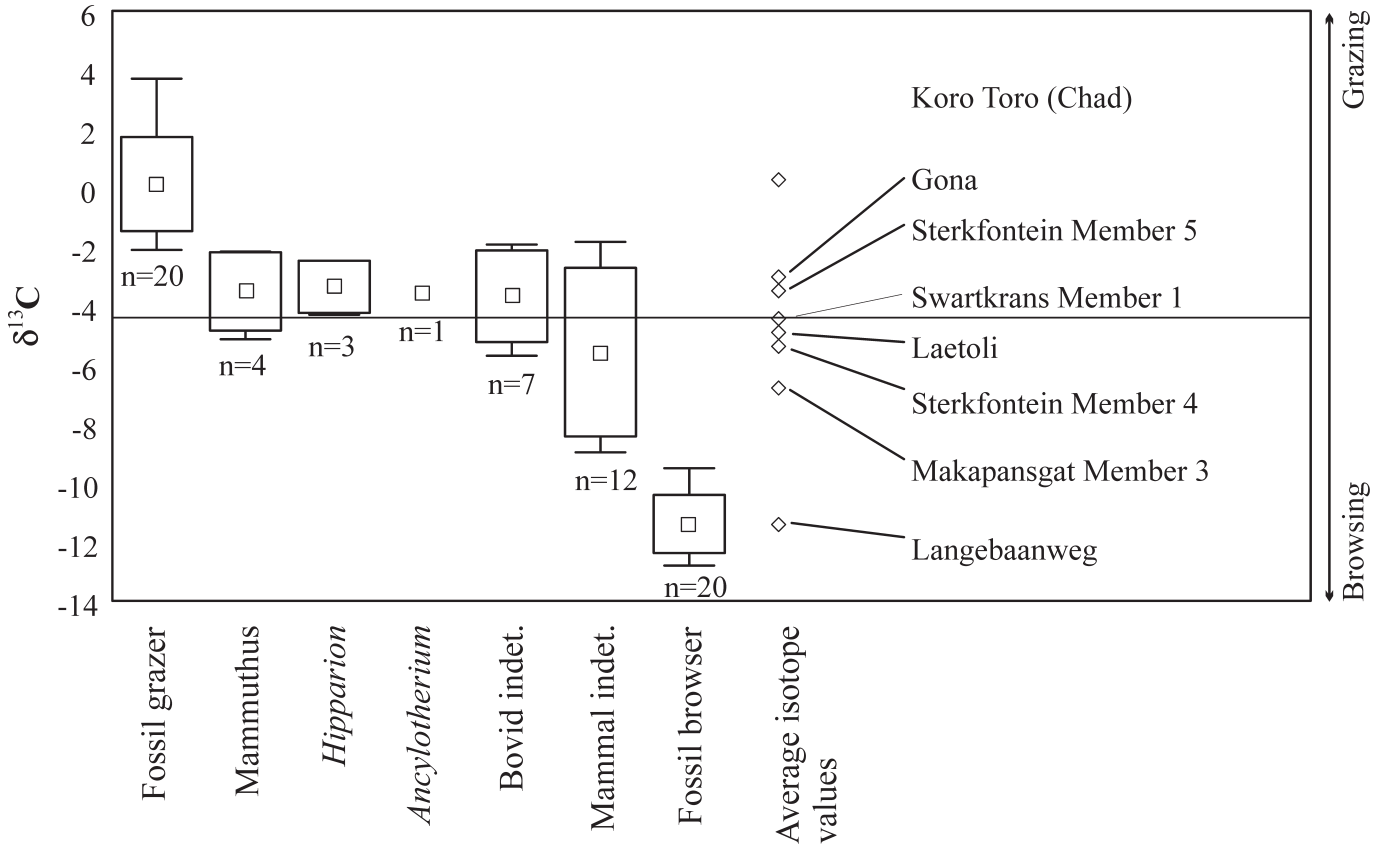


Figure 9. Carbon isotope values for a selection of fossil mammal teeth from Matjhabeng. Comparative 'fossil grazer' and 'fossil browser' data compiled from Swartkrans and Sterkfontein. Grazers are those animals with $\delta^{13}C$ values greater than –2‰, while browsers are those animals with $\delta^{13}C$ values less than –10‰. Animals with values between these ends are referred to as mixed feeders. Average isotope values are calculated by averaging the isotope composition of all specimens sampled from a given site. The grey line represents the average isotope value for all Matjhabeng specimens included in this study, which corresponds to a mixed feeder signal tending towards grazing. These data indicate that grasslands were already extensive by the earlier Pliocene in the Free State, representing the earliest indication of significant grasslands in South Africa. Comparative average isotope values for fossil sites other than Matjhabeng from Sponheimer & Lee-Thorp (2009).

alcelaphines. The presumed browser *Sivatherium* is evident, as is *Ancylotherium,* thus wooded conditions are also indicated. The reptiles and birds demonstrate relatively wetter conditions than are found in the area today. Our isotope data support a primarily mixed feeding/grazing fauna, though the mixed feeding/grazing diet of *Ancylotherium* was unexpected. At present our reconstruction of the paleoenvironment indicates relatively extensive grasslands though these grasslands were part of an environmental mosaic that included notable woodland and probable wetland components. Given that Matjhabeng is a river-deposited locality there is a significant potential for reworking and mixing of materials and thus a potential for time-averaging. We therefore interpret these environmental indicators broadly at the regional scale of the Free State in the earlier Pliocene. Combined with our isotope analysis these data are consistent with a model of major grassland expansion into South Africa by the early Pliocene *c.* 4.0 Ma (Hopley *et al.* 2007; Segalen *et al.* 2007). At present Matjhabeng represents the earliest appearance of significant C_4 grasslands in the central interior of southern Africa. At the same time the Paleo-Sand river was large enough to sustain both hippopotamus and waterfowl. This necessitates perennial channel flow with fresh grasslands available in the vicinity year-round. Periodic fluctuations in river flow are indicated by the interbedded, abandoned channel deposits which developed when the river channel migrated during periods of low stream discharge. Many of the taxa recovered to date are shared by both Langebaanweg and Makapansgat, though some are shared only with Langebaanweg (*Mammuthus*), and some are shared only with Makapansgat (*Ancylotherium, Megalotragus*). These data reflect the intermediary and perhaps transitional nature of this site and highlight the importance of expanding our sample of early Pliocene fossils in South Africa.

We would like to thank James Brink, Lloyd Rossouw and Rick Nuttall of the National Museum, Bloemfontein, and Bruce Rubidge of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, for logistical and scientific support. Izak Thapo and the Florisbad Quaternary Research Department's team of excavators provided invaluable excavation assistance. Steve Churchill and the Duke Paleoanthropology Field School were instrumental in early exploration of the site. Tim Campbell discovered the *Megalotragus* mandible *in situ.* The South African Heritage Resources Agency provided the permit for excavation. We wish to thank Peter Muller, Joy Alec and the Matjhabeng Municipal Council for allowing us unfettered access to the property. We also thank the town of Virginia and the Tikwe Lodge for welcoming our often large team. The following individuals volunteered to assist in the excavations: Benjamin Ashby, Rachael Bible, Lauren Butaric, Tim Campbell, Krista Church, Kelly Forson, Phil Johnson, Aline Lovings, Paul Sandberg, Jill Scott and Rich Tutalo. Generous funding was provided by the Wenner-Gren Foundation and the Palaeontological Scientific Trust of South Africa.

REFERENCES

BERGER, L.R., LACRUZ, R.S. & DE RUITER, D.J. 2002. Brief communication: revised age estimates of *Australopithecus*-bearing deposits at Sterkfontein, South Africa. *American Journal of Physical Anthropology* **119**, 192–197.

BONE, E.L. & SINGER, R. 1965. *Hipparion* from Langebaanweg, Cape Province, and a revision of the genus in South Africa. *Annals of the South African Museum* **48**, 273–397.

BRAIN, C.K. 1981. *The Hunters or the Hunted? An Introduction to African Cave Taphonomy.* Chicago, University of Chicago Press.

BRINK, J.S. 2005. *The evolution of the black wildebeest,* Connochaetes gnou*, and modern large mammal faunas in central southern Africa*. Unpublished Ph.D. dissertation, University of Stellenbosch, Stellenbosch.

BROMAGE, T.G., SCHRENK, F. & JUWAYEYI, Y.M. 1995. Paleobiogeography of the Malawi Rift: age and vertebrate paleontology of the Chiwondo Beds, northern Malawi. *Journal of Human Evolution* **28**, 37–57.

BROOM, R. 1951. *Finding the Missing Link.* London, Watts.

BRUNET, M., GUY, F., PILBEAM, D., MACKAYE, H.T., LIKIUS, A., AHOUNTA, D., BEAUVILAIN A., BLONDEL, C., BOCHERENS, H., BOISSERIE, J.-R., DE BONIS, L., COPPENS, Y., DEJAX, J., DENYS, C., DURINGER, P., EISENMANN, V., FANONE, G., FRONTY, P., GERAADS, D., LEHMANN, T., LIHOREAU, F., LOUCHART, A., MAHAMAT, A., MERCERON, G., MOUCHELIN, G., OTERO, O., CAMPOMANES, P.P., PONCE DE LEON, M., RAGE, J.C., SAPANET, M., SCHUSTER, M., SUDRE, J., TASSY, P., VALENTIN, X., VIGNAUD, P., VIRIOT, L., ZAZZO, A. & ZOLLIKOFER, C. 2002. A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* **418**, 145–151.

BUTLER, P.M. 1978. Chalicotheriidae. **In**: Maglio, V. & Cooke, H.B.S. (eds), *Evolution of African Mammals,* 368–370. Cambridge, MA, Harvard University Press.

BUTZER, K.W. 1973. On the geology of a late Pliocene *Mammuthus* site, Virginia, Orange Free State. *Navorsinge van die Nasional Museum, Bloemfontein* **2**, 386–393.

BUTZER, K.W., HELGREN, D.M., FOCK, G.J. & STUCKENRATH, R. 1973. Alluvial terraces of the lower Vaal River, South Africa: a reappraisal and reinvestigation. *Journal of Geology* **81**, 341–362.

CERLING, T.E. 1992. Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeography, Palaeoclimatology, Palaeoecology* **97**, 241–247.

CERLING, T.E., HARRIS, J.M., MACFADDEN, B.J., LEAKEY, M.G., QUADE, J., EISENMANN, V. & EHLERINGER, J.R. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* **389**, 153–158.

CHURCHER, C.S. 1978. Giraffidae. **In**: Maglio, V.J. & Cooke, H.B.S. (eds), *Evolution of African Mammals,* 509–535. Cambridge, Harvard University Press.

CLARKE, R.J. 1998. First ever discovery of a well-preserved skull and associated skeleton of *Australopithecus. South African Journal of Science* **94**, 460–463.

