

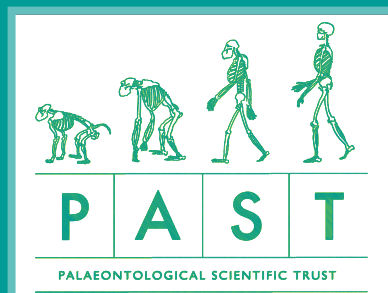
PALAEONTOLOGIA AFRICANA

Volume 47
December 2012

Annals of the
Bernard Price Institute
for
Palaeontological Research



Supported by
PALAEONTOLOGICAL SCIENTIFIC TRUST



ISSN 0078-8554

SCHOOL OF GEOSCIENCES

BERNARD PRICE INSTITUTE FOR PALAEOONTOLOGICAL 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)

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

J. Choiniere BSc (Massachusetts), PhD (GWU).

Collections Manager

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

Post Doctoral Fellows

D. Marchi MSc, PhD (Pisa, Italy)

V. Fernandez MSc (Lyon 1, France), PhD (Paris VI, France)

C.A. Phillips BSc (Hons) (Bournemouth), MSc (Oxford Brookes), PhD (Cambridge)

Editorial Panel

M.K. Bamford: Editor

L.R. Backwell: Associate Editor

B.S. Rubidge: 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

W.P. Germishuizen

Senior Administrative Secretary

S. Sejake

Assistant Research Technician

C.B. Dube

Technicians/Fossil Preparators

P. Chakane

S. Jirah

P.R. Mukanela

G. Ndlovu

T. Nemavhundi

S. Tshabalala

Honorary Staff

Honorary Research Associates

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

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

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

C.A. Sidor BSc (Trinity College) MSc, PhD (University of 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)

L. Wadley MSc (UCT), PhD (Wits)

Administrative and Support Staff

Senior Administrative Secretary

Evlyn Ho

Preparators

T. Dingiswayo

T. Makhele

N. Molefe

A. Mollepolle

S. Motsumi

L. Sekowe

M. Seshoene

Honorary Staff

Honorary Research Associates

Dr Shaw Badenhorst, Transvaal Museum

Prof. Steve Churchill, Duke University, USA

Prof. Francesco d'Errico, Bordeaux University, 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

Dr Peter Ungar, University of Arkansas, USA

PALAEONTOLOGIA AFRICANA

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

ISSN 0078-8554

Volume 47, December 2012

CONTENTS

Articles

- Kennedy, W.J. & Klinger, H.C.** — Cretaceous faunas from Zululand and Natal, South Africa. The ammonite genus *Codazziceras* Etayo-Serna, 1979 1
- Kennedy, W.J. & Klinger, H.C.** — The ammonite genus *Diaziceras* Spath, 1921, from the Campanian of KwaZulu-Natal, South Africa, and Madagascar 3
- Kennedy, W.J. & Klinger, H.C.** — Cretaceous faunas from Zululand and Natal, South Africa. A new species of the ammonite genus *Salaziceras* Breistroffer, 1936, from the Lower Cenomanian Mzinene Formation 15
- Geraads, D., El Boughabi, S. & Zouhri, S.** — A new caprin bovid (Mammalia) from the late Miocene of Morocco 19
- Odes, E.J. & Thackeray, J.F.** — Morphometric analysis of modern human crania: a framework for assessing early Pleistocene hominids 25

Abstracts

- 16th Biennial Conference of the Palaeontological Society of Southern Africa** 29

Standard Bank/PAST First Phillip Tobias Memorial Lecture

- Preface to Prof. Nina Jablonski's public lecture on "Skin: Its Biology in Black and White"* by A. Leenen and R.J. Blumenschine 61
- Jablonski, N.G.** — Skin: Its Biology in Black and White 62

© 2012
BERNARD PRICE INSTITUTE
for
PALAEOONTOLOGICAL 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

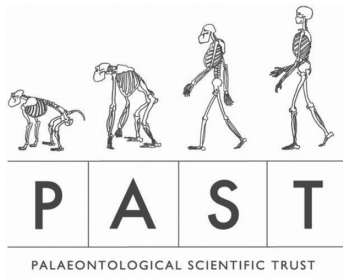
NATIONAL RESEARCH FOUNDATION (NRF)

DEPARTMENT OF SCIENCE AND TECHNOLOGY (DST)

and the

PALAEOONTOLOGICAL SCIENTIFIC TRUST (PAST)

for publication of this journal



Cretaceous faunas from Zululand and Natal, South Africa[‡]. The ammonite genus *Codazziceras* Etayo-Serna, 1979

William James Kennedy^{1*} & Herbert Christian Klinger^{2*}

¹Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, and
Department of Earth Sciences, South Parks Road, Oxford OX1 3AN, United Kingdom

²Natural History Collections Department, Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa

Received 6 August 2012. Accepted 22 October 2012

A new species of the Coniacian ammonite genus *Codazziceras* Etayo-Serna, 1979, previously known with certainty only from Colombia, is described from the St Lucia Formation of northern KwaZulu-Natal.

Keywords: Cretaceous, Coniacian, ammonite, *Codazziceras*, KwaZulu-Natal, South Africa.

INTRODUCTION

The collections of the Iziko South African Museum include a small ammonite, just over 50 mm in diameter, from the western shores of False Bay, Lake St Lucia, in northern KwaZulu-Natal. It is described below as a new species of the genus *Codazziceras* Etayo-Serna, 1979, known previously with certainty only from the type species *Codazziceras scheibei* (Riedel, 1938) (which is a junior synonym of *Ammonites ospinae* Karsten, 1858), and *C. fina* Etayo-Serna, 1979, from the Coniacian of Colombia. *Yubariceras gosavicum* Wiedmann, 1979, from the Coniacian of Austria may also belong to the genus. The present record is thus the first from the Southern Hemisphere.

SYSTEMATIC PALAEOLOGY

Suborder Ammonitina Hyatt, 1889

Superfamily Acanthoceratoidea de Grossouvre, 1894

Family Acanthoceratidae de Grossouvre, 1894

Subfamily Euomphaloceratinae Cooper, 1978

Genus *Codazziceras* Etayo-Serna, 1979

Type species

Lyelliceris scheibei Riedel, 1938, p. 55, pl. 9, figs 7, 8; pl. 13, fig. 17, by the original designation of Etayo-Serna (1979, p. 83) = *Ammonites ospinae* Karsten, 1858, p. 110, pl. 4, fig. 3.

Diagnosis

'Small, very evolute, serpenticonic, whorl section square to rectangular on phragmocone, rounded on body chamber. Innermost whorls smooth and constricted, constrictions persist into early part of ribbed stage. Phragmocone and early body chamber with strong ribs branching from

umbilical bullae or not or intercalated. Primary ribs with weak inner umbilical tubercles that may be indistinct at some stage and strong outer umbilicals; all ribs with inner and outer ventrolateral and siphonal tubercles. All tubercles and ribs weaken on body chamber which resembles inner whorls of *Pedioceras* Gerhardt, 1897 (Crioceratitinae)' (Wright *et al.*, 1983, p. 342).

Occurrence

The type species and *Codazziceras fina* Etayo-Serna, 1979 (p. 84, pl. 13, fig. 17, text-fig. 8M,N,Q,S) occur in the Lower Coniacian of Colombia. *Yubariceras gosavicum* Wiedmann, 1979 (p. 46, pl. 6, figs C,D) from the Coniacian of Brandenburg (Tirol, Austria) may also be a *Codazziceras*. The present record extends the geographic range to northern KwaZulu-Natal.

***Codazziceras africanum* sp. nov.**, Fig. 1

Derivation of name

Africanum: of Africa.

Type

The holotype is SAM-PCZ 022424 (formerly SAS Z1543), from the Middle or Upper Coniacian part of the St Lucia Formation close to locality 86 of Kennedy & Klinger, (1975), on the southwestern shores of False Bay, Lake St Lucia, northern KwaZulu-Natal, coordinates 28°01'45"S, 32°33'03"E approximately.

Diagnosis

A species of *Codazziceras* with inner umbilical bullae, inner and outer ventrolateral and siphonal tubercles on primary ribs alternating regularly with single shorter intercalated ribs with outer ventrolateral and siphonal clavi only.

Dimensions

| | D | Wb | Wh | Wb:Wh | U |
|------------------------------|-------------------|-------|----------------|-------|----------------|
| SAM-PCZ 022424 (ex Z1543) | At: 51.6 (100) | – (–) | 20.2 (38.8) | – | 14.9 (28.9) |

[‡]In current geopolitical terminology Zululand and Pondoland now form parts of the provinces of KwaZulu-Natal and the Eastern Cape respectively. For the sake of continuity we retain the names Zululand and Natal in the title of our series of systematic descriptions of the invertebrate faunas from these regions from 1975 onwards.

*Authors for correspondence
E-mail: jim.kennedy@oum.ox.ac.uk / hklinger@iziko.org.za & hkling@telkomsa.net

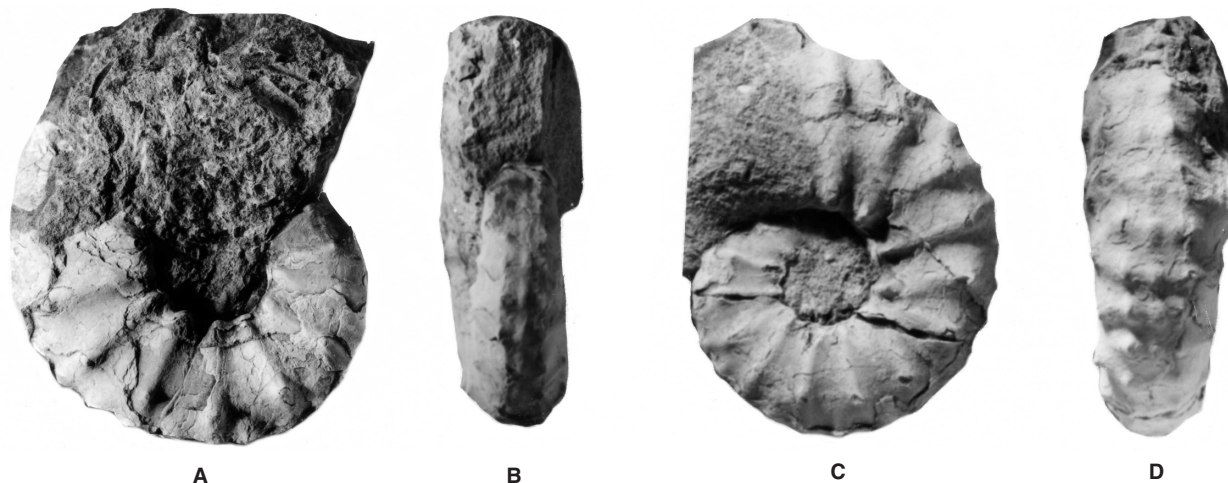


Figure 1. A–D, *Codazziceras africanum* sp. nov., the holotype, SAM-PCZ 022424 (formerly SAS Z1543), from the Middle or Upper Coniacian part of the St Lucia Formation close to locality 86 of Kennedy & Klinger (1975) on the southwestern shores of False Bay, Lake St Lucia, northern KwaZulu-Natal, coordinates 28°01'45"S, 32°33'03"E approximately. Figures are $\times 1$.

Description

The specimen retains well-preserved iridescent nacreous shell. Coiling is moderately evolute, with a moderately wide, shallow umbilicus that comprises 29% of the diameter. The whorl section is slightly compressed in intercostal section, and only slightly wider than high in costal section, with the maximum breadth at the umbilical bullae. The umbilical wall is low and rounded, the flanks flattened and subparallel, with a narrow, flattened venter and rounded ventrolateral shoulder in intercostal section. The costal whorl section is octagonal. There are 12 small, sharp umbilical bullae on the outer whorl. They give rise to a single rib or a pair of distant, straight, narrow, prorsiradial rounded primary ribs that bear small conical inner ventrolateral tubercles and outer ventrolateral clavi. Single intercalated ribs arise on the ventrolateral shoulder and bear outer ventrolateral clavi only. All ribs cross the venter and bear elongated siphonal clavi. One primary rib bifurcates at the inner ventrolateral tubercle. There are an estimated 28 ribs at the ventrolateral shoulder of the outer whorl. The sutures are not exposed.

Discussion

The presence of alternately long and short ribs, the former with umbilical, inner and outer ventrolateral and siphonal clavi, the latter with outer ventrolateral and siphonal clavi only, distinguish the species. *Codazziceras ospinae* (Karsten, 1858) (p. 110, pl. 4, fig. 3), as revised by Wright *et al.* 1983 (p. 343, figs 1–4) has inner and outer umbilical tubercles at the same diameter, and the intercalated ribs bear inner and outer ventrolateral tubercles. *Codazziceras fina* Etayo-Serna, 1979 (p. 84, pl. 123, fig. 17; text-figs 8M,N,Q,S) has an estimated 34–35 crowded ribs that are finer than those of the holotype of *africanum*, the ribs frequently arising in pairs, non-bullate primaries, and all ribs have inner and outer ventrolateral tubercles. *Yubariceras gosavicum* Wiedmann, 1979 (p. 46, pl. 6, figs C, D) may be a *Codazziceras*. It differs from the present species in having inner and outer umbilical tubercles on the primary ribs, inner and outer ventrolateral tubercles on both primary and intercalated ribs, and an incipient to weak outer lateral tubercle on some of the ribs.

Occurrence

As for type.

Kennedy acknowledges the support of the staff of the Geological Collections, Oxford University Museum of Natural History, and the Department of Earth Sciences, Oxford, and the financial assistance of the Oppenheimer Fund (Oxford). Klinger acknowledges the support of the staff of the Natural History Collections Department, Iziko South African Museum and financial support from the NRF (South Africa). Thanks are due to referees for their comments on the manuscript.

ABBREVIATIONS

| | |
|----|--------------------|
| D | diameter (mm) |
| Wb | whorl breadth (mm) |
| Wh | whorl height (mm) |
| U | umbilicus (mm) |

REFERENCES

- COOPER, M.R. 1978. Uppermost Cenomanian-basal Turonian ammonites from Salinas, Angola. *Annals of the South African Museum* **75**, 51–152.
- ETAYO-SERNA, F. 1979. Zonation of the Cretaceous of central Colombia by Ammonites. *Publicaciones Geológicas Especiales del Ingeominas, Bogotá* **2**, 1–186.
- GERHARDT, K. 1897. Beiträge zur Kenntniss der Kreideformation in Columbien. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie Beilage Band* **11**, 118–208.
- GROSSOUVRE, A. de 1894. Recherches sur la Craie supérieure, 2, Paléontologie. Les ammonites de la craie supérieure. *Mémoires du Service de la Carte Géologique détaillée de la France*, 1–264 (misdated 1893). Paris, Imprimerie Nationale.
- HYATT, A. 1889. Genesis of the Arietidae. *Smithsonian Contributions to Knowledge* **673**, xi + 1–239.
- KARSTEN, H. 1858. Über die geognostischen Verhältnisse des westlichen Columbien, der heutigen Republiken Neu-Granada und Equador. *Amthlicher Bericht über die Versammlung Deutscher Naturforscher und Ärzte zu Wien (for 1856)*, 80–117.
- KENNEDY, W.J. & KLINGER, H.C. 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, stratigraphy. *Bulletin of the British Museum (Natural History) Geology* **25**, 263–315.
- RIEDEL, L. 1938. Amonitas del Cretacico inferior de la Cordillera Oriental. In: *Estudios geológicos y paleontológicos sobre la Cordillera Oriental de Colombia* Bogotá **2**, 7–78. Bogotá, Departamento de Minas y Petroleos, Ministerio de Industrias y Trabajo.
- WIEDMANN, J. 1979. Ammonites. Pp. 41–49, In: Herm, D., KAUFFMAN, E.G. & Wiedmann, J. The age and depositional environment of the 'Gosau'-Group (Coniacian-Santonian), Brandenberg/Tirol, Austria. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* **19**, 27–92.
- WRIGHT, C.W., KENNEDY, W.J. & CHANCELLOR, G.R. 1983. The affinities of *Codazziceras* Etayo-Serna, 1979 (Cretaceous Ammonoidea). *Cretaceous Research* **4**, 341–348.

The ammonite genus *Diaziceras* Spath, 1921, from the Campanian of KwaZulu-Natal, South Africa, and Madagascar

William James Kennedy^{1*} & Herbert Christian Klinger^{2*}

¹Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, and
Department of Earth Sciences, South Parks Road, Oxford OX1 3AN, United Kingdom

²Natural History Collections Department, Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa

Received 23 May 2012. Accepted 18 October 2012

The ammonite genus *Diaziceras* Spath, 1921, and the type species, *D. tissotiaeforme* are revised and referred to the subfamily Lenticeratinae Hyatt, 1900, of the family Sphenodiscidae Hyatt, 1900. *Skoumalia* Summesberger, 1979, is interpreted as a junior synonym of *Diaziceras*. *Diaziceras guillantoni* Hourcq, 1949, and *D. spathi* Hourcq, 1949, are regarded as synonyms of *D. tissotiaeforme*, and all are referred to the Lower Campanian on the basis of records from Madagascar.

Keywords: ammonites, *Diaziceras*, Campanian, Cretaceous, KwaZulu, South Africa, Madagascar.

INTRODUCTION

L.F. Spath introduced the genus *Diaziceras* on the basis of a single specimen of the type species, *Diaziceras tissotiaeforme* Spath, 1921 (p. 245, pl. 19, figs 1a–k), collected by A. L. du Toit at Umkwelane Hill, south of Mtubatuba in what is now KwaZulu-Natal.

The holotype (Figs 1C–E, 2A,B, 3, 4F) remains the only specimen of the genus known from South Africa, the systematic position of which has been a matter of debate by subsequent authors. The age of the type specimen is also uncertain. The type locality corresponds to locality 10 of Kennedy & Klinger (1975, p. 282). Here, the basal shell-pebble bed of the St Lucia Formation rests unconformably on deeply weathered basalt of the Lebombo Volcanics. Concretions three metres above the base have yielded *Placenticeras kaffrarium* Etheridge, 1904, and *Forresteria* (*Forresteria*) *alluaudi* (Boule, Lemoine & Thévenin, 1907), indicating a Coniacian date for the base of the sequence (Coniacian II of Kennedy & Klinger (1975)). Taxa recorded from this locality by Spath (1921) also demonstrate the presence of Santonian: i.e. *Pseudoschloenbachia umbulazi* (Baily, 1855), and Lower Campanian: i.e. *Submortonicerases woodsi* Spath, 1921. The *Parapachydiscus* sp. nov. aff. *colligatus* Binkhorst of Spath (1921, p. 226, pl. 22, fig. 1a,b) is the holotype of *Menuites* (*Menuites*) *spathi* (Venzo, 1936) (Kennedy & Klinger, 2006, p. 71, figs 52–68), indicating the presence of an even higher horizon, equivalent to Campanian III of Kennedy & Klinger (1975).

It is argued below, on the basis of records of *Diaziceras* from Madagascar that the type specimen is from the Lower Campanian. It is also argued that *Skoumalia* Summesberger, 1979, from the Santonian of Austria and southern France is a synonym of *Diaziceras*, and that the genus is closely allied to *Eulophoceras*, Hyatt, 1903, and a member of the Subfamily Lenticeratinae Hyatt, 1900.

SYSTEMATIC PALAEOLOGY

Superfamily Acanthoceratoidea de Grossouvre, 1894

Family Sphenodiscidae Hyatt, 1900

(= Libycoceratinae Zaborski, 1982, p. 306)

Subfamily Lenticeratinae Hyatt, 1900

(= Eulophoceratinae Hyatt, 1903;

= Diaziceratinae Basse, 1947)

Genus *Diaziceras* Spath, 1921

(= *Skoumalia* Summesberger, 1979, p. 146)

Type species

Diaziceras tissotiaeforme Spath, 1921, p. 245, pl. 19, figs 1a–k, by original designation.

Diagnosis

Compressed to moderately inflated, involute. Whorl section compressed polygonal, with fastigiate venter and strong siphonal keel. Costal section markedly concave between umbilical and ventral tubercles, and on either side of strong siphonal keel. Weak to strong umbilical bullae give rise to pairs of low, broad, pro-spiral ribs which, together with additional intercalated ribs, all bear conical to bullate ventral tubercles. Suture moderately to deeply incised, with asymmetrically bifid to asymmetrically trifid E/A and bifid A.

Discussion

The holotype of the type species is a stout individual (Figs 1C–E, 2A,B). The holotype of *Diaziceras guillantoni* Hourcq, 1949, p. 22 (108), pl. 12(2), fig. 1; Fig. 9D herein) is compressed, with weaker ornament of the same basic pattern: umbilical bullae that give rise to pairs of ribs on the phragmocone, with additional intercalated ribs. All ribs bear ventral tubercles, but these are elongated and projected forwards, rather than being conical, as in *D. tissotiaeforme*. The venter is markedly concave on either side of the siphonal keel. E/A is asymmetrically trifid,

*Authors for correspondence.

E-mail: jim.kennedy@oum.ox.ac.uk / hklinger@iziko.org.za & hkling@telkomsa.net



Figure 1. A, B, the holotype of *Diaziceras spathi* Hourcq, 1949, p. 107 (21), pl. 12 (2), fig. 2, from the 'region de Berere', Madagascar, an unregistered specimen in the collections of the École des Mines, Paris, now at the collections of the Université Claude Bernard, Lyon. No precise horizon was given. C–E, *Diaziceras tissotiaeforme* Spath, 1921, the holotype, by monotypy, SAM-PCZ19040 (formerly 5478 in Spath 1921), the original of Spath 1921, p. 245, pl. 19, fig. 1a–k, from the St Lucia Formation of Umkwelane Hill, northern KwaZulu-Natal. Figures are $\times 1$.

and A bifid (Fig. 4B). The differences in ornament between *tissotiaeforme* and *guillantoni* reflect the common covariance between whorl inflation and strength ornament; they are clearly congeneric.

Skoumalia Summesberger, 1979, with type species *Skoumalia austriaca* Summesberger, 1979 (p. 141, text-figs 26–30; pl. 9, figs 37–41, text-figs 26–30), from the Upper Santonian of the Sandkalkbank of the Bibereckschichten of the Gosau Basin, Austria, has been regarded as a synonym of *Eulophoceras* Hyatt, 1903 (Kennedy (1987, p. 776; Kennedy in Kennedy *et al.* 1995, p. 425; Wright 1996, p. 204). Summesberger recognised two morphotypes in

Skoumalia austriaca. His Form A, which included the holotype (Summesberger, 1979, pl. 9, figs 37, 38; text-figs. 26–28; Fig. 4A,C; 9A–C herein) has a compressed phragmocone with fastigate venter, strong umbilical bullae that give rise to pairs of straight prorsiradiate ribs that, together with intercalated ribs, terminate in small ventral bullae. The ornament differs in no significant respects from that of *Diaziceras guillantoni* (compare Figs 9A–C and D). The suture of the holotype lacks the ventralward part of E/A (Fig. 4A) which is broad, asymmetric, with narrow deep median incision, a deep narrow A, and, bifid A/U2. The suture of a second specimen referred



Figure 2. A, B, *Diaziceras tissotiaeforme* Spath, 1921, the holotype, by monotypy, SAM-PCZ19040 (formerly 5478 in Spath 1921), the original of Spath (1921, p. 245, pl. 19, fig. 1a–k), from the St Lucia Formation of Umkwelane Hill, northern KwaZulu-Natal. C, D, the holotype of *Diaziceras menabense* Hourcq, 1949, (p. 109 (23), pl. 13 (3)), fig. 3, from the ‘région de Berere, sommet du Santonien’, Madagascar, an unregistered specimen in the collections of the École des Mines, Paris, now housed at the Université Claude Bernard, Lyon. Figures are $\times 1$.

to form A by Summesberger (1979, text-fig. 28; Fig. 4C herein) has a broad asymmetric bifid E/A with a deep narrow incision. The suture is thus less deeply incised than in the holotype of *Diaziceras tissotiaeforme* (Fig. 4F), and lacks the complex folioles adjacent to E, which is obliquely trifid. The bifid E/A and lesser depth of incisions of *Skoumalia austriaca* as opposed to the trifid E/A and deep incisions in *Diaziceras tissotiaeforme* are the only clear distinguishing feature between the two. The sutures of

other *Diaziceras*, e.g. *D. guillantoni* (Fig. 4B) are much less deeply incised than in the holotype of *D. tissotiaeforme*, and that of *D. menabense* (Fig. 4E) is bifid. *Skoumalia* is regarded here as a synonym of *Diaziceras*, rather than *Eulophoceras*. Summesberger recorded what he regarded as a second form, form B, of *Skoumalia austriaca*, that co-occurred with the lectotype (his form A). Form B of Summesberger (1979, p. 143, text-figs 29, 30; pl. 9, figs 39–41; text-figs 29, 30; 1980, p. 280, pl. 2, figs 5–6; pl. 3,

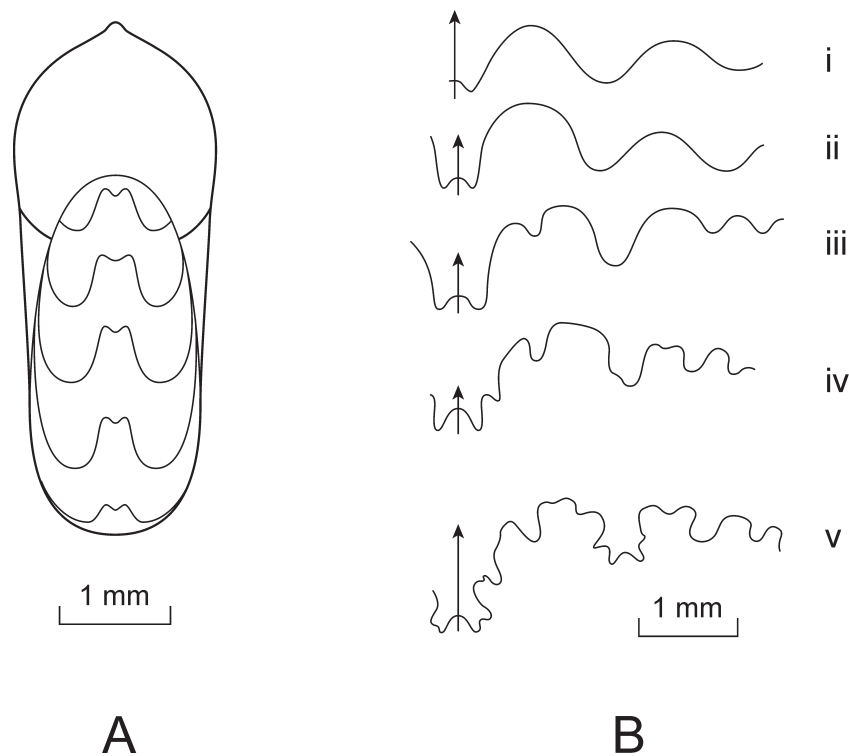


Figure 3. *Diaziceras tissotiaeforme* Spath, 1921, the holotype, by monotypy, SAM-PCZ19040 (formerly 5478 in Spath 1921), the original of Spath (1921, p. 245, pl. 19, fig. 1a–k), from the St Lucia Formation of Umkwelane Hill, northern KwaZulu-Natal. **A**, the inner whorls at a diameter of 3 mm; copy of Spath, (1921, pl. 1, fig. 1d); **B**, development of the suture line at i, a diameter of 1.5 mm; ii at 2 mm; iii at 3 mm; iv at 5.5 mm; v at 8 mm. Copy of Spath, (1921, pl. 1, fig. 1g–1k). Scale bars are 1 mm.

figs 7–8; text-figs 5,6) is ornamented by delicate umbilical bullae on the phragmocone. The outer whorl bears delicate feebly flexuous growth lines and striae, with ten distant outer lateral bullae. Whereas form A has the ornament of *Diaziceras*, Form B (a juvenile from southwest France is shown in Fig. 9E–G for comparison) has delicate ribs and outer lateral bullae, recalling *Eulophoceras*, as discussed elsewhere (Kennedy & Klinger, 2012, in press).

Spath (1921, p. 242) was unequivocal in his view of the affinities of *Diaziceras*: ‘Its suture-line stamps it as being near to the genera *Eulophoceras* Hyatt and *Spheniscoceras*’ Spath also noted the similarity in ornament between *Diaziceras* and certain Tissotidae Hyatt, 1900, specifically *Metatissotia fourneli* (Bayle, 1878) (pl. 40, fig. 3), but dismissed the possibility of affinity, given the pseudo-ceratic suture of the family. In contrast, Hourcq (1949, p. 116 (30)), placed *Diaziceras* and *Eulophoceras* in the family Tissotidae Hyatt, 1900. Basse (1947, p. 159 (63)) introduced a subfamily Diaziceratinae, which she placed in the Tissotidae. Wright (1957, p. L437) assigned the genus to the Lenticeratinae Hyatt, 1900 (= *Eulophoceratinae* Hyatt, 1903). In 1996 (p. 189) he preferred placement in the subfamily Barroisiceratinae Basse, 1947, of the family Collignoniceratidae Wright & Wright, 1951. An orphan genus indeed!

We revert to the views of Spath. The sutures of *Diaziceras* and *Eulophoceras* share an asymmetrically trifold E/A. The weak ribs with no or feeble umbilical bullae, and strengthened rib terminations (but only rarely bullae) of *Eulophoceras* are a reflection of the compressed, oxycone whorl section. *Diaziceras tissotiaeforme* has inflated whorls and strong ribs and tubercles. The ribs and tubercles of

compressed *Diaziceras guillantoni* Hourcq, 1949 (p. 108 (22), pl. 12 (2), fig. 1; text-fig. 15) are intermediate, differences that reflect covariance between ornament strength and whorl section.

Occurrence

Upper Santonian of the Gosau Basin, Austria, and Corbières in southern France. Lower Campanian of Madagascar (following Collignon, 1969, although originally referred to the top of the Santonian by Hourcq, 1949). On the basis of the Madagascan occurrences, the type occurrence in KwaZulu-Natal is inferred to be in the Lower Campanian.

Diaziceras tissotiaeforme Spath, 1921

- Figs 1C–E, 2–3, 4E,F, 5
 1921 *Diaziceras tissotiaeforme* Spath, p. 245, pl. 19, figs 1a–k.
 1949 *Diaziceras spathi* Hourcq, p. 107 (21), pl. 12 (2), fig. 2.
 1949 *Diaziceras menabense* Hourcq, p. 109 (23), pl. 13 (3), fig. 3; text-figs 16, 17.
 1957 *Diaziceras tissotiaeforme* Spath; Wright, p. L437, text-fig. 552, 4a–c.
 1969 *Diaziceras spathi* Hourcq; Collignon, p. 210, pl. 603, fig. 2258.
 1996 *Diaziceras tissotiaeforme* Spath; Wright, p. 189, text-fig. 143, 2a–c.

Type

The holotype, by monotypy, is SAM-PCZ19040 (formerly 5478 in Spath 1921), the original of Spath 1921, p. 245, pl. 19, figs 1a–k, from the St Lucia Formation of Umkwelane Hill, northern KwaZulu-Natal, locality 10 of Kennedy & Klinger (1975, p. 282).

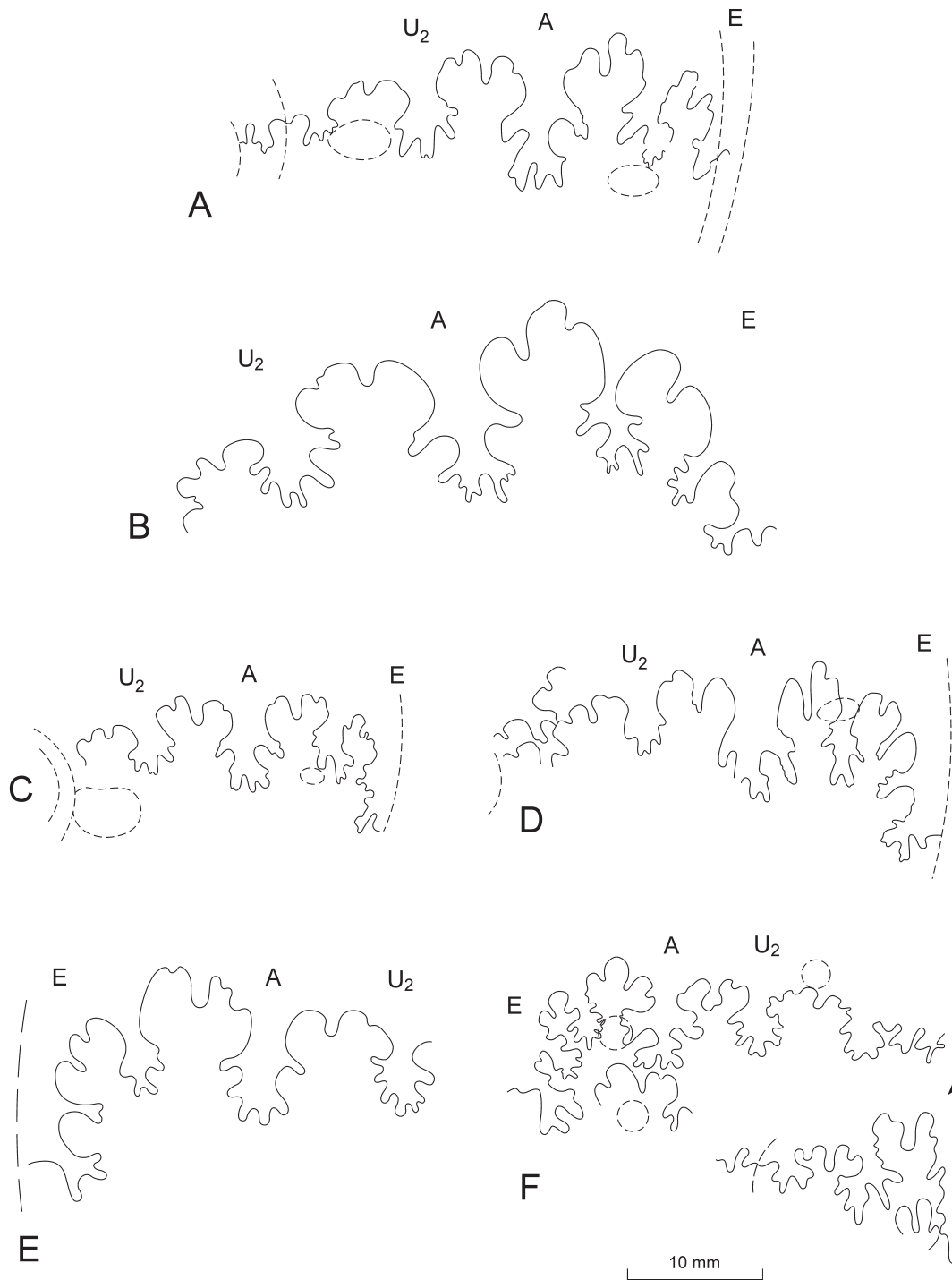


Figure 4. Suture lines. **A**, *Skoumalia austriaca* Summesberger, 1979, form A (copy of Summesberger 1979, text-fig. 27). **B**, the holotype of *Diaziceras guillantoni* Hourcq, 1949, p. 108 (22), pl. 12 (2), fig. 1. **C**, *Skoumalia austriaca* Summesberger, 1979, form A, (copy of Summesberger 1979, text-fig. 28). **D**, *Skoumalia austriaca* Summesberger, 1979, form B (copy of Summesberger 1979, text-fig. 30). **E**, the holotype of *Diaziceras menabense* Hourcq, 1949, p. 109 (23), pl. 13 (3), fig. 3. **F**, the holotype of *Diaziceras tissotiaeforme* Spath, 1921, copy of Spath (1921, pl. 19, fig. 1e, f). Scale bar is 10 mm.

Dimensions of the holotype

| | D | Wb | Wh | Wb:Wh | U |
|-------------|------------|-----------|-----------|-------|-----------|
| PCZ19040,c | 80.6 (100) | 47.7 (59) | 42.1 (52) | 1.13 | 13.6 (16) |
| PCZ19040,ic | 80.6 (100) | 38.6 (47) | 42.1 (52) | 0.92 | 13.6 (16) |

Description

The holotype is a well-preserved undeformed individual retaining traces of the original aragonitic shell. It is septate to a diameter of 81.4 mm, the last few septa crowded,

suggesting the specimen may be the phragmocone of an adult. A short, worn section of body chamber survives, and extends the specimen to a maximum preserved diameter of 84.5 mm. Coiling is very involute, with a small, very deep conical umbilicus that comprises 16.9% of the diameter, the umbilical wall flattened and outwardly-inclined. The umbilical shoulder is broadly rounded. The intercostal whorl section is compressed polygonal, with the greatest breadth just outside the umbilical shoulder and a whorl breadth to height ratio of 0.92. The inner flanks are broadly rounded, the outer flanks flattened and



Figure 5. *Diaziceras tissotiaeforme* Spath, 1921, the original of *Diaziceras spathi* Hourcq, 1941, *sensu* Collignon, (1969, pl. 603, fig. 2258), from the 'base du Campanien Inférieur. Zone à *Anapachydiscus wittekindi* et *Eulophoceras jacobi*. Sous-Zone à *Besairiella besairiei* (base). Gisement 195 de la Coupe de Berere II-B (Belo-sur-Tsiribihina)', Madagascar. The figure is $\times 1$.

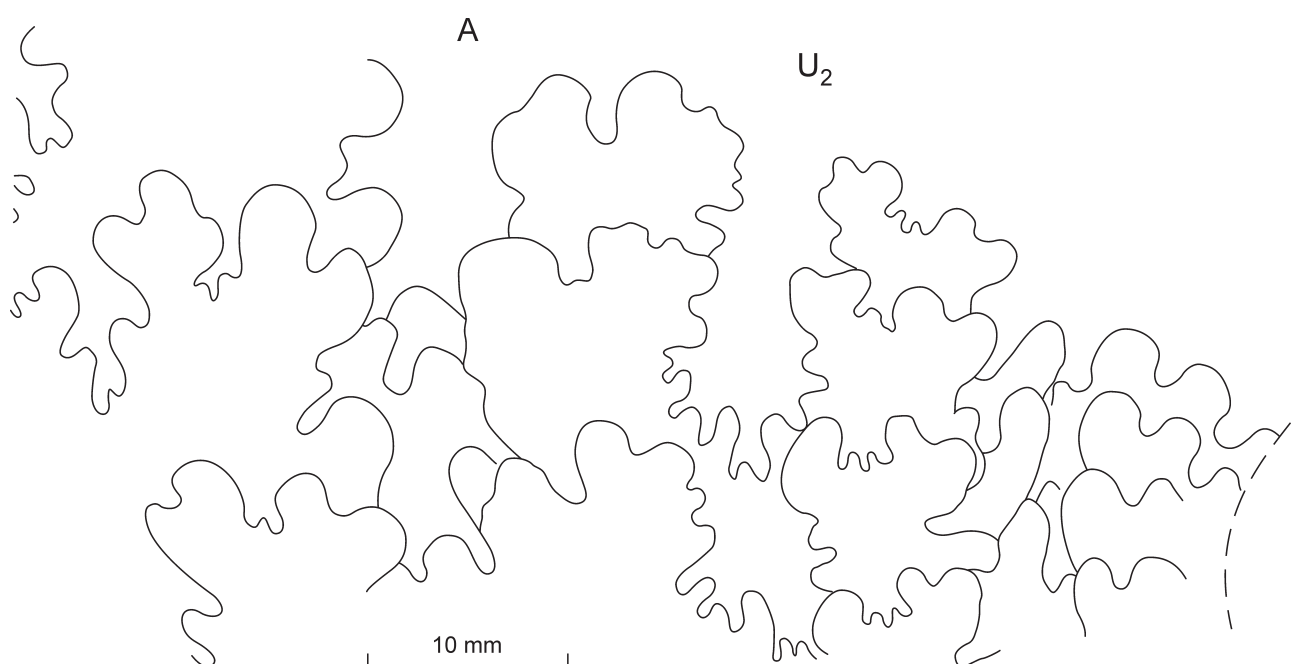


Figure 6. External suture of *Diaziceras guillantoni* Hourcq, 1949, the original of Collignon, (1969, pl. 614, fig. 2261). Scale bar is 10 mm.