COOKE, H.B.S. 1991. *Dinofelis barlowi* (Mammalia, Carnivora, Felidae) cranial material from Bolt's Farm, collected by the University of California African Expedition. *Palaeontologia africana* **28**, 9–21.

COOKE, H.B.S. & MAGLIO, Q.B. 1972. Plio-Pleistocene stratigraphy in East Africa in relation to proboscidean and suid evolution. **In**: Bishop, W.W. & Miller, J.A. (eds), *Calibration of Hominoid Evolution.* University of Toronto Press, Toronto, pp. 303–329.

COPPENS, Y., MAGLIO, V.J., MADDEN, C.T. & BEDEN, M. 1978. Proboscidea. **In**: Maglio, V.J. & Cooke, H.B.S. (eds), *Evolution of African Mammals,* 336–367. Cambridge, Harvard University Press.

DART, R.A. 1925. *Australopithecus africanus*: the man-ape of South Africa. *Nature* **115**, 195–199.

DELSON, E. 1984. Cercopithecid biochronology of the African Plio-Pleistocene: correlation among eastern and southern hominid-bearing localities. *Courier Forschrung Institut Senckenberg* **69**, 199–218.

DELSON, E. 1988. Chronology of South African Australopith site units. **In**: Grine, F.E. (ed.), *Evolutionary History of the Robust Australopithecines,* 317–325. New York, Aldine de Gruyter.

DE RUITER, D.J., COPELAND, S.R., LEE-THORP, J.A. & SPONHEIMER, M. 2010. Investigating the role of eagles as accumulating agents in the dolomitic cave infills of South Africa. *Journal of Taphonomy* **8**: 129–154.

EWER, R.F. 1956. Some fossil carnivores from the Makapansgat Valley. *Palaeontologia africana* **4**, 57–67.

EWER, R.F. 1958. The fossil Suidae of Makapansgat. *Proceedings of the Zoological Society, London* **130**, 329–372.

FRANZ-ODENDAAL, T.A., LEE-THORP, J.A. & CHINSAMY, A. 2002. New evidence for the lack of C_4 grassland expansions during the early Pliocene at Langebaanweg, South Africa. *Paleobiology* **28**, 378–388.

GENTRY, A.W. 1974. A new genus and species of Pliocene boselaphine (Bovidae, Mammalia) from South Africa. *Annals of the South African Museum* **65**, 145–188.

GENTRY, A.W. 1980. Fossil Bovidae (Mammalia) from Langebaanweg, South Africa. *Annals of the South African Museum* **79**, 213–337.

GRINE, F.E. & HENDEY, Q.B. 1981. Earliest primate remains from South Africa. *South African Journal of Science* **77**, 374–376.

HAILE-SELASSIE, Y., SUWA, G. & WHITE, T.D. 2004. Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. *Science* **303**, 1503–1505.

HARRIS, J.M. 1991. *Koobi Fora Research Project Volume 3: The Fossil Ungulates: Geology, Fossil Artiodactyls, and Palaeoenvironments.* Oxford, Clarendon Press.

HELGREN, D. 1977. Geological context of the Vaal River faunas. *South African Journal of Science* **73**, 303–307.

HELGREN, D. 1979. Rivers of diamonds: an alluvial history of the lower Vaal Basin, South Africa. *Research Papers of the University of Chicago, Department of Geography* **185**, 1–389.

HENDEY, Q.B. 1970. A review of the geology and palaeontology of the Plio-Pleistocene deposits at Langebaanweg, Cape Province. (With an appendix on the Langebaanweg Bovidae by A.W. Gentry.) *Annals of the South African Museum* **56**, 75–117.

HENDEY, Q.B. 1972. A Pliocene ursid from South Africa. *Annals of the South African Museum* **9**, 115–132.

HENDEY, Q.B. 1973. Fossil occurrences at Langebaanweg, Cape Province. *Nature* **224**, 13–14.

HENDEY, Q.B. 1974. The late Cenozoic Carnivora of the southwestern Cape Province. *Annals of the South African Museum* **63**, 1–369.

HENDEY, Q.B. 1976a. The Pliocene fossil occurrences in 'E' Quarry, Langebaanweg, South Africa. *Annals of the South African Museum* **69**, 215–247.

HENDEY, Q.B. 1976b. Fossil peccary from the Pliocene of South Africa. *Science* **192**, 787–789.

HENDEY, Q.B. 1978a. Late Tertiary Hyaenidae from Langebaanweg, South Africa, and their relevance to the phylogeny of the family. *Annals of the South African Museum* **76**, 265–297.

HENDEY, Q.B. 1978b. Late Tertiary Mustelidae from (Mammalia, Carnivora) from Langebaanweg, South Africa. *Annals of the South African Museum* **76**, 329–357.

HENDEY, Q.B. 1978c. The age of the fossils from Baard's Quarry, Langebaanweg, South Africa. *Annals of the South African Museum* **75**, 1–24.

HENDEY, Q.B. 1981a. Paleoecology of the late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. *Annals of the South African Museum* **84**, 1–104.

HENDEY, Q.B. 1981b Geological succession at Langebaanweg, Cape Province, and global events of the late Tertiary. *South African Journal of Science* **77**, 33–38.

HENDEY, Q.B. 1982. *Langebaanweg: A Record of Past Life.* Cape Town, South African Museum.

HOPLEY, P.J., LATHAM, A., KUYKENDALL, K. & WEEDON, G. 2007. Orbital forcing and the spread of C4 grasses in the late Neogene: stable isotope evidence from South African speleothems. *Journal of Human Evolution* **53**, 620–634.

HOWELL, F.C. 1972. Pliocene/Pleistocene Hominidae in eastern Africa – absolute and relative ages. **In**: Bishop, W.W. & Miller, J.A. (eds), *Calibration of Hominoid Evolution,* 331–368. Toronto, University of Toronto Press.

HRDLIČKA, A. 1925. The Taungs ape. *American Journal of Physical Anthropology* **8**, 379–392.

KALB, J.E. & MEBRATE, A. 1993. Fossil elephantoids from the hominid-bearing Awash Group, Middle Awash Valley, Afar Depression, Ethiopia. *Transactions of the American Philosophical Society* **83**, 1–114.

KIBII, J.M. 2007. *Comparative taxonomic, taphonomic and palaeoenvironmental analysis of 4–2.3 million year old australopithecine cave infills at Sterkfontein.* Unpublished PhD dissertation, University of the Witwatersrand, Johannesburg.

KUMAN, K., & CLARKE, R.J. 2000. Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. *Journal of Human Evolution* **38**, 827–847.

LATHAM, A.G., McKEE, J.K. & TOBIAS, P.V. 2007. Bone breccias, bone dumps, and sedimentary sequences of the western Limeworks, Makapansgat, South Africa. *Journal of Human Evolution* **52**, 388–400.

LEAKEY, M.G., FEIBEL, C.S., McDOUGALL, I. & WALKER, A. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* **376**, 565–571.

LEAKEY, M.G., FEIBEL, C.S., McDOUGALL, I., WARD, C. & WALKER, A. 1998. New specimens and confirmation of an early age for *Australopithecus anamensis. Nature* **393**, 62–66.

LEE-THORP, J.A. & VAN DER MERWE, N.J. 1991. Aspects of the chemistry of modern and fossil biological apatites. *Journal of Archaeological Science* **18**, 343–354.