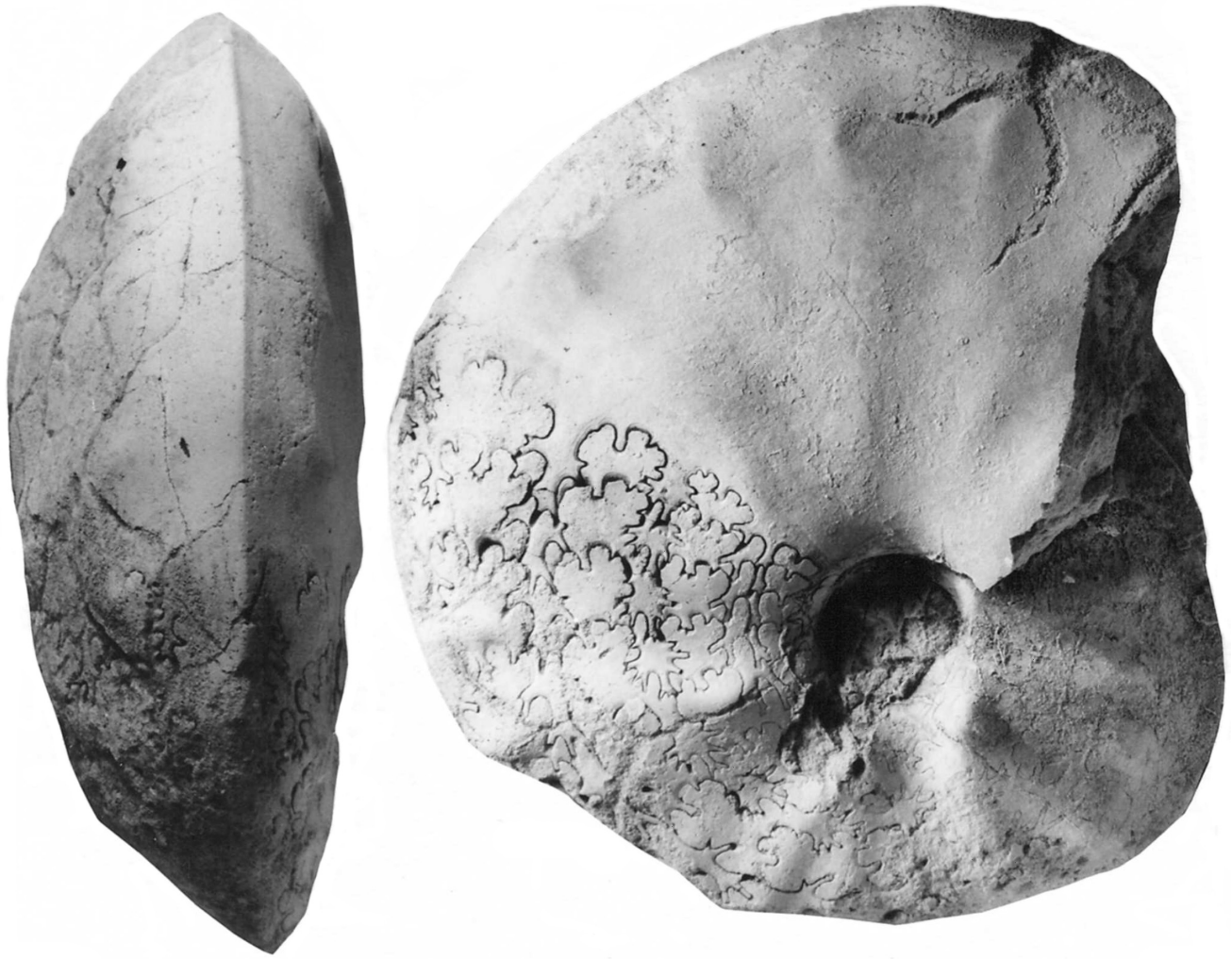


Figure 7. *Diaziceras guillantoni* Hourcq, 1949, the original of Collignon, (1969, pl. 604, fig. 2261), from 'base du Campanien Inférieur. Zone à *Anapachydiscus wittekindi* et *Eulophoceras jacobii*. Sous-Zone à *Hourcquiella hourcqui*. Gisement 195 de la Coupe de Berere II-B (Belo-sur-Tsiribihina)', Madagascar. The figure is $\times 1$.

convergent, the venter obtusely fastigiate, with a strong siphonal keel. The greatest breadth is at the massive umbilical bullae in costal section, with a whorl breadth to height ratio of 1.13. The whorl section is concave between umbilical bullae and ventrolateral tubercles, and between ventrolateral tubercles and keeled venter. There are five massive umbilical bullae, perched on the umbilical shoulder. The bullae give rise to pairs of low, broad, convex prorsiradiate ribs that sweep across the flanks and link to small conical ventral tubercles. One or more short ribs intercalate between the successive pairs of bullate primaries, to give a total of 12 ribs on the adapertural half of the outer whorl, and an estimated 24 per whorl.

The mature suture (Fig. 4F) has a broad, deeply incised asymmetrically trifold E/A, A with deep incisions and a small, bifid U2. The early sutural development is shown in Fig. 3.

Discussion

Diaziceras menabense Hourcq, 1949 (p. 23 (109), text-figs 16,17; pl. 13 (3), fig. 3) is a synonym of *D. tissotiaeforme* in our view. The holotype (Figs 2C,D, 4E) is an unregistered specimen in the collections of the École des Mines, Paris, now housed at the Université Claude

Bernard, Lyon. It is from Berere, Madagascar, and was referred to the top of the Santonian by Hourcq. A worn and battered internal mould with a 60° sector of body chamber preserved, the dimensions are as follows:

Dic: 98.0 (100) Wb: 37.5 (38.3) Wh: 54.0 (55.1) Wb:Wh:0.69 U:10.7 (10.9)

Coiling is very involute, the small deep umbilicus comprising 10.9% of the diameter, with a flattened, outward-inclined wall and a broadly rounded umbilical shoulder. The intercostal whorl section is compressed lanceolate, with the greatest breadth just outside the umbilical shoulder. Nine to 10 conical umbilical tubercles perch on the umbilical shoulder; strong on the phragmocone, they weaken markedly on the body chamber. On the phragmocone, the bullae give rise to pairs of low broad prorsiradiate ribs that terminate in conical outer lateral tubercles. Beyond the tubercles the flanks are concave and converge to the acute venter. The tubercles and flank ribs persist onto the body chamber, but the venter becomes less acute. The suture (Fig. 4E) has a broad, little-incised incipiently obliquely trifold E/A, a narrow A, and little-incised bifid U2. The ornament is slightly weaker, and the whorl section compressed when compared to that of the holotype of *tissotiaeforme* while the



Figure 8. *Diaziceras guillantoni* Hourcq, 1949, the original of Collignon, (1969, pl. 604, fig. 2261), with the previously unfigured body chamber fragment included, from the 'base du Campanien Inférieur. Zone à *Anapachydiscus wittekindi* et *Eulophoceras jacobii*. Sous-Zone à *Hourcquiella hourcqui*. Gisement 195 de la Coupe de Berere II-B (Belo-sur-Tsiribihina)', Madagascar. The figure is $\times 1$.

suture is much less deeply incised, lacking the long complex folioles on E/A adjacent to A, and barely trifid.

Diaziceras spathi Hourcq, 1949 (p. 107 (21), pl. 12 (2), fig. 2) is a further synonym. The holotype, by monotypy (Fig. 1A,B), is an unregistered specimen in the collections of the École des Mines, Paris, now housed at the Université Claude Bernard, Lyon. It from Berere, Madagascar. A worn, wholly septate internal mould, the dimensions are as follows:

Dic: 88.5 (100); Wb: 42.0 (0.47); Wh: 47.5 (0.54) Wb:Wh0.89 U:15.5 (17.5)

Coiling is involute, the deep umbilicus comprising 17.5% of the diameter, with a flattened, outward-inclined umbilical wall and broadly rounded umbilical shoulder. The whorl section is stoutly lanceolate in intercostal section, with the greatest breadth just outside the umbilical shoulder. The greatest breadth is at the umbilical bullae in costal

section. These number eight per whorl, and are perched on the umbilical shoulder. They give rise to pairs of low, broad blunt straight prorsiradiate ribs that terminate in conical outer lateral tubercles, 19–20 per whorl. The flanks are concave in costal section between these tubercles and the obtuse venter. The specimen has a slightly more compressed whorl section than the holotype of *D. tisso-tiaeforme*, but is otherwise identical in our view (compare Figs 1A,B and 1C–E).

Diaziceras guillantoni Hourcq, 1949 (p. 108 (22), pl. 12 (2), fig. 1; text-fig. 15), is a distinct compressed form (Fig. 9D). The holotype by monotypy is an unregistered specimen in the collections of the École des Mines, Paris, now housed at the Université Claude Bernard, Lyon. It is from Berere, Madagascar, and was referred to the top of the Santonian by Hourcq. A worn internal mould with a 180° sector of body chamber preserved, and a near-complete

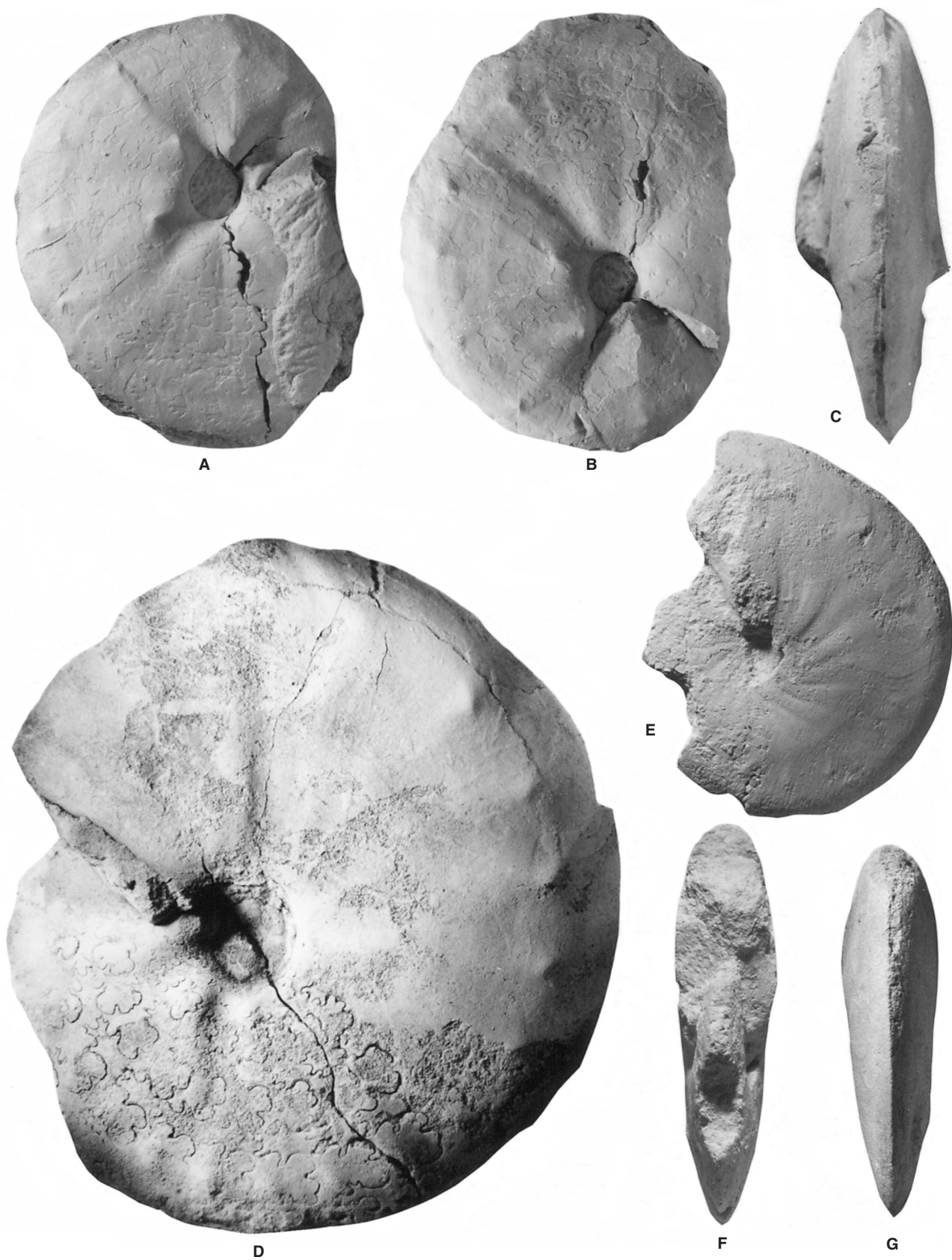


Figure 9. A–C, the holotype of *Skoumalia austriaca* Summesberger, 1979, SK,N.1977/14, the original of Summesberger, (1979, pl. 9, figs 37, 38) from the Upper Santonian Sandkalkbank of the Bibereckschichten of the Gosau Basin, Upper Austria. **D**, the holotype of *Diaziceras guillantoni* Hourcq, 1949, the original of Hourcq, (1949, pl. 12 (2), fig. 1), from the 'Région de Berere, sommet du Santonien.' **E–G**, *Skoumalia austriaca* Summesberger, 1979, form B of Summesberger, (1980), A363, from the Upper Santonian of Autoroute cutting S2, west of Saintes, Charente-Maritime, France in the collections of the Université Claude Bernard. All figures are $\times 1$.

adult, the dimensions of which are as follows:

D: 132.0 (100) Wb: 40.5 (30.7) Wh: 70.0 (53.0) Wb:Wh 0.58 U: 18.0 (13.6)

Coiling is involute, the umbilicus small and deep, comprising 13.6% of the diameter, with an outward-inclined wall and broadly rounded umbilical shoulder. The whorl section is compressed lanceolate, with a whorl breadth to height ratio of 0.58. Four massive bullae perch on the umbilical shoulder of the adapical half of the outer whorl. They give rise to pairs of low, broad, straight prorsiradiate ribs with occasional intercalated ribs arising around mid-flank, to give a total of ten ribs per half whorl on the outer flank, where the ribs strengthen into conical to feebly bullate tubercles. The umbilical bullae efface progressively on the body chamber and the flank ribs weaken. The outer lateral tubercles become markedly bullate and prorsiradiate before weakening at the greatest preserved diameter. The suture (Fig. 4B) has a very broad, obliquely trifid E/A, with deep incisions and plump folioles; A is asymmetrically bifid; U2 is broad, bifid with only minor incisions. It is interpreted as a microconch. The macroconch is represented by the original of Collignon (1969, pl. 604, fig. 2261, see Figs 6–8 herein) from the Lower Campanian *Hourcquiella bererensis* Subzone of Collignon's 'Zone à *Anapachydiscus wittekindi* et *Eulophoceras jacobi*' of Berere (Belo-sur-Tsiribihina), Madagascar. The umbilical bullae are weak and very elongate, the ribs straight and prorsiradiate, arising from the bullae in pairs and intercalating, with an oblique prorsiradiate ventrolateral bulla on the phragmocone. Ribs and tubercles weaken and efface on the body chamber, which occupies a 180° sector and may be incomplete (Fig. 8). The sutures (Fig. 6) are crowded and interfere. The saddles are broad and plump, with A narrower.

Diaziceras austriaca (Summesberger, 1979), is discussed above, and figured here as Figs 4A,C, 9A–C, E–G. It combines a compressed whorl section with massive umbilical tubercles and weak flank ribs in form A of Summesberger, the suture (Figs 4A,C) is a little less deeply incised than that of *D. tissotiaeforme*, and has E/A obliquely asymmetrically bifid, rather than trifid.

The holotype of *Diaziceras tissotiaeforme* is interpreted as a microconch. Collignon (1969, pl. 603, fig. 2258) figured (as *D. spathi*) a worn and battered individual 150 mm in diameter with a 180° sector of body chamber preserved that is interpreted as a near-complete macroconch (Fig. 5). It has seven massive bullae perched on the umbilical shoulder that give rise to pairs of ribs on the phragmocone, the ribs on the body chamber simple, to give a total of 17 ribs on the outer whorl that terminate in strong ventrolateral tubercles. It is from the base of the Campanian, the base of the *Besairiella besairiei* Subzone of Collignon's Zone à *Anapachydiscus wittekindi* et *Eulophoceras jacobi* of Berere (Belo-sur-Tsiribihina), Madagascar.

Occurrence

The type occurrence at Umkwelane Hill in KwaZulu-Natal is imprecisely dated, but inferred to be Lower Campanian on the basis of the record of Collignon (1969) from Madagascar.

Kennedy acknowledges the support of the staff of the Geological Collections, Oxford University Museum of Natural History, and the Department of Earth Sciences, Oxford, and the financial assistance of the Oppenheimer Fund (Oxford). Klinger acknowledges financial support from the NRF (South Africa) and help from the staff of the Natural History Collections Department, Iziko, South African Museum. Thanks are due to the reviewers for constructive comments on the manuscript.

ABBREVIATIONS

Dimensions are given in millimetres.

D diameter
Wb whorl breadth
Wh whorl height
U umbilicus
c costal dimension
ic intercostal dimension

Figures in brackets are dimensions as a percentage of the diameter.

The suture terminology is that of Korn *et al.* (2003):

E external lobe
A adventive lobe (= lateral lobe, L, of Kullmann & Wiedmann 1970)
U umbilical lobe
I internal lobe

REFERENCES

- BAILY, W.H. 1855. Description of some Cretaceous fossils from South Africa. *Quarterly Journal of the Geological Society of London* **11**, 454–465.
- BASSE, E. 1947. Les peuplements Malgaches de *Barroisiceras* (Révision du genre *Barroisiceras* de Gross). *Paléontologie de Madagascar* **26**. *Annales de Paléontologie* **22**, 97–190.
- BAYLE, É. 1878. Fossiles principaux des terrains. *Explication de la Carte Géologique de France* **4(1)** (Atlas), 158 pls. Paris, Service de la Carte Géologique détaillée.
- BOULE, M., LEMOINE, P. and THÉVENIN, A. 1906–1907. Paléontologie de Madagascar III Céphalopodes crétacés des environs de Diego-Suarez. *Annales de Paléontologie* **1**, 173–192 (1–20) **2**, 1–56 (21–76) (1907).
- COLLIGNON, M. 1969. *Atlas des fossiles caractéristiques de Madagascar (Ammonites)*. XV, (Campanien inférieur), xi + 1–216. Tananarive: Service Géologique.
- ETHERIDGE, R. 1904. Cretaceous fossils of Natal. 1. The Umkwelane Hill Deposit. *Report of the Geological Survey of Natal and Zululand* **1**, 71–93.
- GROSSOUVRE, A. de 1894. Recherches sur la craie supérieure, 2, Paléontologie. Les ammonites de la craie supérieure. *Mémoires du Service de la Carte Géologique détaillée de la France* **1**, 1–264 (misdated 1893). Paris, Imprimerie nationale.
- HOURCQ, V. 1949. Paléontologie de Madagascar. XXVIII. Sur quelques ammonites du Sénonien. *Annales de Paléontologie* **35**, 10(87)–31(117).
- HYATT, A. 1900. Cephalopoda. In: Zittel, K.A. von 1896–1900, *Textbook of Palaeontology* (transl. Eastman, C.R.), 502–604. London and New York, Macmillan.
- HYATT, A. 1903. Pseudoceratites of the Cretaceous. *United States Geological Survey Monograph* **44**, 351 pp.
- KENNEDY, W.J. 1987. Ammonites from the type Santonian and adjacent parts of northern Aquitaine, western France. *Palaeontology* **30**, 765–782.
- KENNEDY, W.J., BILOTTE, M. & MELCHIOR, P. 1995. Ammonite faunas, biostratigraphy and sequence stratigraphy of the Coniacian-Santonian of the Corbières. *Bulletin des Centres de Recherche Exploration et Production Elf-Aquitaine* **19**, 377–499.
- KENNEDY, W.J. & KLINGER, H.C. 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, Stratigraphy. *Bulletin of the British Museum (Natural History) Geology* **25**, 263–315.
- KENNEDY, W.J. & KLINGER, H.C. 2006. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Pachydiscidae Spath, 1922. *African Natural History* **2**, 17–168.
- KENNEDY, W.J. & KLINGER, H.C. 2012, in press. Cretaceous faunas from Zululand and Natal, South Africa. The Santonian-Campanian ammonite genus *Eulophoceras* Hyatt, 1903. *African Natural History* **8**.
- KORN, D., EBBIGHAUSEN, V., BOCKWINKEL, J. & KLUG, C. 2003. The A-mode sutural ontogeny in prolecanitid ammonoids. *Palaeontology* **46**, 1123–1132.
- KULLMANN, J. & WIEDMANN, J. 1970. Significance of sutures in phylogeny of Ammonoidea. *University of Kansas, Paleontological Contributions* **42**, 1–32.

- SPATH, L.F. 1921. On Cretaceous Cephalopoda from Zululand. *Annals of the South African Museum* **12**, 217–321.
- SUMMESBERGER, H. 1979. Eine obersantonie Ammonitenfauna aus dem Becken von Gosau (Oberösterreich). *Annalen des Naturhistorischen Museums Wien* **83**, 109–176.
- SUMMESBERGER, H. 1980. Neue Ammoniten aus der Sandkalkbank der Hochmooschichten (Obersanton; Gosau, Austria). *Annalen des naturhistorischen Museums Wien* **83**, 275–383.
- VENZO, S. 1936. Cefalopodi del Cretaceo medio-superiore dello Zululand. *Palaeontographia Italica* **36**, 59–133 (1–75).
- WRIGHT, C.W. 1957. [Cretaceous Ammonoidea]. In: Moore, R.C. (ed.), *Treatise on Invertebrate Paleontology. Part L, Mollusca 4, Cephalopoda Ammonoidea*. Boulder, New York and Lawrence, Geological Society of America and University of Kansas Press.
- WRIGHT, C.W. 1996. In: *Treatise on Invertebrate Paleontology. Part L, Mollusca 4: Cretaceous Ammonoidea* (with contributions by J.H. Calloman (sic) and M.K. Howarth). Boulder, Colorado and Lawrence, Kansas, Geological Society of America and University of Kansas.
- WRIGHT, C.W. & WRIGHT, E.V. 1951. A survey of the fossil Cephalopoda of the Chalk of Great Britain. *Monograph of the Palaeontographical Society Monographs*, London, **140**, 1–40.
- ZABORSKI, P.M.P. 1982. Campanian and Maastrichtian sphenodiscid ammonites from southern Nigeria. *Bulletin of the British Museum (Natural History) Geology* **36**, 303–332.

Cretaceous faunas from Zululand and Natal, South Africa[†]. A new species of the ammonite genus *Salaziceras* Breistroffer, 1936, from the Lower Cenomanian Mzinene Formation

William James Kennedy^{1*} & Herbert Christian Klinger^{2*}

¹Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, and
Department of Earth Sciences, South Parks Road, Oxford OX1 3AN, United Kingdom

²Natural History Collections Department, Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa

Received 6 August 2012. Accepted 18 October 2012

A diminutive ammonite collected by E.C.N. Van Hoepen from the Cenomanian part of the Mzinene Formation of the Skoenberg in northern KwaZulu-Natal, is described as *Salaziceras simplex* sp. nov., and interpreted as one of the last survivors of the genus.

Keywords: Cretaceous, Cenomanian, *Salaziceras*, ammonite, KwaZulu-Natal, South Africa.

INTRODUCTION

We have previously recorded the type species of the diminutive Late Albian ammonite genus *Salaziceras* Breistroffer, 1936, from the Upper Albian part of the Mzinene Formation at Ndumu in northern KwaZulu-Natal (Klinger & Kennedy 1994), and interpreted the enigmatic *Acanthoceras naviculare* from Mont Raynaud, Madagascar, described by Boule *et al.* (1907, p. 30 (10), pl. 1 (8), fig. 1) as a hypermorphic giant species of this normally diminutive genus (Kennedy & Klinger 2008). Revision of the KwaZulu-Natal Stoliczkaiinae (in progress), led to the recognition of a second specimen of this genus from KwaZulu-Natal, which we describe below, and refer to a new species, *Salaziceras simplex*.

SYSTEMATIC PALAEOLOGY

Superfamily Acanthoceratoidea de Grossouvre, 1894

Family Flickiidae Adkins, 1928

Subfamily Salaziceratinae Wright & Kennedy, 1984

Genus *Salaziceras* Breistroffer, 1936

Type species

Ammonites salazacensis Hébert & Munier-Chalmas, 1875, p. 114, pl. 5, fig. 6, by original designation by Breistroffer (1936, p. 64).

Discussion

See Wright & Kennedy (1979, p. 686).

Occurrence

Upper Upper Albian, southern England, southeast France, Hungary, Morocco, Nigeria, northern KwaZulu-

Natal, South Africa, and Madagascar. Lower Cenomanian of northern KwaZulu-Natal, South Africa.

Salaziceras simplex sp. nov., Fig. 1

Derivation of name

Simplex: simple.

Type

The holotype is SAM-PCZ022425 (formerly D 2945, ex E.C.N. Van Hoepen Collection), from the Lower Cenomanian Mzinene Formation at the Skoenberg, corresponding to locality 61 of Kennedy & Klinger (1975, p. 189, fig. 6), NNW of Hluhluwe, northern KwaZulu-Natal, coordinates 27°52'17"S, 32°20'19"E.

Diagnosis

A species of *Salaziceras* in which the earlier phragmocone whorls are ornamented by coarse bullate primary ribs separated by one or two intercalated ribs that extend across the venter, followed by a late phragmocone and early body chamber phase ornamented by bullate primary ribs only that efface on the ventrolateral shoulders and venter.

Dimensions

| | D | Wb | Wh | Wb:Wh | U |
|---------------------------------|------------|-------------|-------------|-------|------------|
| SAM-PCZ 022424 (ex D2945) | 16.4 (100) | 10.4 (64.0) | 9.0 (54.9) | 1.17 | – (–) |
| at | 24.8 (100) | 10.4 (44.0) | 10.0 (40.3) | 1.1 | 6.9 (27.8) |

Description

The holotype is a well-preserved phragmocone and a 120° sector of body chamber, with extensive areas of limonitized shell preserved that largely obscure the sutures. Coiling is evolute, the umbilicus comprising 27.8% of the diameter, of moderate depth, with a convex wall and broadly rounded umbilical shoulder. The whorl section is

[†]In current geopolitical terminology Zululand and Pondoland now form parts of the provinces of KwaZulu-Natal and the Eastern Cape. For the sake of continuity we retain the names Zululand and Natal in the title of our series of systematic descriptions of the invertebrate faunas from these regions from 1975 onwards.

*Authors for correspondence

E-mail: jim.kennedy@oum.ox.ac.uk / hklinger@iziko.org.za & hkling@telkomsa.net

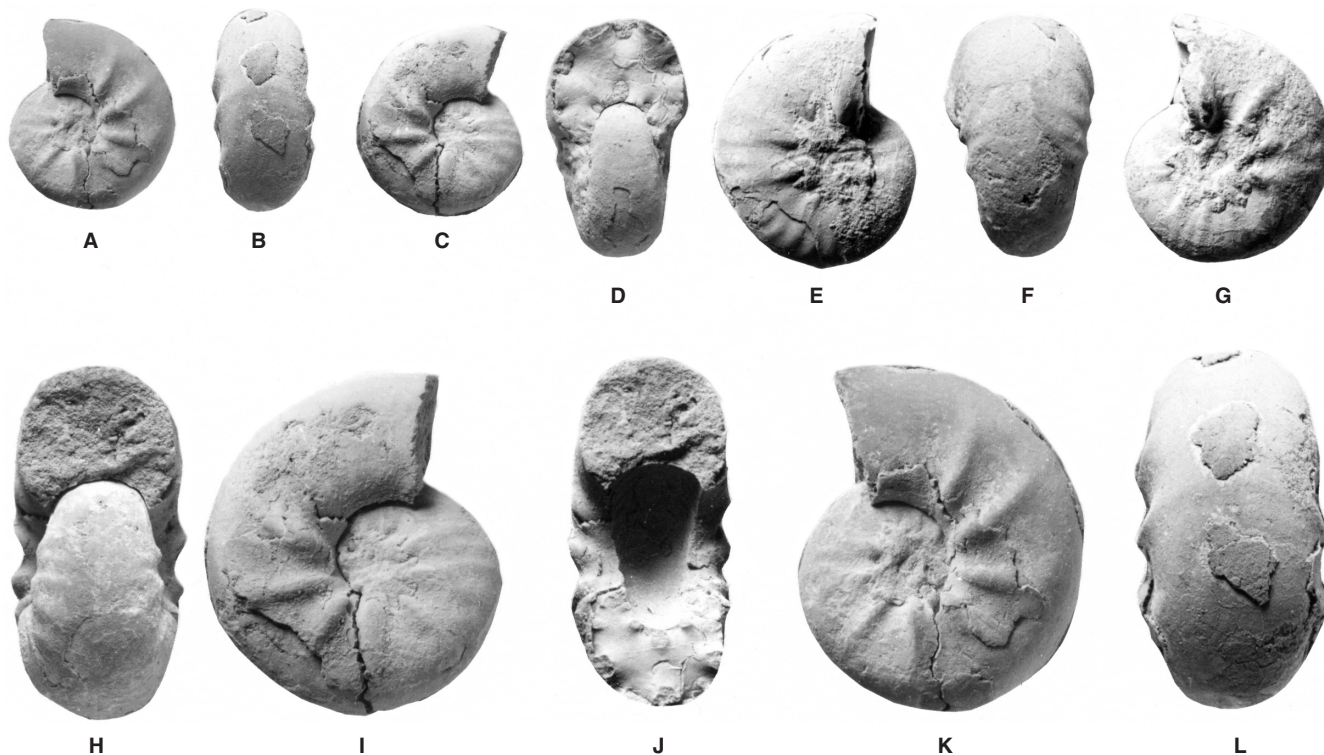


Figure 1. *Salazicerias simplex* sp. nov. The holotype is SAM-PCZ 022425 (formerly D. 2945, ex E.C.N. Van Hoepen Collection), from the Lower Cenomanian Mzinene Formation at the Skoenberg, corresponding to locality 61 of Kennedy & Klinger (1975, p. 189, fig. 6), NNW of Hluhluwe, northern KwaZulu-Natal, coordinates 27°52'17''S, 32°20'19''E. A–C are $\times 1$; D–L are $\times 2$.

depressed reniform, with the greatest breadth at the umbilical bullae and a costal whorl breadth to height ratio of up to 1.3 on the adapertural parts of the phragmocone. The intercostal whorl breadth to height ratio is 1.1 on the body chamber at the greatest preserved diameter. The nucleus of the specimen at 16.4 mm diameter has an estimated 12 progressively strengthening umbilical bullae per whorl. These give rise to low, broad, prorsiradiate ribs or, occasionally, a pair of ribs, while one or two shorter ribs intercalate low on the flank. The ribs strengthen across the outer flank before weakening, and crossing the venter in a very feeble convexity. Towards the end of the nucleus the ribs are near effaced on the venter. On a 120° sector at the adapertural end of the phragmocone and adapical end of the body chamber four strong, distant umbilical bullae give rise to a single prorsiradiate rib that effaces on the ventrolateral shoulders and venter, which are near smooth. The final 60° sector bears a single non-bullate rib, and is thereafter smooth; this change in ornament suggesting the proximity of the adult aperture. The sutures are not seen.

Discussion

Salazicerias simplex differs from typical forms of the type species, *S. salazacense salazacense* in the absence of ribs on the ventrolateral shoulders and venter of the latest parts of the phragmocone and body chamber (see illustrations in Scholz, 1979, p. 92, pl. 21, figs 6–10, 13–15, 17; text-figs 25, 26A, B, H, I, J, L, M, U, V and Szives, 2007, p. 107, pl. 14, fig. 14; pl. 16, figs 7–12; pl. 20, figs 6, 8, 9 and references therein). *Salazicerias salazacense gracilicostatus* Scholz 1979 (p. 95, pl. 21, figs 11, 12; text-fig. 25) is a slender form, with crowded ribs that are well developed across the venter

throughout the known ontogeny, and lack umbilical bullae on the primary ribs. *Salazicerias salazacense peyrolasense* Scholz 1979, (p. 93, pl. 21, figs 16, 18–20; text-figs 25, 26B, 27C–G, K, N, O, P, Q) is near smooth but for constrictions at a diameter that corresponds to the adapertural section of the nucleus of the holotype of *simplex*, thereafter developing very distant flank ribs, three per half whorl, lacking strong bullae. *Salazicerias lemoinei* Kennedy & Klinger, 2008 (p. 115, text-figs 1G–K, 2) is much larger (up to 53 mm in diameter), the primary ribs lacking umbilical bullae, and alternating with short intercalated ribs, all ribs strongly developed on the ventrolateral shoulders and venter of the adult body chamber.

Occurrence

As for type.

ABBREVIATIONS

| | |
|----|--------------------|
| D | diameter (mm) |
| Wb | whorl breadth (mm) |
| Wh | whorl height (mm) |
| U | umbilicus (mm) |

Kennedy acknowledges the support of the staff of the Geological Collections, Oxford University Museum of Natural History, and the Department of Earth Sciences, Oxford, and the financial assistance of the Oppenheimer Fund (Oxford). Klinger acknowledges the technical support of the staff of the Natural History Collections Department, Iziko, South African Museum and financial support from the NRF (South Africa).

REFERENCES

- ADKINS, W.S. 1928. Handbook of Texas Cretaceous fossils. *University of Texas Bulletin* 2838, 1–385.
 BOULE, M., LEMOINE, P. & THÉVENIN, A. 1906–1907. Paléontologie de Madagascar III Céphalopodes crétacés des environs de Diego-Suarez. *Annales de Paléontologie* 1, 173–192 (1–20); 2, 1–56 (21–76).
 BREISTROFFER, M. 1936. Les subdivisions du Vraconien dans le

- Sud-Est de la France. *Bulletin de la Société Géologique de France* (6)5, 63–68.
- GROSSOUVRE, A. de 1894. Recherches sur la craie supérieure, 2, Paléontologie. Les ammonites de la craie supérieure. *Mémoires du Service de la Carte Géologique détaillée de la France*. 264 pp.(misdated 1893). Paris, Imprimerie Nationale.
- HÉBERT, [E.] & MUNIER-CHALMAS, [E.P.A.]. 1875. Fossiles du Bassin d'Uchaux. *Annales des Sciences Géologiques, Paris* 6, 113–132.
- KENNEDY, W.J. & KLINGER, H.C. 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, Stratigraphy. *Bulletin of the British Museum (Natural History) Geology* 25, 263–315.
- KENNEDY, W.J. & KLINGER, H.C. 2008. Hypermorphosis in *Salaziceras*, a Cretaceous ammonite, from Madagascar. *African Natural History* 4, 113–116.
- KLINGER, H.C. & KENNEDY, W.J. 1994. Cretaceous faunas from Zululand and Natal. *Salaziceras salazacense* Hébert & Munier-Chalmas, 1875) from the Mzinene Formation of northern Zululand. *South African Journal of Geology* 97(3), 146–148.
- SCHOLZ, G. 1979. Die Ammoniten des Vracon (Oberalb, *dispar* Zone) des Bakony-Gebirges (Westungarn) und eine Revision der wichtigsten Vracon-Arten der Westmediterranen Faunenprovinz. *Palaeontographica* A165, 1–136.
- SZIVES, O. 2007. Albian Stage. In: Aptian-Campanian ammonites of Hungary. *Geologica Hungarica, Series Palaeontologica* 57, 75–122.
- WRIGHT, C.W. & KENNEDY, W.J. 1979. Origin and evolution of the Cretaceous micromorph ammonite family Flickiidae. *Palaeontology* 22, 685–704.
- WRIGHT, C.W. & KENNEDY, W.J. 1984. The affinities of the Cretaceous ammonite *Neosaynoceras* Breistroffer, 1947. *Palaeontology* 27, 159–167.

A new caprin bovid (Mammalia) from the late Miocene of Morocco

Denis Geraads^{1*}, Siham El Boughabi² & Samir Zouhri²

¹CNRS, UPR 2147, 44 rue de l'Amiral Mouchez, F-75014 Paris, France

²Laboratoire de Géosciences, Faculté des Sciences, Université Hassan II-Casablanca, Km 8, route d'El Jadida, BP 5366 Maârif, 20100 Casablanca, Morocco

Received 23 April 2012. Accepted 20 August 2012

We describe here a bovid skull from the Upper Member of the Aït Kandoula Formation near Ouarzazate, Morocco, which can be dated by biostratigraphy to the late Miocene, Turolian-equivalent. We assign it to a new taxon, *Skouraia helicoides*, gen. nov., sp. nov. It has long horn-cores that are much inclined backwards, strongly spiralled in homonymous direction, very divergent, and have a strong anterolateral keel. The strong cranial flexure, broad basioccipital, and aegodont teeth demand inclusion of this new taxon within the tribe Caprini, a mostly Eurasian group with few African representatives. *Skouraia* must be an early offshoot of this tribe, but its highly derived cranial features suggest that the Caprini may have experienced, in the poorly known late Miocene of Africa, a broader morphological diversification than in Europe.

Keywords: Upper Miocene, Morocco, Africa, Bovidae, Caprinae, Caprini.

INTRODUCTION

With more than 70 living species, the Bovidae are by far the most diverse family of large mammals in Africa today. They include representatives of all major tribes except the Boselaphini, but most of them belong to tribes that are today endemic to the Afro-Arabian domain, namely the Tragelaphini, Cephalophini, Neotragini, Aepycerotini, Reduncini, Hippotragini and Alcelaphini. The Antilopini are also well represented, but they are mainly a Palearctic group. In the Pliocene and Pleistocene, evidence from the whole continent shows that the same groups dominated the bovid assemblages, although the proportions of the various tribes vary sharply with age and location. To these groups, Ethiopian in the terminology of modern faunal provinces, we must add the Bovini, more common and more diverse than today, the Boselaphini that went extinct in Africa by the earliest Pliocene (their last appearance is at Langebaanweg in South Africa, and in the Apak Member of Lothagam in Kenya), and the Caprini that were far less common than in Eurasia. It is likely that the differentiation of the African tribes took place in the Miocene, but it is only by the late Miocene, c. 7 Ma, at Sahabi in Libya, Lothagam in Kenya, and Toros Menalla in Chad, that we find fossils that can be unambiguously assigned to these modern endemic tribes (Lehmann & Thomas 1987; Harris 2003; Geraads *et al.* 2008; Bibi *et al.* 2009; Gentry 2010). At that time, the composition of the bovid assemblage is already fully African in character, with the exception of the last boselaphines.

Earlier late Miocene African bovid faunas are poorly known. The Beglia Formation of Tunisia, mostly, if not fully (Geraads 1989) of late Miocene age, yielded several bovids but only a few have been described (Robinson 1972, 1986); a few fragmentary specimens were described by Geraads (1989) from the slightly younger sites of Jebel Krechem in the same country; Bou Hanifia in Algeria

yielded only the very poorly known *Damalavus boroccoi* Arambourg, 1959. It is noteworthy that none of the fossils from these localities foreshadow the later endemic African tribes. The greatest potential for improving our knowledge of bovids of the first part of the late Miocene (Vallesian – equivalent) in Africa probably rests in the Nakali and Samburu beds of Kenya, but these have not yet been published.

In this paper we describe the most complete known skull of a North African Miocene bovid, and assign it to a new taxon. It comes from the fluvial deposits (coarse sands and conglomerates) of the Upper Member of the Aït Kandoula Formation, near the village of Skoura, East of Ouarzazate, south of the High Atlas of Morocco (Fig. 1); these deposits have been dated to the late Miocene on a faunal basis (Zouhri *et al.* 2012).

SYSTEMATIC PALEONTOLOGY

In the descriptions, the tooth rows are supposed to be horizontal. Upper teeth are in upper case, lower teeth are in lower case.

Family Bovidae Gray, 1821

Subfamily Antilopinae Gray, 1821

Tribe Caprini Gray, 1821

Genus *Skouraia*, gen. nov.

Type species. *Skouraia helicoides*, new species.

Derivatio nominis. From Skoura, the village closest to the area of the type locality.

Diagnosis. That of the type-species.

***Skouraia helicoides* sp. nov., Fig. 2**

Holotype. Almost complete cranium, bearing the complete right horn-core and a large part of the left one, with most of the teeth except the left P2 and all right premolars, but lacking most of the dorsal part of the face anterior to the orbit, and the premaxillae. It is unnumbered and preserved

*Author for correspondence. E-mail: denis.geraads@evolhum.cnrs.fr

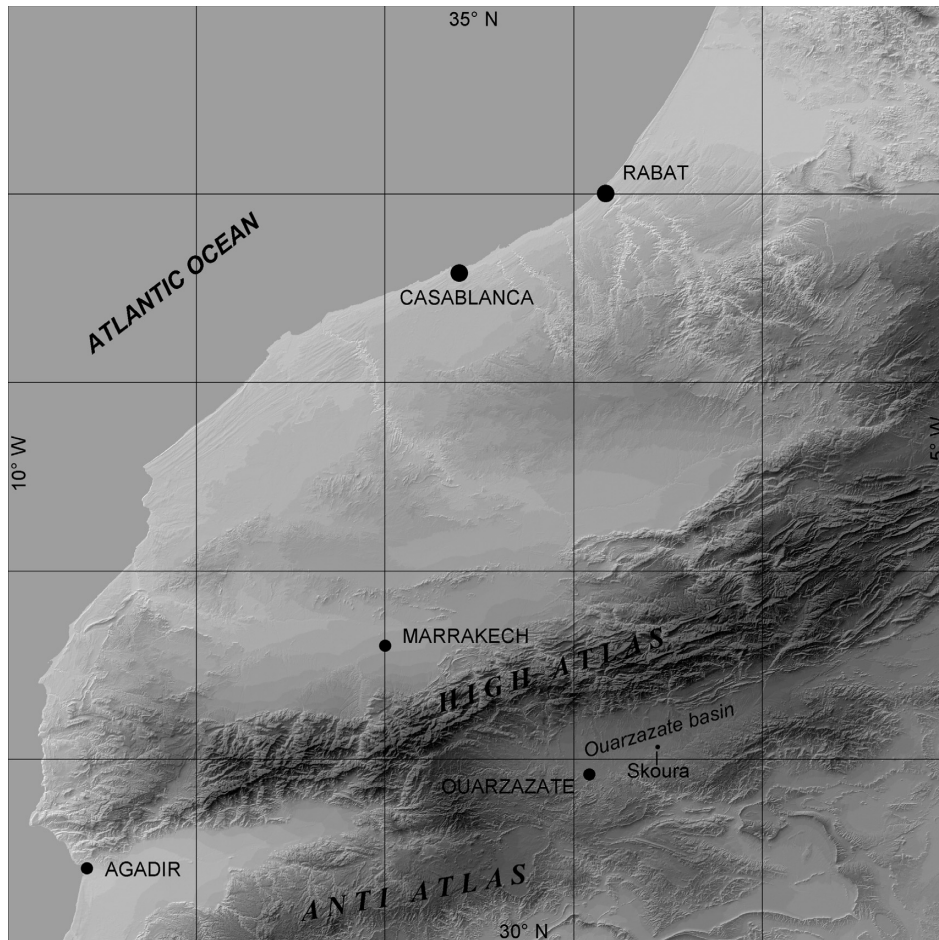


Figure 1. Map of Morocco with the location of Skoura in the Ouarzazate basin. Elevation data from <http://hydrosheds.cr.usgs.gov/>

in the private museum of Mr Brahim Tahiri in Erfoud, Morocco.