LOCKWOOD, C.A. & TOBIAS, P.V. 1999. A large male hominin cranium

from Sterkfontein, South Africa, and the status of *Australopithecus africanus. Journal of Human Evolution* **36**, 637–685.
LOCKWOOD, C.A. & TOBIAS, P.V. 2002. Morphology and affinities of new hominin cranial remains from Member 4 of the Sterkfontein Formation, Gauteng Province, South Africa. *Journal of Human Evolution* **42**, 389–450.
MAGLIO, V.J. 1973. Origin and evolution of the Elephantidae. *Transactions of the American Philosophical Society* **63**, 1–149.
MAGLIO, V.J. & HENDEY, Q.B. 1970. New evidence relating to the supposed stegolophodont ancestry of the Elephantidae. *South African Archaeological Bulletin* **25**, 85–87.
McKEE, J.K. 1993. Faunal dating of the Taung hominid fossil deposit. *Journal of Human Evolution* **25**, 363–376.
McKEE, J.K. & TOBIAS, P.V. 1990. New fieldwork at the Taung hominid site: 1988–1989. *American Journal of Physical Anthropology* **81**, 266–267.
MEIRING, A.J.D. 1955. Fossil Proboscidean teeth and ulna from Virginia, O.F.S. *Navorsinge van die Nasional Museum, Bloemfontein* **1**, 187–201.
OSBORN, H.F. 1928. Mammoths and man in the Transvaal. *Nature* **71**, 672–673.
MOGGI-CECCHI, J., GRINE, F.E. & TOBIAS, P.V. 2006. Early hominid dental remains from Members 4 and 5 of the Sterkfontein Formation (1966–1996 excavations): catalogue, individual associations, morphological descriptions and initial metrical analyses. *Journal of Human Evolution* **50**, 239–328.
PARTRIDGE, T.C., SHAW, J., HESLOP, D. & CLARKE, R.J. 1999. The new hominid skeleton from Sterkfontein, South Africa: age and preliminary assessment. *Journal of Quaternary Science* **14**, 293–298.
PARTRIDGE, T.C., SHAW, J. & HESLOP, D. 2000. Note on recent magnetostratigraphic analyses in Member 2 of the Sterkfontein Formation. **In**: Partridge, T.C. & Maud R.R. (eds), *The Cenozoic of Southern Africa,* 129–130. Oxford, Oxford University Press.
PARTRIDGE, T.C., GRANGER, D.E., CAFFEE, M.W. & CLARKE, R.J. 2003. Lower Pliocene hominid remains from Sterkfontein. *Science* **300**, 607–612.
PICKERING, R. & KRAMERS, J.D. 2010. Re-appraisal of the stratigraphy and determination of new U-Pb dates for the Sterkfontein hominin site, South Africa. *Journal of Human Evolution* **59**: 70–86.
PICKERING, T.R. 1999. *Taphonomic interpretations of the Sterkfontein early hominid site (Gauteng, South Africa) reconsidered in light of recent evidence.* Unpublished PhD dissertation, University of Wisconsin, Madison.
PICKERING, T.R., CLARKE, R.J. & HEATON, J.L. 2004. The context of Stw 573, an early hominid skull and skeleton from Sterkfontein Member 2: taphonomy and paleoenvironment. *Journal of Human Evolution* **46**, 279–297.
QUADE, J., CERLING, T.E., BARRY, J.C., MORGAN, M.M., PILBEAM, D.R., CHIVAS, A.R. & LEE-THORP, J.A. 1992, A 16 million year record of paleodiet from Pakistan using carbon isotopes in fossil teeth. *Chemical Geology* **94**, 183–192.
REED, K.E. 1996. *The paleoecology of Makapansgat and other African Plio-Pleistocene hominid localities.* Unpublished PhD dissertation, State University of New York, Stony Brook.
SCHWARCZ, H.P., GRUN, R. & TOBIAS, P.V. 1994. ESR dating studies of the australopithecine site of Sterkfontein, South Africa. *Journal of Human Evolution* **26**, 175–181.
SEGALEN, L., LEE-THORP, J.A. & CERLING, T. 2007. Timing of C_4 grass expansion across sub-Saharan Africa. *Journal of Human Evolution* **53**, 549–559.
SÉNÉGAS, F. & AVERY, D.M. 1998. New evidence for the murine origins of the Otomyinae (Mammalia, Rodentia) and the age of Bolt's Farm (South Africa). *South African Journal of Scienc*e **94**, 503–507.
SINGER, R. & HOOIJER, D.A. 1958. A stegolophodon from South Africa. *Nature* **182**, 101–102.
SPONHEIMER, M. & LEE-THORP, J.A. 2009. Biogeochemical evidence for the environments of early Homo in South Africa. **In**: Grine, F.E., Fleagle, J.G. & Leakey, R.E.F. (eds), *The First Humans: Origin and Early Evolution of the Genus* Homo. Springer, Dordrecht.
SPONHEIMER, M., LEE-THORP, J.A. & DE RUITER, D.J. 2006. Icarus, isotopes, and australopith diets. **In**: Ungar, P. (ed.), *Evolution of the Human Diet,* 132–149. Oxford, Oxford University Press.
SPONHEIMER, M, LEE-THORP, J., DE RUITER, D.J., CODRON, D., CODRON, J., BAUGH, A. & THACKERAY, J.F. 2005. Hominins, sedges, and termites: new carbon isotope data from the Sterkfontein Valley and Kruger National Park. *Journal of Human Evolution* **48**, 301–312.
SPONHEIMER, M., PASSEY, B.H., DE RUITER, D.J., GUATELLI-STEINBERG, D., CERLING, T.E. & LEE-THORP, J.A. 2006a. Isotopic evidence for dietary variability in the early hominin *Paranthropus robustus. Science* **314**, 980–982.
SPONHEIMER, M., LOUDON, J.E., CODRON, D., HOWELLS, M.E., PRUETZ, J.D., CODRON, J., DE RUITER, D.J. & LEE-THORP, J.A. 2006b. Do 'savanna' chimpanzees consume C_4 resources? *Journal of Human Evolution* **51**, 128–133.
STROMER, E. 1931. Reste susswasser- und land bewohnender wirbeltiere aus den diamante-feldern Klein-Namaqualandes (Sudwest-Afrika). *Sber. Bayern Akademie Wissenschaften* **1931**, 17–47 (from Hendey 1970).
TURNER, A. 1987. New fossil carnivore remains from the Sterkfontein hominid site (Mammalia: Carnivora). *Annals of the Transvaal Museum* **34**, 319–347.
TURNER, A. 1997. Further remains of Carnivora (Mammalia) from the Sterkfontein hominid site. *Palaeontologia africana* **34**, 115–126.
VRBA, E.S. 1976. The fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai. Pretoria. *Transvaal Museum Memoir* No. 21.
VRBA, E.S. 1987. A revision of the Bovini (Bovidae) and a preliminary checklist of Bovidae from Makapansgat. *Palaeontologia africana* **26**, 33–46.
WALKER, J., CLIFF, R.A. & LATHAM, A.G. 2006. U-Pb isotopic age of the Stw 573 hominid from Sterkfontein, South Africa. *Science* **314**, 1592–1594.
WEBB, G.L. 1965. Notes on some chalicothere remains from Makapansgat. *Palaeontologia africana* **9**, 49–73.
WELLS, L.H. & COOKE, H.B.S. 1956. Fossil Bovidae from the Limeworks Quarry, Makapansgat, Potgietersrus. *Palaeontologia africana* **4**, 1–55.
WHITE, T.D. & HARRIS, J.M. 1977. Suid evolution and correlation of African hominid localities. *Science* **198**, 13–21.
WHITE, T.D., SUWA, G. & ASFAW, B. 1994. *Australopithecus ramidus,* a new species of early hominid from Aramis, Ethiopia. *Nature* **371**, 306–312.
WHITE, T.D., SUWA, G. & ASFAW, B. 1995. *Australopithecus ramidus,* a new species of early hominid from Aramis, Ethiopia: Corrigendum. *Nature* **375**, 88.
WHITE, T.D., ASFAW, B., BEYENE, Y., HAILE-SELASSIE, Y., LOVEJOY, C.O., SUWA, G. & WOLDEGABRIEL, G. 2009. *Ardipithecus ramidus* and the paleobiology of early hominids. *Science* **326**, 75–86.
YASUI, K., KUNIMATSU, Y., KUGA, N., BAJOPE, B. & ISHIDA, H. 1992. Fossil mammals from the Neogene strata in the Sinda Basin, eastern Zaire. *African Study Monographs, Supplemental* **17**, 87–107.

Botanical remains from a coprolite from the Pleistocene hominin site of Malapa, Sterkfontein Valley, South Africa

M.K. Bamford[1*], F.H. Neumann[1,2], L.M. Pereira[1], L. Scott[3], P.H.G.M. Dirks [4,5] & L.R. Berger[5]

[1]*Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 Johannesburg, South Africa*

[2]*Steinmann Institute for Geology, Mineralogy and Palaeontology, University of Bonn, Germany*

[3]*Department of Plant Sciences, University of the Free State, Bloemfontein, South Africa*

[4]*School of Earth and Environmental Sciences, James Cook University, Townsville, Australia, 4811*

[5]*Institute for Human Evolution, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050 Johannesburg, South Africa*

Received 8 August 2010. Accepted 10 November 2010

A coprolite probably from a carnivore described in this paper was recovered from the decalcified sediments of Facies D, close to the cranium of a hominid child, *Australopithecus sediba,* at Malapa, and is dated at 1.95–1.78 Ma based on a combination of faunal, U-Pb and palaeomagnetic dating techniques. Maceration of the coprolite yielded wood fragments and pollen of *Podocarpus* sp. as well as phytolith morphotypes that occur in leaves of *Podocarpus* and many other woody taxa. The Malapa site today is in the Grassland Biome, close to the transition to the Savanna Biome. *Podocarpus/Afrocarpus* occurs about 30 km distance in the Northern Afromontane Forest Biome and is restricted to small patches in the mountain kloofs or small canyons (altitude: 1500–1900 m). The occurrence of this vegetation at Malapa in the past implies that the cooler, moister forest vegetation was more widespread.

Keywords: *Podocarpus*, pollen, wood, phytoliths.

INTRODUCTION

The late Pliocene to Pleistocene cave deposits in the Cradle of Humankind World Heritage Site (South Africa) represent one of the world's most important geological settings, hosting hominin fossils and associated faunal and archaeological remains. The recently discovered site of Malapa in the Cradle of Humankind, 15 km NNE of Sterkfontein (Fig. 1), has yielded a remarkable array of fossil hominins attributed to the species *Australopithecus sediba* (Berger *et al.* 2010) together with remains of well-preserved fauna (Dirks *et al.* 2010). The hominin fossils, one juvenile male and one adult female, occur together with the other faunal remains in near-articulated state in the sedimentary remains of a deeply eroded cave system. The hominin remains were deposited in the cave by a single debris flow which occurred shortly after the death of the animals. The fossils of *Au. sediba* are exceptionally well preserved and represent a transitional form, maybe the best yet found, between early australopithecines and early members of the genus *Homo,* thereby replacing other candidates such as *Homo habilis* as our distant ancestor (Berger *et al.* 2010). A reconstruction of the full environment in which *Au. sediba* lived is therefore of great importance.

However, finding fossil plant remains in calcareous hominin sites for reconstructing environments is extremely difficult (Scott & Bonnefille 1986; Carrión & Scott 1999). Amongst the fossils a coprolite, most likely belonging to a carnivore, was discovered during the course of excavations in 2009. Research by Bryant (1974), Scott (1987), Carrión *et al.* (2001), Horrocks *et al.* (2002, 2003), Gonzalez-Samperiz *et al.* (2003) and Ghosh *et al.* (2008) have shown that coprolites may contain preserved pollen, phytoliths and other macerated plant remains. These remains can be from ingestion of plants directly, from ingestion of herbivores by carnivores or from airborne pollen or plant litter that adhered to the fresh, moist faeces before being buried rapidly and preserved. The coprolite from Malapa preserves evidence of floral remains and provides important clues about the local vegetation and environment in which *Au. sediba* lived and died.

*Author for correspondence. E-mail: marion.bamford@wits.ac.za

SITE DESCRIPTION

Geological setting

Cave deposits in the Cradle of Humankind are hosted by stromatolite-rich dolomite of the late Archaean (2.64–2.5 Ga) Malmani Subgroup (Eriksson *et al.* 2006) which is subdivided into five formations based on stromatolite morphology, chert content and the presence of shale and chert-breccia horizons (Eriksson & Truswell 1974). From base to top these formations are: the Oaktree, Monte Christo, Lyttelton, Eccles and Frisco Formations. The Malapa site occurs in well-bedded, chert-free dolomite in the stratigraphic top of the 155 m-thick Lyttelton Formation.

Malapa is positioned within the steep-sided valley of the Grootvleispruit, at an altitude of 1442 masl, and represents an erosion remnant of a de-roofed cave. Dating of the land surface around the fossil site constrains the minimum and maximum erosion rates of the land surface to 4 m/My and 55 m/My, respectively (Dirks *et al.* 2010). This illustrates the dynamic nature of the landscape and indicates that at the time the Malapa fossils were buried, the cave was over 30 m deep (Dirks *et al.* 2010).

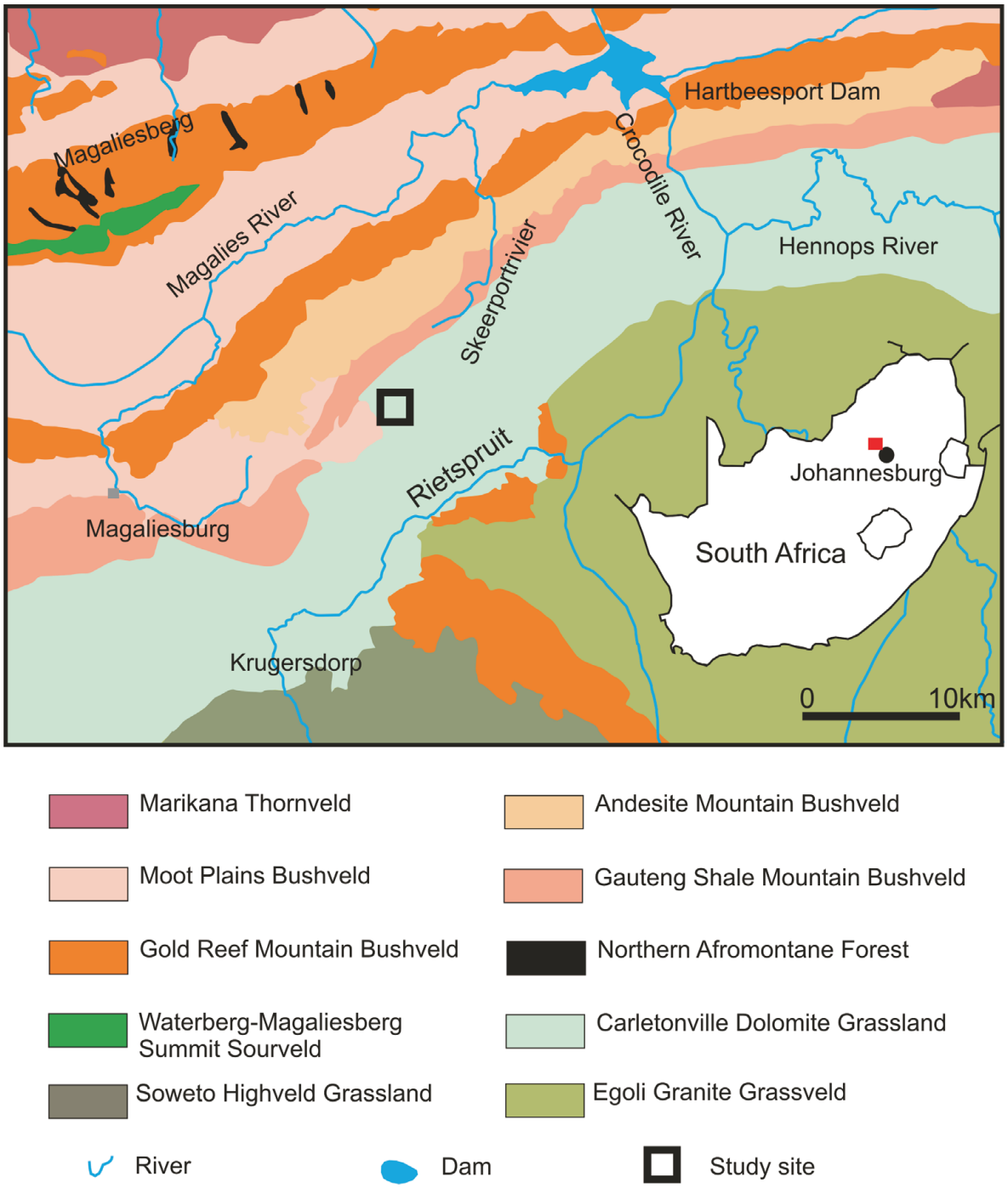


Figure 1. Map of locality with the vegetation biomes indicated (from Mucina & Rutherford 2006).

The fossil remains of *Au. sediba* and associated fauna occur predominantly in two sedimentary facies named Facies D and Facies E (Fig. 2 of Dirks *et al.* 2010) which are positioned stratigraphically above a central flowstone. The fauna includes an unusual abundance of carnivores, several in near-articulated state (Dirks *et al.* 2010). The coprolite described in this paper was recovered from the decalcified sediments of Facies D, close to the child's cranium and probably belonged to a carnivore. The order Carnivora is represented in Facies E and D by four families: Canidae, Felidae, Hyaenidae and Herpestidae. The family Canidae is represented by a single species, *Lycaon pictus*; Felidae is represented by *Dinofelis* sp., *Megantereon whitei* and *Felis silvestris; Parahyaena brunnea* is the sole species representing the Hyaenidae; and Herpestidae is represented by *Atilax mesotes* and *Mungos sp.*

Through a combination of faunal, U-Pb and palaeomagnetic dating techniques the age of the rocks encasing the fossils has been determined at 1.95–1.78 Ma (Dirks *et al.* 2010). Dating involved a U-Pb date for a flowstone sheet below the hominin-bearing sediments of Facies D, and yielded an age of 2.026 ± 0.021 Ma. Paleomagnetic analysis further constrained the age of the fossil-bearing layers above the flowstone to the period coinciding with, or immediately following, a palaeomagnetic reversal at 1.95 Ma (Dirks *et al.* 2010).

Ecological setting

The Malapa site today occurs within the grassland biome, close to the transition to the savanna biome (Fig. 1).

Table 1. Microbotanical remains of the Malapa coprolite.

Micro remains	Outer layer (? local plant debris)	Core (? ingested material)
Wood	2 *Podocarpus/Afrocarpus* sp. 1 dicot wood	1 piece conifer charcoal 1 larger piece with cross-fields 12 woody fragments (indeterminate)
Palynomorphs	1 *Podocarpus* sp. 1 unidentified	barren
Phytoliths	Not tested (insufficient material)	12 orbicular nodulose 6 sub-orbicular nodulose 5 orbicular psilate 3 orbicular rugulose 2 lanceolate psilate 2 tabular psilate 1 irregular nodulose

The hilly region features heavily degraded vegetation due to human activities. Precipitation is around 600 mm per annum (Avery 2001; Mucina *et al.* 2006). The remains of the cave lie within the Carletonville Dolomite Grassland. Poaceae are dominant and species-rich, *Anthospermum rigidum* subsp. *pumilum, Rhus Magalismontana* and *Ziziphus zeyheriana* are typical shrubs (Mucina *et al.* 2006). To the south Egoli Granite Grassland can be found on

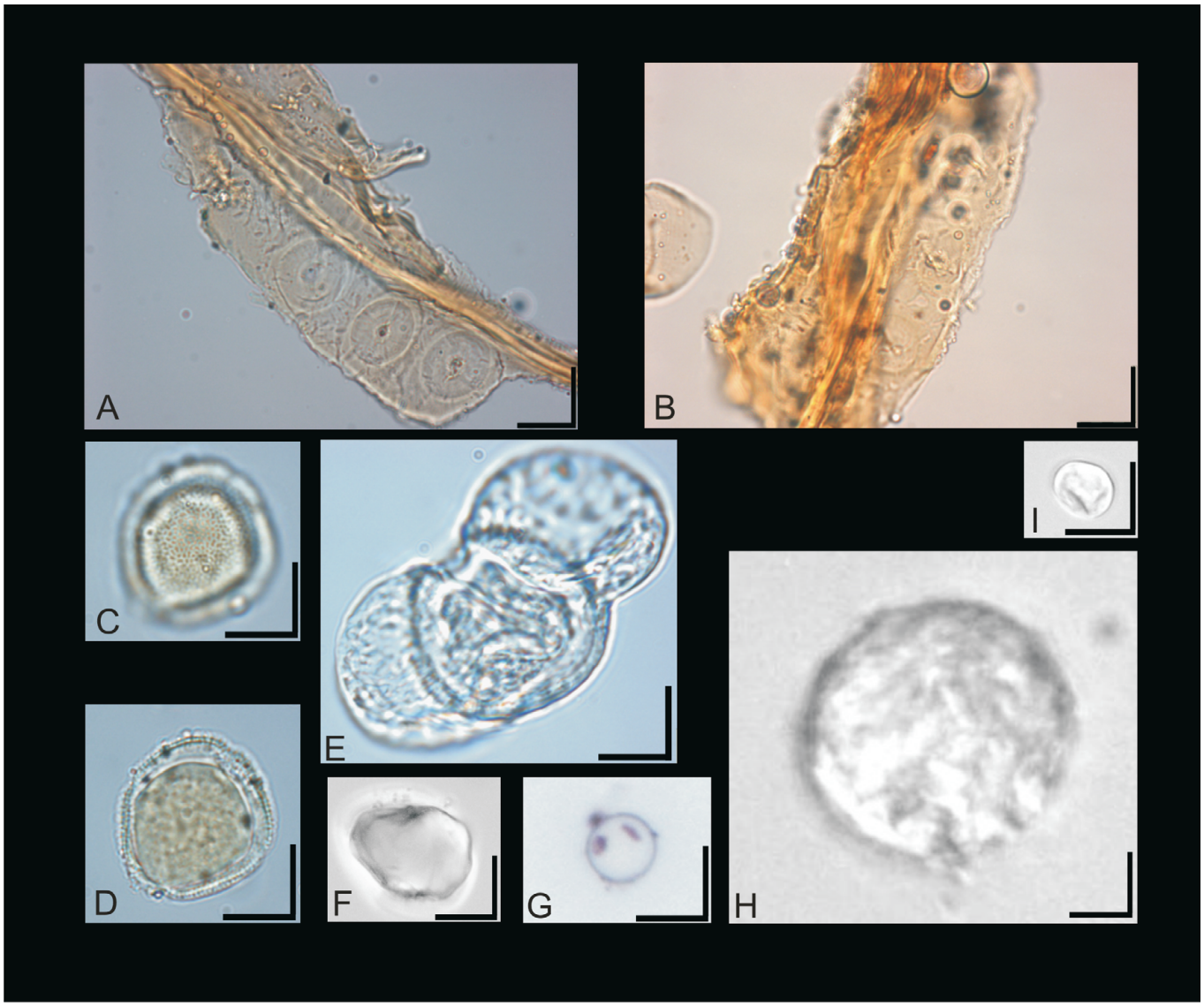


Figure 2. Microbotanical remains from the Malapa coprolite photographed under light microscope. **A, B**, cf. *Podocarpus* sp., tracheid with bordered pits on the radial wall. **C**, **D**, unidentified pollen grain (contaminant?). **E**, *Podocarpus* sp. pollen, bisaccate, length 52 μm. **F**, sub-orbicular irregular phytolith (fossil). **G**, modern *Podocarpus* leaf orbicular psilate phytolith. **H**, orbicular, rugulate fossil phytolith. **I**, orbicular, psilate fossil phytolith. (Scale bar on images A–E is 10 μm; images F–I is 2μm.)

undulating plains and low hills. The grassland is dominated by *Hyparrhenia hirta*, trees and shrubs such as *Rhus pyroides, Vangueria infausta* and *Anthospermum hispidulum* grow on rocky slopes. Soweto Highland Grassland appears in a broad band south of Krugersdorp. *Themeda triandra* is the most important member of the Poaceae; woody species include *Berkheya annectens, Ziziphus zeyheriana* and *Anthospermum* species (Mucina *et al.* 2006). At the precipitation-rich southern slopes of the Magaliesberg the Waterberg–Magaliesberg Summit Sourveld features few small trees and shrubs, e.g. *Englerophytum magalismontanum, Protea caffra* subsp. *caffra, Brachylaena rotundata,* as well as grassland. To the north of the grassland a narrow band of Gauteng Shale Mountain Bushveld appears where trees like *Acacia caffra, Dombeya rotundifolia, Celtis africana* and *Cussonia spicata* as well as a variety of Poaceae are common (Rutherford *et al.* 2006). Andesite Mountain Bushveld, forming small patches to the south of the site and a band north of the Gauteng Shale Mountain Bushveld, are characterized by *Acacia caffra, A. karroo, Celtis africana, Protea caffra* and grasses, e.g. *Themeda triandra.* The vegetation of the Gold Reef Mountain Bushveld, found on east–west trending ridges and close to Krugersdorp, consists of *Acacia* woodland. The herbaceous layer is dominated by Poaceae. The valley of the Magalies River and the region around Magaliesburg is dominated by Moot Plains Bushveld (Rutherford *et al.* 2006, Fig. 1). *Acacia nilotica, A. tortilis* subsp. *heteracantha, Rhus lancea* and *Buddleja saligna* grow on stony soils; grass is common in the herbaceous layer.