Diagnosis. A bovid with strong cranial flexure, early fusion of the bones of the braincase, low occipital, basioccipital broad and rather flat, with a narrow central groove. Horn-cores strongly divergent, much inclined posteriorly, with a virtually circular cross-section except for a strong antero-lateral keel, and describing a strong homonymous spiral. Upper teeth aegodont, with narrow styles, flat or poorly convex labial walls, and short premolars.

Type locality. The specimen was collected near Tizi N'Tadderht, in the Upper Member of the Aït Kandoula Formation of the Ouarzazate basin, Morocco, associated with a fauna dated by biostratigraphy to the youngest part of the late Miocene (equivalent to the European Turolian; Zouhri *et al.* 2012).

Derivatio nominis. Because the horn-cores are strongly spiralled.

Remarks. It is of course unfortunate that the holotype, and only known specimen, be kept in a private (albeit freely accessible as of November 2010) museum. Still, we believe that in spite of this shortcoming, the importance of this new taxon warrants description and formal naming.

Description. The skull is rather large for its geological age, comparable to that of European *Pachytragus* (measurements: Table 1). Its most obvious feature is the strong cranial flexure (Fig. 2A). The angle between the fronto-parietal profile, behind the horn-cores, and that of the (missing) dorsal profile of the face, can be estimated at

about 100°; the angle between the basioccipital and the alveolar plane is about 50°. Correlated with this highly derived skull flexure, the orbit is located far behind the tooth row, and the frontals are strongly elevated between the horn-cores. The anterior part of the frontals, including the supra-orbital foramina, the nasals, the premaxillae, and most of the maxillae, are missing. There is a double postcornual fossa, which is in fact infracornual. All bones of the low, broad braincase are fused, and no suture is visible, but the parietal was certainly short; its dorsal profile is slightly concave. The angle between it and the plane of the occipital is about 130°. The occipital has a rounded outline, and is low and broad, with a central sagittal crest (Fig. 2G). The mastoid and auditory areas are

Table 1. Measurements (in mm) of holotype skull of *Skouraiia helicoides*.

| | |
|---|------|
| Length from occipital condyle to P2 (estimated) | 193 |
| Length from occipital condyle to M3 | 118 |
| Minimum width of braincase | 69 |
| Width of occipital | 82+ |
| Height of occipital (from top of foramen) | 39 |
| Width of basioccipital | 28.6 |
| Bicondylar width | 56 |
| Width over M3s | 75 |
| Width over horn core pedicles | 91 |
| Antero-posterior diameter of horn-core | 47.4 |
| Transverse diameter of horn core | 41.1 |
| Length of right horn core | 260+ |
| Length M1-M3 | 55.8 |
| Length P3-P4 | 21 |

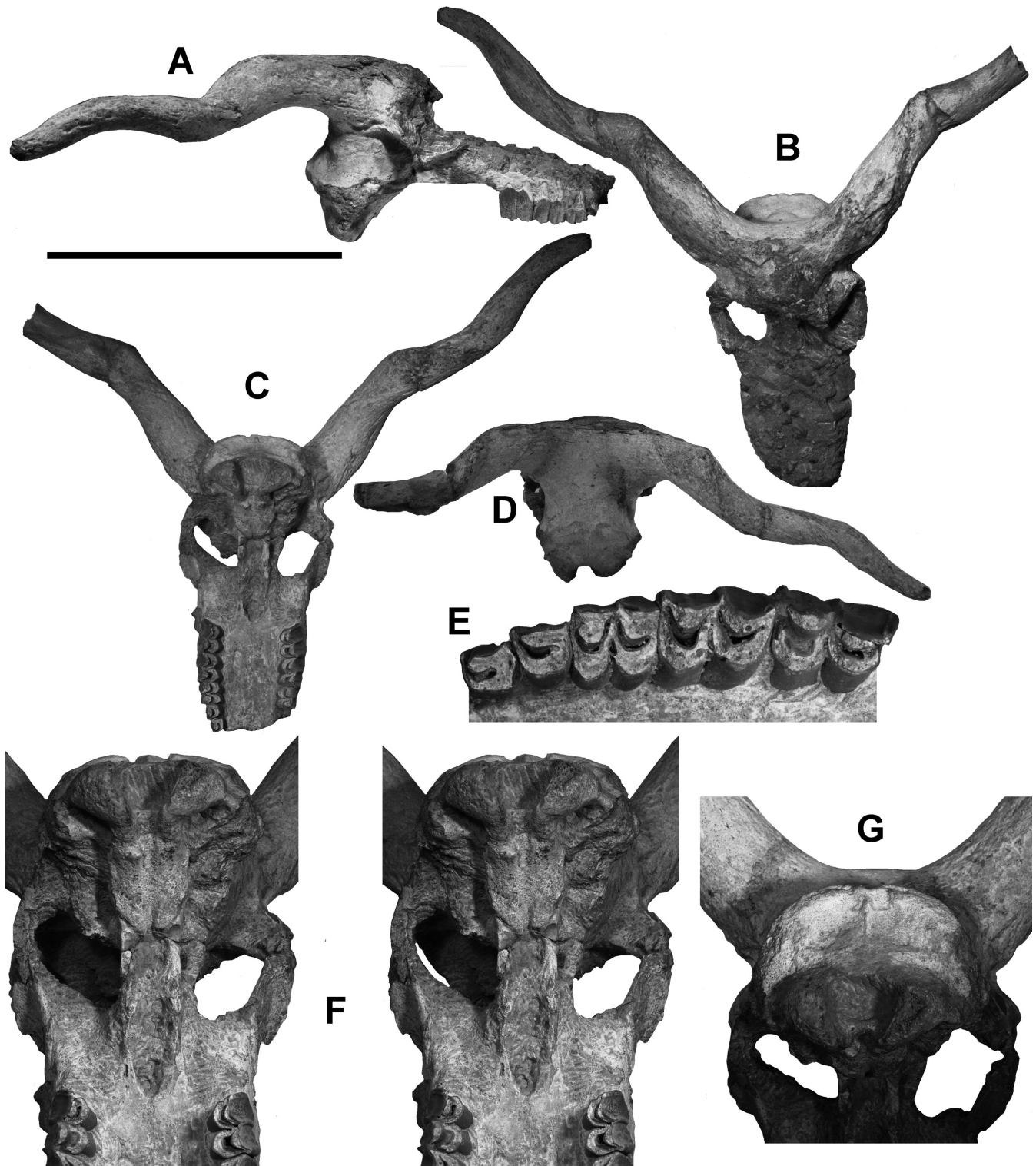


Figure 2. *Skouria helicoides* sp. nov., holotype cranium. **A**, right lateral view; **B**, dorsal view; **C**, central view; **D**, posterior view; **E**, left tooth row P3–M3; **F**, stereo view of the cranial base; **G**, occipital view. Scale = 5 cm for Fig. E, 10 cm for Figs E, G, 20 cm for Figs A–D.

indistinct. On the basioccipital, the usual pairs of anterior and posterior tuberosities are hardly distinct; they are in fact little more than elevations above a pair of rectangular plateaus, only slightly narrower anteriorly than posteriorly, and separated by a long narrow groove in the midline (Fig. 2F); there are no accessory stop facets for the atlas. The choanae reach the level of the posterior border of M3, and the lateral indentations almost reach the same level (Fig. 2F).

The horn-cores are inserted above the orbits, and are

strongly inclined backwards, as their basal part is parallel to the tooth row in lateral view, and their tips are more ventral than their base (Fig. 2A). Basal divergence is about 90°, and slightly increases towards the tips. They are strongly spiralled, but the axis of revolution of the horn core probably remains within the bone, thus forming a closed spiral. Torsion is homonymous, i.e. the right horn has a clockwise torsion (its is perhaps necessary to stress here that, although imperfectly preserved, the skull is wholly devoid of reconstruction, and therefore no error

can have occurred in fitting the horn-cores onto the skull). They have a strong anterolateral keel, which remains strong all the way to the tip, and a weaker anteromedial one; the anterior surface is almost flat between these keels, and the remaining part of the surface is rounded, with only a slight mediolateral compression. Owing to imperfect preservation of these parts, we do not know whether the base of the horn-cores and/or the frontal, were pneumatized.

The premolars are very short compared to the molars (Fig. 2E). The P4 has a rather square outline, being almost as long lingually as labially, and has a moderate, centrally placed, labial rib. This rib is much more mesially placed, and stronger, on P3, which is distinctly smaller than P4, making unlikely that the P2, now missing, was larger. Assuming that it was as large as P3, the index L P2-P4/L M1-M3 100 can be estimated at about 55, a very low value, comparable to that of modern *Capra*. The molars have no entostyles. The paracone has a weak labial rib, but there is none on the metacone, whose labial wall is a flat depressed surface between prominent styles; the metastyle of M3 is remarkably salient. On the whole, the dentition is therefore clearly of the aegodont type.

Comparisons. The most remarkable feature of this new bovid is the homonymous direction of horn torsion. Most spiral-horned bovids, living and fossil, instead have horns with heteronymous torsion, i.e. the right horn-core has an anticlockwise torsion. This is true, in particular, of those antelopes with the most conspicuously spiralled horns, the African Tragelaphini, but also of the modern *Antilope* (Antilopini) and *Addax* (Hippotragini), whose horns are markedly spiralled, and of *Kobus* (Reduncini), *Damaliscus* (Alcelaphini) and *Aepyceros*, where torsion is much weaker. Most of the abundant spiral-horned forms of the Palearctic late Miocene, such as *Palaeoreas*, *Prostrepsiceros*, *Protragelaphus*, and related genera, also have heteronymous torsion. Thus, their few representatives in Africa, such as *Prostrepsiceros libycus* Lehman & Thomas, 1987 from Sahabi (referred to *Dytikodorcas* by Bouvrain & Bonis, 2007), or the '*Palaeoreas*' from the Samburu Hills (Nakaya *et al.* 1987), can be readily excluded from the comparison.

A slight homonymous torsion can be found in many Alcelaphini, especially *Connochaetes*, *Megalotragus* and *Numidocapra*, but no member of this tribe has horns that are strongly spiralled, and they have a characteristic tooth morphology quite distinct from that of *Skouraiia* (although they share the same premolar reduction). It is also detectable, but much weaker than in *Skouraiia*, in some other African bovids that are clearly unconnected to genus, such as *Menelikia* and *Antidorcas*.

Bovids with a clear homonymous horn core torsion can be divided into four groups for convenience, and compared in the same order:

- 1) the *Oioceros* group, mostly of late Miocene age;
- 2) the *Sinotragus* group, also of late Miocene age, perhaps related to the next group, or to the *Pachytragus-Protoryx* group;
- 3) many modern Caprini, including the sheep and some goats;
- 4) a few fossils from northwestern Africa.

1) Among the informal *Oioceros* group, *Hispanodorcas* from Spain (Thomas *et al.* 1982; Alcalá & Morales 2006) and Greece (Bouvrain & Bonis 1988) has slender, almost straight horn-cores with weak torsion and no keels, which are uprightly inserted far from the occipital, and a rounded braincase. *Hispanodorcas* is clearly unrelated to *Skouraiia*.

Pontoceros Verescagin *et al.*, 1971, from the Plio-Pleistocene of the Black Sea and Greece (Verescagin *et al.* 1971; Kostopoulos 1997) also has almost straight horn-cores, not spiralled like those of *Skouraiia*, with a more triangular cross-section underlined by distinct furrows, and they are much less divergent.

Systematics of the late Miocene *Oioceros-Samotragus-Samodorcas* group is still debated, and its discussion is beyond the scope of this paper. '*Oioceros wegneri*' differs from *Oioceros sensu stricto*, and approaches *Skouraiia*, in its stronger cranial flexure and larger size, but differs from *Skouraiia* in several cranial features: the frontal is not strongly elevated between the horn-cores; even the largest '*O. wegneri*' remain of moderate size; the basioccipital has very strong anterior and posterior tuberosities; the occipital condyles are less broad relative to the occipital width. The horn-cores also offer clear distinguishing features between the *Oioceros* group and *Skouraiia*. In the *Oioceros* group, the surface of the horn-cores is not smooth; instead, it is always marked by one or more longitudinal groove(s) and adjacent or intervening ridge(s) that may be acute and become keel-like, but these keels result from the depression of the areas adjacent to them, rather than from their own raising above the horn core surface, so that the cross-section is quite different; in *Oioceros sensu stricto*, it is often comma-shaped. *Oioceros* is also clearly unrelated to *Skouraiia*.

2) *Prosinotragus* and *Sinotragus* from the Upper Miocene of China (Bohlin 1935), Samos (Solounias 1981), and Turkey (Geraads *et al.* 2002) have horn-cores that are short, only slightly divergent and close to each other at the base, with at most an incipient torsion, and with a keel that is anteromedial rather than anterolateral when present (in the Samos and Turkish forms). All these features differ from those of *Skouraiia helicoides*.

The *Pachytragus-Protoryx* group has been revised by Kostopoulos (2009), who considered both names as synonymous and created the new genus *Skoufotragus*. This group, best known from the Turolian (Gentry 2003, and references therein), had long been placed among the Hippotragini, until Gentry (1971, 2000) convincingly argued that it is closer to the Caprini. Kostopoulos (2005, 2009) maintained that its affinities are still open to discussion because the i1 is larger than i2, unlike Caprini, but the size of i1 seems to be unrelated to phylogeny, and we suspect that its small size in modern Caprini is a consequence of its incipient hypsodonty, so that a moderately large i1 might just be primitive. Members of the *Pachytragus-Protoryx* group have a derived skull with a long face, a posteriorly located orbit, a strong cranial flexure, rather simple horn-cores variably curved backwards but without torsion, and an oval cross-section without keels.

Identification of the dentitions at species level is often difficult, but many of them resemble *Skouraiia* in their aegodont pattern, with short premolars, and molars with weak labial ribs and flat metacone, prominent styles, no entostyles, and often a central fossette. *Pachytragus solignaci* Robinson, 1972, from the middle/late Miocene of Tunisia is the only African form; it resembles *Skouraiia* in the slight spiralling of a horn-core figured by Robinson (1972, Fig. 3) but otherwise clearly differs in the strong transverse compression of the horn-cores. Horn-core morphology rules out any close connection between *Skouraiia* and this group.

3) In many modern Caprini, such as *Capricornis*, *Naemorhedus*, *Oreamnos*, *Pseudois*, and *Rupicapra*, the horn-cores are short, conical, and lack keels and torsion, so that they differ completely from those of *Skouraiia*; those of *Hemitragus* have keels but are also short and simple; those of the 'Ovibovini' *Ovibos* and *Budorcas* are very peculiar and completely different, although a clear homonymous torsion can be found in *Euceratherium*, an extinct relative of the musk-ox. *Ammotragus*, *Capra* and *Ovis* deserve greater attention. They have highly derived skulls with a long face and an orbit located posteriorly, and a strongly flexed cranium. Their horn-cores display a wide range of shapes; they are always curved, usually strongly so, and often show some spiralling. In *Capra* and *Ammotragus*, it is only incipient (except in *C. falconeri*, whose horn-cores are tightly twisted), and usually heteronymous, but some (especially domestic forms) may have a weak homonymous torsion. Many *Capra* (especially *C. falconeri* and domestic forms), as well as the probably related *Bouria* from the Ethiopian Pleistocene (Vrba 1997), have a strongly compressed cross-section with an anterior keel; *Capra wodaramoya* Bibi *et al.* 2012, from the early Pleistocene of Ethiopia is similar but without a clear anterior keel. Other *Capra*, and *Ammotragus*, have a more triangular cross-section, with rounded angles, and a tendency to form a flattened anterior face, limited by a poorly indicated anteromedial change of curvature, which may become a keel near the tip, and a better indicated anterolateral one, which may almost be a keel (e.g. in *C. sibirica*). In *Ovis*, the cross-section is similar but often less compressed and without true keels; however, the greater basal divergence that increases above the base and the strong homonymous torsion are resemblances with *Skouraiia*. Thus, among living bovids, it is undoubtedly with the Caprini that we find any possible similarities with *Skouraiia*.

4) In Northwestern Africa, *Parantidorcas latifrons* Arambourg, 1979 from the Pliocene of Aïn Brimba in Tunisia has horn-cores that have a weak but distinct heteronymous torsion, but this is a much smaller species that probably belongs to the Antilopini.

The northwestern African fossil form most similar to *Skouraiia* is *Benicerus theobaldi* Heintz, 1973, from Beni Mellal in Morocco. This site has traditionally been assigned to the middle Miocene because it lacks hipparions, and Jaeger (1977) even concluded that it is not immediately anterior to the Vallesian because another site, Pataniak 6, is also ante-Vallesian but younger than Beni Mellal.

However, Ginsburg (1977), followed by Werdelin & Peigné (2010), noted that its carnivore fauna is similar in composition to late Miocene ones; we estimate the age of Beni Mellal at c. 12 Ma.

The holotype, and only described specimen, of *B. theobaldi* is an incomplete left horn-core with most of the orbit (Heintz 1973, pl. 1); unfortunately, we could not locate it in the Muséum National d'Histoire Naturelle, Paris. From Heintz' description and figures, this horn-core is strongly curved posteriorly, moderately compressed transversely but with a compression that quickly increases above the base; it has a clear anticlockwise torsion, and a sharp anterior keel. It differs from the type of *S. helicoides* in its smaller size, shortness, more upright insertion, greater apical compression, and complete lack of an anteromedial keel and of an anterior surface. *Benicerus* is too poorly known for in-depth comparisons with *Skouraiia*, but they are the only Miocene African bovids with distinctly homonymous torsion, and both are from Morocco.

There are two or three bovid species in the Upper Miocene of Jebel Krechem in Tunisia (Geraads 1989); some horn-cores could belong to a form close to *Prostrepsiceros*, but there are also some fragments of spiralled horn-cores whose direction of spiralling cannot be determined because they lack the base, but one of them looks so similar to the type of *B. theobaldi* that it is hard to believe that torsion was not homonymous, as in this species. The cross-section is ovoid, transversely compressed, with a keel that must have been anterior, and a hint of a posteromedial one. The presence of this second keel is the only difference with *B. theobaldi*, and we consider likely that a species close to that of Beni Mellal was also present at Jebel Krechem, whose age is probably equivalent to European MN10. Unfortunately, no spiral-horned bovid has been found in the Beglia Formation of Tunisia (Robinson 1986), which is of intermediate age, but it is conceivable that *Benicerus* survived into the late Miocene. How closely this genus is related to *Skouraiia* is hard to tell; a *Benicerus theobaldi*-*Skouraiia helicoides* lineage can be hypothesized, but unsubstantiated on the basis of the very poor record from Beni Mellal, and we prefer to propose *Skouraiia* as a distinct genus.

Behaviour. The strong divergence of the horn-cores, and their strong inclination, with no part of them being dorsal to the frontal plane, strongly suggest that *Skouraiia* performed some kind of the agonistic fighting behaviour known as ramming or Rammkampf, in which the opponents violently clash their heads after charging. It is best known in the Caprini *Ovis* and *Ammotragus*, in *Ovibos*, but also occurs in *Connochaetes* and some Bovini. Since *Skouraiia* is obviously unrelated to any of the latter taxa, this inferred behaviour may be taken as supporting an assignment of this new taxon to the Caprini.

CONCLUSION

The most likely scenario is that *Skouraiia* is an early, *Ovis*-like, offshoot of the Caprini, possibly related to *Benicerus*. Phylogenetic relationships between the living members of this tribe have recently been investigated, with limited consistency in the results (Schafer & Hall

2010; Bibi *et al.* 2012, and references therein). Molecular dating suggests that the early diversification within the tribe started in the late Miocene (Ropiquet & Hassanin 2005). The fact that *Myotragus*, which does not occupy a basal position in this group (Lalueza-Fox *et al.* 2005), must have reached the Balearics during the Messinian, implies that this is a minimum date, and if the shortened metapodials of *Aragoral mudejar*, of MN10 age, are indeed a synapomorphy with the Caprini (Alcalá & Morales 1997), the divergence of this tribe from the Hippotragini and Alcelaphini might go back to the middle Miocene (Bibi *et al.* 2009). It is therefore entirely possible that the North African latest Miocene witnessed an early diversification of the Caprini, which filled there a niche occupied in Eurasia by a variety of other antelopes. It is also likely that this group settled earlier and more deeply in Africa than hypothesized by Bibi *et al.* (2012), who regard its spotty record in this continent as mere successive waves of migrations from Eurasia.

We are especially grateful to B. Tahiri for having allowed us to study the specimen in his private museum. Thanks to A.W. Gentry and to an anonymous reviewer for their useful comments that significantly improved the manuscript. Thanks also for giving access to collections in their care to J. Lesur-GebreMariam and C. Argot (Muséum National d'Histoire Naturelle, Paris), and M. Bertling (Geologisch-Paläontologisches Institut, Universität Münster).

REFERENCES

- ALCALÁ, L. & MORALES, J. 1997. A primitive caprine from the Upper Vallesian of La Roma 2 (Alfambra, Teruel, Aragon, Spain). *Comptes rendus de l'Académie des Sciences* **324**, 947–953.
- ALCALÁ, L. & MORALES, J. 2006. Antilopinae (Bovidae, Mammalia) from the lower Pliocene of Teruel Basin (Spain). *Estudios Geológicos* **62**, 559–570.
- ARAMBOURG, C. 1959. Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord. *Publications du Service de la carte géologique de l'Algérie (N.S.), Paléontologie, Mémoire* **4**, 1–159.
- ARAMBOURG, C. 1979. *Vertébrés villafranchiens d'Afrique du Nord (Artiodactyles, Carnivores, Primates, Reptiles, Oiseaux)*. Paris, Fondation Singer-Polignac.
- BIBI, F., BUKHSIANIDZE, M., GENTRY, A.W., GERAADS, D., KOSTOPOULOS, D.S. & VRBA, E. 2009. The fossil record and evolution of Bovidae: State of the field. *Palaeontologia Electronica* **12**, 1–11.
- BIBI, F., VRBA, E. & FACK, F. 2012. A new African fossil caprin and a combined molecular and morphological bayesian phylogenetic analysis of caprini (Mammalia: Bovidae). *Journal of Evolutionary Biology* **25**, 1843–1854.
- BOHLIN, B. 1935. Cavicornier der Hipparion-Fauna Nord Chinas. *Palaeontologia Sinica* **9**, 1–166.
- BOUVRAIN, G. & BONIS, L. DE. 1988. Découverte du genre *Hispanodorcas* (Bovidae, Mammalia) dans le Turolien de Grèce septentrionale. *Annales de Paléontologie* **74**, 97–112.
- BOUVRAIN, G. & BONIS, L. DE. 2007. Ruminants (Mammalia, Artiodactyla: Tragulidae, Cervidae, Bovidae) des gisements du Miocène supérieur (Turolien) de Dytiko (Grèce). *Annales de Paléontologie* **93**, 121–147.
- GENTRY, A.W. 1971. The earliest goats and other antelopes from the Samos Hipparion fauna. *Bulletin of the British Museum (Natural History) – Geology* **20**, 231–296.
- GENTRY, A.W. 2000. Caprinae and Hippotragini (Bovidae, Mammalia) in the Upper Miocene. In: Vrba, E.S. & Schaller, G.B. (eds), *Antelopes, Deer and Relatives: Fossil Record, Behavioral Ecology, Systematics and Conservation*, 65–83. New Haven, Yale University Press.
- GENTRY, A.W. 2003. Ruminantia (Artiodactyla). In: Fortelius, M., Kappelman, J., Sen, S. & Bernor, R.L. (eds), *Geology and Paleontology of the Miocene Sinap Formation, Turkey*, 332–379. New York, Columbia University Press.
- GENTRY, A.W. 2010. 38 – Bovidae. In: Werdelin, L. & Sanders, W.J. (eds), *Cenozoic Mammals of Africa*, 741–796. Berkeley, University of California Press.
- GERAADS, D. 1989. Vertébrés du Miocène supérieur du Djebel Krechem el Artsouma (Tunisie centrale). Comparaisons biostratigraphiques. *Géobios* **22**, 777–801.
- GERAADS, D., GÜLEÇ, E. & KAYA, T. 2002. *Sinotragus* (Bovidae, Mammalia) from Turkey and the late Miocene Middle Asiatic Province. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **8**, 477–489.
- GERAADS, D., BLONDEL, C., LIKIUS, A., TAISSO MACKAYE, H., VIGNAUD, P. & BRUNET, M. 2008. New Hippotragini (Bovidae) from the late Miocene of Toros-Menalla, Chad. *Journal of Vertebrate Palaeontology* **28**, 231–242.
- GINSBURG, L. 1977. Les carnivores du Miocène de Beni Mellal. *Géologie Méditerranéenne* **4**, 225–240.
- GRAY, J.E. 1821. On the natural arrangement of vertebrate animals. *London Medical Repository* **15**, 296–310.
- HARRIS, J.M. 2003. Bovidae from the Lothagam succession. In: Leakey M.G. & Harris J.M. (eds), *Lothagam – The Dawn of Humanity in Eastern Africa*, 531–582. New York, Columbia University Press.
- HEINTZ, E. 1973. Un nouveau bovidé du Miocène de Beni Mellal, Maroc: *Benicercus theobaldi* n.g., n.sp. (Bovidae, Artiodactyla, Mammalia). *Annales Scientifiques de l'Université de Besançon* **18**, 245–248.
- JAEGER, J.-J. 1977. Les rongeurs du Miocène moyen et supérieur du Maghreb. *Palaeovertebrata* **8**, 1–166.
- KOSTOPOULOS, D.S. 1997. The Plio-Pleistocene artiodactyls (Vertebrata, Mammalia) of Macedonia. 1. The fossiliferous site 'Apollonia-1', Mygdonia basin of Greece. *Geodiversitas* **19**, 845–875.
- KOSTOPOULOS, D.S. 2005. The Bovidae (Mammalia, Artiodactyla) from the late Miocene of Akkasdağı, Turkey. *Geodiversitas* **27**, 747–791.
- KOSTOPOULOS, D.S. 2009. The late Miocene Mammal faunas of the Mytilini basin, Samos Island, Greece: new collection. 14. Bovidae. *Beiträge zur Paläontologie* **31**, 305–349.
- LALUEZA-FOX, C., CASTRESANA, J., SAMPIETRO, L., MARQUES-BONET, T., ALCOVER, J.A. & BERTRANPETIT, J. 2005. Molecular dating of caprines using ancient DNA sequences of *Myotragus balearicus*, an extinct endemic Balearic mammal. *BMC Evolutionary Biology* **5**, 70.
- LEHMANN, U. & THOMAS, H. 1987. Fossil Bovidae (Mammalia) from the Mio-Pliocene of Sahabi, Libya. In: Boaz, N.T., El-Arnauti, A., Gaziry, A.W., Heinzelin, J. de & Dechant Boaz, D. (eds), *Neogene Paleontology and Geology of Sahabi*, 323–335. New York, Alan R. Liss.
- NAKAYA, H., PICKFORD, M., YASUI, K. & NAKANO, Y. 1987. Additional large mammalian fauna from the Namurungule Formation, Samburu Hills, Northern Kenya. *African Study Monographs* **5**, 79–129.
- ROBINSON, P. 1972. *Pachytragus solignaci*, a new species of caprine bovid from the Late Miocene Beglia Formation of Tunisia. *Notes du Service Géologique de Tunisie* **37**, 73–94.
- ROBINSON, P. 1986. Very hypsodont antelopes from the Beglia Formation (central Tunisia), with a discussion of the Rupicaprini. *Contributions to Geology, University of Wyoming Special Paper* **3**, 305–315.
- ROPIQUET, A. & HASSANIN, A. 2005. Molecular phylogeny of caprines (Bovidae, Antilopinae): the question of their origin and diversification during the Miocene. *Journal of Zoological Systematics and Evolutionary Research* **43**, 49–60.
- SCHAFFER, A.B.A. & HALL, J.C. 2010. Placing the mountain goat: a total evidence approach to testing alternative hypotheses. *Molecular Phylogenetics and Evolution* **55**, 18–25.
- SOLOUNIAS, N. 1981. The Turolian Fauna from the Island of Samos, Greece, with special emphasis on the hyaenids and the bovids. *Contributions to Vertebrate Evolution* **6**, 1–232.
- THOMAS, H., MORALES, J. & HEINTZ, E. 1982. Un nouveau Bovidé (Artiodactyla, Mammalia), *Hispanodorcas torrubiæ* n.g., n.sp., dans le Miocène supérieur d'Espagne. *Bulletin du Muséum national d'Histoire naturelle* **4**, 209–222.
- VERESCAGIN, N., ALEXEJEVA, L., DAVID, A., BAIGUSHEVA, V. 1971. [Tribe Tragelaphini Sokolov, 1953]. In: Nikiforova, K. (ed.), *Pleistocene of Tiraspol*, 165–170. Shtiintsa, Chisinau [in Russian].
- VRBA, E.S. 1997. New fossils of Alcelaphini and Caprinae (Bovidae: Mammalia) from Awash, Ethiopia, and phylogenetic analysis of Alcelaphini. *Palaeontologia africana* **34**, 127–198.
- WERDELIN, L. & PEIGNÉ, S. 2010. 32 – Carnivora. In: Werdelin, L. & Sanders, W.J. (eds), *Cenozoic Mammals of Africa*, 603–657. Berkeley, University of California Press.
- ZOUHRI, S., GERAADS, D., EL BOUGHABI, S. & EL HARFI, A. 2012. Discovery of an Upper Miocene Vertebrate fauna near Tizi N'Tadderht, Skoura, Ouarzazate Basin (Central High atlas, Morocco). *Comptes-rendus Palevol* **11**, 455–461.

Morphometric analysis of modern human crania: a framework for assessing early Pleistocene hominids

E.J. Odes^{1,2} & J.F. Thackeray^{1*}

¹Institute for Human Evolution, University of the Witwatersrand, P.O. WITS, Johannesburg, 2050 South Africa

²School of Geosciences, University of the Witwatersrand, P.O. WITS, Johannesburg, 2050 South Africa

Received 16 January 2012. Accepted 12 October 2012

Craniofacial measurements have been obtained from modern human skulls from cadavers representing several southern African population groups including Ndebele, Shangaan, Sotho, Swazi, Tswana, Xhosa and Zulu, in addition to European *Homo sapiens*. The measurements were obtained from crania in the Dart Collection housed at the School of Anatomical Sciences of the University of the Witwatersrand. Pairwise comparisons, using least squares linear regression analysis of cranial measurements, were used to calculate the standard error of the m -coefficient associated with the general equation $y = mx + c$, where m is the slope of the regression line. The standard error of the m -coefficient is a measure of the degree of similarity between specimens. Log transformed $s.e._m$ values ($\log s.e._m$) show a normal distribution with a mean value of -1.84 ± 0.087 ($n = 384$ pairwise comparisons). These results can be used as a frame of reference for comparing Early Pleistocene specimens. For example, a comparison between KNM-ER 1813 (attributed to *H. habilis*) and KNM-ER 3733 (attributed to *H. erectus* or *H. ergaster*) is associated with a $\log s.e._m$ value of -1.844 . Despite differences in size, these two penecontemporary hominid fossils are associated with a high probability of conspecificity, since the $\log s.e._m$ value is identical to the mean $\log s.e._m$ value of -1.84 obtained for pairwise comparisons of modern *Homo sapiens*.

Keywords: *Homo sapiens*, *Homo ergaster*, *Homo habilis*, morphology, craniofacial.

INTRODUCTION

Thackeray (2005) has previously examined cranial variation in modern hominoid primates, excluding modern humans, in the context of variation in skulls of extinct African hominins. In this study we obtain cranial data from a sample of modern humans, using more than 100 landmarks, to provide a frame of reference for assessing Plio-Pleistocene hominins.

MATERIALS AND METHODS

The modern comparative human sample in the Dart Collection at the University of the Witwatersrand, from cadavers, includes 24 African crania: Ndebele (two male, two female), Shangaan (two male, two female), Sotho (two male, two female), Swazi (two male, two female), Tswana (one male, one female), Xhosa (two female, two male), Zulu (one male), and one African human cranium; and five crania catalogued as Europeans (Caucasian). The choice of sample size was arbitrary, with the objective of securing a total sample of at least 25 individuals, recognizing that this represents only part of the range of variation that would be expected from a global sample of *H. sapiens*.

The measurements on the modern crania (Table 1) were based on landmarks previously used in Wood's (1991) study of fossil hominins. The landmarks include Prosthion (pr); Nasospinale (ns); Nasion (n); Glabella (g); Bregma (b); Vertex (v); Apex (ap); Lambda (l); Opistocranium (op); Inion (i) Opisthion (o); Basion (ba); Alveolon (alv); Staphylion (sta); Orale (ol); Euryon (eu); Porion (po); Mastoidale (ms); Alare (al); Orbitale (or); Zygion (zy); Ectoconchion (ec); Ectomalare (ecm); Pterion (pt); Endomalare (enm); Frontotemporale (ft).

Measurements were obtained using (1) digital callipers manufactured by the Mitutoyo Corporation (product

name Digimatic Caliper; model no: CD-6 inch CX; code no: 500-171-20; serial no: 09093312; measuring range 0–150 mm; minimum indication 0.01 mm); (2) a two-button digital calliper manufactured by Mitutoyo Corporation, with the same technical specifications (resolution: 0.01 mm); and (3) a Mitutoyo digital linear spreading calliper with a 300 mm digital scale and a throat depth of 150 mm. The modern crania were positioned on a foam base for stability and protection. Measurements were taken using the same calipers throughout the study to minimize measurement error. Curved regions were measured using chord distance.

Statistical method

The method that is used in this study has been developed by Thackeray *et al.* (1997, 2007). Morphological variation within a species can be quantified using least squares linear regression analysis of measurements of pairs of specimens. The degree of similarity between two specimens of the same species can be expressed by comparing measurements of a reference specimen A (associated with the x -axis) and conspecific specimen B (associated with the y -axis). In such cases there is generally little scatter around the regression line, associated with the linear regression equation $y = mx + c$, where m represents the slope of the regression line, and c represents the constant; the log transformed standard error of the slope m is referred to as $\log s.e._m$. The limited scatter around the regression line is associated with similarity in shape of the two conspecific specimens.

The degree of scatter around the regression line is quantified by the standard error of the m -coefficient ($s.e._m$).

The $s.e._m$ value for pairs of conspecific pairs is relatively low. By contrast, when measurements of two specimens representing two different species are compared, there is

*Author for correspondence. E-mail: francis.thackeray@wits.ac.za

Table 1. List of craniofacial measurements.

| Number | Measurement | Number | Measurement |
|--------|---|--------|---|
| 1 | Glabella–opisthocranium | 52 | Bizygomatic breadth |
| 2 | Posthion–inion | 53 | Bimaxillary breadth |
| 3 | Posterior cranial length | 54 | Outer alveolar breadth |
| 4 | Basion–bregma | 55 | Anterior interorbital breadth |
| 5 | Basion–nasion | 56 | Orbital breadth |
| 6 | Porion height | 57 | Orbital height |
| 7 | Mastoid length | 58 | Orbitale–zygomaxillare |
| 8 | Minimum frontal breadth | 59 | Minimum malar height |
| 9 | Maximum parietal breadth | 60 | Malar thickness |
| 10 | Maximum temporal breadth | 61 | Width temporal gutter |
| 11 | Biporionic breadth | 62 | Vertical thickness of supraorbital torus |
| 12 | Supramastoid breadth | 63 | Anteroposterior thickness of supraorbital torus |
| 13 | Maximum breadth across mastoid process | 64 | Anteroposterior thickness of supraorbital torus |
| 14 | Biaterionic breadth | 65 | Anteroposterior thickness of glabella |
| 15 | Interentoglenoid breadth | 66 | Frontal torus breadth |
| 16 | Entoglenoid breadth | 67 | Frontal torus breadth |
| 17 | Glabella–bregma | 68 | Maximum nasal width |
| 18 | Glabella–bregma | 69 | Nasal height |
| 19 | Postglabellar sulcus–bregma | 70 | Rhinion–nasospinale |
| 20 | Postglabellar sulcus–bregma | 71 | Sagittal length of nasal bones |
| 21 | Bregma–left pterion | 72 | Superior breadth of nasal bones |
| 22 | Bregma–left pterion | 74 | Inferior breadth of nasal bones |
| 23 | Bregma–right pterion | 75 | Infratemporal fossa depth |
| 24 | Bregma–right pterion | 76 | Foramen magnum length |
| 25 | Parietal sagittal length | 77 | Foramen magnum maximum width |
| 26 | Parietal sagittal length | 78 | Occipital condyle maximum length |
| 27 | Parietal temporal length | 79 | Occipital condyle maximum width |
| 28 | Parietal temporal length | 80 | Mandibular fossa length |
| 29 | Parietal coronal breadth | 81 | Mandibular fossa length |
| 30 | Parietal coronal breadth | 82 | Mandibular fossa breadth |
| 31 | Parietal lambdoid length | 83 | Mandibular fossa breadth |
| 32 | Parietal lambdoid length | 84 | Mandibular fossa depth |
| 33 | Bregma–asterion | 85 | Depth of postglenoid process |
| 34 | Bregma–asterion | 86 | Depth of articular eminence |
| 35 | Lambda–inion | 87 | Maxillo–alveolar length |
| 36 | Lambda–inion | 88 | Maxillo–alveolar breadth |
| 37 | Inion–opisthion | 89 | Palate length (orale–staphylion) |
| 38 | Inion–opisthion | 90 | Palate length (orale–palatomaxillary suture) |
| 39 | Occipital sagittal length | 91 | Palate breadth |
| 40 | Occipital sagittal length | 92 | Incisive canal–palatomaxillary suture |
| 41 | Biasterionic breadth | 93 | Internal alveolar breadth at M3 |
| 42 | Biasterionic breadth | 94 | I ¹ –I ² alveolar length |
| 43 | Superior facial height | 95 | Canine alveolus breadth |
| 44 | Superior facial length | 96 | P ³ –P ⁴ alveolar length |
| 45 | Alveolar height | 97 | M ¹ –M ³ alveolar length |
| 46 | Subnasale–prosthion | 98 | Inter canine distance |
| 47 | Subnasale–prosthion (horizontal projection) | 99 | P ³ interalveolar distance |
| 48 | Subnasale–prosthion (vertical projection) | 100 | P ⁴ interalveolar distance |
| 49 | Superior facial breadth | 101 | M ² interalveolar distance |
| 50 | Biorbital breadth | 102 | M ³ interalveolar distance |
| 51 | Bijugal breadth | 103 | Palatal height |

a greater degree of scatter around the regression line and the $s.e._m$ value is relatively high (Thackeray et al. 1997; Aiello et al., 2000). The distribution of $s.e._m$ values obtained from pairwise comparisons of extant conspecific pairs of specimens has been examined. Thackeray et al. (1997) showed there is a log normal distribution of $s.e._m$ values when pairwise comparisons are made between conspecific specimens of extant vertebrates including mammals, birds, reptiles and extant invertebrates. In a larger study (Thackeray, 2007), log $s.e._m$ values are inclined to be centrally distributed around a mean log $s.e._m$ value of -1.61 ± 0.23 (including vertebrates and invertebrates where $n = 1424$ specimens), not significantly different from a mean log $s.e._m$ value of -1.66 ± 0.20 for invertebrates ($n = 172$ specimens).

Thackeray (2007) proposed that when comparisons are made between any two specimens of the same species,

the log $s.e._m$ approximates a ‘biological species constant’ ($T = -1.61$) which is considered to prevail over evolutionary time and geographical space. The advantage of this approach is that the mean log $s.e._m$ value of -1.61 ± 0.23 facilitates a definition of a species based on morphometric analysis. It allows for the assessment of probabilities of conspecificity associated with fossil specimens including hominins from South and East Africa, taking into account the fact that there is morphological variation in time and space, and recognizing that there is no clear boundary between hominin species in space and time, and no clear boundary between *Australopithecus* and *Homo*. The method has been used in this study to assess the degree of similarity between a sample of modern specimens of *Homo sapiens*, representing only part of the range of variation that would be expected in a global sample. As an example of the application of this approach, comparisons

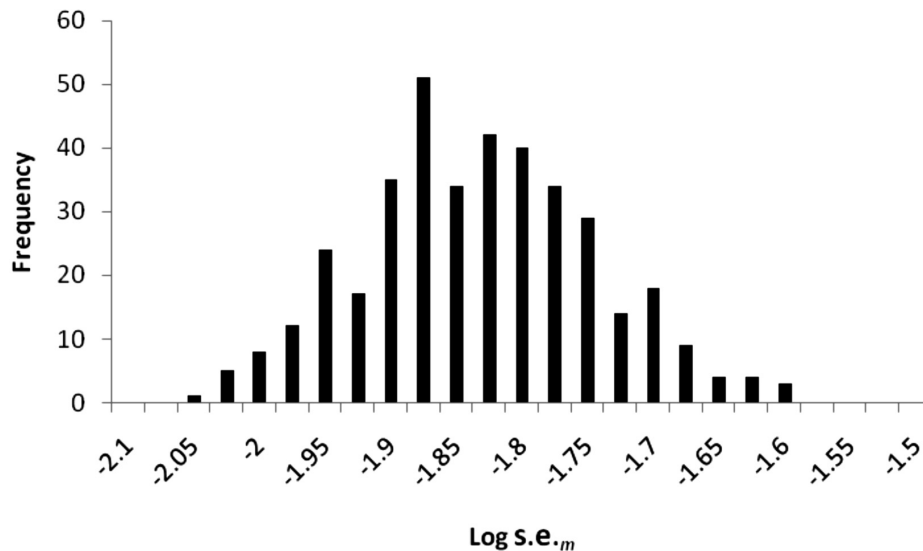


Figure 1. Normal distribution of log s.e._m values obtained from pair-wise comparisons of *Homo sapiens* crania in the Dart Collection. The mean log-transformed s.e._m value based on comparisons of conspecific pairs of *Homo sapiens* is -1.84 ± 0.09 ($n = 384$ comparisons).

are between two penecontemporary Early Pleistocene hominin specimens, KNM-ER 1813 (attributed to *H. habilis*) and KNM-3733 (attributed to *H. ergaster* or *H. erectus*), dated around 1.6 million years, from Koobi Fora (East Turkana) in Kenya (Wood, 1991).