Northern Afromontane Forest is restricted to small patches in the mountain kloofs or small canyons (altitude: 1500–1900 m) of Magaliesberg to the north of the site and completely surrounded by Gold Reef Mountain Bushveld. Two patches border the Waterberg–Magaliesberg Summit Sourveld. In comparison the forest is species-poor: *Podocarpus latifolius, Olinia emarginata, Halleria lucida, Afrocarpus falcatus* and *Ilex mitis* are typical trees (Mucina & Geldenhuys 2006).

MATERIALS AND METHODS

A single, whitish coprolite of a rather undiagnostic, slightly flattened shape (29 mm × 21 mm × 11 mm; 7.71 g after cleaning, catalogue no. UW88-0905-B020) has been macerated in the palynology laboratory of the Bernard Price Institute for Palaeontological Research as a test for botanical remains. More coprolites from the Malapa site, which hopefully will be discovered in the future, will be analysed. The coprolite was first thoroughly cleaned with a brush, soap and distilled water to remove modern dust contamination and it was then weighed. To differentiate between ingested plant matter and external accumulation after expulsion of the faeces by the animal, the cleaned outer layer was dissolved in hydrochloric acid (10% HCl) for 2 minutes and the solution was retained for analysis. The outer layer dissolved in HCl had a thickness of 1–2 mm. The remaining inner core of the coprolite and the dissolved surface layers of the coprolite were processed separately for palynomorphs using a standard procedure which includes the addition of HCl, HF, KOH and heavy liquid separation in a saturated $ZnCl_2$ solution. Two *Lycopodium* spore tablets were added to the samples before processing.

A sub-sample of 1.83 g of the coprolite's inner core was set aside for phytolith processing. The sample was processed in 10% HCl to remove carbonates and 30% H_2O_2 to remove organic matter. The remaining residue was mounted onto one slide. There was insufficient outer surface material for phytolith processing and analysis. The pollen and phytolith slides were studied under a Zeiss Axiophot petrographic microscope and photographs taken with a digital camera at ×400 and ×1000 magnification.

RESULTS

The coprolite dissolved easily in HCl and hence was calcium carbonate-rich. Although not rich in plant remains some identifiable microbotanical remains were found and these are described below. Both the inner and outer layers of the coprolite were productive (Table 1); however, only the inner part of the coprolite was tested for phytoliths, a number of which were found and are described. Observed microfossils including wood, pollen and phytoliths are shown in Fig. 2.

Wood fragments

Fragments of tracheids and fibres of conifer and dicot woods respectively were visible in the sample from the outer layers of the coprolite but the dicot fragments are not diagnostic beyond this level of identification. However, there were two pieces of conifer tracheids with bordered pits arranged in a single vertical line along the length of the tracheid. The pits are well spaced, round in outline with a diameter of 20 μm and circular areole of 5 μm (Fig. 2A,B). Such tracheids are water-conducting tissues typically of conifers and the form and arrangement of the bordered pits are indicative of the family.

In order to identify the fragments of conifer wood that have very few features and are missing the key feature for identification, that of the cross-field pits, a survey of the southern hemisphere taxa was done (Phillips 1941; Greguss 1955; IAWA Committee 2004). Araucariaceae have 2–3 rows of pits, alternately arranged and in contact. The Cupressaceae and Podocarpaceae have uniseriate to biseriate and opposite, well-spaced bordered pits on the radial walls of the tracheids. The Pinaceae bordered pits are similar but the pits tend to be more crowded. Of these families only two are represented in southern Africa today with seven species. *Widdringtonia* (Cupressaceae) has three species and *Podocarpus* (Podocarpaceae) has four species (Germishuisen & Meyer 2003). *Widdringtonia* species have round, separate tracheid bordered pits that range in size from 8–20 μm. The pits in *Podocarpus* species have the same arrangement but tend to be larger, 20–35 μm in diameter. The fossil fragments have round, separate bordered pits that are 20 μm wide.

The three species of *Widdringtonia* (commonly called cedars) have disjunct distributions (Coates Palgrave 2002): *Widdringtonia cedarbergensis* Marsh is restricted to the Cederberg Mountains in the western Cape;

W. nodiflora (L.) Powrie occurs north of Zimbabwe, in eastern Zimbabwe, northern South Africa and inland along the eastern margin of the Cape and southern KwaZulu Natal; and *W. schwarzii* (Marloth.) Mast. occurs in the Eastern–Western Cape junction. The Podocarpaceae (yellowwoods) also have a disjunct distribution (Coates Palgrave 2002). *Podocarpus elongatus* (Ait.) L=Hérit. ex Pers. occurs in the western Cape, *Podocarpus* falcatus, or *Afrocarpus falcatus* (Thunb.) C.N. Page is more widespread, along the eastern side of the Cape, Natal and Mpumalanga. *Podocarpus henkelii* Stapf is restricted to KwaZulu Natal and *Podocarpus latifolius* (Thunb.) R.Br. ex Mirb. has a similar distribution to *P. falcatus* but also occurs in eastern Zimbabwe.

Based on the recorded distributions of these conifers none of them occurs naturally today in the Cradle area; so it likely that in the past at least one of the taxa was more widespread. To the north of the site are relict patches of Northern Afromontane Forest (Fig. 1) that includes *P. latifolius* and *P. (A.) falcatus.* Coates Palgrave (2002) notes that these conifers are not pioneers and most of these species grow to large trees in sheltered or protected areas (*W. cedarbergensis, W. nodifolia, W. schwarzii, A. falcatus, P. latifolius*). Most of the species also occur in moist montane or coastal forest or evergreen forest so it is very likely that the fossil trees did too. *P. falcatus,* for example, occurs at 1500–2400 m in East Africa but grows at lower altitudes in South Africa and it prefers an annual rainfall of (800–) 1200–1800(–2200) mm and a mean annual temperature of 13–20°C (Aerts 2008). *P. latifolius* prefers even higher rainfall (1000–2000 mm per annum; Okeyo 2008). Today the Cradle area (altitude 1300–1600m) has 650–750 mm summer rainfall per annum with temperatures varying between the recorded extremes of –12°C and 39°C with an average of 16°C (Bredenkamp & van Rooyen 1998). This is not very different from the preferred altitude and temperature range of *P. falcatus* or *P. latifolius* but the rainfall is much lower at the fossil site today.

Pollen

The sample from the core of the coprolite is barren with the exception of a few fragments of AOM (amorphous organic matter) and the sample from the outer layers of the coprolite is very poor in palynomorphs. One unidentified pollen grain features four apertures (colpi?) and a microreticulate sculpture. A clearly visible interior structure is reminiscent of cytoplasm, so it cannot be excluded that this pollen grain is a contaminant (Fig. 2C,D). Other evidence for contamination, for example pine pollen, is absent from the sample. A second pollen grain belongs to *Podocarpus* sp. (Fig. 2E). The well-preserved palynomorph has no obvious cell contents, is 52 μm wide and is vesiculate-bisaccate (see Erdtman, 1957). Although it seems rather unlikely that the *Podocarpus* pollen is a contaminant, we cannot exclude this possibility. Podocarp or yellowwood pollen is produced in abundance and they have an excellent dispersal mechanism because the air sacs give them some buoyancy. Consequently, yellowwood pollen is often overrepresented in pollen diagrams (Coetzee 1967). Since it is not possible to easily differentiate between the pollen of different *Podocarpus* species this was not attempted in the current study.

Phytoliths

Thirty one phytoliths were counted on the slide from the core of the coprolite. None of the morphotypes was distinctive to family level. Characteristic short-cell phytoliths from Poaceae (grasses) were absent. The majority of morphotypes (29) were spheres with nodulose, psilate or verrucate surfaces (Fig. 2F-I). Verrucate spheres have not been isolated in grasses (Piperno 2006); however, spherical morphotypes are most commonly observed in arboreal and herbaceous monocots and eudicots (Kindo *et al.* 1994; Kealhofer & Piperno 1998; Piperno 2006). A single unsegmented hair and various undiagnostic, irregularly shaped bodies were also observed. Comparing the fossil phytoliths with those from the modern reference collection housed at the Bernard Price Institute (Pereira 2009) we observed that psilate spheres in the size range 10 to 15 μm are also common in the leaves of *Podocarpus latifolius.* However, it should be noted that they are by no means exclusive to the species.

DISCUSSION

If we assume that the botanical material in the core of the coprolite represents plant material that was ingested by the animal then it was a browser, or a carnivore that ate a browser. The outer layer plant material is either ingested material or debris that adhered to the coprolite before preservation so it could indicate the local environment.

Both pollen and wood microbotanical remains in the coprolite indicate the presence of conifer trees. The phytolith morphotypes do not contradict this interpretation but indicate the presence of some woody species. The conifer is most likely a species of *Podocarpus/Afrocarpus.* All the living southern African species prefer higher rainfall than occurs in the area today. Such trees form a stable forest with medium light levels. It is not possible to determine the extent or height of the forest from these data. On the other hand it seems likely that Northern Afromontane Forests with *Podocarpus* also existed in the early Pleistocene, and were perhaps more widespread than today. Generally the genus *Podocarpus* must have been prominent in southern Africa around 2 Ma as its long distance-transported pollen occurs in marine sediments of this age off the Namibian coast (Dupont 2006). Out of a series of modern pollen surface samples from the 1980s in the Sterkfontein/Kromdraai area adjacent to Malapa, it only occurs rarely (0.4%) in one count from September 1988 (Scott 1995). Therefore it is remarkable that only one of the two pollen grains in the Malapa coprolite was a *Podocarpus.* Its apparent prominence in the study area might be a consequence of higher rainfall in the past and suppressed fire. Today the Afromontane Forest in the Magaliesberg is restricted to mountain kloofs. In strong summer rainfall regions forests can only grow if precipitation is greater than 725 mm. Today the distribution of Afromontane Forest is also limited by fire and is limited to areas protected from the wind (Mucina & Geldenhuys 2006). Therefore the borders to fire-prone ecosystems, e.g.

grassland and savannas, are naturally sharp. A more humid climate might have lead to the expansion of *Podocarpus* forest beyond Magaliesberg in the past. This trend has been noted from other Quaternary pollen archives from the same region in the Holocene (e.g. Scott & Vogel 1983) and in the Late Pleistocene where *Podocarpus* were quite prominent in certain periods before the last Glacial Maximum (Scott 1999). Apart from a slightly contaminated travertine sample from Kromdraai Member 3 (0.6%), it was only found in a very low concentration (0.4%) in a more reliable travertine sample from Sterkfontein Member 5 suggesting it was not a prominent part of the vegetation, which included Proteaceae at the time (Scott 1995).

The Pleistocene topography of the Malapa area was not static (Dirks *et al*. 2010). There may have been significant Karoo remnants remaining on top of the dolomite, the valleys in the area would have been less deep, the Magaliesberg was probably less pronounced and the overall altitude could have been lower, considering postulated rapid uplift in the late Pliocene (Partridge & Maud 2000). Direct comparisons with the current settings need some qualification and the past vegetation may well have been richer and more diverse.

We thank the South African Heritage Resources Agency for a permit to work at the Malapa site and the Nash Family for permission to work on their land. The Department of Science and Technology, the National Research Foundation of South Africa, the Institute for Human Evolution, the Palaeontological Scientific Trust, the University of the Witwatersrand, Sir Richard Branson and the Mellon Foundation are thanked for their financial support. Lucy Pereira thanks the Oppenheimer Memorial Trust and Palaeontological Scientific Trust for financial assistance. Frank Neumann is supported by a University of the Witwatersrand URC post-doctoral fellowship.

REFERENCES

AERTS, R., 2008. *Afrocarpus falcatus* (Thunb.) C.N.Page. [Internet] Record from Protabase. Louppe, D., Oteng-Amoako, A.A. & Brink, M. (eds), PROTA (Plant Resources of Tropical Africa / Resources végétales de l'Afrique tropicale), Wageningen, Netherlands. Online at: http://database.prota.org/search.htm (accessed 4 February 2010).

BERGER, L.R., DE RUITER, D.J., CHURCHILL, S.E., SCHMID, P., CARLSON, K.J., DIRKS, P.H.G.M. & KIBII, J.M. 2010. *Australopithecus sediba*: a new species of *Homo*-like australopith from South Africa. *Science* **328**, 195–204.

BREDENKAMP, G. & VAN ROOYEN, N. 1998. Rocky Highveld Grassland. **In**: Low, A.B. & Rebelo, A.G. (eds), *Vegetation of South Africa, Lesotho and Swaziland.* Pretoria, Department of Environmental Affairs and Tourism.

BRYANT, V.M. Jr., 1974. Prehistoric diet in southwest Texas: the coprolite evidence. *American Antiquity* **39**, 407–420.

CARRION, J.S., RIQUELME, J.A., NAVARRO, C. & MUNUERA, M. 2001. Pollen in hyaena coprolites reflects late glacial landscape in southern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* **176**, 193–205.

CARRION, J.S. & SCOTT, L. 1999. The challenge of pollen analysis in palaeoenvironmental studies of hominid beds: the record from Sterkfontein Caves. *Journal of Human Evolution* **36**, 401–408.

COATES PALGRAVE, M. 2002. *Keith Coates Palgrave Trees of Southern Africa* (3rd edn). Cape Town, Struik Publishers.

COETZEE, J.A. 1967. Pollen analytical studies in East and southern Africa. *Palaeoecology of Africa* **3**, 1–146.

DIRKS, P.H.G.M., KIBII, J.M., KUHN, B.F., STEININGER, C., CHURCHILL, S.E., KRAMERS, J.D., PICKERING, R., FARBER, D.L., MERIAUX, A-S., HERRIES, A.I.R., KING, G.C.P. & BERGER, L.R. 2010. Geological setting and age of *Australopithecus sediba* from southern Africa. *Science* **328**, 205–208.

DUPONT, L.M. 2006. Late Pliocene vegetation and climate in Namibia (southern Africa) derived from palynology of ODP Site 1082. *Geochemistry, Geophysics and Geosystems* **7**, Q05007, doi:10.1029/2005GC001208

ERDTMAN, G. 1957. *Pollen and Spore Morphology. Plant Taxonomy, Gymnospermae, Pteridophyta Bryophyta.* Stockholm, Almqvist and Wiksell.

ERIKSSON, P.G., ALTERMANN, W. & HARTZER, F.J. 2006. The Transvaal Supergroup and its precursors. **In**: Johnson, M.R., Anhaeusser, C.R. & Thomas, R.J. (eds), *The Geology of South Africa,* 237–260. Pretoria, Geological Society of South Africa and Council for Geoscience.

ERIKSSON, K.A. & TRUSWELL, J.F., 1974. Tidal flat associations from the lower Proterozoic carbonate sequence in South Africa. *Sedimentology* **21**, 293–309.

GERMISHUISEN, G. & MEYER, N.L. (eds) 2003. Plants of southern Africa. An annoted checklist. *Strelitzia* **14**, National Botanical Institute, Pretoria. 1231 pp.

GHOSH, R., GUPTA, S., BERA, S., JIANG, H., LI, X. & LI, C. 2008. Ovi-caprid dung as an indicator of palaeovegetation and palaeoclimate in northwestern China. *Quaternary Research* **70**, 149–157.

GONZALEZ-SAMPIREZ, P., MONTEZ, L. & UTRILLA, P. 2003. Pollen in hyaena coprolites from Gabasa Cave (northern Spain). *Review of Palaeobotany and Palynology* **126**, 7–15.

GREGUSS, P. 1955. *Identification of Living Gymnosperms on the Basis of Xylotomy.* Budapest, Akadémiai Kiadó.

HORROCKS, M., JONES, M.D., BEEVER, R.E. & SUTTON, D.G. 2002. Analysis of plant microfossils in prehistoric coprolites from Haratoanga Bay, Great Barrier Island, New Zealand. *Journal of the Royal Society of New Zealand* **32**(4), 617–628.

HORROCKS, M., IRWIN, G.J., McGLONE, M.S., NICHOL, S.L. & WILLIAMS, L. 2003. Pollen, phytoliths and diatoms in prehistoric coprolites from Kohika Bay of Plenty, New Zealand. *Journal of Archaeological Science* **30**, 13–20.

IAWA Committee. 2004. IAWA list of microscopic features for softwood identification. *IAWA Journal* **25**, 1–70.

KEALHOFER, L. & PIPERNO, D.R. 1998. Opal phytoliths in Southeast Asian flora. *Smithsonian Contributions to Botany.* **88**. Smithsonian Institution Press. Washington, D.C.

KONDO, R., CHILDS, C. & ATKINSON, I. 1994. *Opal Phytoliths of New Zealand.* Lincoln, New Zealand, Manaaki Press.

MUCINA, L. & RUTHERFORD, M.C. (eds), 2006. The Vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* **19**. Pretoria, South African National Biodiversity Institute.

OKEYO, J.M., 2008. *Podocarpus latifolius* (Thunb.) R.Br. ex Mirb. [Internet] Record from Protabase. Louppe, D., Oteng-Amoako, A.A. & Brink, M. (eds), PROTA (Plant Resources of Tropical Africa / Resources végétales de l'Afrique tropicale), Wageningen, Netherlands. Online at: http://database.prota.org/search.htm (accessed 4 February 2010).

PARTRIDGE, T.C. & MAUD, R.R., 2000. Macro-scale geomorphic evolution of southern Africa. **In**: Partridge, T.C & Maud, R.R. (eds), *The Cenozoic of Southern Africa,* 3–18. New York, Oxford University Press.

PERIERA, L.M., 2009. The Wits Online Phytolith Database. University of the Witwatersrand, Johannesburg, South Africa. Online at: http://web.wits.ac.za/Academic/Science/GeoSciences/BPI/Research/WOPD/ (accessed 15 February 2010).

PHILLIPS, E.W.J., 1941. The identification of coniferous woods by their microscopic structure. *Botanical Journal of the Linnean Society* **52**, 259–320.

PIPERNO, D.R. 2006. *Phytoliths: A Comprehensive Guide for Archaeologists and Paleoecologists.* Lanham, Maryland, Altamira Press.

SCOTT, L. 1987. Pollen analysis of hyaena coprolites and sediments from Equus Cave, Taung, southern Kalahari (S. Africa). *Quaternary Research* **28,** 144–156.

SCOTT, L. 1995. Pollen evidence for vegetational and climatic change in southern Africa during the Neogene and Quaternary. **In**: Vrba E.S., Denton, G.H., Partridge, T.C. & Burckle, L.H. (eds), *Paleoclimate and Evolution with Emphasis on Human Origins,* 65–76. Yale: Yale University Press.

SCOTT, L. 1999.The vegetation history and climate in the Savanna Biome, South Africa, since 190 000 Ka: A comparison of pollen data from the Tswaing Crater (the Pretoria Saltpan) and Wonderkrater. *Quaternary International* **57–58**, 215–223.

SCOTT, L. & BONNEFILLE, R. 1986. A search for pollen from the hominid deposits of Kromdraai, Sterkfontein and Swartkrans: some problems and preliminary results. *South African Journal of Science* **82,** 380–382.

SCOTT, L. & VOGEL, J.C., 1983. Late Quaternary pollen profile from the Transvaal Highveld, South Africa. *South African Journal of Science* **79**, 266–272.

Technical note

A case of vertebrate fossil forgery from Madagascar

Bernhard Zipfel*, Celeste Yates & Adam M. Yates

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, WITS, 2050 Johannesburg, South Africa

Received 19 July 2010. Accepted 3 December 2010

INTRODUCTION

The high value of rare fossil specimens results in some fossil dealers and collectors purchasing these specimens from dubious and even illegal sources. Complete vertebrate fossils in particular are rare, and are therefore more easily sold at relatively high prices. As a result there is a demand for the production of fake fossils particularly in developing countries where the trade in fossils represents a means to economic survival (Mateus *et al.* 2008). Most dealers, however, have little or no scientific knowledge on the fossils they purchase and may therefore inadvertently purchase fake fossils. Both China and Morocco, for example, are known to produce both genuine and fake fossils (Dalton 2000, 2004a, b; Milner *et al.* 2001; Padin 2000). As a result, China, among many other countries, including South Africa, has instituted very strict legislation regarding the trade and export of fossils. Fraudulent fossils do not just affect dealers and collectors, but have also embarrassingly deceived scientists. The best known of these is the famous 'Piltdown Man' from England, a forgery merging the cranium of a modern human and the mandible of an orangutan. This forgery was put forward as an early human ancestor that confused the scientific community for decades (Weiner 1955), whilst the first genuine early hominin, the now famous 'Taung Skull', holotype of *Australopithecus africanus* from South Africa (Dart 1925, 1929; Dart & Craig 1959; Hrdlicka 1925), was forced to take a 'back seat' for many years. More recently, the famous *Archaeoraptor* specimen from the Lianoing Province of China received coverage by a number of publications including *National Geographic* and *Nature* (Sloan 1999; Rowe *et al.* 2001) but in reality the specimen represents at least two and perhaps up to five separate individuals of two or more different species fraudulently merged into a single specimen (Zhou *et al.* 2002).