RESULTS

Results obtained from pair-wise comparisons of crania of modern humans (Table 2) are presented in Fig. 1.

Table 2. Human specimens from the Dart Collection, School of Anatomical Sciences, University of the Witwatersrand. This list includes catalogue numbers, population affinities, age and sex.

| Catalogue number | Population affinity | Age | Sex |
|------------------|---------------------|-----|-----|
| 4011 | Tswana | 54 | m |
| 4069 | Tswana | 20 | f |
| 3955 | Zulu | 56 | m |
| 1532 | Ndebele | 69 | f |
| 1549 | Ndebele | 28 | f |
| 1274 | Ndebele | 39 | m |
| 1535 | Ndebele | 35 | m |
| 172 | Shangaan | 60 | m |
| 58 | Shangaan | 38 | m |
| 263 | Shangaan | 30 | f |
| 3057 | Shangaan | 30 | f |
| 2492 | Sotho | 21 | f |
| 2307 | Sotho | 60 | f |
| 2248 | Sotho | 48 | m |
| 2077 | Sotho | 48 | m |
| 1360 | Swazi | 19 | f |
| 1534 | Swazi | 24 | f |
| 2014 | Swazi | 42 | m |
| 1362 | Swazi | 49 | m |
| 1333 | Xhosa | 48 | m |
| 400 | Xhosa | 36 | m |
| 22 | Xhosa | 30 | f |
| 761 | Xhosa | 37 | f |
| 4035 | African | 22 | f |
| 2179 | Caucasian | 19 | f |
| 3902 | Caucasian | 40 | m |
| 3129 | Caucasian | 29 | f |
| 2186 | Caucasian | 57 | m |
| 3545 | Caucasian | 40 | m |

COMPARISON BETWEEN FOSSIL CRANIA

A log s.e._m value of -1.84 has been obtained from a comparison of two early Pleistocene hominid crania, KNM-ER 1813 (attributed to *H. habilis*) and KNM-ER 3733 (attributed to *H. ergaster* or *H. erectus*).

DISCUSSION AND CONCLUSION

The results of this study show that the log s.e._m values obtained from 384 pairwise comparisons of human crania display a normal distribution, similar to results obtained from previous studies of both vertebrates and invertebrates (Thackeray *et al.* 1997; Thackeray 2007). The mean log s.e._m value of -1.84 ± 0.09 obtained from the human crania provides a frame of reference for assessing Early Pleistocene hominids.

Thackeray *et al.* (1997) compared conspecific specimens of extant vertebrates including mammals such as primates, rodents and ungulates; birds; reptiles; and invertebrates (Coleoptera and Lepidoptera). In a preliminary study the mean log-transformed s.e._m value calculated by Thackeray *et al.* (1997) from comparisons of measurements of conspecific pairs of vertebrates and invertebrates was -1.78 ± 0.27 for 1260 specimens (70 extant species). Extending this approach Thackeray (2007) provided a statistical definition of a species, taking advantage of a substantially larger sample of vertebrates. Using that enlarged sample Thackeray (2007) calculated a mean log s.e._m of -1.61 ± 0.23 ($n = 1424$ specimens), which is not significantly different from the mean value obtained from the initial study.

The result of -1.84 obtained from *Homo sapiens* crania in this study is lower than the mean log s.e._m value of -1.78 (Thackeray *et al.* 1997) and -1.61 (Thackeray, 2007) obtained for large samples of a diversity of vertebrates and invertebrates.

Despite differences in size, KNM-ER 1813 and KNM-ER 3733 are examples of early Pleistocene hominid fossils which are associated with a high degree of similarity. The log s.e._m value of -1.84 obtained from the comparison of these two specimens is identical to the mean log s.e._m.

value of -1.84 obtained for pairwise comparisons of modern *Homo sapiens*. The implication is that there is a high probability that KNM-ER 1813 and KNM-ER 3733 are conspecifics, despite the fact that they have previously been attributed to different species of *Homo* (*H. habilis* and *H. erectus/ergaster*). This serves as one example demonstrating the applicability of a morphometric approach to assess probabilities of conspecificity in fossil hominids.

Thackeray (2005) has previously suggested that KNM-ER 1813 is a small female of a species also represented by KNM-ER-3733, considered to be a large male. Both are dated to about 1.6 million years before present (BP).

We are grateful to the NRF, the University of the Witwatersrand, the Andrew Mellon Foundation, and the French Embassy in South Africa for financial support.

We thank Brendon Billings for access to material in the Dart Collection. We also thank Alan Morris and an anonymous referee for helpful comments.

REFERENCES

- THACKERAY, J.F. 2005. Probabilities of conspecificity: an application of a morphometric approach to extant and extinct hominoids. In: Štrkalj, G., Pather, N. & Kramer, B. (eds), *Voyages in Science. Essays by South African Anatomists in Honour of Phillip V. Tobias's 80th Birthday*, 85–97. Pretoria, Content Solutions.
- THACKERAY, J.F., 2007. Approximation of a biological species constant? *South African Journal of Science* **103**, 489.
- THACKERAY, J.F., BELLAMY, C.L., BELLARS, D., BRONNER, G., CHIMIMBA, C., FOURIE, H., KEMP, A., KRUGER M., PLUG, I., PRINSLOO, S., TOMS, R., VAN ZYL, A.J., & WHITING, M.J. 1997. Probabilities of conspecificity: application of a morphometric technique to modern taxa and fossil specimens attributed to *Australopithecus* and *Homo*. *South African Journal of Science* **93**: 195–196.
- WOOD, B. 1991. *Koobi Fora Research Project*, Vol. 4. *Hominid Cranial remains*. Oxford, Clarendon Press.

Palaeontological Society of Southern Africa

16th Biennial Conference, University of Cape Town

5–8 September 2012

(An index to authors is given on page 58)

Basal therocephalian from the Middle Permian of South Africa: taxonomy and geographic and temporal distribution

Abdala, Fernando; Day, Michael; Rubidge, Bruce

Bernard Price Institute for Palaeontological Research, Palaeosciences Centre, University of the Witwatersrand, East Campus, Private Bag 3, WITS 2050, Johannesburg, South Africa
nestor.abdala@wits.ac.za

Important changes in amniote taxonomic representation occurred during the Middle Permian, the most significant being an explosive emergence of therapsids. The Middle Permian tetrapod record of the South African Karoo Supergroup has the oldest advanced theriodonts, including gorgonopsians and therocephalians. The oldest therocephalians are the largest members of this lineage and clearly were top predators in the Middle Permian. Two main basal therocephalian families are present at this age and can readily be distinguished by snout proportions: Scylacosauridae with a long and comparatively narrow snout, and Lycosuchidae with a short and broad snout. New findings of representatives of these two groups of basal therocephalians in the Karoo Basin prompted a revision of the taxonomy, and geographic and temporal distribution in the Karoo Basin. In the *Eodicynodon* Assemblage Zone (AZ), the lowermost biozone of the Beaufort Group, they are represented by two scylacosaurid taxa. The overlying *Tapinocephalus* AZ, by far the thickest vertebrate biozone of the Group, shows a great increase in diversity and abundance of basal therocephalians. Thus from only two specimens represented in the *Eodicynodon* AZ, more than 100 specimens are known from the *Tapinocephalus* AZ. The last record of basal therocephalians is represented in the *Pristerognathus* AZ in which the diversity and abundance is clearly diminished. Lycosuchids are generally considered in phylogenetic analyses as the most basal therocephalians; however, their fossil records (apart from three uncertain localities) are restricted to the upper *Tapinocephalus* and the overlying *Pristerognathus* Assemblage Zones. The most advanced scylacosaurids are known from the basal *Eodicynodon* AZ until the *Pristerognathus* AZ. This revision will allow exploration of the actual extension of the first important diversification of therocephalians, and will provide a better knowledge of the distribution, temporal and geographic, of these early representatives of therocephalians in the Karoo Basin.

Ontogeny of the Early Triassic *Thrinaxodon liorhinus* (Therapsida, Cynodontia): dental morphology and replacement

Abdala, Fernando¹; Jasinowski, Sandra²; Fernandez, Vincent¹

¹ Bernard Price Institute for Palaeontological Research, Palaeosciences Centre, University of the Witwatersrand, East Campus, Private Bag 3, WITS 2050, Johannesburg, South Africa
nestor.abdala@wits.ac.za

² Vancouver, British Columbia, Canada. Former postdoctoral fellow in the Zoology Department, University of Cape Town, Rondebosch, South Africa
sandra_jas@hotmail.com

We present a detailed study on variation of the dental morphology and replacement in the Early Triassic cynodont *Thrinaxodon liorhinus*. For this study we analysed five specimens ranging from 37–87 mm in skull length using micro computed tomography (microCT) scanning techniques, which were supplemented by detailed anatomical analysis of 41 specimens with a basal skull length of 30–96 mm. Our results confirm the alternate replacement of the postcanines and the posterior migration of the postcanine series (including the loss without replacement of the anteriormost postcanines). Even when most of the observations point to a posterior-to-anterior replacement wave, the evidence is not clear-cut. Lower postcanines are more numerous and present a more complex morphology than the upper postcanines, even in the same individual; only the lower postcanines have more than three sectorial cusps and a cingular collar on the lingual margin. Complexity of the postcanines increases from the smallest individual to specimens of 75 mm of skull length, but complexity decreases in larger specimens. The virtual extraction of functional and replacement teeth permitted us to conclude that in most of the cases, the upper canines were replaced anteriorly while lower canines were replaced posteriorly. The presence of two simultaneous replacements of the upper canine tooth was observed in two small juveniles, suggesting a higher rate of canine replacement at younger age. Incisors also had a sequential replacement pattern, and more replacement teeth were present in medium-sized individuals.

New vertebrates from the Permian Pedra de Fogo Formation, Parnaíba Basin, northeastern Brazil

Angielczyk, Kenneth¹; Cisneros, Juan C.²; Mariscano, Claudia A.³; Richter, Martha⁴; Fröbisch, Jörg⁵; Kammerer, Christian F.⁵; Smith, Roger M.H.⁶; da Conceição, Domingas, M.²; de Castro Silva, Mayana²

¹ Field Museum of Natural History, Chicago, U.S.A.
kangielczyk@fieldmuseum.org

² Universidade Federal do Piauí, Piauí, Brazil.
juan.cisneros@ufpi.edu.br / mayanacastro@hotmail.com

³ CONICET Universidad de Buenos Aires, Buenos Aires, Argentina
clamar@gl.fcen.uba.ar / domingasmayra@hotmail.com

⁴ Natural History Museum, London, United Kingdom
m.richter@nhm.ac.uk

⁵ Museum für Naturkunde, Humboldt-Universität zu Berlin, Berlin, Germany
joerg.froebisch@mfn-berlin.de / christian.kammerer@mfn-berlin.de

⁶ Iziko South African Museum, Cape Town, South Africa
rsmith@iziko.org.za

The Permian assemblage of the Pedra de Fogo Formation (PFF) includes petrified wood, fish, and a temnospondyl amphibian. The assemblage has received little attention, however, and its precise age is uncertain, with estimates spanning most of the Permian. In 2011 and 2012 we con-

ducted fieldwork in the Parnaíba Basin (Maranhão, Piauí and Tocantins states), to better understand the chronological and palaeoenvironmental contexts of the PFF fauna.

The PFF accumulated in a large shallow intra-continental depression, the Parnaíba Basin. Palaeoenvironments changed with progressive aridification and continentality, from a large shallow epeiric sea that supported a flourishing chondrichthyan community, to isolated continental water bodies between aeolian dune fields.

Fish are the most abundant vertebrate fossils. Chondrichthyes dominate in wavy-bedded sandstones and siltstones that accumulated towards the basin's depocentre. Ctenacanth, xenacanth, and other chondrichthyans include new taxa. The holocephalan (petalodont) *Itapyrodus puctatus* proved ubiquitous in the nearshore and evaporitic shoreline facies, where teeth of *Anisopleurodontis pricei*, a large, endemic, shark-like predator are also common. In Tocantins, we collected specimens of the shark *Glikmanius*, also known from the Lower Permian of the U.S.A. and the Carboniferous of Russia and Europe. Dipnoan fossils are relatively rare, but we tentatively recognize at least four distinct tooth plate morphologies. In more continental deposits in the upper PFF, we collected osteichthyans (lower actinopterygians and coelacanthiforms) with close affinities to Mesozoic taxa.

The putative archegosaurid *Prionosuchus* is the only tetrapod previously known from the PFF. We have additional amphibians from two areas, representing at least three new taxa. Specimens from the eastern edge of the basin show some affinities with tupilakosaurids, whereas those from the more central part of the basin may represent brachyopids and rhitidosteids, all best known from the Triassic. During the Permian the Parnaíba Basin was located in the equatorial regions of Pangaea, comparable to the Moradi Formation of Niger, which includes an anachronistic mixture of taxa that may have been common in central Pangaea. The PFF appears to include a mix of clades best known from the Early Permian and Mesozoic. The PFF has the potential to yield new insights into Permian biogeography and the end-Permian extinction and recovery.

Improved biostratigraphic correlations between Upper Permian rocks in the Karoo, Luangwa and Ruhuhu Basins: implications for biogeography and the end-Permian extinction

Angielczyk, Kenneth¹; Sidor, Christian²; Steyer, Jean-Sebastien³; Smith, Roger⁴

¹ Department of Geology, Field Museum of Natural History, Chicago, U.S.A.
kangielczyk@fieldmuseum.org

² Burke Museum and Department of Biology, University of Washington, Seattle, U.S.A.

³ Department Earth History, CNRS-Museum national d'Histoire naturelle Paris, France

⁴ Department of Karoo Palaeontology, Iziko South African Museum, Cape Town, South Africa

Upper Permian tetrapod fossils were discovered in the Karoo Basin in the mid-19th century, but similar faunal assemblages were only found in the Luangwa (Zambia) and the Ruhuhu (Tanzania) Basins in the early 20th century. The number of faunal assemblages present in the latter

basins and their correlation with the Karoo are uncertain, with two to three assemblages typically recognized in the Usili (formerly Kawinga) Formation of Tanzania and up to four in the Upper Madumabisa Mudstone of Zambia. A variety of correlations with the Karoo have been proposed, with both basins potentially preserving time equivalents of the *Pristerognathus* to *Dicynodon* Assemblage Zones. Taxonomic confusion surrounding key groups, such as dicynodont therapsids, has hampered the development of more refined correlations.

Since 2007 we have worked in the Luangwa and Ruhuhu Basins. These data, combined with those from earlier collections and recent taxonomic revisions, provide new insights into these Upper Permian faunas. Co-occurrence of species indicates that the Usili Formation and the Upper Madumabisa Mudstone each host a single Permian assemblage, although their preservation varies; e.g. specimens from the basal conglomerate unit of the Usili Formation tend to be fragmentary and encrusted with a thin hematite rind, whereas those higher in the section are more complete. A Middle Permian-age fauna is also present in the Ruhuhu Basin Ruhuhu Formation.

Stratigraphically long-ranging taxa like *Dicynodontoides* or *Pristerodon* are present in the Upper Madumabisa Mudstone and the Usili Formation, but the occurrence of more restricted taxa such as *Odontocylops* and *Kitching-anomodon* in the Luangwa Basin strongly suggests a correlation between the *Cistecephalus* Assemblage Zone of the Karoo and the Madumabisa assemblage. *Dicynodon huenei* and *Katumbia* in both basins suggests that the Usili assemblage also correlates with the *Cistecephalus* Zone.

Revised faunal lists for the *Cistecephalus* Zone, the Upper Madumabisa Mudstone, and the Usili Formation show that each has similar proportions of endemic species. The Madumabisa fauna, however, is more similar to that *Cistecephalus* Zone than to the Usili Formation, indicating that geographic proximity was not the sole factor controlling distribution of these tetrapods. Ecological structure and taxonomic composition, with therapsids numerically and taxonomically dominant, are shared. This diversity contrasts strongly with the early Middle Triassic assemblages from the same basins, suggesting that disruptions associated with the end-Permian extinction caused divergent recoveries.

Cretaceous and Tertiary gymnosperm and angiosperm woods from southern Africa

Bamford, Marion

BPI Palaeontology, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS 2050, South Africa
marion.bamford@wits.ac.za

The Cretaceous and Tertiary fossil wood record for southern Africa is not extensive but there is a variety of taxa from sites widely distributed over the southern part of the continent. Early Cretaceous woods are preserved onshore and offshore along the west coast, and onshore along the east coast. These include woods of the Araucariaceae, Cheirolepidiaceae and Podocarpaceae, the latter of which there are at least five species. Late Early and early Late Cretaceous woods from the east coast

include a variety of Podocarpaceae woods as well as tree ferns of *Osmundacaulis* species. This diversity of ferns extends into the Late Cretaceous and the gymnosperm taxa, although still of the Podocarpaceae, are mostly different species from the older taxa. The most common Upper Cretaceous species is *Podocarpoxydon umzambense* Schultze-Motel and it was widespread in southern Africa. Some of these specimens have indistinct growth rings and others have clear rings but variable in width. The climatic implications are explored further. From the Upper Cretaceous Umzamba beds (southern coast) there are fossil logs of angiosperms: Monimiaceae and Euphorbiaceae. Gymnosperm woods of the Araucariaceae and Podocarpaceae are also abundant from this locality. Tertiary woods are predominantly angiospermous. There is only one known Eocene locality and it has a mix of woods with well-defined family affiliations and some indeterminate woods. Oligocene woods are very rare but there are abundant Miocene sites with wood and faunal remains. The common families in the fossil record are still common today and include Anacardiaceae, Burseraceae, Combretaceae, Dipterocarpaceae, Fabaceae, Myrtaceae and Oleaceae. These wood specimens do not have clear growth rings but their taxonomic affinities and wood structure, such as size and density of vessel members, can be used to infer local climate. There are no silicified gymnosperm woods from the Miocene but new records from the Cape region show the continued presence of carbonized Podocarpaceae. Today the only indigenous conifers in southern Africa are four species of Podocarpaceae and one of Cupressaceae.

A Cenozoic foraminiferal record and its associated palaeoenvironmental conditions from the Namibian outer shelf

Bergh, Eugene^{1,2}

¹ Department of Geological Sciences, University of Cape Town

² Natural History Department, Iziko South African Museum, Cape Town. ebergh@iziko.org.za

The Benguela Current is one of four major eastern boundary current regions worldwide where coastal upwelling dominates. The cold Benguela Current has a marked influence on the Namibian shelf and micro-faunal distributions. Depocentres may have shifted between the inner and outer shelf over geologic time as attested by foraminiferal assemblages. Cenozoic-aged sediments from the Namibian phosphogenic belt between Lüderitz and Walvis Bay on the outer shelf revealed three distinctive foraminiferal assemblages suggesting three geological ages (Miocene, Pliocene and Holocene) and the absence of the Pleistocene record. Sixteen 1.8 m long cores, from a depth of 199 to 309 m exhibit a coarsening-upward sequence with an increase of foraminiferal abundance in the Holocene-aged units. The lower units of the cores revealed the occurrence of the extinct families Stilostomellidae and Nodosariidae suggesting an age of Miocene to Pliocene sedimentation. *Uvigerina* sp. together with *Nodogenerina* sp. and *Stilostomella* sp. suggest Pliocene sedimentation. Complete mollusc shells *Dosinia lupinus* and *Lucinoma capensis*

confirm a Holocene age for the upper core units correlating with the dominant foraminiferal species *Ammonia japonica* and *Elphidium advenum*. The biostratigraphic ages can further be constrained with Sr-isotope data. The microfossil and mollusc occurrences indicate that bottom-water conditions had variable oxygen content throughout geologic time. Benthic foraminifera display an inverse correlation with pelletal phosphorite components. The micropalaeontology of the cores suggests a heterogeneous Namibian outer shelf with variable sedimentation and erosional rates.

Osteohistology of Triassic archosauromorphs in South Africa

Botha-Brink, Jennifer¹; Smith, Roger²

¹ Karoo Palaeontology, National Museum, P. O. Box 266, Bloemfontein, 9300 South Africa
jbotha@nasmus.co.za

² Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa

The archosauromorphs of the South African Karoo Basin formed important constituents of the Early to Middle Triassic ecosystems following the end-Permian mass extinction event. We present data on the osteohistology of the stem archosaurs *Prolacerta*, *Proterosuchus*, *Erythrosuchus*, *Garjania* and *Euparkeria*. Results reveal that the Early Triassic non-archosauriform archosauromorph *Prolacerta* exhibits a poorly defined fibro-lamellar complex, with parallel-fibred bone in some regions. The contemporaneous *Proterosuchus* exhibits rapidly forming uninterrupted fibro-lamellar bone early in ontogeny, which becomes slow and cyclical with increasing age. The early Middle Triassic erythrosuchid *Garjania* deposited highly vascularized fibro-lamellar bone interrupted by annuli, whereas the Middle Triassic *Erythrosuchus* exhibited highly vascularized, uninterrupted fibro-lamellar bone throughout ontogeny. In contrast, the growth of the Middle Triassic *Euparkeria* was relatively slow and cyclical throughout ontogeny. When our data are combined with those of previous studies, preliminary results reveal that Early and Middle Triassic non-crown group archosauromorphs generally exhibit faster growth rates than many of those of the Late Triassic. Early rapid growth and rapid attainment of sexual maturity are consistent with life history predictions for taxa living in the unpredictable conditions following the end-Permian mass extinction. Further research with larger sample sizes will be required to determine the nature of the environmental pressures on these basal archosaurs.

Palaeobiology of the Lower Triassic stereospondyl *Lydekkerina* (Tetrapoda: Temnospondyli) inferred from long bone histology and microanatomy

Canoville, Aurore; Chinsamy-Turan, Anusuya

Department of Zoology, University of Cape Town, Rondebosch, Cape Town
canoville.aurore08@gmail.com

Long bone microstructure (histology and microanatomy) provides insight to assess various aspects of tetrapod palaeobiology, such as ontogeny, growth patterns, and lifestyle. Histology has been extensively applied to the diverse and abundant non-mammalian therapsids from the exceptional vertebrate fossil-bearing sequence of the

Karoo Basin (South Africa), but few studies have been conducted on amphibians, which were fairly abundant in the Permo-Triassic terrestrial ecosystems.

Lydekkerina huxleyi, a basal and paedomorphic stereospondyl dominated the amphibian fauna from the Lower Triassic *Lystrosaurus* assemblage Zone. Even though the anatomy of this taxon has been well described, it remains enigmatic in term of its growth strategies and lifestyle habits.

Earlier studies based on anatomical and taphonomical data suggested that the unusually small size of this genus, compared to its Permo-Triassic relatives could be linked to a fast, but shortened development to maintain large and successful breeding populations under difficult environmental conditions and may explain the success of these animals after the end Permian extinction event. Moreover, *Lydekkerina* has alternatively been described as aquatic and mostly terrestrial – a controversial hypothesis, since Triassic stereospondyls are generally considered to be predominantly aquatic or semi-aquatic.

In order to document growth patterns and palaeoecological adaptations of this taxon, our study examined various long bones (humerus, radius, femur, tibia, rib) of several specimens of different ontogenetic stages.

Our results show that during early ontogeny, *Lydekkerina* had a rapid rate of growth, which slowed down during later development. The microanatomy of the long bones with their thick bone walls and distinctive vacant medullary cavity suggests that *Lydekkerina* may have been amphibious with a tendency to be more terrestrial.

Was *Thrinaxodon liorhinus* a digger?

**Carlson, Kristian¹; Fernandez, Vincent²;
Abdala, Fernando²; Rubidge, Bruce²; Tafforeau, Paul³**

¹ Institute for Human Evolution, University of the Witwatersrand, Johannesburg, South Africa
kristian.carlson@wits.ac.za

² Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa

³ European Synchrotron Radiation Facility, 6 Rue Horowitz Bp 220, 38046 Grenoble Cedex, France

Attributing fossorial behaviour to the mammal-like cynodont *Thrinaxodon liorhinus* has traditionally drawn from indirect behavioural evidence. *Thrinaxodon* specimens have been found inside ichnofossils (i.e. burrow casts) (Damiani *et al.* 2003) and often fossilize exhibiting curled-up postures. At stake is whether these distant ancestors of mammals may have survived harsh climates during the mass extinction event at the Permian-Triassic boundary, approximately 251 million years ago, because of their proficiency in creating burrows. Alternatively, *Thrinaxodon* may have utilized previously constructed burrows, but done so secondarily because they were incapable of creating new ones, leading to a very different reconstruction of *Thrinaxodon* activity patterns and life history. Recent recovery of a complete *Thrinaxodon* skeleton inside a burrow cast (Fernandez *et al.* 2012), plus a second relatively complete *Thrinaxodon* skeleton (Damiani *et al.* 2003), provide two sets of associated postcrania for analysis. Using synchrotron scanning from the European Synchrotron Radiation Facility (Grenoble,

France), virtual renderings of postcranial elements were produced. Structural comparisons between *Thrinaxodon* and extant wombats (Genera *Vombatus* and *Lasiiorhinus*) were performed to identify potential fossorial adaptations in limbs of the former. Wombats are well-known fossorial animals roughly equivalent in body size to *Thrinaxodon*. Such comparisons permit assessment of direct structural evidence for fossorial adaptations in *Thrinaxodon liorhinus*, or determine whether their digging ability has been inaccurately attributed because of guilt by association.

Damiani R, Modesto S, Yates A. & Neveling J. 2003. Earliest evidence of cynodont burrowing. *Proceedings of the Royal Society of London B* **270**, 1747–1751.

Fernandez, V., Abdala, F., Carlson, K.J., Collins Cook, D., Rubidge, B., Yates, A. & Tafforeau, P. 2012. Synchrotron radiation sheds light on mammal forerunners entombed in their burrow. *Palaeontologia africana* **47**: 35.

Bone microstructure of polar and temperate *Edmontosaurus*

**Chinsamy, Anusuya¹; Thomas, Daniel B.¹;
Tumarkin-Deratzian, Allison R.²; Fiorillo, Anthony R.³**

¹ University of Cape Town, Zoology Department, Rondebosch, South Africa
anusuya.chinsamy-turan@uct.ac.za

² Dallas Museum of Natural History, Dallas, TX 75315, U.S.A.

³ Temple University, Department of Earth and Environmental Science, Philadelphia, Pennsylvania 19122, U.S.A.
tfiorillo@natureandscience.org / altd@temple.edu

Dinosaurs have a worldwide distribution, and appear to have inhabited a range of latitudinal zones, including high latitudinal localities that were well within the Arctic and Antarctic regions, i.e. areas today known to have dramatic changes in temperature and light during the course of a single year. The Upper Cretaceous Prince Creek Formation of the North Slope of Alaska is one of the richest high latitudinal dinosaur-bearing deposits. Skeletal material and track assemblages of a wide diversity of nonavian dinosaurs (e.g. large and small bodied theropods, ceratopsians, pachycephalosaurs, hypsilophodontids, and hadrosaurs) have been recovered from this locality. One of the major questions is whether these high-latitude dinosaurs overwintered or migrated during the winters.

Since it is well documented that various aspects of the biology and life history of extinct vertebrates is recorded in the microstructure of their fossilized bones, we compared the long bone histology of *Edmontosaurus* from the Prince Creek Formation (69.5 ± 1.5 Ma) with that of *Edmontosaurus* from the more temperate, Horseshoe Canyon Formation (70.0 ± 3.0 Ma) of Canada. Our sample comprised seven femora, four humeri and two tibiae from the polar *Edmontosaurus*, and three femora and one tibia from temperate *Edmontosaurus*.

We found that the bone microstructure of the polar *Edmontosaurus* exhibited highly vascularized, fibro-lamellar bone with periodic changes in channel organization i.e. from a reticular oriented 'vascularization' to a more circumferential orientation. In contrast, such alternating changes in the vascularization were not consistently observed in the bones of *Edmontosaurus* from the more temperate Canadian locality.

The differences observed in the microstructure of *Edmontosaurus* from the high and low latitude localities,

suggests that they grew differently. From the type of bone microstructure evident, we deduce that polar *Edmontosaurus* endured the long winter night, while temperate *Edmontosaurus* lived in a perennially moderate environment. Thus, we propose that the regular alternating vascularization pattern observed in the polar dinosaurs is an overwintering signal in response to an annual change in the prevailing environmental conditions.

A new pareiasaur reptile from the *Tapinocephalus* Assemblage Zone, middle Permian of the Karoo

Cisneros, Juan Carlos¹; Rubidge, Bruce²

¹ Centro de Ciências da Natureza, Universidade Federal do Piauí, Teresina, Brazil
juan.cisneros@ufpi.edu.br

² Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa
bruce.rubidge@wits.ac.za

Pareiasaurs are large, heavily-built members of the Parareptilia, that had a global distribution and constituted important components of the herbivore niche in terrestrial faunas during middle to late Permian times. We report a new pareiasaur species from the middle Permian of South Africa. The fossil was found in the Prince Albert District, Western Cape, in the Abrahamskalk Formation, upper *Tapinocephalus* Assemblage Zone (AZ). The specimen consists of a fragmentary cranium with mandible in occlusion, and an articulated postcranium including most of the vertebral column, ribs, pectoral and pelvic girdles, and some long bones. Despite being very damaged, the skull of the new specimen has a well-preserved marginal dentition that allows direct comparisons with most pareiasaurs known in the Karoo and elsewhere. The new fossil is easily distinguished from other pareiasaurs by having only five cusps on each upper marginal tooth, being the lowest number of dental cusps in any known species of pareiasaur. Other pareiasaurs have upper tooth cusp numbers ranging from seven (*Bradysaurus* spp. and *Nochelesaurus alexanderi*) to fifteen (*Anthodon serrarius*). Another notable feature in the teeth of the new specimen is their shape, having three closely spaced cusps – second, third and fourth – that rise well beyond the level of the first and fifth cusp, providing altogether a rather elongated outline to each marginal tooth that contrasts with a wider outline in the teeth of most pareiasaur species. These characteristics allow us to recognize a new species of pareiasaur in the *Tapinocephalus* AZ. The extreme low number of dental cusps present on this pareiasaur is reminiscent of the condition in the nycteroleters, a group of parareptiles that is well represented in the Middle Permian of the Russian Platform, which is considered to constitute the sister group of the Pareiasauria. In most nycteroleters the marginal teeth are thin, elongated and monocuspid, and in the genera *Bashkyroleter* and *Riphaeosaurus*, three cusps are present. The teeth of the new pareiasaur, thus, constitute an intermediary condition between the elongated, mono- or tri-cuspid teeth of the nycteroleters and the wide teeth, with several cusps, present in all other pareiasaurs. In this way, the teeth of the new pareiasaur fill a gap in tooth evolution towards herbivory in the Nycteroleter-Pareiasaur clade of the Parareptilia.

Actualistic investigation of bone modification by caracal (*Caracal caracal*) and honey badger (*Mellivora capensis*) on domestic rabbit carcasses

Cohen, Brigitte; Kibii, Job

Institute for Human Evolution, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa.
jet-cohen@hotmail.com / job.kibii@wits.ac.za

The involvement of carnivores and birds of prey in bone accumulation in archaeological and palaeontological fossil assemblages has often been inferred through diagnostic bone modification. The bulk of actualistic and field work investigation, has concentrated on assessing the nature of bone modifications by large carnivores on large bodied mammals, much to the neglect of smaller predators and prey. This study investigated the nature of bone modification of mesomammal (Ieporid) carcasses by captive small carnivores including the caracal (*Caracal caracal*) and the hitherto taphonomically undocumented honey badger (*Mellivora capensis*). Domestic rabbit carcasses were fed to the two captive carnivore species at the Johannesburg Zoo. Scatological remains were collected, the bones removed, cleaned and taphonomically assessed. Preliminary analysis indicates that the honey badger is highly destructive of rabbit remains. A total of 392 identifiable bone fragments were recovered from the honey badger scats, representing only 16% of the recovered bones. Average bone length was 10.3 mm and the maximum length recovered was 28.1 mm. The assemblage was made up primarily of vertebral fragments, particularly from the lumbar region, and rib fragments. Cranial and femoral remains are also high as were phalanges. There was a total of 237 tooth marks in the assemblage, the majority made up of crush marks and scours. The majority of bones showed evidence of digestive damage. A template deriving from actualistic investigation is crucial in the assessment of fossil assemblages, particularly in determining taphonomic agents and processes involved in the accumulation of mesomammals in fossil assemblages.

Corked! The history and importance of humanities' favourite beverage

Cohen, Brigitte; Val, Aurore

Institute for Human Evolution, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa
jet-cohen@hotmail.com / aurore_val@yahoo.com

It was common practice 20 years ago for archaeologists to clean out the sediments contained in any recovered containers or jars and to analyse only the potsherds themselves. However, recent research by such experts as Patrick McGovern has shown the importance in preserving and analysing the surrounding sediments, a principle that has also been successfully applied to palaeontological excavations. Today it has become just as important, if not superior, to analyse residues found within jars and containers. Indeed the contents of sealed containers can last surprising lengths of time under the right conditions; in 2011 soup was recovered from 2000-year old bronze and clay containers in China (Hilgers 2012). Thus this research in conjunction with ancient engravings and texts gave rise to the field of 'dipsology'. Chemical analysis of potsherds

has revealed the oldest beers, wines and grogs (Finally a use for them!). Not only that but independent brewers have got on the experimental archaeology bandwagon attempting to recreate such forgotten masterpieces (gee and I thought archaeologists were nerdy!). Dipsology provides us with more than just a peek into how our favorite beverage may have looked or tasted or even what it was made from. It provides an understanding of when domestic fermentation began and even indicates that it may have performed a fundamental role in the creation of the modern static civilization. What if this behaviour went back even further? Recent archaeological research in South Africa has been pushing back the boundaries of earliest modern human behaviour with the recovery of etchings, jewellery and even paint containers. Perhaps one of the most important modern human behaviours also began in Africa.

Hilgers, L. 2012. Ancient Chinese takeout. *Archaeology Magazine*, January/February.

Middle Permian biodiversity in the Karoo: a biostratigraphic review of the *Tapinocephalus* Assemblage Zone

Day, Mike; Rubidge, Bruce; Güven, Saniye

Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa
 michael.day@students.wits.ac.za / bruce.rubidge@wits.ac.za / saniye.guven@students.wits.ac.za

The Beaufort Group of South Africa contains one of the most complete Permo-Triassic tetrapod fossil records in the world. Its lower strata are of late Middle Permian age, comprising up to 2700 m of sediment at its thickest point along the Cape Fold Belt. These sediments fall within three faunal assemblage zones of which the second, the *Tapinocephalus* Zone, is stratigraphically the thickest and has the highest diversity of fossil genera (Rubidge 1995). In addition, the fauna in the *Tapinocephalus* Zone is dominated by the Dinocephalia, a group which was highly successful towards the end of this stage but which became extinct before the beginning of the Late Permian. A link between the disappearance of the Dinocephalia and a marine extinction in China has already been proposed (Retallack *et al.* 2006), but there is no direct evidence to support this. An understanding of the *Tapinocephalus* Zone is therefore crucial to understanding Middle Permian tetrapod diversity, while the transition into the succeeding *Pristerognathus* Zone provides the opportunity to study the extinction of the Dinocephalia.

The outcrop area of the *Tapinocephalus* Zone extends from the Eastern Cape near East London, west to Laingsburg in the Western Cape and northwest to Victoria West in the Northern Cape Province. Over such a wide area, the stratigraphy varies laterally as well as thinning rapidly towards the north. The strata in the south are also heavily folded and together these have made it difficult to conduct accurate biostratigraphic studies. Utilization of the Beaufort Vertebrate Database housed at the BPI combined with satellite imagery, extensive fieldwork and stratigraphic collecting conducted over many years, has enabled examination of the the *Tapinocephalus* Zone at a far higher biostratigraphic resolution. Stratigraphic

ranges of vertebrate taxa are more distinct from each other than is currently understood with the ranges of most genera restricted to the upper part of the zone. Dinocephalians also extend higher in the stratigraphic succession than previously documented.

Retallack, G.J., Metzger C.A. *et al.* 2006. Middle-Late Permian mass extinction on land. *Geological Society of America Bulletin* 118(11-12), 1398–1411.

Rubidge, B.S. (ed.) 1995. Biostratigraphy of the Beaufort Group (Karoo Supergroup). South African Committee for Stratigraphy Biostratigraphic Series.

Early diagenesis in Late Jurassic sauropod teeth revealed by transmission electron microscopy

Dumont, Maitena¹; Kostka, Aleksander¹; Tütken, Thomas²

¹ Abteilung für Werkstoffdiagnostik und Technologie der Stähle, Max-Planck-Institut für Eisenforschung, Düsseldorf, Germany
 m.dumont@mpie.de

² Steinmann Institute of Geology, Mineralogy and Palaeontology, University of Bonn, Germany

The stable isotope compositions ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$, ^{13}C - ^{18}O) of dinosaur tooth enamel is widely used to study the diet, thermophysiology and paleoenvironment of the dinosaurs. It is then important to determine if original isotope compositions are still preserved in the fossil teeth and to understand possible geochemical and mineralogical modifications during the fossilization process. For this purpose the microstructure of dental tissues of teeth from large Jurassic sauropods such as *Branchiosaurus brancai* from the Tendaguru beds in Tanzania (Africa) and *Camarasaurus* sp. from the Morrison Formation (U.S.A.) were investigated using transmission electron microscopy (TEM). Recently, clumped isotope thermometry of the enamel bioapatite from the same teeth determined physiologically plausible, mammalian-like body temperatures for the sauropods that suggest good preservation of these teeth and their stable isotope compositions (Eagle *et al.* 2011).

Our TEM results show different stages of diagenetic alteration between the investigated tooth samples. The Tendaguru teeth are well preserved compared to the Morrison material, confirming previous conclusions drawn by stable and clumped isotope compositions (Eagle *et al.* 2011).

Furthermore, enamel is generally less altered by diagenesis than the dentine of the same teeth. Indeed, the crystal size in the enamel does not change drastically between altered and well-preserved tooth areas, whereas an increase of the dentine crystals in size and in their width/thickness is observed. TEM results coupled with EDX (energy dispersive X-ray) analysis of the chemical composition and diffraction pattern allow us to discern precisely changes in the apatite crystal structure during diagenesis. Secondary mineral infillings, when present in the dentine tubuli, are also analysed and identified precisely by indexing their diffraction patterns.

This approach enables to characterize the history of the diagenetic alteration in teeth of different taphonomic settings.

Eagle, R.A., Tütken, T., Martin, T.S., Tripathi, A.K., Fricke, H.C., Connely, M., Cifelli, R.L. & Eilen, J.M. 2011. Dinosaur body temperatures determined from isotopic (^{13}C - ^{18}O) ordering in fossil biominerals. *Science* 333(6041), 443–445.

The impact of mining on the Cradle of humankind World Heritage Site

Durand, Francois

Department of Zoology, University of Johannesburg
fdurand@uj.ac.za

South Africa has an exceptional cultural and natural heritage; the largest astrobleme in the world, the largest layered igneous intrusion in the world containing some of the richest ore deposits in the world, the largest gold repository in the world, some of the oldest fossils in the world, the largest terrestrial Permo-Triassic sequence in the world containing the most synapsids and some of the oldest dinosaurs in the world, the most hominin fossils, spanning the largest part of human prehistory, in the world and an unparalleled diversity of fauna and flora. This geological, palaeontological, archaeological and ecological wealth has spawned two industries – mining and tourism which are in conflict with each other. Conservation of our natural and cultural resources is threatened by short-term opportunism and mismanagement. It is proposed that this conflict arises from the fact that the connections between the geological, ecological and cultural wealth are not appreciated nor understood. In the recent past the threat of acid mine drainage (AMD) from the mine void adjacent to the Cradle of Humankind World Heritage Site (COHWHS) was ignored. The influx of megalitres of AMD into the COHWHS in 2011 served as a wakeup call to everybody. The climate change led to higher rainfall in the region which resulted in the elevation of the water table and an increase in the efflux of AMD from the mine void on the West Rand. This can be seen in the rise of the level of the 'underground lake' in Sterkfontein Caves and the Rietspruit which has turned into a perennial river carrying AMD at a pH below 3. The Rietspruit is a tributary of the Bloubaan which flows through the southern part of the COHWHS past several palaeontological sites. The groundwater in the region is similarly affected as a plume of AMD is spreading from the mine void into the Swartkrans dolomitic compartment underlying the southern part of the COHWHS.

Synchrotron radiation sheds light on mammal forerunners entombed in their burrow

Fernandez, Vincent¹; Abdala, Fernando¹;
Carlson, Kristian J.²; Collins Cook, Della³;
Rubidge, Bruce¹; Yates, Adam¹; Tafforeau, Paul⁴

¹ Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, South Africa
vincent.fernandez@wits.ac.za / nestor.abdala@wits.ac.za /
bruce.rubidge@wits.ac.za / yatesam@gmail.com

² Institute for Human Evolution, University of the Witwatersrand, South Africa
kristian.carlson@wits.ac.za

³ Department of Anthropology, Indiana University, U.S.A.
cook@indiana.edu

⁴ European Synchrotron Radiation Facility, France
paul.tafforeau@esrf.fr

The Karoo Basin of southern Africa has provided numerous examples of vertebrate burrowing behaviours in strata spanning the Permo-Triassic boundary (PT, ~251 Myr). The use of underground shelters has been interpreted as evidence of their importance in providing a stable envi-

ronment that protected occupants against harsh conditions during the PT mass extinction event. During the last decade, several burrow casts with occupants have been discovered; some include aggregations of several individuals or even different species. A key observation was the fact that several of these specimens were therapsids, the very distant ancestors of mammals. Fifty per cent of modern mammals are capable of burrowing; this is viewed as an ancient behavioural trait that pre-conditioned burrower survival under the harsh environments and successive global Permo-Triassic extinctions.

A major limitation with such specimens is the fact that the fossils are enclosed in burrow casts and therefore invisible without preparation. However, classic preparation (physical or chemical removal of the surrounding rock) destroys all information about the sediment infill. Moreover, observations on prepared skeletal remains are often limited to a single side because it is necessary to leave intact matrix in order to maintain the integrity of specimens.

In the last few years, third generation synchrotron radiation-based X-ray microtomography (SR-CT) has provided new ways to increase the quality of data obtained from fossil specimens. Synchrotrons allow use of other methods that are thousands of times more sensitive and utilize phase-contrast effects, such as propagation phase contrast microtomography (PPC-SR- μ CT). While many synchrotron X-ray imaging beamlines are interested in developing narrow X-ray beams, the European Synchrotron Radiation Facility (ESRF) offers the possibility to scan large specimens and keeps improving the possibilities for non-destructive investigations of fossils.

Here we present results obtained using the large X-ray beam of the ID17 beamline of the ESRF on fossilized tetrapods preserved in burrow-casts from the Early Triassic of the Karoo Basin. Images produced by PPC-SR CT exhibit a high degree of contrast and accuracy. Whole burrows were imaged with a voxel size of 45 μ m, revealing every structure of the skeletons as well as fine structure of the sediment infill. The images and resultant rendering allow us to understand the thanatocoenose or death assemblage and observe information about the behaviour of mammal forerunners.

Distribution patterns of Devonian tetrapodomorphs revealed by study of pectoral girdle morphologies

Gess, Robert

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, South Africa
robg@imaginnet.co.za

Sarcopterygians include 'fish-like' sarcopterygians (lobe finned fishes) and tetrapods. Intermediate forms, loosely grouped as panderichthyids or elpistostegids, provide clues regarding arguably the most important transition in vertebrate evolution, that from finned fish to digit-bearing tetrapods. The most important morphological changes include those affecting the shoulder girdle, which permitted critical changes in paired appendage use.

The pectoral girdle of sarcopterygians includes an endoskeletal scapulocoracoid and a number of dermal elements, most importantly the cleithrum and clavicle. In 'fish-like' sarcopterygians these bones and other dermal shoulder girdle bones (which may include an anocleithrum, extracleithrum, supracleithrum and interclavicle) form a rigid dermal skeleton articulating with the skull. The scapulocoracoid is attached to the medial face of the cleithrum and sometimes also the clavicle. It has a posteriorly directed glenoid for articulation of the pectoral fin, which does not protrude far beyond the posterior margin of the dermal girdle.

Tristichoperid fish, the most derived 'fish-like' sarcopterygians, in terms of tetrapod evolution, include *Eusthenopteron*. The two halves of the dermal pectoral girdle of *Eusthenopteron* are linked by a thin interclavicle, on either side of which the girdle includes a clavicle, cleithrum, anocleithrum and supracleithrum. The cleithrum dominates the dermal girdle and is subrectangular and upright (in lateral view) with a ventromedial extension at the attachment point of the clavicle. The scapulocoracoid is attached to the medial wall of the ventrolateral angle of the cleithrum.

The cleithrum of the elpistostegids *Panderichthys* and *Tiktaalik* is more dorso-posteriorly angled and lacks a ventromedial extension. It is ventrolaterally reduced to allow extensive exposure of the scapulocoracoid. This is much larger than that of *Eusthenopteron*, has extensive contact with the clavicle and a more laterally orientated articulation for the pectoral appendage. Greater exposure of the scapulocoracoid permitted the fin not only to assume postures suitable for swimming but also for a substrate supported upright stance.

In *Acanthostega*, the best known early tetrapod (with digits), the pectoral girdle is detached from the back of the skull. The cleithrum is unornamented and far more reduced posteroventrally, further exposing the scapulocoracoid. In anterior view a distinct postbranchial lamina forms an anteromedially directed flange. A ridge extends posteroventrally from the cleithrum onto the scapulocoracoid.

Rapid morphological changes spanning the emergence of tetrapods give cleithra diagnostic value in the study of disarticulated Devonian sarcopterygians. More than one grade of 'advanced' sarcopterygian is thereby identified from the Late Devonian Waterloo Farm locality, with important implications for the range of environmental settings in which transitional forms occurred.

Palynofacies patterns of the Northern Witbank Basin (South Africa): clue to decipher Permian palaeoenvironmental and climate change

Götz, Annette E.¹; Ruckwied, Katrin²

¹ Department of Geology, Rhodes University, South Africa
a.gotz@ru.ac.za

² Shell International Exploration and Production B.V., the Netherlands

The Main Karoo Basin hosts an important coal resource of South Africa, the Witbank coal field, which comprises the basin's northeasternmost economic coal deposits.

These sediments are part of the Ecca Group and were deposited subsequent to the melting of the Dwyka ice. One of the most important coal seams of the Witbank Basin, the No. 2 coal seam, represents postglacial fluvio-deltaic deposits and here, we report on new palynological data from a highly proximal setting of the northern basin margin.

The sedimentary series includes coarse-grained to pebbly-sandstones, with an abrupt upward transition into fine-grained sediments and coal, through cross-stratified medium- to coarse-grained sandstones, and horizontally-laminated fine- to medium-grained sandstones and siltstones. The highly volatile bituminous coals are characterized by significant amounts of inertinite and low maturity, with a vitrinite reflectance ranging from 0.62% to 0.8%, and medium to high ash content, ranging between 7.8 wt% and 73.6 wt%. The sedimentary organic matter content clearly documents changes in the palynomorph assemblage and variations in the amount and the type, size and shape of plant debris. Generally, the palynofacies are characterized by high proportions of opaque phytoclasts. Amorphous organic matter is characteristic of laminated siltstones and coals. The palynological record indicates a cold climate fern wetland community characteristic of lowland alluvial plains with an upland conifer community in the lower part of the coal seam. In the upper section, these communities are replaced by a cool-temperate cycad-like lowland vegetation and gymnospermous upland flora.

Our data establish a base for further integrated palynological-palaeobotanical studies on terrestrial plant vegetation and its response to climate amelioration. The cyclic patterns recognized in the sedimentary series we studied will, furthermore, allow interpretation of palaeoenvironmental change at greater time resolution, which will lead to a better understanding of the timing of floral change.

Five million-year-old Cetacean population from Langebaanweg, west coast of South Africa

Govender, Romala¹; Chinsamy-Turan, Anusuya²

¹ Natural History Department, Iziko South African Museum, Cape Town
rgovender@iziko.org.za

² Department of Zoology, University of Cape Town, Rondebosch
anusuya.chinsamy-turan@uct.ac.za

Langebaanweg (LBW) is a world renowned and prolific African Tertiary fossil site. It records local Mio-Pliocene the fauna, flora and environment. Among this treasure trove of fossil vertebrates are the remains of marine mammals. Our improved understanding of the terrestrial vertebrate fauna and palaeoenvironment has highlighted a lack of knowledge of the marine context. We report here on the preliminary results of my analysis of the cetacean remains from LBW's 'E' Quarry.

The condition of the fossils ranges from fragmentary to well preserved; the latter, in particular, being bones of the petrotympanic region. Our study focusses on these bones as they are reasonably readily identified, at least to generic level. The ear bones are predominantly of mystecetes

and include balaenopterid and balaenid forms. Five million years ago a lagoon or estuarine system existed at Langebaanweg. Hypothetically the occurrence of cetacean remains appears to be the result of their larger size and 'floatability', which allowed carcasses to be beached; thereafter, storm surges refloated partially skeletonized carcasses, which further disintegrated and fragmented before being moved upstream where some came to rest in the channels or scour pools in which they were found.

Taxonomy of tapinocephalid Dinocephalia from the South African Karoo Basin

Güven, Saniye; Rubidge, Bruce; Abdala, Fernando

Bernard Price Institute for Palaeontological Research, Palaeosciences Centre, University of the Witwatersrand, South Africa
guven.saniye@gmail.com / bruce.rubidge@wits.ac.za / nestor.abdala@wits.ac.za

Tapinocephalids (Therapsida: Dinocephalia) are an important component of the Middle Permian terrestrial ecosystem. They are known from South Africa, Zimbabwe, Tanzania, Russia, and Brazil. South Africa contains by far the most abundant and morphologically varied fauna of this group which are the most important herbivorous component from the fauna of the *Tapinocephalus* Assemblage Zone. Recent studies indicate a large number of tapinocephalid genera compared to other herbivorous therapsids in any particular biozone of the Beaufort Group. Additionally, most tapinocephalian taxa are based on either fragmentary or heavily weathered types, suggesting the need for taxonomic re-examination. As a result of our taxonomic survey we reduced the recognized genera of tapinocephalids from 18 to 9. This revision indicates that the diversity of tapinocephalid dinocephalians in the *Tapinocephalus* AZ was overestimated. This will modify our understanding of the Middle Permian extinction event that appears to have affected dinocephalians in particular.

First tapinocephalid dinocephalian from the Pristerognathus Assemblage Zone (Karoo Supergroup, South Africa), including new information on *Criocephalosaurus* (Therapsida: Dinocephalia) (Poster)

Güven, Saniye¹; Day, Michael¹; Almond, John E.²; Abdala, Fernando¹; Rubidge, Bruce S.¹

¹ Bernard Price Institute for Palaeontological Research, Palaeosciences Centre, University of the Witwatersrand, South Africa
guven.saniye@gmail.com / michael.day@students.wits.ac.za / nestor.abdala@wits.ac.za / bruce.rubidge@wits.ac.za

² Natura Viva CC, P.O. Box 12410 Mill Street, Cape Town, 8010 South Africa
naturaviva@universe.co.za

Tapinocephalid dinocephalians were impressively large herbivores from the Middle Permian of South Africa and are considered to be stratigraphically restricted to the *Eodicynodon* and *Tapinocephalus* Assemblage Zones of the Karoo basin. We report the first tapinocephalid from the lower *Pristerognathus* Assemblage Zone. The specimen, which comprises the posterior portion of the skull, is identified as *Criocephalosaurus* (*Criocephalus* Broom, 1928 [*nomen nudum*]). This poorly-known genus comprises two species: *C. vanderbyli* represented by a weathered incom-

plete posterior cranial roof (holotype) and some cranial fragments; and *C. gunyankaensis* based on posterior cranial roof fragments. The first species is known from strata of the Abrahamskraal Formation, South Africa and stratigraphically occurs in the *Tapinocephalus* Assemblage Zone; whereas *C. gunyankaensis* was discovered in Gunyankas Kraal, Zimbabwe, from horizons considered to be equivalent to the *Tapinocephalus* Assemblage Zone of South Africa. Due to the fragmentary and poorly preserved nature of the specimens this genus has not received much attention. The issue is further complicated by the fact that the holotype of *C. gunyankaensis* is missing. This specimen was described in a very short paper without any diagnosis. Accordingly the only reliable morphological data of the genus is based on the genotype. In addition to the new fossil from the *Pristerognathus* Assemblage Zone, a specimen referable to *Criocephalosaurus* has been discovered in the palaeontological collection of the Natural History Museum, London. Both specimens allow revision of the cranial description of *Criocephalosaurus* and have facilitated additional characters which are not present in the holotype. This discovery raises the possibility of the unexpected survival of dinocephalians beyond the *Tapinocephalus* Assemblage Zone age. It also highlights the necessity for more-detailed palaeontological sampling in the lower levels of the *Pristerognathus* Assemblage Zone of the Karoo Basin.

Mosasaur long bone microanatomical and histological features

Houssaye, Alexandra¹; Lindgren, Johan²

¹ Steinmann Institute of Geology, Mineralogy and Palaeontology, University of Bonn, Germany
houssaye@uni-bonn.de

² Department of Geology, GeoBiosphere Science Centre, Lund University, Sweden

Mosasauroids are an extinct group of medium-sized to giant squamates that succeeded in establishing themselves as the dominant marine reptiles in a brief 27 million years at the end of the Cretaceous. Osteohistological studies of mosasauroids have hitherto been limited to ribs and vertebrae. Here we present data on long bone microanatomical and histological features of various hydropelvic (i.e. with no sacrum) forms, including the plesio pedal (i.e. with terrestrial-like limbs) *Dallasaurus* and hydropedal (i.e. with paddle-like limbs) *Angolasaurus*, *Globidens*, *Halisaurus*, *Mosasaurus*, *Platecarpus*, *Plotosaurus*, and *Prognathodon*. In all hydropedal genera, the bone microanatomy is characterized by a spongy organization with no medullary cavity; a condition which is conspicuously different from that in *Dallasaurus*. The histology shows a dominance of lamellar-zonal bone (although fibrous bone can occur locally), and a well-developed vascular network with a predominantly longitudinal orientation. Comparisons are made with extant terrestrial and semi-aquatic lizards, such as *Amblyrhynchus*, *Tupinambis*, and *Varanus*, as well as obligate aquatic tetrapods, such as ichthyosaurs, plesiosaurs and cetaceans. Histological features suggest relatively low metabolic rates in mosasaurs, where high body temperatures presumably were maintained by gigantothermy.

Do body size trends in nonmammalian therapsids reveal the influence of the end-Permian extinction?

Huttenlocker, Adam¹; Sidor, Christian²; Botha-Brink, Jennifer³

¹ Department of Biology, University of Washington, U.S.A.
afrahuttenla@uw.edu

² Burke Museum and Department of Biology, University of Washington, Seattle, Washington 98195, U.S.A.

³ Karoo Palaeontology, National Museum, Bloemfontein, 9300 South Africa

Post-extinction body size reductions in animals (or 'Lilliput phenomena') represent a recently identified feature of mass extinctions. Such have been identified in earliest Triassic marine invertebrates and anecdotally in South African temnospondyls and nonmammalian therapsids following the end-Permian extinction (*ca.* 252 Ma). However, field observations of post-extinction size reductions in terrestrial vertebrate communities have not previously been subjected to rigorous statistical testing. Here, we characterize body size trends in Permian and early-to-mid-Triassic eutheriodonts, an ecologically varied therapsid subclade which outnumbered contemporary dicynodont herbivores in terms of species richness during the earliest Triassic and eventually gave rise to mammals. This research addresses the simple question: Are body size decreases observed among and/or within eutheriodont taxa following the end-Permian extinction?

Preliminary analysis on a database of measurements from more than 343 eutheriodont specimens indicates large body sizes and increasing size disparity in Permian *Cistecephalus* and *Dicynodon* Assemblage Zones, followed by a slight decrease in size disparity and reduced overall body size in the Triassic *Lystrosaurus* Assemblage Zone. Basal skull length (BSL) as well as femur and humerus midshaft diameter were used as relative proxies for size as (1) complete skeletons were not always available for precise mass estimates and (2) their proportions share an approximate relationship with body mass. Our findings corroborate earlier results on BSL in the Permo-Triassic (P-Tr) therocephalian *Moschorhinus*, which suggested significant within-lineage cranial size reductions in P-Tr survivor lineages. More general trends corroborate significant decreases in BSL and limb bone dimensions in eutheriodonts as a whole. Finally, to correct for the impacts of longer term phylogenetic trends, it is necessary to recognize potential phylogenetic constraints on observed body size distributions. In other words, are observed body size trends stochastic or 'driven' and, if driven, are they explainable by extrinsic processes acting on body size distributions during the P-Tr transition? We will explore statistical approaches which include (1) regression on dissimilarity matrices (Mantel tests) and (2) model-based tree randomization procedures in order to identify the extent to which size distributions are explainable by phylogenetic distance and tree structure. Our null prediction is that size shifts are stochastic and largely reflect tree structure (i.e. closely related clades should be more similar in size than phylogenetically disparate clades). However, initial results from Mantel tests indicate that size disparity correlates poorly with pairwise phylogenetic distance within the therocephalian subclade.

Alternatively, if extrinsic factors indiscriminately accelerated rates of life history evolution across clades, then observed size distributions should show significant anti-signal in earliest Triassic clades (a signature of adaptive radiations).

Morphological variation of Sterkfontein and Swartkrans first metatarsals by linear feature extraction on morphometric colour maps

Jashashvili, Tea¹; Dowdeswell, Mark R.²; Carlson, Kristian J.¹; Marchi, Damiano¹; Nshimirimana, Robert³

¹ Institute for Human Evolution, University of the Witwatersrand, South Africa
tea.jashashvili@wits.ac.za

² School of Statistics and Actuarial Science, University of the Witwatersrand, South Africa
mark.dowdeswell@wits.ac.za

³ NECSA, Radiation Sciences Department, Pretoria, South Africa

Four first metatarsals, two from Sterkfontein (StW562, StW595) and two from Swartkrans (SKX5017, SK1813) are analysed. SKX5017 is attributed to *Paranthropus robustus*. Taxonomical attribution of SK1813 is unsure although morphological comparisons show similarity with SKX5017. StW562 and StW595 are from Member 4 deposits at Sterkfontein and are described as intermediate in morphology between modern humans and apes. Unfortunately, they have yet to be attributed to a genus or species. The mosaic nature of morphological trait distribution on the metatarsals complicates functional interpretations: early hominins were unquestionably bipedal but possessed a unique toe-off mechanism different to modern humans. This paper shows preliminary results of first metatarsal shaft cortical thickness distribution in living hominoids. This information is used to provide a better interpretation of the bending and compressive stress patterns in early australopithecines.

First metatarsals of chimpanzees, gorillas and modern humans are compared to those of fossils. For each metatarsal we took 17 cross-sections from 25–65% of the shaft mechanical length. Distance between consecutive cross sections is 2.5% of metatarsal mechanical length. We measured cortical thickness at different radii of each cross section at 1° increment. Cortical thicknesses are standardized by size and normalized between 0 and 1. Distribution of thicknesses along shafts is shown using colour maps. We subsequently perform Linear Feature Extraction on morphometric colour maps of the shafts in order to show the differences between presented taxa.

Results show that chimpanzees and gorillas differ from modern humans in that great apes have much thicker cortical bone distribution distally on the shaft, dorso-lateral thicker cortical shafts proximally, and dorso-plantar thicker cortical bone distally. Modern humans do not show much variation along the shaft with predominantly thicker cross sections along the dorso-plantar direction. Both Swartkrans (SKX5017, SK1813) and Sterkfontein (StW562) metatarsals have similar distribution patterns to chimpanzees and gorillas. StW959 from Sterkfontein has a much more human-like distribution. We confirm that StW562 represents the 'robust' form of hominin fossil from Sterkfontein Member 4. StW959

represents the 'gracile' form (*Au. africanus*) from Sterkfontein, and has modern human characteristics in the distribution of cortical thickness that could be associated to a similar shaft bending regime.

Sediment sources of the aeolian Clarens Formation, Karoo Supergroup

Jinnah, Zubair¹; Roberts, Eric²; Dirks, Paul²

¹ School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa
zubair.jinnah@wits.ac.za

² School of Earth and Environmental Sciences, James Cook University, Townsville, Australia
eric.roberts@jcu.edu.au / paul.dirks@jcu.edu.au

Detrital zircon geochronology is a widely used technique in sedimentary basin analysis and has become important in finding maximum depositional ages and source areas for otherwise poorly constrained stratigraphic units. The aeolian Clarens Formation, which is the uppermost sedimentary unit in the Karoo Supergroup, is a prime locality for detrital zircon analysis because Clarens sediment is derived largely from reworking of sediment from older Karoo units. Zircons in the Clarens Formation thus contain populations from all significant sources of the Karoo Basin.

The Clarens Formation was sampled in the northwest (Free State), south (Eastern Cape) and east (KwaZulu-Natal) of the extent of outcrop. Zircon populations are dominated by groups originally derived from Pan-African age (approximately 700–500 Ma) and Namaqua-Natal age (approximately 1 Ga). A small population of Archaean zircons are also present in the Clarens Formation. Phanerozoic zircons include populations from the Ordovician, Silurian, Permian and Triassic. Ordovician and Silurian grains are potentially recycled from the Cape Supergroup, and may be ultimately derived from Antarctica or South America, whereas Permian zircons may potentially be derived from reworked ash beds in the lower parts (Ecca and Beaufort Groups) of the Karoo Supergroup. One Triassic grain, with an age of 212.7 ± 5.6 Ma, is enigmatic as it is much younger than any ash documented from the Karoo Supergroup, and does not overlap temporally with any kimberlites in the region. The exact source of this grain remains uncertain but its presence highlights the potential of detrital zircons to provide age constraint for the Triassic-Jurassic fill of the Karoo Basin with continued detrital zircon geochronology.

Stratigraphy and sedimentology of the Tapinocephalus Assemblage Zone (Abrahamskraal Formation) in the area around Merweville, South Africa

Jirah, Sifelani; Rubidge, Bruce

Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa
sifelani.jirah@wits.ac.za / bruce.rubidge@wits.ac.za

By far the thickest biozone of the Beaufort Group is the *Tapinocephalus* Assemblage Zone, which, despite its thickness and the presence of tetrapod fossils, has not yet been biostratigraphically subdivided in a satisfactory way. Rossouw & De Villiers (1953) proposed a threefold subdivi-

vision of the *Tapinocephalus* Biozone and Boonstra (1969) confirmed this subdivision. Keyser & Smith (1978) define the upper limit of the *Tapinocephalus* Biozone by the last occurrence of dinocephalians which they say coincides with an extensive green 'chert' band about 120 m below the Poortjie Sandstone.

Recent stratigraphic and sedimentological analysis of the *Tapinocephalus* Assemblage Zone rocks around Merweville has led to the subdivision of the study area into mapable lithological units. The study area is situated in the southwestern corner of the Karoo Basin and is bounded by the longitudes 21°19' and 21°45' east and latitudes 32°20' and 33°00' south. Initial geological mapping of the area was accomplished in the laboratory with the aid of aerial photographs as well as mosaics of Google Earth satellite imagery in order to recognize prominent lithological units. This map of the study area was subsequently checked through fieldwork. Two stratigraphic sections were measured through the entire Abrahamskraal Formation in the study area, and information documented includes lithofacies type, sedimentary structures, grain size, palaeocurrent directions, and ranges of vertebrate fossils. Although no Lower Beaufort lithological units are continuous (Rossouw & De Villiers 1953) in the study area, it was possible, based on their lithology, to recognize several prominent stratigraphic units which extend across the entire study area and have been coded. Biostratigraphically the study area is dominated by dinocephalia and small dicynodonts *Robertia*, *Eosimops* and *Diictodon* as well as therocephalians. The last occurrence of dinocephalia in the study area is 21 m below the Poortjie sandstone.

Boonstra, L.D. 1969. The fauna of the Tapinocephalus Zone (Beaufort beds of the Karoo). *Annals of the South African Museum* 56, 1–73.

Keyser, A.W. & Smith, R.M.H. 1978. Vertebrate biozonation of the Beaufort Group with special reference to the western Karoo Basin. *Annals of the Geological Survey of South Africa* 12, 1–36.

Rossouw, P.J. & De Villiers, J. 1953. The geology of the Merweville area, Cape Province. An explanation of Sheet 198 (Merweville). 78 pp. Pretoria, Geological Survey of South Africa.

Investigating the evidence for soft organic tissue preserved with the MH1 and MH2 Australopithecus sediba fossils from the Malapa Cave site

Keeling, Rachelle; Berger, Lee R.

Institute for Human Evolution, School of GeoSciences, University of the Witwatersrand, Johannesburg, South Africa
rachelle.keeling@gmail.com / proflieberger@yahoo.com

The well-preserved remains of the *Australopithecus sediba* specimens from the Malapa Cave site, in South Africa, might have retained soft tissue in the form of fossilized skin. A multi-disciplinary approach combining morphological and molecular imaging techniques was utilized to investigate whether or not original organics might be recovered. Two primary samples were investigated. The first lay above the posterior surface of MH1's cranium, while the second was derived from the mandible of MH2. Six diverse, non-destructive techniques, combining micro-CT scans, Raman spectroscopy and more, build a provocative body of evidence. Any soft original material discovered from the 2 Myr Malapa hominins will be a first in the field of paleoanthropology.

Histology of sauropod cervical ribs: implications for neck posture?

Klein, Nicole¹; Sander, P. Martin¹; Christian, Andreas²

¹ Steinmann Institute of Geology, Mineralogy and Palaeontology, University of Bonn, Germany
nklein@uni-bonn.de

² Institut für Biologie und Sachunterricht und ihre Didaktik, University of Flensburg, Germany

The long neck of sauropod dinosaurs is probably the most distinctive feature of their anatomy and one of the key evolutionary innovations, permitting their unique gigantism by reducing the energy spent feeding. However, the position in which the neck was held is still controversial, with either a nearly horizontal or a distinctly raised neck. Arguments put forth have centred on the constraints imposed by the cardiovascular system, the mobility of the intervertebral joints, and on biomechanical considerations. Surprisingly, the distinctive and in some taxa extremely elongated cervical ribs, that can extend over three vertebrae, have not been studied in this regard, although a bracing function has been hypothesized for the cervical ribs before.

For the first time bone histology of the extremely long cervical ribs of *Brachiosaurus/Giraffatitan* and *Mamenchisaurus* as well as the shorter cervical ribs of a diplodocid sauropod is studied in detail. Besides an expected strong remodeling by secondary osteons, we found no primary bone tissue in the cervical ribs but there was metaplastic bone. However, most of the microstructure of the anterior and posterior processes of the cervical ribs is made up of longitudinal running fibres, identical to those known from the microstructure of ossified tendons. The longitudinal orientation of the fibres implies that the cervical ribs had transported tension forces and clearly contradicts the bracing hypothesis, because in the case of a bracing function of the cervical ribs the fibres would be expected to run vertically. The main function of the cervical ribs as transporter for tension forces is also supported by the fact that the anterior and posterior processes of the cervical ribs show morphological structures such as striations and shallow depressions, which indicate multiple and close overlap of the long cervical ribs which are also preserved on the fossils. On the basis of our histological results we hypothesize that the processes of the cervical ribs were only loosely connected by soft tissue and movable along their long axis against each other; this would make the neck much more flexible than previously thought.

A redescription of a burnetiamorph (Therapsida – Biarmosuchia) from Karoo rocks of Malawi (Poster)

Kruger, Ashley; Rubidge, Bruce; Abdala, Fernando

Bernard Price Institute for Paleontological Research, University of the Witwatersrand, Johannesburg, South Africa
ashleykruger@gmail.com / nestor.abdala@wits.ac.za / bruce.rubidge@wits.ac.za

Exposures of Karoo-age Supergroup are represented in the northern and southern regions of Malawi. The fauna discovered in the Chiweta Beds of northern Malawi includes typical representatives of Late Permian age, which suggest that it is coeval with the *Cistecephalus* Assemblage Zone of the South African Karoo. The Chiweta fauna reported by Jacobs and colleagues in

2005 includes the dicynodont *Oudenodon* and a new biarmosuchian. The latter taxon is represented by the skull and lower jaw of a burnetiamorph, a group of biarmosuchians that present numerous bosses and swellings on the skull. Burnetiamorphs are currently known from seven genera of Middle to Late Permian age, five of which are known from the Beaufort Group of South Africa, the other two from Russian deposits. MAL 290 represents the first burnetiamorph from Malawi. A preliminary description of this material, MAL 290, including a phylogenetic analysis was presented by Jacobs and colleagues in 2005, who found the Malawi specimen to be the sister taxon to *Proburnetia*, *Burnetia* and *Bullacephalus*. Additional preparation of the skull of the burnetiamorph from Malawi, allows a full description of the material and has enabled a revised phylogenetic analysis.

Large burrows and palaeoenvironmental reconstruction of the Early Triassic Katberg Formation, southeastern Main Karoo Basin, South Africa (Poster)

Krummeck, William; Bordy, Emese

Department of Geological Sciences, 13 University Avenue, Upper Campus, University of Cape Town, Rondebosch, 7700 South Africa
willkrummeck@yahoo.com / emese.bordy@uct.ac.za

The Early Triassic Katberg Formation (*Lystrosaurus* Assemblage Zone) of the Beaufort Group records the period when life recovered from the Permo-Triassic extinction event during which nearly 90% of all life was wiped out. Several burrow casts of ~11 cm in diameter and up to 2 m in length, and morphologically similar to those described from the Triassic of Antarctica, were found in the Katberg Formation in the Free State and Eastern Cape (South Africa). The latter locality (NW of Cathcart) previously produced several vertebrate fossils and *Kitchingnathus untabeni* (holotype BP/1/1187).

This study seeks to: 1) reconstruct the local palaeoenvironments, 2) determine the purpose of the burrows and 3) the possible burrow makers. The analyses of the burrow casts, vertebrate fossils and host sedimentary rocks have been undertaken through a multidisciplinary approach based on ichnological, sedimentological, petrographical, stratigraphic, taphonomic and paleontological evidence gathered in the field and laboratory observations.

Some of the findings related to the burrows include: diamond-shaped pattern of incised scratches (bioglyphs) on the surface of burrow casts indicating the alternating scratching directions by the burrow maker; bilobate cross-sectional shape suggesting travel wear due to a semi-sprawling locomotion by the burrow maker; multi-stage passive filling of burrows implying that the burrows were filled up in several flooding events. Furthermore, a ~0.5 mm calcite rim around some of the casts, the 'cement-supported' grain fabric in the burrow fill, the deformation of burrows by calcite concretions and preferential calcitization of the burrow casts relative to the host rocks are all indicative of the high permeabilities of the burrow fill before cementation, a process that likely occurred within soil profiles in very early diagenesis due to evaporation. The burrows tend to occur in floodplain

mudstones overlain by channel fill and crevasse splay sandstones. The close proximity to such sandy deposits and the sedimentary and ichnofacies of the host mudstones and coarse-grained burrow fills suggest that the burrowing occurred in parts of the floodplain that were in fairly close proximity to the higher energy fluvial channels.

With this on-going study, we hope to gain further insights into the earliest Triassic ecosystems of the Karoo and the behaviours (e.g. survival strategies) of the organisms after 'the Great Dying' at the Permian-Triassic boundary.

Preliminary analysis of a Triassic dinosaur from the Lower Elliot Formation of Lesotho

Krupandan, Emil; Chinsamy-Turan, Anusuya

Department of Zoology, University of Cape Town, Rondebosch, 7700 South Africa
emilkrupandan@hotmail.com

The Lower Elliot Formation (LEF) of South Africa is the richest known Triassic assemblage dominated by relatively large sauropodomorph dinosaur remains of *Antetonitrus ingenipes*, *Blikanasaurus cromptoni*, *Melanorosaurus readi*, *Plateosaurus cullingworthi*, *Eucnemesaurus fortis* and *Aardonyx celestae*. *Massospondylus*, a prosauropod, is most abundant in these deposits, with a number of individuals of different ontogenetic sizes (adults, juveniles, embryos within eggs). We investigate undescribed material from the site, Maphutseng in Lesotho. During the 1950s and 1960s Francois and Paul Ellenberger studied the LEF at Maphutseng in the Mohale's Hoek region and recovered numbers of presumed prosauropod remains from a bone-bearing lens.

Apart from three cursory descriptions by the Ellenbergers and Gauffre of some of the material, not much work has been done on the bones excavated. Ellenberger & Ellenberger reported that the bones recovered from the site numbered in the high hundreds and were identified as a 'new' prosauropod similar to a *Plateosaurus* or *Melanosaurus*.

We assess the postcranial remains to provide an anatomical and taxonomic description. We apply histological methods to ascertain biological aspects of this large sauropodomorph. We hope this multi-dimensional approach will provide a better understanding of the Maphutseng dinosaur, and its relationship to contemporaneous sauropodomorphs in the Lower Triassic of South Africa.

- Sereno, P.C. 1999. The Evolution of Dinosaurs. *Science* **284**, 2137–2147.
- Yates, A.M. 2006. Solving a dinosaurian puzzle: the identity of *Aliwaliaxer* Galton. *Historical Biology*, 1–31. **19**(1), 93–123
- Gauffre, F. 1993. Biostratigraphy of the lower Elliot Formation (southern Africa) and preliminary results on the Maphutseng dinosaur (Saurischia: Prosauropoda) from the same formation of Lesotho. In: Lucas, S.G. & Morales, M. (eds), *The Nonmarine Triassic. New Mexico Museum of Natural History and Science Bulletin* **3**, 147–149.
- Ellenberger, F., Ellenberger, P. 1956. Le gisement de Dinosauriens de Maphutseng (Basutoland, Afrique du Sud). *Comptes Rendus de la Société Géologique de France* **8**, 99–101
- Reisz, R.R., Scott, D., Sues, H., Evans, D.C., Raath, M.A. 2005. Embryos of an Early Jurassic prosauropod dinosaur and their evolutionary significance. *Science* **309**, 761–764.
- Brusatte, S.L., Nesbitt, S.J., Irmis, R.B., Butler, R.J., Benton, M.J., Norell, M.A. 2010. The origin and early radiation of dinosaurs. *Earth-Science Reviews* **101**, 68–100.

- Upchurch, P., Barret, P.M., Galton, P.M. 2007. A phylogenetic analysis of basal sauropodomorph relationships: implications for the origin of sauropod dinosaurs. *Special Papers in Palaeontology* **77**, 57–90.

Insect herbivore diversification after the end-Permian crisis: evidence from leaf miners

Labandeira, Conrad^{1,2,3}; Prevec, Rose²

¹ Smithsonian Institution; Washington, DC, U.S.A.
labandec@si.edu

² Rhodes University, Grahamstown, 6140 South Africa
r.prevec@ru.ac.za

³ University of Maryland, College Park, MD 207, U.S.A.

One of the ecological consequences of the end-Permian biotic turnover was the origin on land of new plant communities during the Triassic dominated by clades overwhelmingly different from those occurring during the Permian. Insects also underwent a major diversification and new herbivore clades arose, either opportunistically or in tandem with their plant hosts. Nowhere is this plant-and-insect pattern of radiation and colonization better demonstrated than in the Karoo Basin of South Africa. In an ongoing examination of plant damage in floras spanning an approximately 50-million-year interval from the late Early Permian through the early Late Triassic, we have initially selected the colonization patterns of leaf-mining insects, as evidenced by their distinctive and diagnosable mines preserved on a broad spectrum of vascular plant hosts. In the future, we will compare patterns of plant-host colonization by leaf miners to gallers, piercer-and suckers, seed predators, and other insect functional feeding groups that exhibit elevated levels of host specificity.

Our leaf-mine sub-dataset begins during the latest Permian in which a distinctive blotch mine has been recorded on a glossopterid leaf taxon found at a single locality in the Emakwezini Formation (Normandien Formation), followed by the absence of leaf mining (or for that matter, hardly any specialist herbivores) in the Anisian Burgersdorp Formation. However, throughout the early Carnian Molteno Formation, seven leaf-mining damage types (DTs) occur in 30 stratigraphic levels from 22 localities. The 27 leaf-mined plant-host species include sphenopsids, ferns, and a particularly rich spectrum of seed plants comprising broadleaved voltzialean conifers, cycads, five major lineages of ginkgoopsids, corystosperms, and taxa possibly affiliated with bennettitopsids and gnetopsids. Our data preliminarily indicate dietary partitioning of foliar tissues, including full-depth and epidermal mines in leaf blades, rachides and midribs, and rarely in horsetail stems. Three distinctive mine DTs occur exclusively on herbaceous plants, notably horsetails, ferns and kannaskoppiaceous ginkgophytes in Horsetail Marsh and Fern Kannaskoppia Meadow habitats. One very abundant damage type, DT71, is centred on the broadleaved voltzialean conifer *Heidiphyllum elongatum* in *Heidiphyllum* Thicket, but also occurs in other seed-plant lineages, particularly cycads, ginkgophytes and corystosperms, occurring in *Dicroidium* dominated riparian forests and in *Dicroidium*- and *Sphenobaiera*-dominated woodland. The distinct ecological centre of leaf mining distribution is *Heidiphyllum* Thicket, from which other habitats were

possibly colonized. These data indicate an evolutionarily dynamic pattern of plant-host colonization by herbivorous insects, paralleling the associational diversity the Angiosperm Revolution that began approximately 100 million years later.

The small mammal fauna from Koanaka South, Botswana, and the implications for reconstructing Pleistocene environments

Lewis, Patrick

Department of Biological Sciences, Sam Houston State University,
Huntsville, TX 77340, U.S.A.
pjl001@shsu.edu

Recent excavations of fossiliferous deposits from Bone Cave have produced a diverse Plio-Pleistocene mammalian fauna. The cave is located in the southernmost section of Koanaka Hills, northwestern Ngamiland, Botswana, an area under-represented for the period. A large assemblage consisting primarily of rodents and shrews was excavated. Similar to many of the Plio-Pleistocene small mammal assemblages in South Africa, taphonomy of these fossils is consistent with an owl accumulation and *Tyto alba* (barn owl) is the most likely agent. Our goal was to better inform on the regional paleoenvironment during the Plio-Pleistocene.

Specimens attributed to *Mus* sp., *Gerbilliscus* sp., and *Otomys* sp. were identified, but much of the material could not be confidently diagnosed below subfamily based only on dentition as has been standard practice in the region; to the level of genus and, frequently, to species. Comparison of the Koanaka Hills fossil material with recently trapped modern specimens from the area and comparative specimens from the Ditsong National Museum of Natural History (formerly Transvaal Museum) in Pretoria failed to identify reliable apomorphies for many clades. This result suggests that diagnosing these rodents based on dentition alone is precarious, particularly for many murine taxa.

In addition, genetic work on the modern Koanaka rodents finds genetically distinct cryptic taxa of murines that are morphologically indistinguishable. As such, a lack of distinct dental morphologies may not be sufficient to rule out multiple taxa. Further morphological analyses, using specimens identified to species by molecular methods, also suggest that some modern specimens in South African museum collections may be misidentified. As these specimens have been the primary source of comparative material for the diagnosis of small mammals in the region, any misidentified specimens in these collections could distort ranges of variation and lead to incorrect identification of fossil specimens.

Once identifications are made and taxonomic lists created for a locality the environmental preferences of modern taxa are used to guide paleoenvironmental reconstruction. Misdiagnosis of these taxa obviously distorts this reconstruction but, in addition recent examinations of modern South African rodent distributions suggest that many taxa do not appear to be constrained by factors such as rainfall and temperature. The presumed environmental preferences of modern taxa may be poor indicators of past environments, and their use certainly

assumes a level of stasis in preferences that appears unwarranted.

Our data call into question prior paleoenvironmental reconstructions in the South African Plio-Pleistocene. Well-defined ranges for dental characters must be established and clear apomorphies defined for modern South African murine taxa relied upon to guide the interpretation of regional fossil specimens. The variables constraining rodent ranges must also be more clearly defined. Until then current taxonomic lists and their associated paleoenvironmental reconstructions for Plio-Pleistocene localities should be used with caution.

Evolutionary developmental model for the origin of the turtle shell and a novel functional hypothesis for the origin of the chelonian lung ventilation mechanism

**Lyson, Tyler¹; Bever, Gabe¹; Scheyer, Torsten²;
Hsiang, Allison¹; Gauthier, Jacques¹**

¹ Department of Geology and Geophysics, Yale University, New Haven,
CT 06511, U.S.A.
tyler.lyson@yale.edu

² Palaeontological Institute and Museum, University of Zurich, Zurich, Switzerland

The origin of the turtle shell and the constraints it places on how turtles breathe are interdependent problems that have fascinated scientists for the past three centuries. The discovery of the stem turtle *Odontochelys semitestacea* supports the developmental *de novo* hypothesis, because it confirms that the costals and neurals are produced through the outgrowth of (sub) dermal bone from the perichondral collar of the dorsal ribs and vertebrae. This discovery allows for the integration of developmental and fossil data into an evolutionary developmental (evo-devo) model for the shell's origin that makes explicit predictions for the contentious early history of the turtle stem. We expand this model by integrating novel anatomical and histological data for *Eunotosaurus africanus*, a species recovered as a stem turtle in both global phylogenetic analyses of amniotes and parareptiles. We consider the phylogenetic signal within a dataset based on shell-related characters and shelled taxa currently considered as potential relatives of turtles. This analysis tests the hypotheses that the *de novo* shell appeared once in amniote history and that *E. africanus* is a stem turtle.

Results support the hypotheses that the *de novo* shell appeared only once in vertebrate evolution and that *E. africanus* is a stem turtle. Characters *E. africanus* shares with stem turtles include: ten or less elongate dorsal vertebrae, nine pairs of anterior-posterior broadened ribs, loss of intercostal muscles, insertion of muscles on the ventral side of the dorsal ribs, and (sub) dermal outgrowth of bone from the developing perichondral collar of the dorsal ribs. The successive divergences of *E. africanus* (broadened ribs; dermal outgrowth of bone from the ribs; re-organization of locomotion/respiratory muscles), *O. semitestacea* (broadened ribs/neurals), and finally *Proganochelys quenstedti* (fully ossified carapace) results in a sequence of character acquisitions that is fully congruent with predictions drawn from the evo-devo model.