Invertebrates from Morocco, for example trilobites have been skillfully carved out of rock and sold as genuine fossils. As most trilobites from Morocco are genuine, and the trade in these invertebrates from that country is legal, it is understandable that a fossil trader may be deceived. In other cases, a genuine fossil of a common living species, such as the tooth of a great white shark (*Carcharodon carcharias*), may be sold as a representative of a similar, but extinct species such as a megalodon (*Carcharocles megalodon*). Fossil frauds are therefore committed not only for profit, but also for publicity (Mateus *et al.* 2008).

Mateus *et al.* (2008) suggest a number of methods of fraud recognition and describe three kinds of hoaxes:

1) Those that contain no original fossil material, such as shapes carved in rock;
2) Those that contain original fossil material, but are entirely or partially altered in order to give the appearance of a more complete specimen, for example, a skull carved from a limb bone.
3) Those that are true fossils but a combination of multiple individuals, mostly from the same species.

Here we report on a specimen that was brought to the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand by a fossil dealer for identification. The specimen had been obtained illegally in Madagascar by the fossil dealer, reportedly from the vicinity of known dinosaur localities in the Cretaceous Maevarano Formation of the Mahajanga Basin (Depéret 1896; Besairie 1936, 1972), with the intention of having it prepared in South Africa. The fauna of this formation is well known and is the subject of ongoing research programmes (e.g. Forster *et al.* 1998; Krause & Hartman 1996; Sampson *et al.* 2001; Krause *et al.* 1999; Buckley *et al.* 2000; Curry-Rogers & Forster 2001; Rogers 2005; Fanti & Therrien 2007).

DESCRIPTION

The specimen initially appeared to consist of two articulated vertebral centra in a nodule of matrix. It measured approximately 23 cm by 15 cm. A superficial resemblance to a small skull could be seen. After removal of the 'matrix' it became apparent that the specimen was a forgery using genuine pieces of dinosaur bone that attempted the construction of a vertebrate skull (Fig. 1). The 'matrix' proved to be crushed rock, probably from the Maevarano Formation mixed with commercial cement covering inner layers of resin and plaster of Paris (Fig. 2). The construction of the skull consisted of an 'orbit', a pig-like 'snout', crude 'teeth' a lower 'jaw' and a 'post-orbital' region. The snout and post-orbital region were constructed from genuine fossils of dinosaur vertebral centra (Fig. 2). These are most probably from a titanosaur sauropod; however, this is purely speculative as there is not enough material to be diagnostic. The teeth were constructed with a series of roughly shaped stones cemented to the upper and lower 'jaws' (Fig. 2).

DISCUSSION

Clearly, this forgery was a poor attempt at creating what seemed to have been intended to resemble a vertebrate skull. As the 'skull' was bound by matrix, it appears that the intent of the forgery was probably not to convince anyone that this was a genuine fossil assemblage, but rather to give a vague impression that the matrix block was indeed fossiliferous and superficially gave the impression that it potentially contained what seemed to be a vertebrate skull. This resulted in the sale of the specimen before the complete contents of the matrix could be determined by the purchaser. According to the classification of fossil forgeries by Mateus *et al.* (2008), this forgery would

*Author for correspondence. E-mail: bernhard.zipfel@wits.ac.za



Figure 1. Fossil forgery from Madagascar: **a**, left view; **b**, right view; **c**, inferior view.

fall into the second group; being one that contains original fossil material, but is entirely or partially altered in order to give the appearance of a more complete specimen. As long as fossils are permitted to be legally traded by some countries, it appears that fossil forgeries and similar frauds will occur. Where fossils are purchased for both private and public collections, the legality of the purchase in the absence of formal heritage agency approval, will remain doubtful. A recent debate highlights this where fossils in private collections of questionable origin subjected to scientific study were not accepted for publication in reputable peer-reviewed journals. A controversial new

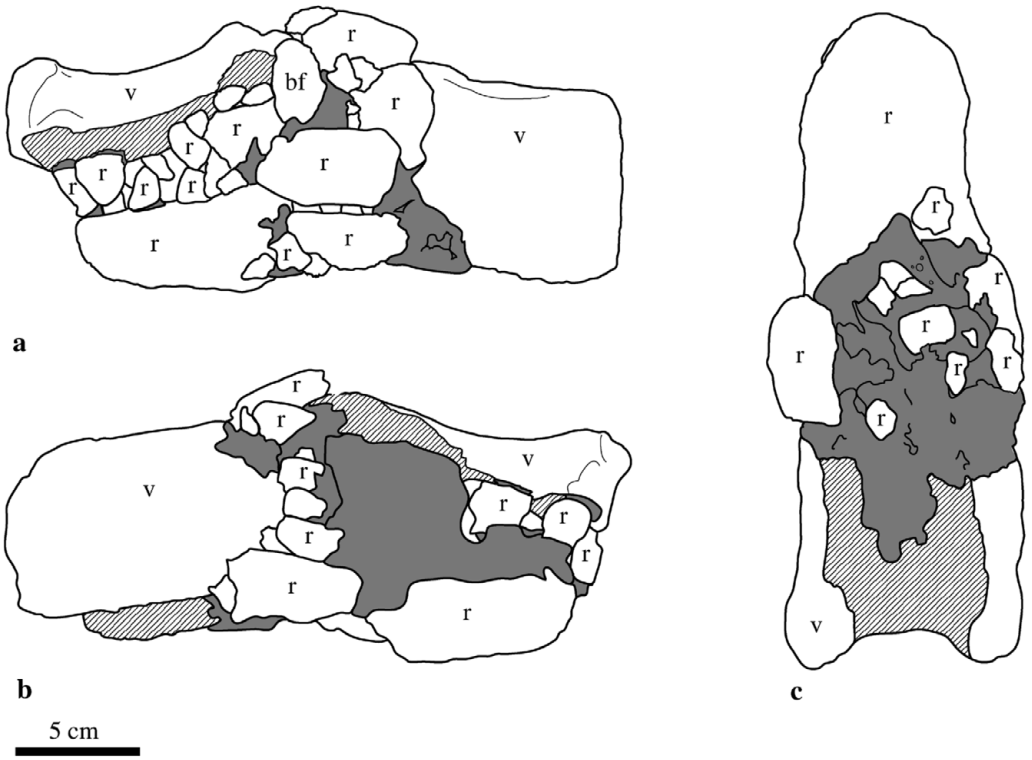


Figure 2. Key to main components of the fossil forgery from Madagascar: **a**, left view; **b**, right view; **c**, inferior view. Hatched area represents artificially ground or cut surfaces of fossil bone, grey areas represent areas of resin or plaster. Abbreviations: bf, fossil bone fragment; r, rock; v, fossil vertebra.

'amateur' journal, the *Journal of Paleontological Sciences*, has angered academic researchers who fear that the project will give some scientific legitimacy to the dealings of commercial fossil hunters (Hopkin 2007). The organizers of the *Journal of Paleontological Sciences* said that they will publish details of privately held fossils, bringing them in from the 'scientific darkness'. Traditional palaeontologists feel that this undermines the field and could fuel the black market in fossil specimens. Triebold (2007) counters this argument and explains that the journal's submission guidelines state that the *JPS* will not publish fossils that cannot be legally exported from their home country, or where ownership cannot be verified.

It appears that to date South Africa has no obviously overt illegal fossil trade. This, however, by no means indicates that such a trade may not exist. South African legislation (National Heritage Resources Act 25 of 1999) is primarily concerned with the protection and preservation of national heritage resources which allows for the trade of foreign fossils, provided that they were obtained legally in the country of origin. This is often difficult to prove, as was the case with the fossil forgery presented here.

CONCLUSION

Here we have reported the first published fossil fraud from Madagascar of which we are aware. Although this crude forgery was easily identified, the possibilities of more sophisticated forgeries of this nature are possible. This serves to draw attention to the potential problem and encourage palaeontologists to report such cases when they occur.

Our thanks go to an anonymous reviewer for helpful comments.

REFERENCES

BESAIRIE, H. 1936. Recherches géologiques à Madagascar – La géologie du Nord-Ouest. *Mémoires de l'Académie Malgache* **21,** 9–259.

BESAIRIE, H. 1972. Géologie de Madagascar I. Les terrains sédimentaires. *Annales Géologique de Madagascar* **35**, 1–463.

BUCKLEY, G., BROCHU, C., KRAUSE, D. & POL, D. 2000. A pug-nosed crocodyli-form from the Late Cretaceous of Madagascar. *Nature* **405**, 941–944.

CURRY-ROGERS, K. & FORSTER, C. 2001. The last dinosaur titans: a new sauropod from Madagascar. *Nature* **412**, 530–534.

DALTON, R. 2000. Chasing the dragons. *Nature* **406**, 930–932.

DALTON, R. 2004. Feathered fossils cause a flap in museums. *Nature* **429**, 5.

DALTON, R. 2004. Feathers fly as China cracks down on illegal fossils sales. *Nature* **431**, 496.

DART, R.A. 1925. *Australopithecus africanus*: the man-ape of South Africa. *Nature* **115**, 195–199.

DART, R.A. 1929. A note on the Taung skull. *South African Journal of Science* **26**, 648–658.

DART, R.A. & CRAIG, D. 1959. *Adventures with the Missing Link.* New York, Harper Brothers.

DEPÉRET, C. 1896. Note sur les dinosauriens sauropodes et théropodes du Crétacé Superieur de Madagascar. *Bulletin de la Société géologique de France* **21**, 176–194.

FANTI, F. & THERRIEN, F. 2007. Theropod tooth assemblages from the Late Cretaceous Maevarano Formation and the possible presence of dromaeosaurids in Madagascar. *Acta Palaeontol. Pol.* **52** (1), 155–166.

FORSTER, C., CHIAPPE, L., KRAUSE, D. & SAMPSON, S. 1996. The first Cretaceous bird from Madagascar. *Nature* **382**, 532–534.

FORSTER, C., SAMPSON, S., CHIAPPE, L. & KRAUSE, D. 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* **279**, 1915–1919.

HARRUB, B. & THOMPSON, B. 2001. *Archaeopteryx, Archaeoraptor,* and the dinosaur-to-birds' theory. *Reason and Revelation* **21**, 25–31.

HOPKIN, M. 2007. Palaeontology journal will 'fuel black market'. *Nature* **445**, 234–235.

HRDLICKA, A. 1925. The Taung ape. *American Journal of Physical Anthropology* **8**, 379–392.