The evo-devo model further provides a transitional and mechanistic hypothesis for the origin of the unique

abdominal muscle lung ventilation system in turtles. As the ribs broaden along the turtle stem, they increasingly support the abdomen, while simultaneously becoming less effective lung ventilators due to mechanical conflict created between adjacent overlapping ribs. As the ribs broaden, the dual functioning abdominal muscles are slowly freed from their role of providing additional support to the abdominal cavity against torsion and are delegated into a purely respiratory function. There was a shift from the dual functions found in both the ribs and abdominal muscles of early amniotes, to a division of function in turtles with the ribs taking on a purely support role and the abdominal muscles functioning to only ventilate the lungs.

The avifauna of Langebaanweg (early Pliocene, South Africa)

Manegold, Albrecht¹; Louchart, Antoine^{2,3}

¹ Senckenberg Forschungsinstitut und Naturmuseum, Senckenberganlage 25, Frankfurt/Main, Germany
albrecht.manegold@senckenberg.de

² Department of Cenozoic Palaeontology, Iziko South African Museum, Cape Town, South Africa

³ Institut de Génétique Fonctionnelle de Lyon, CNRS, UMR 5242, Université de Lyon, École Normale Supérieure de Lyon, 46 Allée d'Italie, 69364 Lyon, France
antoine.louchart@ens-lyon.fr

The present paper provides an overview on the already famous, but still insufficiently known avifauna from the early Pliocene Varswater Formation at Langebaanweg (South Africa). This site yielded one of the largest pre-Pleistocene bird bone accumulations worldwide. According to conservative estimates, at least 60 bird species of 25 family-taxa are represented here, and most of them mark the earliest record for these taxa on the African continent. Especially diverse is the fossil record of seabirds such as petrels, prions, and shearwaters (Procellariidae), penguins (Spheniscidae), as well as terrestrial taxa such as shorebirds (Charadriiformes) and songbirds (Oscines, Passeriformes). Recent identifications of new bird species have shed new light on current hypotheses on the palaeoenvironment and palaeoecology at Langebaanweg. For instance, honeyguides and several cavity nesting birds such as parrots and woodpeckers indicate the presence of forested habitats, but evidence for two species of sandgrouse (Pteroclididae), a taxon generally associated with arid to semi-arid landscapes, reveal a little known component of the palaeoenvironment of Langebaanweg area during the Early Pliocene.

Bone microstructure of metapodial bones reveals growth pattern and life history features of Miocene *Hipparion* from Spain

Martinez-Maza, Cayetana¹; Alberdi, Maria Teresa¹; Gomez, Santiago²; Prado, Jose Luis³

¹ Department of Palaeobiology, Museo Nacional Ciencias Naturales (CSIC), Madrid, Spain
martinezmaza.cayetana@gmail.com

² Department of Pathological Anatomy, University of Cádiz, Cádiz, Spain

³ INCUAPA, Departamento de Arqueología, Universidad Nacional del Centro, Del Valle, Olavarría, Argentina

Hipparions characterizes the Upper Miocene and Pliocene faunas of Eurasia and Africa. They represent an intermediate stage in horse evolution towards higher crowns, larger size and reduced autopodials. They present

an autopodial composed by a major central toe and two reduced lateral ones. Their morphology has been studied, but until now not histologically. Bone microstructure reflects development, growth and adaptive changes during life. These aspects of the life history of an extinct animal, can be assessed as fossil bone generally maintains its histological integrity. We characterize the microstructure from 50 central and lateral metacarpal and metatarsal bones of *Hipparion concudense* from the Vallesian and Turolian fossil sites of Valles de Fuentidueña (Segovia) and Concué (Teruel) of Spain. All analysed bones have fused epiphyses. Bright field and circular polarized light microscopy of transverse ground sections of midshafts reveals that central metapodials are formed of cortical compact bone made of primary bone tissue with variable extension of secondary bone. Primary bone tissue is composed by many layers of primary osteons formed during growth by periosteal apposition. Secondary bone shows several generations of haversian osteons which mainly display a hooked and alternate collagen pattern; one individuals show multiple primary osteon system and few secondary osteons in the posterior area. Other specimens show similar histology but haversian bone extends both in the posterior and the inner area of the dorsal region. Some specimens show secondary osteons throughout the cortical bone. The microstructure of lateral metapodials is similar to that in the central metapodials, but in the lateral one the marrow cavity is reduced to a small space or completely absent. Primary and secondary bone is present in variable proportions. In particular, large areas of secondary bone are found in the medial side facing the central metapodial. Lines of arrested growth (LAG) in primary bone in the cortical bone of central and lateral metapodials, may have formed on an annual basis. The number of LAGs is variable; in the less remodeled cortical bone of a few young individuals we identified from 4 to 6. Structural changes in the cortical bone suggest different age-related bone maturation associated with broad developmental stages in *Hipparion concudense*. At early stages of development, metapodial bones show appositional periosteal associated with fast growth together with secondary osteons in the posterior region. In young specimens, the short distance between LAGs and the increase of haversian bone area could indicate a decelerating growth. The adult specimens present completely remodeled cortical bone. Secondary osteons in the central metapodials of young individuals occur in areas associated with lateral metapodials. Lateral metapodials may inter-relate biomechanically with the central metapodials.

Using geometric morphometrics to clarify the relationship between modern soricid and murid taxa and fossil species from Langebaanweg (5.2 Ma)

Matthews, Thalassa¹; Stynder, Deano D.²

¹ Iziko South African Museum, Cape Town South Africa
tmatthews@iziko.org.za

² Department of Archaeology, Faculty of Science, University of Cape Town, Rondebosch, South Africa
deano.stynder@uct.ac.za

We used geometric morphometrics to compare mandib-

ular shape and size of two extinct forest shrew (Soricidae) species found at Langebaanweg (LBW) with extant species, to elucidate the relationship between the upper first molars from rats (Muridae) belonging to the genus *Aethomys*, which were represented by an anomalously large number of species and/or morphs.

Soricids: This research represented the first study of the soricid community from LBW, which is represented by four species. Using geometric morphometrics, the ascending rami of the two *Myosorex* fossil species were compared with each other, and with the extant western and eastern Cape species *Myosorex varius* and *M. cafer*, as well as the elusive *M. longicaudatus*, which was discovered only in the late 1970s in the Knysna area, south coast. The mandibles of the fossil species are characterized by ascending rami which are relatively gracile and differ in shape and size from modern species, and the existence of a number of primitive mandibular and dental features. This evidence was interpreted as indicating that the Langebaanweg Forest shrews represent an archaic lineage now extinct in southern Africa.

Murids: Initial work described two *Aethomys* species (*Aethomys adamanticola* and *Aethomys modernis*) at LBW. Subsequent research led to the secure identification of a third, as yet, undescribed species, and in addition, three morphs of existing species were also recognized which showed sufficient differences to raise the possibility that they were different species. Geometric morphometrics was used to explore the relationship of fossil species and morphs with extant *Aethomys* species, and to assess the intra and inter-specific variation in the size and shape of modern and fossil *Aethomys* specimens. Geometric morphometrics indicated a marked similarity in the upper first molar (M1) shape between all the analysed species, extant and extinct, and suggests the persistence, over a significant period of time, of a prototype *Aethomys* M1 shape. The relative warp analyses indicated some interspecific variation between the two modern species, *Aethomys chrysophilus* and *Aethomys namaquensis*, and some overlap in shape, although they differed significantly from one another in terms of size. Variability in terms of size and to a minor extent, shape, was also evident in the fossil *Aethomys*, and it was concluded that the various fossil morphs investigated represented intra-specific variability in size and shape rather than intra-specific sexual dimorphism, or a new *Aethomys* species.

Assessing an exhibition and hands-on fossil fuel workshop as a tool to promote learners' understanding of palaeontology

McKay, Ian

School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa
witsgeoutreach@gmail.com

Public understanding of the possible role of human activities in causing climate change and the need for sustainable energy sources to mitigate this change is related to their understanding of the origin, use of, supply and hazards associated with fuels. However, a proper understanding of fossil fuels requires a basic knowledge of Earth

history, geological time, evolution, and chemistry which is taught at schools. In South Africa palaeontology, climate change and fossil fuels are covered at both primary and secondary levels. This paper describes the efficacy of a programme on fossil fuels presented to primary and high school pupils at a Science Centre in South Africa as part of a Sustainable Energy Week. The programme consisted of a fossil fuel exhibition with a five minute overview on fossil fuels presented by a postgraduate student. In addition there was a hands-on workshop consisting of a presentation explaining the origin of fossil fuels, future supplies, and their probable role in influencing climate change. Students compared crude oil with engine oil, as well as peat with different types of coal and also used polystyrene balls to model hydrocarbons. Pre- and post-workshop questionnaires were used to assess the programme. Results suggest that the learners' understanding of fossil fuels and their possible relationship to climate change is poor, resulting in their opinions being shaped by societal pressure rather than actual understanding of the concepts involved. The programme was partially successful in assisting learners to understand fossil fuels and their relationship to climate change.

The anatomy and phylogenetic relationships of *Antetonitrus ingenipes* (Dinosauria, Sauropodomorpha) from the Late Triassic of South Africa: implications for the origins of Sauropoda

McPhee, Blair

BPI Palaeontology, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa
blair.mcphee@gmail.com

The sauropods were the dominant herbivorous dinosaurs for the majority of the Mesozoic, representing the largest terrestrial animals to have ever evolved. How the group rose to such an important role is a question of much interest. However, until recently the anatomy – including the basic osteological framework of the most basal members of the Sauropoda had remained something of a mystery. Exacerbating the problem was a scarcity of good specimens and a lack of consensus on the wider relationships of the Sauropoda among the more inclusive sauropodomorph clade. The situation has improved in recent years, and new discoveries from Thailand, Argentina, China, and South Africa have begun to provide palaeontologists with the means of unravelling the origins of this fascinating group of animals. One of these discoveries, *Antetonitrus ingenipes* from the lower Elliot Formation of South Africa, preserves significant elements of both the axial and appendicular skeleton and therefore represents one of the most significant early sauropod discoveries. Dating to the Norian of the late Triassic, *Antetonitrus* displays an intermediate morphology between later sauropods and their 'prosauropod' forebears. This intermediate morphology and early age uniquely informs us on the pattern and timing of the acquisition of numerous sauropod traits, and several recent phylogenies have resolved *Antetonitrus* as the most basal of all Sauropoda. However, our understanding of

basal sauropodomorph interrelationships – particularly at the sauropodomorph/sauropod transition – continues to remain controversial, and the full informational significance of *Antetonitrus* is yet to be fully explored. A comprehensive description of the *Antetonitrus* fossil assemblage is therefore considered a necessary and timely undertaking in light of the current state of basal sauropodomorph studies, and will form the essence of my current Masters of Science project at the University of the Witwatersrand. Additionally, as the character states of *Antetonitrus* have yet to be based upon a full osteological description, a revised cladistic analysis may yield additional insight into the precise evolutionary context of this important transitional taxon, especially in light of the recent advances in sauropodomorph phylogenetics.

Note on the fossil fauna and flora at Ongongo Springs, Damaraland (Poster)

Mocke, Helke

National Earth Science Museum, Geological Survey of Namibia,
Windhoek, Namibia
hmocke@mme.gov.na

Knowledge of Quaternary-aged fossils in Namibia is somewhat lacking, although several such sites were identified, for example, by Hermann Korn and Henno Martin. The community-run Ongongo Springs in Western Namibia yielded thick layers of tufa (freshwater carbonate) containing a rich collection of impressions of macroscopic fossil plant leaves, roots, branches and trunks. The leaf impressions show mostly primary venation, making their identification very difficult. The absence of organic material within the preserved leaves, roots, stems and trunks makes C^{14} dating impossible. However, dating of the tufas will ascertain when the plant matter was covered by the precipitated material. A possible sedge leaf was noted and impressions of what appear to be those of the sycamore fig, *Ficus sycomorus* (Family Moraceae) and Mopane, *Colophospermum mopane* (Family Fabaceae) leaves. However, no fruits or seeds were found. To date only a single vertebrate fossil has been reported by a visitor to the springs. It has been suggested that it is the impression of a frog skeleton. Land snails were observed in the tufas and surrounding calcretes and are comparable to the modern species *Sculptaria* in general morphology. No dating has as yet been done on the tufa, due to an absence of dating equipment in Namibia.

Microstructural differences in femoral bone of *Abrothrix longipilis* (Cricetidae, Sigmodontidae) populations from different altitudes (Poster)

Montoya, Germán¹; Iturra-Cid, Myriam¹; D'Elía, Guillermo²

¹ Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción-Chile
gemontoya@udec.cl / myiturra@udec.cl

² Instituto de Ciencias Ambientales y Evolutivas, Universidad Austral de Chile, Casilla 567, Valdivia-Chile.
guille.delia@gmail.com

Bone is a plastic and highly responsive tissue that changes in response to different mechanical and environmental conditions. Considering this, bone microstructure (BM) of vertebrates is useful to assess the ecological and

life history characteristics of extant and extinct species. However, accurate knowledge about geographic and climatic variation on the arrangement of cellular and structural components of bone is scarce; we do not know the effects of high-elevation conditions e.g. hypoxia and derived process as angiogenesis and osteoclastogenesis, upon BM. Knowing these effects on BM could be very useful to identify and estimate ecological and paleoecological traits in extinct assemblages (bonebeds) associated with orogenic uplifts. We compare BM from populations exposed to different environmental pressures associated with atmospheric oxygen availability at low and high elevations.

We assessed quantitative and qualitative differences in bone vascularization in populations of long-haired grass mouse *Abrothrix longipilis* from two localities; one at moderate elevation ($n = 5$; 1420 m) and another at sea level ($n = 5$; 15–32 m). We hypothesized that the hypoxic conditions encountered by the high elevation population (*He*) would be reflected by the presence of more Haversian systems and vascular canals than the sea-level population (*Le*).

Osteohistological sections of femora were made, and prepared. BM was described in terms of the number of Haversian systems and vascular canals structures, in addition to description of their arrangement and pattern. A nonparametric Mann-Whitney *U*-test was used to compare whether the mean values corresponding to the *He* and *Le* samples were significantly different ($P < 0.05$).

Populations differed in the proportion and frequency of the microstructural components and in the arrangement and distribution of such elements. Similar to other rodents and mammals, both populations exhibited a small number of Haversian systems (38) and a considerable abundance of vascular canals (242). Individuals of *Le* (5.8 ± 4.14 , $P = 0.028$) had a tendency to have more Haversian systems than those of *He* (1.8 ± 1.48). Inversely, *He* individuals have a higher frequency of vascular canals (39.6 ± 19.91 , $P = 0.036$) than *Le* (8.8 ± 3.27). It is likely that the increased frequency of vascular canals is associated with increased blood supply in populations at high and moderate altitude, where oxygen levels are lower than at sea level. Moreover, the slightly larger number of Haversian systems in the *Le* opposed to the *He* population indicates possible differential metabolic dynamics in bone remodeling associated with altitudinal gradients.

There are significant differences in the BM pattern of *A. longipilis* at different altitudes and BM could be used as a proxy for high altitude environments. This is an interesting and useful tool for interpreting adaptive and paleoecological aspects of organisms related to topographic variables such as in the Andean Altiplane.

The hominin thoracic shape

Nalla, Shahed^{1,2,3}; Zipfel, Bernhard³

¹ Department of Human Anatomy and Physiology, Faculty of Health Sciences, University of Johannesburg
shahedn@uj.ac.za

² Institute for Human Evolution, University of the Witwatersrand

³ Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa
bernhard.zipfel@wits.ac.za

Understanding the locomotory and postural changes

that affected the early hominins is important in order to gain an understanding of primate evolutionary processes. It has been hypothesized that, specifically among hominins, major evolutionary changes have taken place in rib form and structure, which, in turn influenced thoracic shape. Examination of the partial thorax of the *Australopithecus afarensis* skeleton ('Lucy') had contradicted the previous suggestion that the thoracic shape of this species was more 'ape-like than human-like'. This prompted significant debate and highlighted the importance of understanding and interpreting thoracic shape in the fossil hominin record. Earlier ideas of the dimension and shape of the hominin thorax and its evolution have been further challenged by subsequent studies of the more-complete thoracic remains of the Kebara 2 Neanderthal and the Nariokotome *Homo erectus* juvenile.

The complex geometric and dynamic relationship between the thorax, the clavicle and the scapula has also never been fully understood, even in humans, let alone its variation and implications among primate species with diverse locomotor behaviours.

The present study undertook to determine the shape of the hominoid thorax and its influence on the position of the upper limb. The morphology of the thoracic and the upper limb elements (the proximal end of vertebro-sternal ribs, the sternum and associated costal cartilages, the clavicles and the scapulae) of selected extant primate species was analysed by taking 21 linear measurements (from which 12 indices were derived so as to quantify morphometric information from homologous points). These measures were then compared to those found in the fossil record in order to determine whether there are any structural correlates between the extant and the extinct hominin species.

Preliminary results indicate a generalized consensus that modern humans exhibit a narrow upper and lower thoracic shape, when compared to the primitive ape-like thorax which is narrow at the top and wider at the bottom. The observed thoracic shapes facilitate optimal positioning of the upper limb for efficient locomotion and behavioural requirements.

The coprolites from the Early Triassic fossil site Driefontein, eastern Free State

Neumann, Frank H.^{1,2}, Yates, Adam^{2,3}, Hancox, John²

¹ Forschungsstelle Palaeobotanik, University of Münster, Germany
fneum_01@uni-muenster.de

² Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa
jhancox@cciconline.com

³ Museum of Central Australia, Alice Springs, Australia
yatesam@gmail.com

The Driefontein locality comprises lacustrine muds and fluviatile sandstones of the Burgersdorp Formation, which was deposited in the main Karoo Basin from the Early Triassic through to the early Middle Triassic. The fossil site is of special importance since it shows one of the worldwide rare examples of Early Triassic recovery fauna following the End-Permian extinction event. These harsh conditions are reflected by the depauperate nature of

Early Triassic ecosystems and the small sizes of their constituent species, a phenomenon known as the Lilliput effect.

Our aim is to contribute to a better understanding of the palaeoecology by looking at the coprolites in a thin bonebed, which are 400 μm to several centimetres in diameter with an array of methods including light and electron microscopy, thin section and silicon peels. Hybodont sharks, lungfish, several temnospondyl amphibians and a large basal archosauriform, all evidenced at the site by fossil findings, are possible producers of the coprolites.

We documented numerous fossils which were within the coprolites, including an insect wing impression, dipnoan tooth plates, arthropod remains, bone fragments, fish scales, dermal bones and plant remains. Among the most outstanding findings are bivalve impressions which might belong to unionids although they are unusually small and the identification is hampered by limited preservation. If the specimens do represent unionoids then these Early Triassic examples may be an example of the Lilliput effect. Since the oldest incontrovertible unionoids are also from sub-Saharan Africa, it is possible that this subcontinent hosted the initial radiation of the Unionoida.

Our findings demonstrate the importance of coprolites as microenvironments of exceptional preservation that contain fossils of organisms that would otherwise have left no trace.

A proposed palynostratigraphic scheme for the Karoo Supergroup of South Africa

Nicoletti, Natasha; Bamford, Marion; Rubidge, Bruce

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa
nicoletti.natasha@gmail.com

The Karoo Basin is an excellent source of palaeobotanical fossils, including palynomorphs, but previous research has concluded that the abundance of palynomorphs in some Karoo rocks is not sufficient to establish a biozonation for the entire Karoo sequence. Recent extensive sampling from the Karoo stratigraphic succession has yielded numerous palynomorphs, and it appears possible to generate a palynostratigraphic scheme for the Karoo sedimentary sequence from both the proximal and distal facies (Catuneanu *et al.* 1998). The palynological signatures of the Ecca Group, Permian Beaufort Group, Triassic Beaufort Group, Molteno Formation and Elliot Formation are described. The recent determination of radiometric dates for most of the Permian vertebrate biozones of the Beaufort Group (Rubidge *et al.* 2010) will enable precise dating for some palynological zones. Comparison of the Karoo palynological biozonation with the existing Australian scheme and other Gondwana palynomorphs reveals similarities at the generic level but South Africa possesses some unique species that have not been recovered from other Gondwana deposits. The taphonomy of palynomorphs may prove useful for palaeoenvironmental determination within different deposits of the Karoo Supergroup

and is expected to corroborate geological evidence of Permian and Triassic palaeo-environments.

Catuneanu, O., Hancox, P.J. & Rubidge, B.S. 1998. Reciprocal flexural behaviour and contrasting stratigraphies: a new basin development model for the Karoo retroarc foreland system, South Africa. *Basin Research* **10**, 417–439.

Rubidge, B.S., Erwin, D.H., Ramezani, J., Bowring, S.A. & de Klerk, W.J. 2010. The first radiometric dates for the Beaufort Group, Karoo Supergroup of South Africa. *Proceedings of the 16th Conference of the Palaeontological Society of southern Africa*, Howick, 5–8 August 2010.

Variation of cranial morphology and size in the gorgonopsian *Aelurognathus*

Norton, Luke; Rubidge, Bruce; Abdala, Fernando

Bernard Price Institute for Palaeontological Research, Palaeosciences Centre, University of the Witwatersrand, Johannesburg, South Africa
luke.norton@students.wits.ac.za

The Gorgonopsia were a group of highly specialized carnivores that lived approximately 265–250 Ma ago, during the Late Permian. Skulls belonging to Gorgonopsia range in size from those of a domestic cat, to larger than any extant terrestrial predator. Despite this wide range in size, morphological variation of the gorgonopsian skull is relatively conservative. The aim of this study was to identify and describe the extent of morphological variation occurring in a sample of gorgonopsian skulls attributed to the genus *Aelurognathus*. *Aelurognathus* represents the gorgonopsian genus with 16 assigned specimens which are attributed to six species. The length of the skull in this sample varies from approximately 18 cm to 34 cm. Specimens were examined in order to elucidate intra and interspecific variation. Differences observed at the interspecific level allowed for the recognition of three morphotaxa, based predominantly on characters of the skull roof. These characters included the state of a preparietal, and a contribution of the frontal to the supraorbital margin. A high degree of variability in the morphology and state of the preparietal has been well documented in various taxa of extinct and extant synapsids. Sutural boundaries between elements of the skull roof have also been demonstrated to be highly plastic. The extent of sutural variation has been shown to differ considerably, even between opposite sides of the same skull in a specimen of lemur. Taking these observations into account, the hypothesis that all specimens represented a single taxon exhibiting a high degree of morphological variation was tested using allometric techniques. Twenty-seven linear measurements were chosen, such that variability in skull size and shape could be accounted for in all dimensions. Results of the bivariate allometric analyses showed a high level of correlation of the plotted measurements with the calculated best-fit lines, supporting the single taxon hypothesis. While *Aelurognathus* has previously been divided into six species using only morphological characters, this study has shown that the characters used exhibit a high amount of variability. Excessive taxonomic importance has been placed on characters that now seem trivial, leading to a high number of described species of *Aelurognathus*. As such, it is proposed that all species currently attributed to the genus *Aelurognathus* be synonymized with the type, *Aelurognathus tigriceps*.

Establishing incidences of dental calculus and associated plant microfossils in South African Plio-Pleistocene hominin dentition

Odes, Edward¹; Berger, Lee²; Henry, Amanda³; Bamford, Marion¹

¹ Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa
eddieodes@gmail.com / marion.bamford@wits.ac.za

² Institute of Human Evolution, School of Geosciences, University of the Witwatersrand, Private Bag 3, Johannesburg, 2050 South Africa
lee.berger@wits.ac.za

³ Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
amanda_henry@eva.mpg.de

Study of the dental remains from Malapa, a fossil-bearing karstic cave site located in the Cradle of Humankind (Berger *et al.* 2010), have revealed the presence of dental calculus and associated phytoliths preserved on the teeth of *Australopithecus sediba* (MH1) (Henry *et al.*, in press). This raises the possibility that dental calculus and plant microremains may be present on hominin material from other cave sites, where fossils are preserved under similar conditions. Our aim was to establish whether dental calculus is present on the teeth of other southern African Plio-Pleistocene early hominins, and if so, how widespread it is, and how it manifests. We examined the dental collections of the Plio-Pleistocene age group of hominin sites of South Africa. For those fossils on which we found adherent material, we performed several analyses to determine whether this material is calculus or not.

As in previous studies, we performed a visual examination of the location and appearance of the calculus, and where possible, a comparison with the texture of the sediment matrix surrounding the fossil. In addition, we employed other methods, such as scanning electron microscopy with energy dispersive X-ray spectroscopy (SEM/EDX), which can establish whether the material was chiefly calcium phosphate (calculus) or something else. In certain cases, we removed small quantities of this material to determine whether it included food particulates and microfossils. In these cases, we also looked for microfossils in the surrounding matrix as a control. For those fossils on which no calculus material was found, we explored the possible causes for the lack of calculus, including preservation environments and potential preparation.

The results from this study will benefit future analysis by providing a list of target fossils, and a protocol for establishing the presence of calculus. These future studies may be able to obtain direct evidence of consumed food that can directly be associated with the individual hominins' feeding behaviours. This could result in significant clues to the diet and ecology of not only individual hominins, but populations, species and comparisons of diet and behaviour between species and genera.

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 australopit from South Africa. *Science* **328**, 195–204.

Henry, A.G., Ungar, P.S., Passey, B.H., Sponheimer, M., Rossouw, L., Bamford, M., Sandberg, P., de Ruiter, D.J., Berger, L. 2012. The diet of *Australopithecus sediba*. *Nature* **487**, 80–93.

Application of spore-pollen biostratigraphy in the deep offshore Cenozoic Niger Delta

Olayiwola, Moshood; Bamford, Marion

Bernard Price Institute for Palaeontological Research, Palaeosciences Centre, School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa
moshood.olayiwola@students.wits.ac.za / marion.bamford@wits.ac.za

The application of spore and pollen biostratigraphy in the deep offshore Miocene to Pliocene Niger Delta strata are of immense importance especially when other taxa make little or no significant impact. Much research has been done on the onshore deposits but the offshore deposits are now the focal point as these oil and gas reserves are now being exploited.

The purpose of this study is to analyse ditch-cutting offshore samples for their palynomorph contents to create a palynomorph biostratigraphic framework to complement the existing microfossil and nannofossil biostratigraphy in the Niger Delta. The published and unpublished literature on the palynology of Cenozoic sediments has been reviewed and synthesized with a view to identify and describe all the offshore palynomorphs in order to establish pollen biozones and ages of strata penetrated by the studied well A.

Biostratigraphic studies of spores and pollen recently carried out on well A from the southeastern Niger delta basin resulted in identification of over 112 spores and pollen taxa with their respective frequency distributions. This in turn resulted in a palynostratigraphic zonation of the strata penetrated by well A. Three distinctive zones comprise of seven subzones, ranging from Upper Miocene to Lower–Upper Pliocene Series, were established in this study.

The Upper Cretaceous calcareous nannoplankton of the St Lucia Formation at Nibela Peninsula, KwaZulu-Natal (Poster)

Ovechkina, Maria^{1,2,3}; Mostovski, Mike^{2,3,4}

¹ Discipline of Geology, School of Agricultural, Earth and Environmental Sciences, University of KwaZulu-Natal, Durban, South Africa
saccamina@gmail.com

² Paleontological Institute, Russian Academy of Sciences, Moscow, Russia

³ KwaZulu-Natal Museum, Private Bag 9070, Pietermaritzburg, South Africa.
mmostovski@nmsa.org.za

⁴ School of Life Sciences, University of KwaZulu-Natal, Scottsville, South Africa

The Upper Cretaceous St Lucia Formation at Nibela Peninsula is represented by poorly cemented silty finely grained sandstones with distinct layers of concretions. The beds are rich in invertebrate fossils and have yielded various cephalopods, bivalves, gastropods, scaphopods, rare echinoids and brachiopods.

One of the sections (S27°59.555' E32°25.533') was lithologically described and sampled for calcareous nannoplankton at 0.3–0.5 m intervals. Nineteen beds were recognized and 40 sediment samples were collected. Subsamples (ca. 100–200 g) were crushed, and smear slides were made for further identification. Calcareous nanno-fossils were identified using a Zeiss Axioskop microscope with crossed nicols at ×1200–1920 magnification. Almost the entire section contains a rich fossil assemblage, including 80 species with moderate to poor

preservation of nannoplankton. The most common species are *Watznaueria barnesae*, *Gartnerago obliquum*, *Reinhardtites anthophorus*, *Micula decussata*, *Eiffellithus turriseiffelii*, *Tranolithus orionatus*, *T. manifestus*, *Lithraphidites carniolensis*, *Microrhabdulus decoratus*, *M. belgicus*, *Prediscosphaera grandis*, and *Cretarhabdus crenulatus*. Less common are *Eiffellithus eximius*, *Cribrosphaerella ehrenbergii*, *Broinsonia matalosa*, *Calculites obscurus*, *Lucianorhabdus cayeuxii*, *Biscutum magnum*, and *Arkhangelskiella cymbiformis*, whereas *Broinsonia parca parca*, *B. p. constricta*, *B. p. expansa*, *Marthasterites furcatus*, and *Orastrum campanensis* are rare.

According to Perch-Nielsen (1985), the lowermost part of the section (Beds 1–3) is referred to the transitional Upper Santonian–Lower Campanian Zone CC17 due to the presence of *Calculites obscurus*, the first occurrence characterizing the lower boundary.

The Lower Campanian Zone CC18 from bed 4 to the mid. bed 15. Its lower boundary is identified by the first occurrence of *Broinsonia parca parca* and its upper boundary is defined by the last occurrence of *Marthasterites furcatus*. Bed 4 and the lower part of bed 5 belong to Subzone CC18a due to the presence of *Broinsonia parca parca*, the first occurrence of which is in sample 4. The interval from the upper part of bed 5 to the middle part of bed 15 belongs to undivided Lower Campanian Subzones CC18b–c with *Broinsonia parca constricta*, the first occurrence of which is in sample 7. *Ceralithoides verbeekii*, which occurrence defines the lower boundary of Subzone CC18c, is not found.

The upper section, from upper Bed 15 to Bed 19 is the Lower Campanian Zone CC19, the lower boundary being identified by the disappearance of *Marthasterites furcatus*.

The calcareous nannoplankton offers an older age of the sediments than it has been suggested previously by ammonites and inoceramids.

The usual suspect: experimental taphonomy vindicates the humble dermestid

Parkinson, Alexander Haig

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa
palaeoparky@gmail.com

The family Dermestidae of the order Coleoptera and the genus *Dermestes*, was first described by Linnaeus in 1758. The involvement of *Dermestes* in the animal decomposition process typifies members of this genus. The oldest recorded occurrence of Dermestidae dates back to the Late Triassic, but they are more reliably found in Cretaceous ambers. *Dermestes ater*, *Dermestes carnivorus*, *Dermestes frischii* and *Dermestes maculatus* are known to modify bone, but not substantially. Despite this known trait little work has been done to record the distinctive ways in which *Dermestes* modify bone. As a result a large body of palaeontological literature has arisen in which they are inferred as agents of bone modification without actualistic data to support such claims. This prompted our investigation in which bone specimens of various types, conditions and levels of preservation were exposed to *Dermestes maculatus*. Experimental tanks were established in a dedi-

cated insectary which maintained a constant temperature of 28°C at 40% humidity. The bone specimens were exposed to 100 larvae and 35 adults for a period of four months. Specimens were subsequently removed and analysed using an Olympus SZX 16 Multifocus microscope fitted with a digital camera at magnifications between $\times 7$ and $\times 115$. The modifications identified in this study were then classified, described and compared with those attributed to dermestids in the palaeontological literature. We show that the distinctive ways in which bones are modified by dermestids (bone destruction, irregular surface tunnels on cortical bone, pits without associated striations on cancellous bone, surface pits with associated striations on cortical bone as well as distinctive gnawing-related damage in the form of clusters of multiple striations) as well as the distribution thereof (periosteal surfaces, along edges, on cortical or only present on cancellous bone, etc.), are not comparable to modifications ascribed to dermestids in the palaeontological literature. Hence, experimental taphonomy has vindicated the humble dermestid as the modifier of many fossil remains in prehistory. However, the question still remains, who is responsible for the modifications described in existing literature? Ongoing actualistic research, based on the principle of uniformitarianism, promises to identify the agent(s) in question, but one has to consider that dermestid behaviour may have changed, or that the responsible agent is extinct.

Anisian (Middle Triassic) archosaur assemblages from Antarctica, Tanzania and Zambia: how do they relate to the Karoo?

Peacock, Brandon¹; Sidor, Christian¹; Nesbitt, Sterling²; Angielczyk, Kenneth³; Smith, Roger⁴

¹ Burke Museum and Department of Biology, University of Washington, Seattle, U.S.A.
bpeacock@uw.edu

² Department of Biology, University of Washington, Seattle, U.S.A.

³ Field Museum of Natural History, Chicago, Illinois, U.S.A.

⁴ Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa

The beginning of the Triassic (~252–237 Ma) was a critical interval in vertebrate history. Our understanding of how terrestrial ecosystems across southern Pangaea recovered from the end-Permian extinction is based almost exclusively on the well-sampled Karoo Basin of South Africa. Southern Pangaea has historically been viewed as relatively homogenous in community composition, especially during the Late Permian and Early Triassic, because sampling outside the Karoo yielded the same or similar taxa. However, paleontologists have qualitatively noted that by the Middle Triassic new clades had radiated and dissimilarity of taxonomic assemblages across the supercontinent had become a major feature of terrestrial ecosystems.

We sampled Middle Triassic localities in the Ntawere Formation of Zambia, Manda Beds of Tanzania, and Fremouw Formation of the Transantarctic Mountains and have assemblages that greatly differ from those of the Karoo *Cynognathus* Assemblage Zone, subzones B and C. Perhaps most significantly, these assemblages contain members of crown-group Archosauria, which is not

recovered in the better sampled Karoo. From Zambia we have teeth, a large vertebra belonging to a paracrocodylomorph pseudosuchian, a proximal femur of the first shuvosaurid poposauroid outside of the Late Triassic of the Americas, and postcranial material of a new genus of silesaurid dinosauriform. From Tanzania there is material from a number of pseudosuchians including representatives of aetosaur and ctenosauriscid lineages, as well as a silesaurid dinosauriform, *Asilisaurus kongwe*. From Antarctica we have a bizarre pseudosuchian femur of the first crown archosaur from the Triassic of the continent. These records support the idea that far from being homogenous, Pangaea was regionally diverse and supported provincial assemblages.

We have developed new metrics in biogeographic analysis to quantify assemblage dissimilarity, focusing on co-occurrences of taxa across basins and applying network methods. We have mapped terrestrial assemblages across distinct regional bins in southern Pangaea throughout the Triassic and can track increasing assemblage dissimilarity via the increased modularity score in our taxonomic co-occurrences. Modules within a network can be assigned to meaningful groupings in the real world (e.g. geographic location). Traditional biogeographic methods, including Simpson's Coefficient, Bray-Curtis index, and other distance-matrix methods support the contention that the Karoo Basin is not representative of the composition of taxonomic assemblages across southern Pangaea during the Anisian. To better understand the radiation of important Mesozoic clades, like Archosauria, we must look to traditionally under-sampled areas.

New small skeletal fossils from the Terreneuvian (Early Cambrian)-aged Sellick Hill Formation (Normanville Group) of South Australia

Penn-Clarke, Cameron; Yates, Adam

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa
cpennclarke@gmail.com

The Cambrian Period is a critical time in Earth's history where fossils of all major phyla of the Metazoa made their first tangible appearance in the rock record. A major factor for this phenomenon is tied in with advent of biomineralization, with the development of harder chitinous or calcareous or phosphatic exoskeletons, i.e. a scleritome composed of many sclerites, or shells over their soft bodies, and, as seen in later vertebrates, a cartilaginous or phosphatic endoskeleton, possibly as a line of defence. Individual skeletal elements usually are disarticulated from their original position in life, making anatomical interpretations and phylogenetic relationships of these metazoans obscure. Collectively, these skeletal elements are referred to as small skeletal fossils (SSF). Estimating the phylogenetic relationships of these SSF's is plagued by discrepancies in calibrating early Cambrian time. Formal global epoch and stage subdivision schemes for the Cambrian Period have been suggested, but are poorly defined and not yet widely implemented. Sedimentary strata of the eastern Officer and Warburton Basins as well as the Stansbury and Arrowie Basins and Stuart and Spencer Shelves of the uppermost Adelaide Rift Complex

of South Australia are well known to contain fossils of the earliest protostome and deuterostome metazoans and are an arena of active research. The Sellick Hill Formation is part of the Normanville Group of the Stansbury Basin. This study considers the palaeontological, taphonomic, sedimentological and biostratigraphic implications of a hyolith rich, intraclast conglomerate horizon in the lower Sellick Hill Formation. Here, three new coeloscleritophorans are described, as well as the validity of previously described specimens, since these fossils share no resemblance with those previously described. The seemingly unique nature of these fossils, although from one horizon, may have dire biostratigraphic implications and are discussed in terms of their intra- and inter-basin and international correlations. The diagenetic and taphonomic history is also discussed in an attempt to understand the environment of deposition and post depositional history of this horizon. Here up to 14 diagenetic and taphonomic stages have been identified. The disarticulated and highly damaged nature of recovered fossils, in addition to the sedimentology of this horizon implies a thanatocoenotic assemblage accumulated under periodic storm activity. The genesis of these seemingly unique fossils is, however, unknown. It is suggested that these sclerites were brought into the Normanville Basin from elsewhere under a period of storm activity. This study has also attempted to place the biota and lower Sellick Hill Formation within the context of earliest Cambrian time. Based on the sum of all data from the Sellick Hill Formation, in addition to described specimens, an Atdabanian, if not earlier, age is suggested for the Formation as opposed to the currently accepted Botoman age.

Basin analysis, palaeontology and biostratigraphy of the Early to Middle Devonian Bokkeveld Group (Cape Supergroup), Western Cape (Poster)

Penn-Clarke, Cameron¹; Rubidge, Bruce¹; Jinnah, Zubair¹; Almond, John²

¹ Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa
cpennclarke@gmail.com

² Natura Viva CC, P.O. Box 12410 Mill Street, Cape Town, 8010 South Africa

Worldwide the Devonian Period is marked by the *en masse* colonization and diversification of terrestrial embryophytes, the so-called 'Devonian Explosion'. Body fossils, as well as ichnofossils indicate that by the Late Devonian to Early Carboniferous, fully terrestrial-adapted arthropods (the arachnids, isopods, myriapods and hexapods), as well as tetrapods, were adapted to living on land. In the oceans, fish also underwent radiation with many ancient orders existing concomitantly with more derived orders, in particular actinopterygian and sarcopterygian fish as well as true sharks (Neoselachii). Ammonoid cephalopods also made their first appearance during the Devonian Period. From palaeontological evidence, rocks of the South African Bokkeveld Group (Cape Supergroup) are considered to have been deposited between the Early to Middle Devonian. Considering the aerial extent of the Group, relatively little research has been undertaken on the sedimentology, stratigraphy and

palaeontology of this very important aspect of the South African fossil record. The rocks of the Bokkeveld Group contain a rich fossil fauna of Malvinokaffric Realm invertebrates, fish and plants. The Bokkeveld Group records sedimentation as a series of five upward coarsening megacycles. Each megacycle is composed of a basal horizontally-bedded mudstone-siltstone. Lenticular and wavy bedding is also present. These units grade upwards into an overlying amalgamated sandstone body with a lateral (along strike) extent of >150 km. Initiation of each megacycle is related to a combination of reduction in sediment supply and basin deepening, most likely from extensional subsidence. Overall the Bokkeveld Group is a shallowing upward sequence with the overlying, conformable, and increasingly terrestrial Witteberg Group. The pre-cursors and events leading up to potential terrestrial environments in the Witteberg Group, although hinted at by previous work done on the Bokkeveld Group, have not yet been recognized and remain a field of potential study. This project aims to reassess the sedimentology of the Bokkeveld Group, in addition to discussing lithological relationships within a sequence stratigraphic framework in order to understand dynamics of the Cape Basin at time of sedimentation at a section in the Cederberg Range, Western Cape. Fossil assemblages of the Bokkeveld Group too shall be addressed as well as any temporal or spatial controls over their occurrences/ranges in order to discuss any environmental and/or ecologic controls present during this time frame.

A reconstruction of the sphenophyte *Trizygia speciosa* from the latest Permian Wapadsberg Pass locality in the Eastern Cape

Prevec, Rose¹; Looy, Cindy²; Gastaldo, Robert³

¹ Geology Department, Rhodes University, and Albany Museum, Grahamstown, South Africa.
r.prevec@ru.ac.za

² Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, U.S.A.

³ Department of Geology, Colby College, Waterville, U.S.A.

The Wapadsberg Pass plant fossil locality, Eastern Cape Province, has produced one of the youngest *Glossopteris*-dominated floras in the world, situated 70 m below what is generally considered to be the Permian/Triassic boundary on the basis of regional vertebrate biostratigraphy. Although of unusually low diversity for a glossopterid flora, the quality of impression fossil preservation is high in this autochthonous deposit that is preserved in a possible reworked ash. This has resulted in the preservation of very delicate structures including over 40 cones attributed here to the sphenopsid *Trizygia speciosa*. Although this sphenophyte is widespread across Gondwana (it was first described from India by Royle in 1839), fertile organs have not been reported previously. The cones are mostly dispersed, but several are attached to stems typical of *Trizygia*, that are gracile with expanded nodes. This differs from the broader forms of *Paracalamites* that can be attributed to *Phyllothea australis*, the only other, fairly rare, sphenophyte found at the locality. Spores have been isolated from compression material within cones. Although known from a number of Late

Permian (Lopingian) localities in South Africa, well-preserved specimens of *T. speciosa* are rare, typically with only one or a few consecutive leaf whorls preserved. However, dense mats of stems with multiple leaf whorls are present at the Old Wapadsberg Pass. Examination of this unusual fossil flora has provided insights into the morphology of a little-understood sphenopsid, as well as providing a glimpse of life prior to the greatest extinction event in Earth's history.