KRAUSE, D. & HARTMAN, J. 1996. Late Cretaceous fossils form Madagascar and their implication for biogeographic relationship with the Indian subcontinent. **In**: Sahni, A. (ed.), *Cretaceous Stratigraphy and Palaeo-environments. Memoir Geological Society of India* **37**, 135–154.

KRAUSE, D., ROGERS, R., FORSTER, A., HARTMAN, J., BUCKLEY, G. & SAMPSON, S. 1999. The Late Cretaceous vertebrate fauna of Madagascar: implications for Gondwanan paleobiogeography. *GSA Today* **9**, 1–7.

MATEUS, O., OVERBEEKE, M. & RITA, F. 2008. Dinosaur frauds and 'Frankensteins': how to distinguish fake and genuine vertebrate fossils. *Journal of Palaeontological Techniques* **2**, 1–5.

MILNER, A.C., FROREY, P.L., GREENWOOD, T. & WILLIAMS, C.T. 2001. Caveat emptor – fake fossils from the far east. *Geology Today* **17**, 52–57.

PADIAN, K. 2000. Feathers, fakes and fossil dealers: How the commertial sale of fosssils erodes science and education. *Palaeontologia Electronica* **3** Online at: http://palaeoelectronica.org

ROGERS, R. 2005. Fine-grained flows and extraordinary vertebrate burials in the Late Cretaceous if Madagascar. *Geology* **33**, 207–230.

ROWE, T., KETCHAM, R.A., DENISON, C., COLBERT, M., XU, X. & CURRIE, P.J. 2001. The Archaeoraptor forgery. *Nature* **410**, 539–540.

SAMPSON, S., CARRANO, M. & FORSTER, C. 2001. A bizarre predatory dinosaur from the Late Cretaceous of Madagascar. *Nature* **409**, 504–506.

SLOAN, C.P. 1999. Feathers for *T. rex*? *National Geographic* **196**, 98–107.

TRIEBOLD, M. 2007. Fossils: new journal will oppose illegal trade. *Nature* **446**, 136.

WEINER, J.S. 1955. *The Piltdown Forgery.* London, Oxford University Press.

ZHOU, Z., CLARKE, J.A. & ZHANG, F. 2002. Archaeoraptor's better half. *Nature* **420**, 285.

STYLE GUIDE FOR AUTHORS — REVISED 2010

GENERAL

Palaeontologia africana publishes papers in the field of palaeontological research and in related branches of the earth sciences. Copies are available for purchase individually or in sets. There is no set subscription rate; prices vary according to the size of each issue. Direct all enquiries, including enquiries about exchange agreements, to:

The Editor
Palaeontologia africana
Bernard Price Institute for Palaeontological Research
University of the Witwatersrand
Private Bag 3
WITS 2050
South Africa
Telephone: [+27-11] 717-6690/6682
Fax: [27-11] 717-6694
E-mail: marion.bamford@wits.ac.za

Submission of a manuscript for publication will be taken to indicate that the material is original and has not been submitted for publication elsewhere.

Authors wishing to reserve copyright to themselves should stipulate this at the time of submission of a manuscript.

PREPARATION AND SUBMISSION OF MANUSCRIPTS

Manuscripts

Manuscripts should be typewritten in English on one side of A4 size paper in double spacing throughout and with margins at least 25 mm wide all round. All pages must be numbered consecutively in the top margin (central), beginning with page 1 on the title page.

One hard copy of each manuscript plus illustrations and an electronic copy by e-mail and/or on CD are required by the Editor. The text should be composed in 'MS Word' or 'WordPerfect', or saved in 'Rich Text Format'). We are unable to accept files on disks formatted for MAC-OS.

Layout

Except in the case of short communications, manuscripts should normally be divided into appropriate conventional sections set out in the following order: title, abstract, introduction, body of text (subdivided as appropriate), acknowledgements, references.

Title

The title should be concise and should reflect the contents clearly. Names of new biological taxa proposed in the manuscript should not be included in the title. If the title is long a suitable abbreviated running title must be provided.

The title must be followed on a separate line by the authors' name/s and institutional address/es (the e-mail address of the first-named author should also be included if possible). In multi-authored contributions, the institutional address of each individual must be linked to the relevant name using superscript numbers.

Abstract

An informative abstract not exceeding 300 words must be provided.

Keywords

At least three keywords should be provided immediately after the abstract.

Introduction and main text

The manuscript should be divided as appropriate into conventional sections (e.g. Introduction, Materials and Methods, Results, Discussion, References, etc).

Acknowledgements

Authors should include only those acknowledgements that are truly warranted.

References

References are listed at the end of the manuscript, beginning on a new page. Under this heading, authors must list only published works that have been cited in the text.

Unpublished works, even those that are 'in press', must not be included unless full bibliographic details can be provided, including pagination. However, formal theses and dissertations, even though unpublished, may be listed provided full details are supplied; this must include reference to the institution where the master copy is lodged. Work that is 'in preparation' and 'personal communications' may be referred to in the text, but must not be included in the list of references.

The list of references must be arranged alphabetically, then chronologically, according to the layout of the examples below. Leave one blank line between each reference, and do not indent or otherwise format each entry. The layout sequence is:

(i) Author's name(s) and initials (in uppercase only). In the case of multi-authored manuscripts, successive authors' names should be separated by commas, with an ampersand (&) between the penultimate and last name;
(ii) Year of publication (not in brackets). If more than one paper by the same author is listed for the same year, successive entries must be designated by placing the letters a, b, c, etc., after the year of publication;
(iii) Full title of paper. Use capitals only for the first letter and for proper names. Generic and specific names must be italicized, unless such names themselves fall within an italicized title, in which case the names should be in regular (non-italic) script. If your equipment is unable to produce italics, please underline those words that should be italicized;
(iv) Full (*unabbreviated)* title of journal, book or other source, in italics. Book titles should be followed by the edition (if other than the first), the place of publication and the name of the publisher.
(v) Volume specification of journal: i.e. series (if applicable), volume number (in bold), part number (if any) in brackets, pagination (first and last page).

Examples of reference citations (to save space, the blank line between successive entries has been omitted):

ANDERSON, H.M. 1976. *A revision of the genus* Dicroidium *from the Molteno Formation.* Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.

ANDERSON, H.M. & ANDERSON, J.M. 1970. A preliminary review of the biostratigraphy of the uppermost Permian, Triassic and lowermost Jurassic of Gondwanaland. *Palaeontologia africana* **13**, 1–22.

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

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

ROMER, A.S. 1966. *Vertebrate Palaeontology* (3rd edn). Chicago, University of Chicago Press.

ROMER, A.S. 1973. Permian reptiles. **In**: Hallam, A. (ed.), *Atlas of Palaeobiogeography,* 159–168. Amsterdam, Elsevier.

VAN DER MERWE, N.J., LEE-THORP, J.A., THACKERAY, J.F., HALL-MARTIN, A., KRUGER, F.J., COETZEE, H., BELL, R.H.V. & LINDEQUE, M. 1990. Source-area determination of elephant ivory by isotopic analysis. *Nature* **346**, 744–746.

PERIERA, L.M. 2009. The Wits Online Phytolith Database. University of the Witwatersrand, Johannesburg, South Africa. Online at: http://web.wits.ac.za/Academic/Science/GeoSciences/BPI/Research/WOPD/ (accessed 15 February 2010).

Reference citations in the text should give the name of the author and the date on each occasion, and substitutes such as *op. cit., loc. cit.* should not be used, e.g. 'Smith & Jones (1943) suggested that ...', '... extinction rates (Smith & Jones 1972) and other factors ...'. In the text, successive references by the same author should be separated by commas, and those of different authors by semi-colons: (Brain 1990, 1991; Hughes 1961; Smith & Jones 1972).

Headings

Three orders of headings are used.
FIRST ORDER, printed in bold capitals and left-aligned.
Second order, printed in bold upper and lower case and left-aligned.
Third order, printed in upper and lower case italics and left-aligned.

Headed sections and paragraphs should not otherwise be numbered or lettered in the manuscript.

Tables

Tables must be set out on separate sheets, with their headings in lower case. They are numbered consecutively in arabic numerals. Please indicate the position of each table by appropriate pencil notation in the margin of the text.

When referring to Tables in the text the word 'Table' is spelt out in full and given a capital initial letter, e.g. Table 2.

Illustrations

All illustrations are termed Figures (the word is to be spelt out in full with a capital initial letter), and they are numbered consecutively with arabic numerals. Each illustration must bear in pencil on the reverse side the author's name, a key word(s) from the title, the figure number and the word 'top' in the appropriate position to indicate orientation.

Please mark the position of figures by pencil notation in the margin of the text. When referring to figures in the text the word is abbreviated with a capital initial letter, e.g. Fig. 23.

All artwork should be submitted as camera-ready originals. The use of computer-generated lettering (high-quality laser or ink-jet) or dry transfer lettering is preferred for labelling, and stencil or hand-lettering is to be avoided.

Drawings, maps and diagrams should be in black drawing ink on high quality tracing paper or good quality white card. If drawings are submitted on translucent draughting film, labels and other lettering should *not* be stuck onto the original. Instead they should be clearly written on a submitted photocopy of the original, showing their correct positions clearly, for typesetting by the printers. All illustrations should be designed for same-size printing or slight reduction (by no more than 1/3) in the final form. The maximum acceptable size for illustrations on the printed page is 245 × 175 mm. Tip-ins and fold-outs are not accepted except under very special circumstances, and generally any additional costs will be for the account of the author.

Photographs should be high quality glossy b/w prints of good contrast made from critically focused negatives, and similar constraints on size apply as in the case of drawings. Colour illustrations are acceptable, provided the cost (R3750 per page) is borne by the author.

Good quality digital images in TIF and EPS format (at least 350 dpi for photographs and 1200 dpi for line drawings) may also be accepted. They may be submitted on PC-format disks or CD-ROM.

Scale should be represented by suitably labelled scale bars of appropriate size, with the units of measurement specified in the caption; avoid reference to magnification in captions.

Authors must submit the original of each figure plus two copies, which may be photocopies provided the quality is good and all details are clear.

Numerical data

The metric system (SI units) is to be used throughout for all numerical data. If there is good reason for using units other than metric, the SI metric equivalents must be given in brackets. Authors should familiarize themselves with the standard abbreviations of SI metric units; non-standard abbreviations are not acceptable.

ACCEPTANCE OF PAPERS

All manuscripts offered to the Editor are submitted to two or more referees for critical appraisal, and the substance of the referees' comments is forwarded to the author in the event that the manuscript is rejected or requires revision. The Editor will advise the author whether or not the manuscript is accepted for publication.

If the manuscript is accepted, one set of proofs (usually page proofs) will be submitted to the author for careful checking and these must be returned as soon as possible. The cost of any additions or major alterations to the text at proof stage may be charged to the author. Further proofs may be submitted to the author if the Editor considers it to be necessary or desirable, but at this stage any postal