Bone histology of the stegosaur, *Kentrosaurus aethiopicus* (Ornithischia: Thyreophora), from the Upper Jurassic of Tanzania

Redelstorff, Ragna¹; Hübner, Tom²;
Chinsamy-Turan, Anusuya¹

¹ Department of Zoology, University of Cape Town, Rondebosch, Cape Town
ragna.redelstorff@uct.ac.za

² Niedersächsisches Landesmuseum Hannover, Hannover, Germany

Using bone histology, a slow growth rate, atypical of most dinosaurs, has been interpreted for the highly derived stegosaur, *Stegosaurus* (Ornithischia: Thyreophora), and the basal thyreophoran *Scutellosaurus* (Redelstorff & Sander 2009; Padian *et al.* 2004). As the Thyreophora are basal within the Dinosauria, this growth rate may reflect a plesiomorphic growth pattern within the clade and has direct implications for their biology. It is therefore imperative that further analyses of Thyreophoran bone histology are conducted. To this end, we analysed the bone histology of the stegosaur *Kentrosaurus* from the Early Jurassic deposits of the Tendaguru beds of Tanzania. *Kentrosaurus* is both intermediate in size and phylogenetic position between *Scutellosaurus* and *Stegosaurus*. We studied the morphology and dimensions of all the *Kentrosaurus* femora at the Berlin Museum of Natural history, and we were permitted to sample five femora for histological analyses. Our histological samples of *Kentrosaurus* reflect an ontogenetic series from subadult to adult specimens. We found that primary bone in *Kentrosaurus* consists mainly of highly vascularized fibro-lamellar bone with reticular vascular channels. In addition to LAGs and annuli, distinctive changes in the organization of vascularization occur in the compacta, which seem to depict a regular cyclicality. This variation in vascularity may reflect annual climatic fluctuations. The bone deposition and growth rate in *Kentrosaurus* is significantly faster than that observed in *Stegosaurus* and *Scutellosaurus*. Considering that *Stegosaurus* is the larger-sized of the two stegosaurs, this contrasts with the deductions made previously that small dinosaurs have slower growth rates than large dinosaurs (Padian *et al.* 2004). Our analysis of *Kentrosaurus* suggests that the slow growth rate is, not a phylogenetic characteristic of the Thyreophora but may rather indicate a secondarily reduced growth rate in the highly derived *Stegosaurus*.

First biarmosuchian therapsid from the Pristerognathus Assemblage Zone of the Karoo Basin, South Africa

Rubidge, Bruce; Day, Mike; Abdala, Fernando

BPI Palaeontology, School for Geosciences, University of the Witwatersrand,
Johannesburg, South Africa

bruce.rubidge@wits.ac.za / michael.day@students.wits.ac.za /
nestor.abdala@wits.ac.za

The Biarmosuchia, previously known from only a few poorly preserved specimens from South Africa and Russia (Sigogneau-Russell 1989), are considered to be the most basal therapsid clade and have recently been the subject of renewed investigation with the description of several new genera (e.g. Rubidge & Kitching 2003; Rubidge *et al.* 2006; Sidor & Rubidge 2006; Sidor *et al.* 2004; Sidor & Smith 2007; Smith *et al.* 2006). Most of these new genera belong to the Burnetiamorpha, a bizarre and apparently derived clade of the biarmosuchia characterized by pachyostotic bosses on the skull roof. This group now comprises ten genera including *Lemurossaurus*, *Lobalopex*, *Lophorhinus*, *Paraburnetia*, *Burnetia*, *Niuksenitia*, *Bullacephalus*, *Pachydictes* and a new undescribed form from Malawi. Apart from *Lemurossaurus*, which comprises two specimens, the rest of the genera are known from only a single holotype specimen. Two of these genera are from Russia, one from Malawi, and eight are from South Africa.

Burnetiamorphs have a Mid-Late Permian stratigraphic range and in South Africa are known from all the Permian biozones of the Beaufort Group, save the Eodicynodon and Pristerognathus Assemblage Zones (Sidor & Smith 2007), with some of these biozones having more than one genus. Previous phylogenetic analyses have linked *Pachydictes* and *Bullacephalus*, the stratigraphically lowest occurring genera, with *Burnetia*, the burnetiamorph from the latest Permian of South Africa; such a result suggests that most of the biarmosuchian lineage is unrecorded. This paper describes a new specimen, the first from the Pristerognathus Assemblage Zone, which adds to our understanding of the taxonomic diversity and biostratigraphic distribution of the taxon.

Rubidge, B.S. & Kitching, J.W. 2003. A new burnetiamorph (Therapsida: Biarmosuchia) from the lower Beaufort Group of South Africa. *Palaeontology* **46**, 199–210.

Sidor, C.A., Hopson J.A. & Keyser, A. 2004. A new burnetiamorph (Therapsida: Biarmosuchia) from the Teekloof Formation, Permian of South Africa. *Journal of Vertebrate Paleontology* **24**, 938–950.

Sidor, C.A. & Rubidge, B.S. 2006. A new biarmosuchian (Therapsida: Biarmosuchia) from the Beaufort Group of South Africa pp. 76–113. In: Carrano, M.T., Gaudin, T., Blob, R. & Wible, J. (eds), *Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles*. Chicago, University of Chicago Press.

Sidor, C.A. & Smith, R.M.H. 2007. A second burnetiamorph therapsid from the Permian Teekloof Formation of South Africa and its associated fauna. *Journal of Vertebrate Paleontology* **27**, 420–430.

Sidor, C.A. & Welman, J. 2003. A second specimen of *Lemurossaurus pricei* (Therapsida: Burnetiamorpha). *Journal of Vertebrate Paleontology* **23**, 631–642.

Sigogneau-Russell, D. 1989. Theriodontia I. In: Wellnhofer, P. (ed.), *Encyclopedia of Paleoherpetology*, Part 17B, 1–127. Stuttgart, Gustav Fischer.

Smith, R.M.H., Rubidge, B.S. & Sidor, C.A. 2006. A new burnetiid (Therapsida: Biarmosuchia) from the Upper Permian of South Africa and its biogeographic implications. *Journal of Vertebrate Paleontology* **26**, 331–343.

The gigantism in fossil amphibians

Sanchez, Sophie

Uppsala University, Sweden
sophie.sanchez@ebc.uu.se

The appearance of large, even giant, animals in the evolutionary history of vertebrates has long raised the attention of biologists and paleontologists, especially

when regarding fishes, marine reptiles, dinosaurs and mammals. Gigantism is defined as an excessive growth of the stature compared to the mean size of the adult individuals of the same clade which is equal to or more than two standard deviations. During their evolution, amphibians (as non-amniotic tetrapods) also exhibited giant body lengths, attaining up to six or seven metres during the Triassic period. Understanding how such giant sizes could have been reached in fossil amphibians is of major interest, especially when regarding the size distribution of the lissamphibians (1.8 m for the larger lissamphibian: *Andrias davidianus*, the so-called giant Chinese salamander). In order to find some explanations for this gigantism in fossil amphibians, I have performed a preliminary histological study on the long-bone midshafts of fourteen species among the various clades of the Temnospondyli, Seymouriamorpha and Embolomeri. It seems that gigantism in fossil amphibians may have been a hyperpituitary gigantism observable at the histological level, i.e. a combination of 1) an increase of growth rates (which can be 50–80 times higher in *Wetlugasaurus angustifrons* than in *Apateon pedestris*, for example), as suggested in this study by skeletochronology; and 2) a blocking of the development suggested by the retention of juvenile histological features in adults (=paedomorphosis). These histological phenomena could certainly be linked to environmental conditions; increases in size and hypothyroid activity have already been observed in tetrapods, which have secondarily returned to the aquatic environment. It is now necessary to focus on the ecological changes, which occurred during the Permian-Triassic crisis, in order to better understand the physiological reactions of these giant fossil amphibians, especially among temnospondyls, which lived up to the Early Cretaceous.

The global biogeography, taxonomy and chronological distribution of insular proboscideans
(Poster)

Scarborough, Matthew E.

Department of Zoology, University of Cape Town, Rondebosch, South Africa
matthew.archaeology@gmail.com

Proboscidean fossils are known from many islands around the world, including many of the Mediterranean and southeast Asian islands, dating from the Miocene to Mid-Holocene. A checklist of the global occurrence of proboscideans on islands is presented, and the chronology, taxonomy and presence of size-reduction in insular endemics is reviewed. The greatest diversity in insular proboscideans occurs in the genera *Palaeoloxon*, *Stegodon* and *Mammuthus* during the Pleistocene, all of which repeatedly evolved endemic species on islands. Homoplastic traits in endemic proboscideans and their possible heterochronic evolutionary mechanisms are discussed.

Fluctuating Miocene climates and ecosystems at the southern tip of Africa: a multiproxy approach

Sciscio, Lara¹; Neumann, Frank H.²; Roberts, David³; Tsikos, Hari¹; Scott, Louis⁴; Bamford, Marion⁵

¹ Department of Geology, Rhodes University, Grahamstown, South Africa
l.sciscio@gmail.com

² Forschungsstelle Palaeobotanik, University of Münster, Germany

³ Council for Geoscience, Bellville, South Africa

⁴ Department of Plant Sciences, University of the Free State, Bloemfontein, South Africa

⁵ BPI Palaeontology, School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa

The largest Lagerstätte of excellently preserved Mio-Pliocene terrestrial fauna in South Africa is located at Langebaanweg (LBW), now the West Coast Fossil Park situated ~120 km north of Cape Town. This research deals with a core drilled at Langebaanweg 'E' Quarry, which captures Miocene fluvial deposits of the Elandsfontyn Formation (Sandveld Group), unconformably underlying the Mio-Pliocene faunal deposits. The work aims to constrain fluctuations in climate and ecosystems in the region during the Miocene, using palynological, biogeochemical, stable isotope (C, N) and sedimentological approaches. A novel proxy for the reconstruction of terrestrial palaeoclimates, which examines branched glycerol dialkyl glycerol tetraether (GDGTs) membrane lipids produced by soil bacteria, has been used. We have applied these biomarkers (or molecular 'fossils') in conjunction with palynology to the organic sediments of the poorly studied Elandsfontyn Formation.

The mean annual temperature (MAT) and ambient pH values of the organic-rich horizons, at time of deposition, were calculated using the Methylation index of branched tetraethers (MBT) and cyclization ratio of branched tetraethers (CBT) proxies. LBW samples, which span 17–33 m below sea level, had MATs ranging between 12.4°C to 26.6°C and pH range from 4.4 to 6.4 over the 16 m of core studied. Furthermore, samples showed a narrow, light (from -25.52‰ to -24.27‰) $\delta^{13}\text{C}$ value distribution and overall low C/N ratios. Palynological investigation supplemented earlier studies, reaffirming alternating sequences of tropical and subtropical elements and complementing calculated MAT results. Pollen results from the subsection 1 (30.89–33 m) provide evidence of a species rich *Podocarpus*-dominated forest with MATs at 16.2°C. The pollen-bearing section between 16.45 m and 20.35 m depth (subsection 2) shows initially less humid conditions, with MATs between 15.4–26.6°C, similar to the bottom of the section with high podocarp percentages, low Restionaceae and aquatics. The results suggest that the regional Miocene climate showed high amplitude fluctuations (possibly driven by orbital forcing as seen in marine cores), underscoring the potential of biogeochemistry for unravelling past climates and ecosystems.

Early Jurassic trace fossil and conchostracan-bearing lacustrine deposits: refining the ancient dryland ecosystem of the Upper Elliot Formation (Karoo Supergroup) in Lesotho
(Poster)

Sciscio, Lara¹; Bordy, Emese M.¹; Knoll, Fabien²; de Cock, Michiel³

¹ Department of Geological Sciences, University of Cape Town, Rondebosch, South Africa
lara.sciscio@uct.ac.za / emese.bordy@uct.ac.za /

² Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, Madrid, Spain
mcnfk854@mncn.csic.es

³ Department of Geology, University of Johannesburg, South Africa.
mdekock@uj.ac.za

The Elliot Formation (Late Triassic – Early Jurassic) of the

Karoo Supergroup is a fossiliferous, fluvio-lacustrine red bed succession that is believed to capture the end-Triassic mass extinction event and subsequent biotic recovery in the Early Jurassic of southern Africa. A new study site in south-western part of Lesotho (Ha Seeiso, near Matelile, Mafeteng District) reveals a previously unreported lacustrine deposit within the upper Elliot Formation. This interbedded succession of fine-grained sandstones and mudstones is ~17 m thick, and is characterized by laterally persistent, tabular beds that show no evidence for channelling. The grain sizes, sedimentary structures, facies architecture and invertebrate and vertebrate ichnofossil assemblage suggest energy level fluctuations in an otherwise low energy depositional setting. Furthermore blue-black, finely laminated organic-rich mudstones which lack any pedogenic alteration features imply a lake system with multiple anoxic periods. These unique organic units also contain conchostracan (*Cyzicus*) and ostracod valve impressions which suggest seasonal evaporation events. Ostracod-bearing beds have only previously been mentioned in the Clarens Formation. This new fossil locality encapsulates the life and events of an ephemeral lake in the arid depositional environment of the uppermost Elliot Formation. Further geochemical and palynological examinations of the organic units are being undertaken in order to improve our understating of the dynamics of this Early Jurassic lacustrine ecosystem.

A new method to determine volume of spiral bromalites

(Poster)

Shelton, Christen D.

Steinmann Institut of Geology, Mineralogy and Palaeontology,
University of Bonn, Germany
drcarter12@aol.com

Lower Permian vertebrates from both terrestrial and aquatic organisms have been collected from Archer County, Texas, U.S.A. for over a century. This includes preserved shark cartilage and spiral bromalites presumed to have been produced by freshwater sharks of the genus *Orthacanthus*. Specimens were collected in the newly named Archer City Bone Bed V (Archer City Formation). Physical characteristics (length, width, height, mass, eccentricity, volume, and density) were measured and recorded for 300 spiral heteropolar bromalites and compared by linear regression analysis. The spiral bromalites had an average length of 31.74 mm; width 14.43 mm; height 10.51 mm, and mass 7.971 g. Eccentricity around the longest axis was between 0.9399 and 0.0602. In addition to the statistical collection, a new formula is proposed to help determine the volume of the elliptical fossils when volume determination by water displacement is not an option. The regression analysis between the observed volumes obtained by water displacement and the calculated volumes showed $R^2 = 0.9836$. The percentage difference between the two measurements ranged from 0.04% to 56% (95% of the statistical sample had a percentage difference of <30). Data from this study and the formula developed here will help to understand not only the spiral bromalites from this area, but also bromalites from different localities, geological ages, and different

origins. Problems with this formula include accuracy of the physical measurements, which would be skewed due to any extra matrix on the specimen. Also, the formula assumes that all specimens terminate in a point, but many bromalites are incomplete or have blunt tips, due to destructive forces of nature, erosion, or lack of preservation. This would allow some room for error and perhaps explain the extreme percentage difference in some specimens. These data, if compiled with data from the analysis of specimens from other localities, may ultimately reveal size groupings that could reflect the presence of previously unknown taxa that possessed a spiral valve and coexisted with the *Orhtacanthus* sharks. From the data we can only conclude that a single species produced the heteropolar bromalites at this bone bed. A standard precedent for classifying these fossils based on external as well as internal morphometric data is crucial to understanding their origin and producers.

***Ophiacodon* long bone histology – testing the Brinkman hypothesis**

Shelton, Christen D.; Sander, P. Martin

Steinmann Institute of Geology, Mineralogy and Palaeontology,
University of Bonn, Germany.
drcarter12@aol.com

The validity of species in a genus that only differ in size has always come into question. Histological analysis is one of the most definitive methods of species determination based on ontogenetic stages of the diaphyseal mid-shaft of long bones, usually femora or humeri, which are known to contain the best record of growth. In non-therapsid synapsids (pelycosaur), some species have been identified solely on the basis of size regardless of the degree of ossification observed in the epiphysis. Brinkman (1988) attempted to overcome this problem by establishing size-independent morphological criteria on putative growth series of pelycosaur including *Ophiacodon*. Based on degree of ossification of the epiphyses and the development of specific anatomical structures, he subdivided the putative growth series into five stages. Here we test his hypothetical growth series using histological indicators. The growth series comes from the Rattlesnake Canyon locality (Nocona Formation, Lower Permian) in Archer County, Texas, U.S.A.. We conclude that the histology of the *Ophiacodon* humerus growth series of Brinkman does support the morphological ontogenetic stages he assigned to those specimens. The general histology of the humeri consist of a cortical bone matrix made up of parallel-fibred and woven bone and is highly vascularized by radial canals with varying degrees of lamellar bone infilling. This gives the cortex a 'spoked bicycle wheel' appearance. The medullary cavity is filled with a network of trabecular bone. The outer most cortex of the largest humerus, assigned to stage five by Brinkman, contains an external fundamental system (EFS) and a sharp decrease in vascularization. This unequivocally indicates that the animal had passed sexual maturity. However, the time represented by the EFS is unknown. The smallest humerus examined was determined by Brinkman to be a stage two and its histology preserves the neonatal line in the deep cortex. This is an indicator of the time when the animal

presumably hatched, and is the boundary between original embryonic bone and tissue deposited postnatally. The histology and vascularization of the cortex is very similar to that seen in *Dimetrodon natalis* and, surprisingly, basal sauroptrygians. This tissue has been named incipient fibro-lamellar bone. It is the precursor to the true fibro-lamellar bone seen later in therapsids and mammals.

Field evidence for stepped mass extinction in the South African Karoo Basin at the end-Permian

Smith, Roger¹; Botha-Brink, Jennifer²

¹ Iziko South African Museum, Cape Town, South Africa
rsmith@iziko.org.za

² Karoo Palaeontology, National Museum, Bloemfontein, South Africa

The southern Karoo Basin of South Africa contains an uninterrupted terrestrial record of the Permo-Triassic boundary (PTB). Isotope- and magneto-stratigraphy confirm that these fluvial strata are approximately the same age as zircon-dated marine PTB sections (252 Ma). To date, our team has found 580 identifiable, *in situ* vertebrate fossils, mostly therapsids, in PTB exposures at four separate locations. Biostratigraphic range plots reveal a pronounced extinction event within the same stratigraphic interval in each of the PTB sections as well as a regular sequence of taxon disappearances and taphonomic signatures that are interpreted as reflecting real changes in the original populations due to rapid climatic drying and drought. Within the uppermost 45 metres of the Balfour Formation, the sequence of sedimentological facies reflects progressive straightening of the channels and floodplain rubification. Although thicknesses vary, this sequence remains consistent across all sections and is interpreted as indicative of a rapid climatic warming and drying with the onset of a monsoon-type rainfall regime. In the lowlands of the Karoo basin ground-level ferns, clubmosses and liverworts were the most susceptible to the lowering of groundwater. Consequently the formerly flourishing populations of small gregarious herbivorous dicynodonts such as *Diictodon* and *Pristerodon* decreased and eventually disappeared along with their medium-sized gorgonopsian predators (*Aelurognathus*, *Cyonosaurus*). As droughts became more frequent the *Glossopteris* riparian woodlands thinned out causing large-bodied dicynodonts (*Dicynodon*, *Aulacephalodon*, *Dinanomodon*) and their attendant carnivores to die off. A terminal drought phase is recognizable in all the sections as a roughly 5 metre-thick interval containing 1–3 beds of generally rubified finely laminated mudrocks with very little pedogenic modification. Rare skulls and fragmental caniniform processes of the larger Permian taxa *L. maccaigi*, *Moschorhinus* and a very rare skull of *Dicynodontoides* occur in this interval, the top of which is regarded as a reliable lithostratigraphic marker of end of the End-Permian mass extinction in the Karoo Basin.

The dietary behaviour of mammals from Cooper's Cave

Steininger, Christine

Institute of Human Evolution, School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa
christine.steinger@wits.ac.za

Preliminary ecological reconstructions based on com-

parisons of fossil and modern mammals suggests this site is a predominately a grassland environment (deRuiter *et al.* 2009). This argument is flawed, as the behaviour of a mammal in the past may not be the same as the present. For example, the modern impala is considered a savanna antelope that consumes a mixture of grass and leaves; however, using a direct method, stable carbon isotope analysis, this same species fed primarily on tree leaves in the past. In addition, based on its dietary preference we can infer that this species may have favoured a woodland environment. Research conducted for my doctoral dissertation based on the dietary behaviour of several bovid species from Cooper's Cave (locality D) and Swartkrans (Members 1–3) suggests that, while grass was a component of the landscape, woody vegetation predominated, at least in the immediate vicinity of these caves. Research is under way to sample the dietary behaviour of a larger component of the mammal community from Cooper's Cave. This site has a diversity of mammals, including hominins and early stone tools with uranium series dates of 1.5–1.4 Ma. Two questions are addressed: (1) will a representative sample of diverse mammals from Cooper's Cave show a predominately-woody vegetation structure and (2) How are mammals including hominins partitioned within this environment based on their dietary behaviour?

Tooth root morphology in the giant African bear *Agriotherium africanum* (Mammalia, Carnivora, Ursidae) and its implications for feeding ecology

Stynder, Deano¹; Kupczik, Kornelius²

¹ Department of Archaeology, Faculty of Science, University of Cape Town, Rondebosch, South Africa
deano.stynder@uct.ac.za

² Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Universität Jena, Jena, Germany

Tooth root surface areas serve as a proxy for bite force potentials, and by extension, dietary specialization in extant carnivorans. In this study, we investigate the feeding ecology of the extinct ursid *Agriotherium africanum* by comparing its root surface areas (reconstructed with the aid of computed tomography and three-dimensional image processing) and bite force estimates, with those of extant carnivorans. Our results show that in absolute terms, *A. africanum* exhibited higher canine and carnassial bite forces and root surface areas than the extant carnivorans used in this study. However, when adjusted for skull size, *A. africanum*'s canine roots were smaller than those of extant large predators. As teeth are the limiting factor in the masticatory system, low canine root surface areas suggest that *A. africanum* struggled to bring down large terrestrial prey. In addition, its adjusted carnassial root sizes were found to be smaller than those of extant hard and tough object feeders, but larger than those of extant mesocarnivorous ursids and *Ursus maritimus*. The fact that it also possessed carnassials with hyaena-like (pointed) cusps and exhibited its highest post-canine root surface areas in the carnassial region, suggest that *A. africanum* was more competent at scavenging than extant ursids. As the largest carnivore on the early Pliocene African landscape there was an ecological opportu-

nity for it to develop into a specialist scavenger of large terrestrial vertebrates, a niche that it likely occupied given its dental root morphology. Be this as it may, the presence of premasseteric fossae on its mandible suggests that it would have consumed plant material on occasions.

Piltdown Man and Teilhard de Chardin

Thackeray, Francis

Institute of Human Evolution, School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa
francis.thackeray@wits.ac.za

On January 5, 1913, the French palaeontologist, philosopher and priest, Pierre Teilhard de Chardin, wrote an essay in a French Jesuit journal called *Etudes*. The essay was written within a few weeks of the official announcement in London of the discovery of 'Piltdown Man', assigned to *Eoanthropus*, which included a human cranium and a carefully modified mandible and isolated canine of an orangutan. The opening sentence of Teilhard's essay is as follows: 'Il fut un temps où la préhistoire méritait d'être suspectée ou plaisantée'. This can be translated to mean 'There was a time when the study of prehistory deserved to be suspected, or deserved to be the subject of jokes'. Attention is drawn to the mere possibility that almost immediately after the official announcement of 'Piltdown Man' in Burlington House in London (December 18, 1912), Teilhard wrote this sentence in Paris when he may have been disturbed by the fact that English palaeontologists, including Smith Woodward of the British Museum (Natural History), may have been 'taken in' by a joke. If Teilhard had known even before January 1913 that Piltdown was intended as a joke, he could have been deeply concerned by the potential adverse impact if the 'Piltdown joke' was taken seriously. It is suggested that he was writing with Piltdown in mind when he wrote the opening sentence of his essay in January 1913, referring to the study of prehistory, including palaeo-anthropology, as a field which deserved to be 'suspected' and which deserved to be a 'subject of jokes'. Within the Jesuit order, it was considered acceptable to lie provided it was a joke (Thackeray 2012). 'Piltdown Man', announced 100 years ago, is likely to have been a joke associated not only with Teilhard de Chardin but also Martin Hinton and Charles Dawson. The latter was known to have been a perpetrator of forgeries, and is also likely to have been involved in Piltdown (perhaps in the case of 'Piltdown II').

New data on the cranial anatomy, phylogenetic position and biogeography of *Bunostegos akokanensis*

Tsuji, Linda¹; Sidor, Christian¹; Smith, Roger²; Steyer, Jean-Sébastien³

¹ Burke Museum and Department of Biology, University of Washington, Seattle, U.S.A.
latsuji@uw.edu

² Iziko South African Museum, Cape Town, South Africa

³ Department Earth History, CNRS-Museum National d'Histoire Naturelle, Paris, France

Newly recovered cranial material of *Bunostegos akokanensis*, a pareiasaurian reptile known only from the Upper Permian Moradi Formation of northern Niger, permits a redescription of the taxon in addition to inclusion of new

information in a phylogenetic analysis of pareiasauro-morphs. *Bunostegos* is highly autapomorphic, with diagnostic cranial features including: two or three hemispherical bosses located at the anterior end of the snout; elongate, laterally projecting supraorbital 'horn' formed by an enlarged postfrontal; large foramen on ventral surface of postfrontal; hemispherical supratemporal boss at posterolateral corner of skull roof. We addressed the phylogenetic position of *Bunostegos* by incorporating it into a cladistic analysis of 29 parareptilian taxa (including all 21 currently valid named pareiasaurs) and 127 cranial and postcranial characters. The results place *Bunostegos* as more derived than the South African Middle Permian forms such as *Bradysaurus* and *Embrithosaurus*, and as the sister taxon to the Upper Permian taxa including the Russian *Deltavjatia* plus *Velosauria*. Characters related to the cranial sculpture and to the size and placement of the tabulars appear to be similar to more derived pareiasaurs such as *Elginia* from Scotland and *Arganaceras* from Morocco, but parsimony indicates that these features appeared independently in *Bunostegos*. The relationships of velosaurian pareiasaurs, including *Anthodon*, *Pumilio-paraia*, and *Scutosaurus*, were consistent with those of previous analyses.

Pareiasaurs are important biostratigraphic markers within the five Permian assemblage zones established for South Africa's Beaufort Group. In addition, the occurrence of *Pareiasuchus* and *Anthodon* in the Ruhuhu Basin of Tanzania and *Pareiasuchus* in the Luangwa Basin of Zambia has contributed to the regional correlation of these strata. The tetrapod fauna of the Moradi Formation, however, has proven difficult to correlate to other African assemblages because it contains endemic genera (viz. *Bunostegos*, *Moradisaurus*, *Nigerpeton*, and *Saharastega*). The single therapsid known from Niger, an indeterminate gorgonopsid, is suggestive of an Upper Permian assignment, but is hardly definitive. Moreover, the lack of both dicynodont herbivores and *Glossopteris* in the Permian of Niger indicates a markedly different community structure and supports the theory that central Pangaea was biogeographically isolated from the rest of the supercontinent by desert-like conditions. Our improved understanding of the morphology and phylogenetic position of *Bunostegos* helps to piece together a more complete picture of Permian tetrapod evolution.

Post-mortem in 3D: new methods to assess the spatial taphonomy of the early hominins from the Malapa site

Val, Aurore^{1,2}; Backwell, Lucinda R.¹; Berger, Lee³; d'Errico, Francesco^{2,4}

¹ Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa
aurore_val@yahoo.com / lucinda.backwell@wits.ac.za

² PACEA UMR 5199-CNRS, Université Bordeaux 1, France

³ Institute for Human Evolution, University of the Witwatersrand, Johannesburg, South Africa
profleeberger@yahoo.com

⁴ Department of Archaeology, History, Cultural Studies and Religion, University of Bergen, Postboks 7805, NO-5020 Bergen, Norway
f.derrico@pacea.u-bordeaux1.fr

Two nearly complete skeletons of early hominins

(*Australopithecus sediba*; Berger *et al.* 2010) were found at the Malapa cave site (Bloubaank Valley, Gauteng Province, South Africa), in a deposit dated at 1.977 Ma (Dirks *et al.* 2010; Pickering *et al.* 2011). Some anatomical elements were still in articulation and their bone surface shows a good state of preservation. This case scenario (high number of remains per individual, preservation of some articulations, good preservation of the outer bone morphology, high percentage of complete bones) is extremely rare in the context of early hominin discoveries. In order to understand the fossilization processes that have led to such an unusual level of preservation, a comprehensive taphonomical analysis of the hominins and associated faunal remains is currently being conducted. We summarize here the techniques and methods used to investigate the taphonomic implications of the spatial arrangement and orientation of the hominin remains.

The remains of two near-complete individuals (Malapa Hominid 1, a juvenile male and Malapa Hominid 2, an adult female) include 183 specimens, 46 of which were recovered *in situ* and 137 in various *ex situ* blocks of clastic calcified sediment. Each phase of the excavation and preparation processes, including the spatial coordinates of the *in situ* remains, was recorded. By combining this information and the 3D virtual renderings of each specimen to geological and sedimentary data, we are able to propose a best-fit 3D model of the original position of the two *A. sediba* individuals within the deposit, prior to mining damage. This model has been created by applying CT and micro-CT scanning techniques and 3D rendering software (Avizo 6.3).

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 australopit from South Africa. *Science* **328**, 195–204.
 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.
 Pickering, R., Dirks, P.H.G.M., Jinnah, Z., de Ruiter, D.J., Churchill, S.E., Herries, A.I.R., Woodhead, J.D., Hellstrom, J.C. & Berger, L.R. 2011. *Australopithecus sediba* at 1.977 Ma and implications for the origins of the genus *Homo*. *Science* **333**, 1421–1423.

Trackways of bipedal reptiles from Giant's Castle, KwaZulu-Natal (Poster)

Van Dijk, D. Eduard

Department of Plant and Animal Biology, University of Stellenbosch, Stellenbosch
 eddie@vandijks.com

Among trackways in Lesotho described by Paul Ellenberger in 1970 was a genus of reptiles, *Molapopentopodiscus*, with type species *M. pilosus*, which was considered to be bipedal. A second species, *M. supersaltator*, from Giant's Castle, KwaZulu-Natal, was described by Ellenberger from photographs sent to him. Each species was illustrated by drawings of a pair of prints and indications of the length of a leap (hop). The upper and lower surfaces of a slab with *M. supersaltator* tracks was subsequently illustrated (Van Dijk 1978), making it quite clear that the mode of locomotion had been correctly interpreted. In the same publication was an illustration of the upper surface of a slab which included what were considered to be

prints of a biped with distinctly curved toes. In the absence of a slab with a sequence of underprints which could be related to upper prints with curled toes, description of a distinct taxon was deferred. A slab assembled from scree fragments that has a single pair of upper and lower prints, and another slab with both upper and lower prints of one side of a short sequence has made it possible to describe a second taxon

The bipedal prints have variously been attributed to mammals and pterosaurs. There is evidence to support the latter view.

Calcified wood from Mkuze, KwaZulu-Natal (Poster)

Van Dijk, D. Eduard¹; Bamford, Marion²

¹ Department of Plant and Animal Biology, University of Stellenbosch, Stellenbosch
 eddie@vandijks.com

² BPI Palaeontology, School of Geosciences, University of the Witwatersrand, Johannesburg
 marion.bamford@wits.ac.za

In the late 1950s staff at the entrance of Mkuze Reserve, KwaZulu-Natal, were aware of fossil tree trunks not far from the offices. One such trunk was photographed at the time and loose pieces collected. The site has been identified as Nhlohlela Hill and Swamp, now some distance from the present entrance to the reserve.

Large calcite crystals suggested that histological detail was not retained. However, thin chips showed cellular detail. When pieces were sectioned and section surfaces were polished, and lightly etched with acid, it was found possible to detect detail in cellulose acetate peels. Ground sections were also made. Transverse sections showed some variation in cell size and cell wall thickness, but tree rings were not obvious. Tangential sections showed narrow groups of radial sections, mostly only one cell wide and about ten cells high. Repeated attempts at producing radial sections as peels or sections have yielded no useful ones.

In 2011 narrow regions that appeared to be iron oxide were observed and sections along them were attempted. Bordered pits were observed as well as other microscopic details.

Origin of Early Triassic *Lystrosaurus* bonebeds from the Karoo Basin, South Africa: their significance for faunal recovery in a post-extinction world

Viglietti, Pia A.¹; Smith, Roger, M.H.²; Compton, John S.¹

¹ Department of Geological Sciences, University of Cape Town, Rondebosch, South Africa
 pia.viglietti@uct.ac.za / john.compton@uct.ac.za

² Iziko South African Museum, Cape Town, South Africa
 rsmith@iziko.org.za

The most devastating mass-extinction event Earth has experienced occurred at the end of the Permian period approximately 252 Ma ago. The southern Karoo Basin is one of the few places in the world that preserves an almost continuous stratigraphic record of terrestrial sedimentation through the Permian-Triassic Boundary (PTB). Emphasis on the rapid annihilation of marine and tetrapod faunas during the PTB extinction event has generally overshadowed the nearly as rapid radiation and

regeneration of fauna in earliest Triassic Karoo environments. The expansion of mammal-like reptiles (therapsids) of the *Lystrosaurus* Assemblage Zone fauna into an increasingly arid Karoo Basin is associated with a change in fossilization mode from isolated skulls in the latest Permian and bone material to articulated 'curled up' skeletons and multi-individual accumulations (bonebeds) in the early Triassic. Lack of epiphyses and skull sizes suggest only subadult *Lystrosaurus* are present in bonebeds. Clustered articulated ribs among disarticulated material and minor weathering of bones are evidence of a period of desiccation where bones lay on the surface for up to five years before burial (Botha & Smith 2005). The lithology surrounding the bonebeds consists of floodplain mudrocks, carbonate nodules, and sand-filled mudcracks capped by coarse sediments indicative of rapid deposition following floods. Carbonate nodules were sampled and showed $\delta^{13}\text{C}$ values ranging from -8.5 to -5% and $\delta^{18}\text{O}$ values of 13.5 to 16. These values support the formation of the carbonate nodules under a cool semi-arid climate at higher latitude ($\sim 50^\circ\text{S}$) than the current Karoo Basin. This study agrees with previous studies arguing for the formation of bonebeds during extended episodic periods of drought in the earliest Triassic Karoo Basin. The presence of ichnofossils such as vertebrate burrow-fills suggests the use of burrows possibly by *Lystrosaurus* and other fauna (such as cynodonts) to escape extreme environmental conditions. Being able to adapt to these extreme conditions was key to the survival of certain species into the Earliest Triassic, but some species appeared to have been better adapted than others. This is shown by the disappearance of *Lystrosaurus* by the Middle Triassic and the survival of the cynodonts, the ancestors of the mammal lineage.

Anatomical fine structure of brain cases: application in international biostratigraphy

Welman, Johann

University of Limpopo, South Africa
johann.welman@ul.ac.za

In classical South African biostratigraphical studies, strata were characterized by the presence of index fossils. In more recent times, biostratigraphic characterization of strata has been done using the fossil assemblages and the ranges of fossils that indicate boundaries of biostratigraphic divisions.

In the international context, however, a species sometimes occurs in different-aged faunal assemblages and in anomalous stratigraphic positions (i.e. in more than one teichron). These anomalous occurrences may be a function of the time and space aspects of evolution, the longevity of species and the time it took for a species to disperse geographically over Pangaea. This creates questions about the relative age of species in the different localities, since the mere presence or absence of the species apparently has limited significance for refined terrestrial biostratigraphy.

The introduction of international phylozones based upon informed anatomical studies presents a way out of this dilemma. If the anatomy of closely related forms in

evolutionary lineages can be studied, trends in their evolution can be determined and landmark developments identified so that this succession of irreversible anatomical evolutionary events can be used in chronostratigraphy. In this way refined functional-anatomical studies of the diversification of reptiles can pave the way to a better determination of the biochronozones of terrestrial strata.

In the early diapsid reptile lineages leading up to birds and dinosaurs, the fine structure of the brain cases of a series of reptiles has been studied and the anatomical changes identified that gradually and irreversibly developed between 290 and 150 Ma. Assuming the origin of birds from early archosauromorph reptiles, the origin of flight in an arboreal setting caused changes in the anatomy of the brain and ear that happened in a logical functional-morphological progression. The increase in the brain size during the origin and early evolution of birds is characterized by the gradual co-evolution of otic and basicranial structures. The presence or absence of apomorphic structures that resulted from these evolutionary changes serve as precise indicators of relative age within the lineage composed of related species from localities internationally that could consequently serve as indicators of the relative age of the terrestrial sedimentary rocks in which different taxa occur.

In the diverse dinosaur lineages and their Pangaeian archosauromorph ancestors, the gradual evolution of the complex median Eustachian system driven either by thermoregulation or pressure equilization as possible functional impetus, gave rise to well-defined clades with specific landmark anatomical apomorphies. These developments open up the possibility of high resolution stratigraphic correlation of the Lower Triassic to Cretaceous aquatic and terrestrial sediments internationally.

The Olduvai Hominid 8 (OH 8) foot and the status of *Homo habilis*: Where do we stand?

Zipfel, Bernhard¹; DeSilva, Jeremy²; Van Arsdale, Adam³; Tocheri, Matthew⁴; Weiss, Elizabeth⁵

¹ Institute of Human Evolution, School of Geosciences, University of the Witwatersrand, Private Bag 3, Johannesburg, 2050 South Africa
bernhard.zipfel@wits.ac.za

² Anthropology Department, Boston University, 232 Bay State Road, Boston, MA 02215, U.S.A.

³ Department of Anthropology, Wellesley College, Wellesley, MA, U.S.A.

⁴ Human Origins Program, Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington D.C. 20013-7012, U.S.A.

⁵ Department of Anthropology, San Jose State University, One Washington Square, San Jose, CA 95192-0113, U.S.A.

The OH 8 fossil foot assemblage has been important for interpreting foot evolution and the evolution of hominin locomotion. It is generally accepted that OH 8 belongs to a single bipedal individual but debates, both past and present, are centred on maturity and taxonomic attribution. It has been suggested by some, that the presence of what are perceived as unfused metatarsal epiphyses, that OH 8 was a juvenile, associated with the *Homo habilis* type OH 7. It has also been associated with the OH 35 tibia and fibula, but this has been refuted. Accurately assessing the age of the OH 8 individual at death is important for interpreting

the functional morphology of these fossils and the locomotion practiced by early Pleistocene hominins. Here, we review the debate around the juvenile and adult status of the OH 8 foot and present evidence that strongly suggests that the OH 8 assemblage is that of an adult. A study of the patterns of epiphyseal fusion of the original OH 8 fossils, subadult feet from modern humans, chimpanzees, and gorillas suggest that the original interpretation of the OH 8 foot as an adult individual may be the correct one. Based on the timing of epiphyseal fusion in the ape and human foot, if the OH 8 foot is from a juvenile with unfused metatarsal heads, the epiphysis of the first metatarsal base should also be unfused. However, the epiphysis of the first metatarsal of OH 8 is fully obliterated and none of the sample of feet studied shared this pattern of metatarsal

fusion. A radiographically visible epiphyseal scar on the OH 8 first metatarsal has been used as evidence for recent fusion and thus subadult status. To this end, a radiographic study of first metatarsals of humans from ages 17 to 88 years was carried out. The results show that the basal epiphyseal line is visible past the age of epiphyseal fusion in 29% of the radiographed first metatarsals. Statistically, there was no relationship between the loss of the epiphyseal scar and age. The presence of the epiphyseal scar therefore does not necessarily indicate subadult age. We conclude that, together with other compelling evidence, given the metatarsal fusion pattern of OH 8, and the dental development of the OH 7 mandible, it is highly unlikely that the OH 8 foot and the OH 7 mandible are from the same individual.

Author index

| | | | |
|----------------------------|----------------------------|-------------------------|--------|
| Abdala, Fernando | 29, 32, 35, 37, 40, 47, 51 | Govender, Romala | 36 |
| Alberdi, Maria Teresa | 43 | Güven, Saniye | 34, 37 |
| Albrecht Manegold | 43 | Hancox, John | 46 |
| Almond, John E. | 37, 50 | Henry, Amanda | 47 |
| Angielczyk, Kenneth | 29, 30, 49 | Houssaye, Alexandra | 37 |
| Antoine Louchart | 43 | Hsiang, Allison | 42 |
| Backwell, Lucinda R. | 55 | Hübner, Tom | 51 |
| Bamford, Marion | 30, 46, 47, 48, 52, 56 | Huttenlocker, Adam | 38 |
| Berger, Lee | 47, 55 | Iturra-Cid, Myriam | 45 |
| Bergh, Eugene | 31 | Jashashvili, Tea | 38 |
| Bever, Gabe | 42 | Jasinoski, Sandra | 29 |
| Bordy, Emese M. | 40, 52 | Jinnah, Zubair | 39, 50 |
| Botha-Brink, Jennifer | 31, 38, 54 | Jirah, Sifelani | 39 |
| Canoville, Aurore | 31 | Kammerer, Christian E. | 29 |
| Carlson, Kristian J. | 32, 35, 38 | Keeling, Rachelle | 39 |
| Chinsamy-Turan, Anusuya | 31, 32, 36, 41, 51 | Kibii, Job | 33 |
| Christian, Andreas | 40 | Klein, Nicole | 40 |
| Cisneros, Juan C. | 29, 33 | Knoll, Fabien | 52 |
| Cohen, Brigitte | 33 | Kostka, Aleksander | 34 |
| Collins Cook, Della | 35 | Kruger, Ashley | 40 |
| Compton, John S. | 56 | Krummeck, William | 40 |
| D'Elia, Guillermo | 45 | Krupandan, Emil | 41 |
| d'Errico, Francesco | 55 | Kupczik, Kornelius | 54 |
| da Conceição, Domingas, M. | 29 | Labandeira, Conrad | 41 |
| Day, Michael | 29, 34, 37, 51 | Lewis, Patrick | 42 |
| de Castro Silva, Mayana | 29 | Lindgren, Johan | 37 |
| de Cock, Michiel | 52 | Looy, Cindy | 50 |
| DeSilva, Jeremy | 57 | Lyson, Tyler | 42 |
| Dirks, Paul | 39 | Marchi, Damiano | 38 |
| Dowdeswell, Mark R. | 38 | Mariscano, Claudia A. | 29 |
| Dumont, Maitena | 34 | Martinez-Maza, Cayetana | 43 |
| Durand, Francois | 35 | Matthews, Thalassa | 43 |
| Fernandez, Vincent | 29, 32, 35 | McKay, Ian | 44 |
| Fiorillo, Anthony R. | 32 | McPhee, Blair | 44 |
| Fröbisch, Jörg | 29 | Mocke, Helke | 45 |
| Gastaldo, Robert | 50 | Montoya, Germán | 45 |
| Gauthier, Jacques | 42 | Mostovski, Mike | 48 |
| Gess, Robert | 35 | Nalla, Shahed | 46 |
| Gomez, Santiago | 43 | Nesbitt, Sterling | 49 |
| Götz, Annette E. | 36 | Neumann, Frank H. | 46, 52 |

| | | | |
|---------------------------|--|--------------------------------|--------------------|
| Nicoletti, Natasha | 46 | Shelton, Christen D. | 53 |
| Norton, Luke | 47 | Sidor, Christian | 30, 38, 49, 55 |
| Nshimirimana, Robert | 38 | Smith, Roger M.H. | 29, 56 |
| Odes, Edward | 47 | Smith, Roger | 30, 31, 49, 54, 55 |
| Olayiwola, Moshood | 48 | Steininger, Christine | 54 |
| Ovechkina, Maria | 48 | Steyer, Jean-Sebastien | 30, 55 |
| Parkinson, Alexander Haig | 48 | Stynder, Deano D. | 43, 54 |
| Peacock, Brandon | 49 | Tafforeau, Paul | 32, 35 |
| Penn-Clarke, Cameron | 49, 50 | Thackeray, Francis | 55 |
| Prado, Jose Luis | 43 | Thomas, Daniel B. | 32 |
| Prevec, Rose | 41, 50 | Tocheri, Matthew | 57 |
| Redelstorff, Ragna | 51 | Tsikos, Hari | 52 |
| Richter, Martha | 29 | Tsuji, Linda | 55 |
| Roberts, David | 52 | Tumarkin-Deratzian, Allison R. | 32 |
| Roberts, Eric | 39 | Tütken, Thomas | 34 |
| Rubdige, Bruce | 37, 29, 32, 33, 34, 35, 39, 40, 46, 47, 50, 51 | Val, Aurore | 33, 55 |
| Ruckwied, Katrin | 36 | Van Arsdale, Adam | 57 |
| Sanchez, Sophie | 51 | Van Dijk, D. Eduard | 56 |
| Sander, P. Martin | 40, 53 | Viglietti, Pia A. | 56 |
| Scarborough, Matthew E. | 52 | Weiss, Elizabeth | 57 |
| Scheyer, Torsten | 42 | Welman, Johann | 57 |
| Sciscio, Lara | 52 | Yates, Adam | 35, 46, 49 |
| Scott, Louis | 52 | Zipfel, Bernhard | 46, 57 |

Preface to Professor Nina Jablonski's public lecture on "Skin: Its Biology in Black and White"

The Palaeontological Scientific Trust (PAST) has regularly presented a keynote scientific lecture for the public, in fulfilment of its mission to preserve, promote and protect Africa's ancient heritage, and as part of its mandate to integrate education, research and outreach in the origin sciences (palaeontology, palaeo-anthropology and archaeology). The public lecture, which falls under PAST's Public Understanding and Engagement Programme, has since its inception been supported by the Standard Bank, who through PAST remains a founding and major supporter of the origin sciences. The lecture has gained tremendous popularity due to its high-profile scientific speakers presenting complex scientific information in an understandable manner. Previous speakers include Berhane Asfaw, Ron Clarke, Richard Dawkins, Richard Leakey, Paul Sereno, Phillip Tobias and Tim White.

In honour of the late Phillip Tobias, PAST's founding Scientific Advisor and more recently its Scientific Patron, the 2012 lecture is the first in the series to be renamed the Phillip Tobias Memorial Lecture. As a reflection of PAST's efforts to promote the social relevance of the origin sciences, we had endeavoured to make this lecture feature a scientific topic that comments on the complex and challenging social issues facing humanity today. It is therefore fitting that the lecture commemorates not only Phillip Tobias' scientific prowess, but also his life-long advocacy of human rights and social justice.

The 8th Standard Bank/PAST Keynote Lecture was presented by scientist and author, Professor Nina Jablonski, at the Soweto Theatre, Johannesburg, on 19 September 2012. Prof. Jablonski, of the Anthropology Department, Pennsylvania State University, U.S.A., is a biological anthropologist and head of her department. She is well-known for her research on the evolution of skin colour, and she has published numerous papers and books on primate and human evolution. She conducts fieldwork in Asia and Africa, and in 2002 was elected a Fellow of the American Association for the Advancement of Science. She is also an associate of the Stellenbosch Institute for Advanced Study. Her PAST keynote lecture was entitled 'Skin: Its Biology in Black and White' and was delivered to an audience in excess of 350 individuals. Rick Menell, Chairman of PAST, served as the Master of Ceremonies, and Derek Hanekom, the then Deputy Minister of Science and Technology (promoted to the post of Minister in this Department in October 2012), delivered opening remarks.

PAST would like to thank Prof. Jablonski, and her collaborator and husband, Dr George Chaplin, for their efforts to help the organization promote the understanding and relevance of origin sciences in the modern world. Prof. Jablonski's lecture underscored the message of our common human origins in Africa, a message that PAST sees as core to its mission and the seven programmes it supports. It is individuals and institutions such as Prof. Jablonski and the Standard Bank, that ensure PAST's ability to teach the youth of Africa and indeed the world, that they can proudly proclaim Africa to be home.

To celebrate the broader pan-African mission of PAST since the 2011 launch of its Scatterlings of Africa project, PAST wanted to ensure the more widespread distribution of the lecture content through its publication in an African-based academic journal. Given PAST's longstanding support of *Palaeontologia africana*, this journal was the preferred choice for the first publication of the Standard Bank/PAST keynote lecture. Copies of this article will be disseminated through PAST's foundational education programme, the Walking Tall Schools Project, to educators, learners and members of the public lacking access to the journal. For information on PAST and the seven programmes it supports, please refer to www.past.org.za.

Andrea Leenen

CEO, PAST, P.O. Box 203, Parklands, Johannesburg, 2121 South Africa

&

Robert J. Blumenshine

Chief Scientific and Educational Strategist, PAST, and Professor of Anthropology,
Rutgers University, New Brunswick, New Jersey, U.S.A.

Skin: Its Biology in Black and White

Nina G. Jablonski

Department of Anthropology, 409 Carpenter Building, The Pennsylvania State University, University Park, PA 16802, U.S.A., and
Stellenbosch Institute of Advanced Study (STIAS), 19 Jonkershoek Road, Stellenbosch, 7600 South Africa
E-mail: ngj2@psu.edu

Human skin comes in a range of colours, grading from very dark brown near the equator to near ivory near the poles. This colour gradient resulted from the action of natural selection. The original skin tone for members of the *Homo* lineage, including *Homo sapiens*, was dark brown. Diversification of skin colouration occurred as some *Homo sapiens* populations dispersed to regions of lower ultraviolet radiation (UVR), mostly outside of Africa. Humans who began to inhabit higher latitudes faced reduced opportunities to make vitamin D in the skin because of lower and more seasonal levels of UVB from ambient sunlight. Depigmented skin evolved under these conditions, and genetic evidence indicates that mutations leading to loss of melanin pigmentation occurred multiple times in hominin history when groups invaded regions of lower UVB. Because similar skin colours have evolved multiple times under the same environmental conditions, classification of humans according to skin colour is fraught with problems. The colour-based races defined in the 18th century are congeries of physical and behavioural traits that do not exist. The persistence and propagation of these concepts has caused serious problems in many places, and can only be countered by effective education.

Keywords: evolution, natural selection, pigmentation, melanin, eumelanin, ultraviolet radiation, UVB, folate, vitamin D, depigmentation, convergent evolution, race.

Human skin comes in a wide range of sepia tones, from darkest brown to near ivory, but not in black or white. The sepia rainbow of skin colours grades from dark to light, from the equator to the poles. The geographic distribution of skin pigmentation has been known and studied by many people over nearly three centuries, but only in the last 20 years have new kinds of data become available that allow skin colour variation to be well understood. Skin pigmentation is a topic where 'the rubber meets the road' because it is at the meeting point of evolutionary biology and human experience. Scientists and the general public alike are engaged by skin colour diversity, and the social sensitivity that once inhibited both scientific research and social discourse on the topic has now ebbed. People want to know how skin colour evolved and why it has come to have the meaning it has in modern societies.

One of the biggest challenges in studying the evolution of skin is that there is very little actual preserved ancient human skin to study. There is no fossilized human skin yet confirmed, only the skin associated with mummified, frozen, or bog-preserved corpses dating to no more than a few thousand years old (Jablonski 2006). The study of skin and skin colour evolution in humans thus relies on evidence from comparative study of the anatomical and physiological characteristics of the skin of living people and primates, along with the comparative study of the genes that determine these characteristics. A lot of information has been inferred about the nature of the skin and hair in the last common ancestor (LCA) of humans and chimpanzees, for instance, by examining these features and some of the genes associated with them in humans, apes, and monkeys (Jablonski 2004). This examination shows that the LCA probably had dark hair covering lightly pigmented skin, very much like a modern chimpanzee. Exposed skin on the face and hands would have darkened by tanning when the skin was exposed to strong sunlight, but the skin covered by hair would have remained untanned. We can extend the same inference to the appearance of the skin in one of the best known the

early fossil hominin species, *Australopithecus afarensis*, known from middle Pliocene sites in Ethiopia and Tanzania. The skeletal evidence of *A. afarensis* indicates that, although the species was habitually bipedal, it was not an energetic bipedal strider and runner. Rather, the species had ape-like body proportions, retained abilities to climb trees, and probably was not a long-distance runner or fast walker. These aspects of hominin lifestyles are important because body temperature is elevated during vigorous exercise, and problems of dissipation of heat can become critical especially when hominins are exercising in hot environments. The likely cause of the loss of most functional body hair in hominins was the need for more efficient cooling from evaporation of sweat from the surface of the body (Jablonski 2004). Evaporation of expressed sweat works extremely well if the skin is naked, but not well if the skin is covered with dense hair (Folk & Semken 1991). When the skeletons of early members of the genus *Homo* are compared with those of *Australopithecus*, the differences between the two in the likely modes of locomotion are immediately apparent (Crompton *et al.* 1998; Ruff 2008; Ruff 1991). Unlike *Australopithecus*, early *Homo* was a bipedal strider and runner (Bramble & Lieberman 2004). These activities raised metabolic levels and generated body heat that had to be liberated from the body's surface. Dissipation of excess body heat probably was accomplished primarily by evaporation of sweat, and the sweat was produced by a high density of eccrine sweat glands on the body's surface (Jablonski 2004). Keeping cool is of particular importance in highly encephalized primates: the brain is sensitive to elevated core temperature. Eccrine sweat evaporating on nearly naked skin creates a whole-body cooling system that helps to maintain the brain's thermal homeostasis during intense exercise (Caputa & Cabanac 1988; Shibasaki & Crandall 2010), and enhanced body cooling through sweating no doubt released a physiological constraint that made

possible increased brain size in the human lineage (Jablonski 2010a).

The evolution of functional nakedness was not the only major change that occurred in the early evolution of the genus *Homo*. Naked skin was vulnerable to the damaging effects of ultraviolet radiation, and so we reasoned from first principles that permanent dark pigmentation in the skin would have had to have evolved in early *Homo* at the same time as hairlessness in order to protect individuals from these effects (Jablonski & Chaplin 2000). This inference was later supported by genetic evidence indicating that the form of the *MC1R* pigmentation that produces permanent dark pigmentation in darkly pigmented Africans today had been invariant for as long as 1.2 million years (Rogers *et al.* 2004). Early members of the genus *Homo* living under equatorial or near-equatorial sunlight containing abundant ultraviolet radiation (UVR) were, thus, hairless and darkly pigmented (Jablonski & Chaplin 2000).

The pigment melanin, specifically, the intensely dark brown form of melanin called eumelanin, is a natural sunscreen that confers superior protection against the damaging effects of UVR (Brenner & Hearing 2008; Kollias *et al.* 1991). The intensity of UVR at the earth's surface is related to latitude and humidity, with arid areas near the equator having the highest levels (Chaplin 2004). Outside of the tropics, UVR levels decline significantly, and the amount of UVR that falls on any particular area depends on the energy of the radiation emitted by the sun. The most biologically significant types of UVR that fall on the earth are long wavelength UVR called UVA and medium wavelength UVR called UVB. The more energetic of these is UVB and it is readily absorbed and scattered by oxygen and ozone in the atmosphere. Outside of the tropics, when the sunlight passes obliquely through the atmosphere during the winter months, little or no UVB reaches the earth's surface, while most UVA passes through the atmosphere with visible light (Madronich *et al.* 1998). Ultraviolet radiation is mostly harmful to living systems because it damages DNA, cell membranes, and connective tissues, and biological systems have evolved elaborate mechanisms to repair damage caused by UVR (Cleaver & Crowley 2002; Rothschild 1999). For vertebrate animals, one of the most effective means of preventing damage from UVR is eumelanin pigment in the integument. When incorporated into the epidermis of the skin, eumelanin absorbs and scatters most UVB, thereby sparing damage to deeper layers including the blood flowing through the cutaneous blood vessels (Brenner & Hearing 2008; Tadokoro *et al.* 2003; Zmudzka *et al.* 2006).

It was long thought that dark, eumelanin-rich pigmentation originally evolved in humans in order to protect against skin cancer caused by damage to DNA in the skin. When it was demonstrated that this was unlikely because most skin cancers afflict people after their reproductive years (Blum 1961), a rethinking of the role of eumelanin was required. A key discovery was published in 1978, when it was shown that the B vitamin folate was sensitive to ultraviolet radiation (Branda & Eaton 1978). Folate is a vitamin that is obtained from green leafy vegetables,

citrus fruits, and whole grains, and is of critical importance to health because it is necessary for making and repairing DNA (Lucock & Daskalakis 2000). Folate sufficiency is important for normal reproduction because it is a precondition for healthy sperm production in men and for normal development of early embryos in women (Bower & Stanley 1992; Fleming & Copp 1998; Mathur *et al.* 1977). Folate deficiency is one of the main causes of the family of birth defects called neural tube defects (Bower & Stanley 1992; Fleming & Copp 1998). Because of the important role played by folate and related compounds in successful reproduction, we reasoned that protection of these important biomolecules was the primary cause for the evolution of permanent eumelanin protection in the skin (Jablonski & Chaplin 2000). Eumelanin-rich skin protected all members of the genus *Homo*, from the species of the Early Pleistocene through *Homo sapiens*. The evolution of the *Homo* lineage leading to anatomically modern humans, *Homo sapiens*, occurred in Africa, and all members of this lineage were darkly pigmented (Jablonski & Chaplin 2000). The question then arises as to how and when the modern pattern of skin colour diversity arose. For the answer to this question, we must examine the pattern of dispersals of modern people outside of tropical Africa, and the UVR conditions that obtained in these environments.

Modern humans, *Homo sapiens*, evolved in Africa between 200 000 and 120 000 years ago, and the first half of our species existence was spent only in Africa. During this time, populations expanded and dispersals into the extremities of the continent proceeded, accompanied by extensive genetic diversification (Tishkoff *et al.* 2009). The changes that occurred in human populations during this period would have included subtle changes in pigmentation, as populations adapted to local UVR conditions or experienced genetic bottlenecks due to small population sizes. The genetic basis for evolutionary changes in pigmentation among modern people living in Africa is not well understood. Approximately 80 000 years ago, small populations of modern people left Africa, taking with them a small fraction of the continent's genetic diversity. These people were culturally sophisticated and their movements – into southeast and east Asia first, then later into Europe – occurred quickly by sea and over land (Stringer 2000). These movements saw people entering highly diverse solar regimes, including those with very low levels of UVR. A large fraction of the land mass of Eurasia lies at high latitudes which receive low UVR, and particularly low UVB (Chaplin & Jablonski 1998). As people entered these lands, they were subjected to lower and more strongly seasonal levels of UVR than they had ever experienced, and this had profound effects on human health (Chaplin & Jablonski 2009).

Ultraviolet radiation is not a universally malign influence. Its single most important positive action is initiation of the process of vitamin D formation in the skin by UVB. This process occurs in all terrestrial vertebrates and is essential for life (Holick 2003). Vitamin D is necessary because it permits absorption of calcium from the diet. Vitamin D deficiency is a serious problem that leads to skeletal malformation and weakness that manifests itself

as rickets in children and osteomalacia in adults (Dimitri & Bishop 2007). Serious and persistent rickets in young women leads to pelvic deformities that impair or prevent natural childbirth, so vitamin D deficiency can directly impact reproductive success. Because vitamin D is also responsible for maintenance of the health of the immune system, vitamin D deficiencies are related to increased susceptibility to infectious diseases, certain cancers, and autoimmune disorders (Holick 2005; Ponsonby *et al.* 2005) (Holick 2007; Holick & Chen 2008).

On the continent of Africa, the region experiencing the lowest and most seasonal levels of UVB is the southern coast of South Africa. At and near the winter solstice, there is no UVB in the sunlight over this region, and no vitamin D production can take place in human skin, regardless of skin colour (Jablonski & Chaplin, unpubl. obs.). The absence or attenuation of UVB reaching middle and high latitudes during the winter months had profound influences for the evolution of skin pigmentation. Because eumelanin is a superior sunscreensing agent, and because UVB is necessary to make vitamin D in the skin, it would have been beneficial for people living under conditions of weak and highly seasonal sunlight to have less eumelanin in their skin (Jablonski 2004; Jablonski & Chaplin 2000; Loomis 1967; Murray 1934). In any given period of time, more vitamin D precursor can be in lightly pigmented skin than in darkly pigmented skin, and so lighter skin was favoured by natural selection under low UVB conditions (Norton *et al.* 2007; Webb & Holick 1988). Light skin is actually depigmented skin, and genetic mutations leading to depigmentation evolved independently in the ancestors of modern east Asians and modern western Europeans (Lamason *et al.* 2005; Norton *et al.* 2007). The importance of vitamin D production in the skin is attested by the fact that genetic fixation of the pigmentation gene mutations leading to loss of pigmentation occurred through selective sweeps resulting from positive selection (Norton *et al.* 2007). Loss of eumelanin pigmentation has also been inferred to have occurred earlier and independently in *Homo neanderthalensis*, the distant cousin of *Homo sapiens* that inhabited low and moderate UVB environments Europe and the circum-Mediterranean (Lalueza-Fox *et al.* 2007).

The convergent evolution of light pigmentation on at least three occasions in hominin history – in the ancestors of modern western Europeans, modern east Asians, and Neanderthals is remarkable, and has important consequences for the use of skin colour as a feature in human classification. Similarly, the evolution of repigmentation is equally important. As people have moved around in the last 20 000 years, some depigmented populations have re-entered regions with strong UVR and have undergone genetic mutations leading to enhanced tanning abilities and darker baseline pigmentation. This has been demonstrated for some New World populations (Quillen 2010) and is strongly suspected for some groups that now inhabit southern reaches of the Indian subcontinent.

Through time, people have become increasingly mobile as the result of innovations in transportation technology, spurred on by interests in distant resources and trade.

This has resulted in people moving around over longer distances at faster speeds, especially in the last 500 years. The mismatches between skin pigmentation and environmental UVR that have arisen because of these rapid movements have resulted in profound and mostly negative effects on health (Chaplin & Jablonski 2009; Jablonski & Chaplin 2012). People living in earlier times were less mobile, and would not have been exposed to solar regimes significantly different from those experienced by their ancestors. But this situation is common for modern people, whether they are vacationing or are living permanently in a region distant from their ancestral homeland. Even for people who have not moved far in recent millennia, there is often a mismatch between skin pigmentation and sun exposure because of indoor lifestyles in cities and a lack of sun exposure. Lightly pigmented people living in high UVR environments face significantly elevated risk of skin cancer (De Gruijl 1999; Rees 2000; Rigel 2008). Darkly pigmented people living under low or seasonal UVB conditions face an elevated risk of vitamin D deficiency (Brunvand & Haug 1993; Fogelman *et al.* 1995; Fonseca *et al.* 1984). Vitamin D deficiencies are also increasingly common among city dwellers of all skin colours who spend most of their time indoors, or among people who routinely wear concealing clothing and chemical sunscreen when outdoors (Chatfield *et al.* 2007; Davies *et al.* 1986; Forrest & Stuhldreher 2011; Le Goaziou *et al.* 2011). Although relatively few epidemiological studies on vitamin D status have been conducted in South Africa, preliminary indications are that vitamin D deficiency is common and has serious consequences for disease susceptibility (Martineau *et al.* 2011).

Skin is the interface between the body and the physical environment, and skin pigmentation evolved to regulate the penetration of UVR into body under different environmental conditions. The gradient of skin pigmentation seen in modern people, from darker tones near the equator to lighter ones closer to the poles, is the product of two competing clines, one favouring photoprotection in areas of high UVR, the other favouring photosynthesis of vitamin D in areas of low UVR (Chaplin & Jablonski 2009; Jablonski 2010b; Jablonski & Chaplin 2010). People with moderate pigmentation living in middle latitudes (between about 23° and 37°) generally have good abilities to tan, thereby gaining a measure of increased protection from summer sun. Skin pigmentation is a superb example of natural selection acting on the human body, and should be used as a model system for teaching evolution at all levels of the curriculum.

What skin colour does not provide is a unique marker of ancestry for purposes of classification of people into groups. Visibly identical skin phenotypes have evolved from distinct genotypes that arose from independent mutations. This means that skin colour itself cannot be used as a unique indicator of genetic ancestry or as a characteristic for sorting people into races because the same colour is associated with multiple ancestries and races. We recognize this now, but this fact was not known to the naturalists who composed the first classifications of humans and the philosophers who first defined races.

When Carolus Linnaeus created the first scientific classification of humans, he placed them into four groups, sorted by skin colour and continent. The variations of *Homo* he named in 1748 in the 6th edition of his *Systema Naturae* were *Europaeus albus* (white), *Americanus rubescens* (red), *Asiaticus fuscus* (brown), and *Africanus niger* (black). Linnaeus had limited information on which to base a classification of humankind, and so this simple classification must not be judged too harshly. What is significant is what happens in subsequent editions of the *Systema Naturae*. By the 10th edition of 1758, Linnaeus had changed his classification to include more characteristics of each group. Physical traits other than skin colour, such as eye colour and hair texture were added, but he also included behavioural attributes. Europeans were *sanguineus* (sanguine), [Native] Americans were *cholericus* (choleric), Asians were *melancholicus* (melancholy), and Africans were *phlegmaticus* (phlegmatic). He also characterized the four varieties of people according to *regitur* or how they were governed, so that Europeans were described as being ruled by *ritibus* (rites), Americans by *consuetudine* (custom), Asians by *opinionibus* (opinion), and Africans by *arbitrio* (will). Linnaeus was a naturalist and *Systema Naturae* was considered the first 'scientific' classification of living things. It was extraordinary, therefore, that Linnaeus departed from his usual custom of describing organisms on the basis of only their physical attributes to describe people on the basis of dispositions and cultural behaviour as well as physical traits (Broberg 1983). The mixing of physical and behavioural traits that Linnaeus introduced heralded a new era in human classification, and presaged the first description of races.

Linnaeus's classifications of humans were widely read and discussed by scholars of his day. Other naturalists and philosophers took up the challenge of human diversity, and by the late 18th century, no less a figure than Immanuel Kant had published his own classification of humans. Kant was the first person to place people into races (*Rassen* in German), which were defined by skin colour and place of origin (Bernasconi 2001; Shell 2006). Kant placed great importance on place of origin because climate (and sun exposure) had purposeful influences on physical traits – notably skin colour – and on the collective motivation exhibited by a race and the level of civilization it could attain (Bernasconi 2006). Kant considered races and racial characteristics to be fixed and immutable, and on this point he clashed with many of his contemporaries (Bernasconi 2006). He was also the first to rank races clearly and unambiguously: 'Humanity is at its greatest perfection in the race of the whites. The yellow Indians do have a meagre talent. The Negroes are far below them and at the lowest point are a part of the American peoples' (Bernasconi 2002).

The most significant aspect of Linnaeus's and Kant's taxonomies in the context of this paper is that both Linnaeus and Kant considered that the colours of skin they recognized were unique to geographical groups of humans, and that skin colour was unerringly connected with other physical and behavioural traits. They conceived of defined varieties or races of humans as discrete pack-

ages of biosocial attributes. These conceptions have lasted and have been propagated, despite the accumulation of two centuries of evidence showing that discrete races do not exist. The study of skin pigmentation evolution has revealed that similar skin colours evolved independently many times in hominin history, and that pigmentation is not, for the most part, genetically connected to other physical traits. Further, there is no genetic relationship between physical, behavioural, and cultural traits. Thus, the original conception of colour-based human races which many societies have operated under for over 200 years is flawed and baseless.

Skin colour is a trait of great biological significance that illustrates action of evolution by natural selection on the human body. It is also a trait that has been used, incorrectly and persistently, for classifying people into groups which were considered to be elevated or diminished in status because of colour. This unfortunate state of affairs can be changed, if there is motivation and a commitment to change through education. We are one people, and skin colour unites us, not divides us, through the process of evolution.

This paper is based upon a transcription by Ann Smilkstein of the 8th PAST/Standard Bank Annual Lecture I delivered on 19 September 2012 at the Soweto Theatre. I am very grateful to PAST and to Standard Bank for inviting me to give this lecture. With the renaming of the lecture series, I am especially honoured to have been invited to give the 1st Philip V. Tobias Memorial PAST/Standard Bank Annual Lecture. Andrea Leenen, Robert Blumenschine, and Ann Smilkstein of PAST masterfully organized the lecture and the events surrounding it. My stay in South Africa was made possible by a Guggenheim Fellowship and by a fellowship from the Stellenbosch Institute for Advanced Study. My deep thanks go to my senior research technician, Tess Wilson, for continuing support with research and presentation materials, and to George Chaplin for many fruitful discussions, ongoing collaboration, and comprehensive support.

REFERENCES

- BERNASCONI, R. 2001. Who invented the concept of race? Kant's role in the Enlightenment construction of race. In: R. Bernasconi (ed.), *Race*, 11–36. Malden (MA), Blackwell Publishers.
- BERNASCONI, R. 2002. Kant as an unfamiliar source of racism. In: J.K. Ward & T.L. Lott (eds), *Philosophers on Race: Critical Essays*, 145–166. Oxford, Blackwell Publishing.
- BERNASCONI, R. 2006. Kant and Blumenbach's polyyps: a neglected chapter in the history of the concept of race. In: S. Eigen & M. Larrimore (eds), *The German Invention of Race*, 73–90. Albany (NY), State University of New York Press.
- BLUM, H. F. 1961. Does the melanin pigment of human skin have adaptive value? *Quarterly Review of Biology* **36**(1), 50–63.
- BOWER, C. & STANLEY, F. 1992. The role of nutritional factors in the aetiology of neural tube defects. *Journal of Paediatrics and Child Health* **28**, 12–16.
- BRAMBLE, D.M. & LIEBERMAN, D.E. 2004. Endurance running and the evolution of *Homo*. *Nature* **432**(7015), 345–352.
- BRANDA, R.F. & EATON, J.W. 1978. Skin colour and nutrient photolysis: an evolutionary hypothesis. *Science* **201**(4356), 625–626. DOI: 10.1126/science.675247
- BRENNER, M. & HEARING, V.J. 2008. The protective role of melanin against UV damage in human skin. *Photochemistry and Photobiology* **84**(3), 539–549. DOI: 10.1111/j.1751-1097.2007.00226.x
- BROBERG, G. 1983. *Homo sapiens*: Linnaeus's classification of man. In: T. Frangmyr (ed.), *Linnaeus: The Man and His Work*, 156–194. Berkeley (CA), University of California Press.
- BRUNVAND, L. & HAUG, E. 1993. Vitamin D deficiency amongst Pakistani women in Oslo. *Acta Obstetrica et Gynecologica Scandinavica*, **72**(4), 264–268.
- CAPUTA, M. & CABANAC, M. 1988. Precedence of head homoeothermia over trunk homoeothermia in dehydrated men. *European Journal of Applied Physiology* **57**(5), 611–615. DOI: 10.1007/BF00418471
- CHAPLIN, G. 2004. Geographic distribution of environmental factors influencing human skin colouration. *American Journal of Physical*

- Anthropology* **125**(3), 292–302. DOI: 10.1002/ajpa.10263
- CHAPLIN, G. & JABLONSKI, N.G. 1998. Hemispheric difference in human skin colour. *American Journal of Physical Anthropology* **107**(2), 221–224. DOI: 10.1002/(SICI)1096-8644(199810)107:2<221::AID-AJPA8>3.0.CO;2-X
- CHAPLIN, G. & JABLONSKI, N.G. 2009. Vitamin D and the evolution of human depigmentation. *American Journal of Physical Anthropology*, **139**(4), 451–461. DOI: 10.1002/ajpa.21079
- CHATFIELD, S.M., BRAND, C., EBELING, P.R. & RUSSELL, D.M. 2007. Vitamin D deficiency in general medical inpatients in summer and winter. *Internal Medicine Journal* **37**(6), 377–382. DOI: 10.1111/j.1445-5994.2007.01339.x
- CLEAVER, J.E. & CROWLEY, E. 2002. UV damage, DNA repair and skin carcinogenesis. *Frontiers in Bioscience* **7**, 1024–1043.
- CROMPTON, R.H., YU, L., WEIJIE, W., GUNTHER, M. & SAVAGE, R.J.G. 1998. The mechanical effectiveness of erect and “bent-hip, bent-knee” bipedal walking in *Australopithecus afarensis*. *Journal of Human Evolution* **35**(1), 55–74.
- DAVIES, M., MAWER, E.B., HANN, J.T. & TAYLOR, J.L. 1986. Seasonal changes in the biochemical indices of vitamin D deficiency in the elderly: a comparison of people in residential homes, long-stay wards and attending a day hospital. *Age and Ageing* **15**(2), 77–83. DOI: 10.1093/ageing/15.2.77
- De GRUIJL, F.R. 1999. Skin cancer and solar UV radiation. *European Journal of Cancer* **35**(14), 2003–2009. DOI: 10.1016/s0959-8049(99)00283-x
- DIMITRI, P. & BISHOP, N. 2007. Rickets. *Paediatrics and Child Health* **17**(7), 279–287. DOI:10.1016/j.paed.2007.04.004
- FLEMMING, A. & COPP, A.J. 1998. Embryonic folate metabolism and mouse neural tube defects. *Science* **280**, 2107–2109.
- FOGELMAN, Y., RAKOVER, Y. & LUBOSHITSKY, R. 1995. High prevalence of vitamin D deficiency among Ethiopian women immigrants to Israel: exacerbation during pregnancy and lactation. *Israel Journal of Medical Sciences* **31**(4), 221–224.
- FOLK, G.E. Jr. & SEMKEN, H.A. Jr. 1991. The evolution of sweat glands. *International Journal of Biometeorology* **35**(3), 180–186. DOI: 10.1007/BF01049065
- FONSECA, V., TONGIA, R., EL-HAZMI, M. & ABU-AISHA, H. 1984. Exposure to sunlight and vitamin D deficiency in Saudi Arabian women. *Postgraduate Medical Journal* **60**(707), 589–591.
- FORREST, K.Y.Z. & STUHLREHER, W.L. 2011. Prevalence and correlates of vitamin D deficiency in US adults. *Nutrition Research* **31**(1), 48–54. DOI: 10.1016/j.nutres.2010.12.001
- HOLICK, M.F. 2003. Evolution and function of vitamin D. *Recent Results in Cancer Research* **164**, 3–28.
- HOLICK, M.F. 2005. Vitamin D: important for prevention of osteoporosis, cardiovascular heart disease, type 1 diabetes, autoimmune diseases, and some cancers. *Southern Medical Journal* **98**(10), 1024–1026.
- HOLICK, M.F. 2007. Vitamin D deficiency. *New England Journal of Medicine* **357**(3), 266–281. DOI: 10.1056/NEJMr070553
- HOLICK, M.F. & CHEN, T.C. 2008. Vitamin D deficiency: a worldwide problem with health consequences. *American Journal of Clinical Nutrition* **87**(4), 1080S–1086S.
- JABLONSKI, N.G. 2004. The evolution of human skin and skin colour. *Annual Review of Anthropology* **33**, 585–623. DOI: 10.1146/annurev.anthro.33.070203.143955
- JABLONSKI, N.G. 2006. *Skin: A Natural History*. Berkeley (CA), University of California Press.
- JABLONSKI, N.G. 2010a. The naked truth. *Scientific American* **302**, 28–35.
- JABLONSKI, N.G. 2010b. Skin colouration. In: M.I. Muehlenbein (ed.), *Human Evolutionary Biology*, 192–213. Cambridge, Cambridge University Press.
- JABLONSKI, N.G. & CHAPLIN, G. 2000. The evolution of human skin colouration. *Journal of Human Evolution* **39**(1), 57–106. DOI: 10.1006/jhev.2000.0403
- JABLONSKI, N.G. & CHAPLIN, G. 2010. Human skin pigmentation as an adaptation to UV radiation. *Proceedings of the National Academy of Sciences* **107**(Suppl. 2), 8962–8968. DOI: 10.1073/pnas.0914628107
- JABLONSKI, N.G. & CHAPLIN, G. 2012. Human skin pigmentation, migration and disease susceptibility. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**(1590), 785–792. DOI: 10.1098/rstb.2011.0308
- KOLLIAS, N., SAYRE, R.M., ZEISE, L. & CHEDEKEL, M.R. 1991. New trends in photobiology: photoprotection by melanin. *Journal of Photochemistry and Photobiology B: Biology* **9**(2), 135–160. DOI: 10.1016/1011-1344(91)80147-a
- LALUEZA-FOX, C., ROMPLER, H., CARAMELLI, D., STAUBERT, C., et al. 2007. A melanocortin 1 receptor allele suggests varying pigmentation among Neanderthals. *Science* **318**(5855), 1453–1455. DOI: 10.1126/science.1147417
- LAMASON, R.L., MOHIDEEN, M.A.P.K., MEST, J.R., WONG, A.C., et al. 2005. SLC24A5, a putative cation exchanger, affects pigmentation in zebrafish and humans. *Science* **310**(5755), 1782–1786. DOI: 10.1126/science.1116238
- Le GOAZIOU, M.F., CONTARDO, G., DUPRAZ, C., MARTIN, A., LAVILLE, M. & SCHOTT-PETHALEZ, A.M. 2011. Risk factors for vitamin D deficiency in women aged 20–50 years consulting in general practice: a cross-sectional study. *European Journal of General Practice* **17**(3), 146–152. DOI: 10.3109/13814788.2011.560663
- LOOMIS, W.F. 1967. Skin-pigment regulation of vitamin-D biosynthesis in man. *Science* **157**(3788), 501–506. DOI: 10.1126/science.157.3788.501
- LUCOCK, M. & DASKALAKIS, I. 2000. New perspectives on folate status: a differential role for the vitamin in cardiovascular disease, birth defects and other conditions. *British Journal of Biomedical Science* **57**(3), 254–260.
- MADRONICH, S., MCKENZIE, R.L., BJORN, L.O. & CALDWELL, M.M. 1998. Changes in biologically active ultraviolet radiation reaching the Earth's surface. *Journal of Photochemistry and Photobiology B: Biology* **46**(1-3), 5–19. DOI:10.1016/S1011-1344(98)00182-1
- MARTINEAU, A.R., NHAMOYEBONDE, S., ONI, T., RANGAKA, M.X., et al. R.J. 2011. Reciprocal seasonal variation in vitamin D status and tuberculosis notifications in Cape Town, South Africa. *Proceedings of the National Academy of Sciences* **108**(47), 19013–19017. DOI: 10.1073/pnas.1111825108
- MATHUR, U., DATTA, S.L. & MATHUR, B.B. 1977. The effect of aminopterin-induced folic acid deficiency on spermatogenesis. *Fertility and Sterility* **28**(12), 1356–1360.
- MURRAY, F.G. 1934. Pigmentation, sunlight, and nutritional disease. *American Anthropologist* **36**(3), 438–445.
- NORTON, H.L., KITTLES, R.A., PARRA, E., MCKEIGUE, P., MAO, X., et al. 2007. Genetic evidence for the convergent evolution of light skin in Europeans and East Asians. *Molecular Biology and Evolution* **24**(3), 710–722. DOI: 10.1093/molbev/msl203
- PONSONBY, A.-L., LUCAS, R.M. & VAN DER MEI, I.A.F. 2005. UVR, vitamin D and three autoimmune diseases – multiple sclerosis, type 1 diabetes, rheumatoid arthritis. *Photochemistry and Photobiology* **81**(6), 1267–1275. DOI: 10.1562/2005-02-15-IR-441
- QUILLEN, E. 2010. *Identifying genes related to Indigenous American-specific changes in skin pigmentation*. Ph.D. thesis, The Pennsylvania State University, University Park, PA.
- REES, J.L. 2000. The melanocortin 1 receptor (MC1R): more than just red hair. *Pigment Cell Research* **13**(3), 135–140. DOI: 10.1034/j.1600-0749.2000.130303.x
- RIGEL, D.S. 2008. Cutaneous ultraviolet exposure and its relationship to the development of skin cancer. *Journal of the American Academy of Dermatology* **58**(5, Suppl. 2), S129–S132. DOI: 10.1016/j.jaad.2007.04.034
- ROGERS, A.R., ILTIS, D. & WOODING, S. 2004. Genetic variation at the MC1R locus and the time since loss of human body hair. *Current Anthropology* **45**(1), 105–124. DOI: 10.1086/381006
- ROTHSCHILD, L.J. 1999. The influence of UV radiation on protistan evolution. *Journal of Eukaryotic Microbiology* **46**(5), 548–555.
- RUFF, C. 2008. Femoral/humeral strength in early African *Homo erectus*. *Journal of Human Evolution* **54**(3), 383–390. DOI: 10.1016/j.jhev.2007.09.001
- RUFF, C.B. 1991. Climate and body shape in hominid evolution. *Journal of Human Evolution* **21**(2), 81–105. DOI: 10.1016/0047-2484(91)90001-C
- SHELL, S.M. 2006. Kant's concept of a human race. In: S. Eigen & M. Larrimore (eds), *The German Invention of Race*, 55–72. Albany (NY), State University of New York Press.
- SHIBASAKI, M. & CRANDALL, C.G. 2010. Mechanisms and controllers of eccrine sweating in humans. *Frontiers in Bioscience* **2**, 685–696.
- STRINGER, C. 2000. Human evolution: how an African primate became global. In: S.J. Culver & P.F. Rawson (eds), *Biotic Response to Global Change: The Last 145 Million Years*, 379–390. Cambridge (UK), Cambridge University Press.
- TADOKORO, T., KOBAYASHI, N., ZMUDZKA, B.Z., ITO, S., et al. 2003. UV-induced DNA damage and melanin content in human skin differing in racial/ethnic origin. *The FASEB Journal* **17**, 1177–1179. DOI: 10.1096/fj.02-0865fje
- TISHKOFF, S.A., REED, F.A., FRIEDLAENDER, F.R., EHRET, C., et al. 2009. The genetic structure and history of Africans and African Americans. *Science* **324**(5930), 1035–1044. DOI: 10.1126/science.1172257
- WEBB, A.R. & HOLICK, M.F. 1988. The role of sunlight in the cutaneous production of vitamin D₃. *Annual Review of Nutrition* **8**, 375–399. DOI: 10.1146/annurev.nu.08.070188.002111
- ZMUDZKA, B.Z., HEARING, V.J. & BEER, J.Z. 2006. Photobiologic role of melanin distribution in the epidermis. *Journal of Photochemistry and Photobiology B: Biology* **84**(3), 231.

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.

RÖMER, 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.

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.

Digital images are preferred but hardcopy photographic images may be accepted after consultation with the editor. Low-resolution image files are acceptable for review, but images for printing must be of high resolution, and in TIFF, EPS, WMF or EMF formats. Graphs should preferably be in one of the vector (not bitmap) formats (EPS, WMF or EMF). Diagrams prepared in Excel should be saved in Microsoft Word as Windows metafiles or enhanced metafiles (WMF/EMF); EPS (encapsulated PostScript files) are also acceptable. Black and white drawings should be scanned at 1200 dpi as line art, not in RGB colour mode, and zipped. Photographs and colour artwork should be supplied at high resolution (at least 300 dpi) in either TIFF or JPEG formats.

Print-quality digital images may be submitted on CD-ROM or via FTP sites such as Dropbox.com.

Numerical data

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

ACCEPTANCE OF PAPERS

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

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