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# Proceedings of the 20th Biennial Conference of the Palaeontological Society of Southern Africa, Bloemfontein, 4–6 July 2018

**Multiple authors**

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# Proceedings of the 20th Biennial Conference of the Palaeontological Society of Southern Africa, Bloemfontein, 4–6 July 2018

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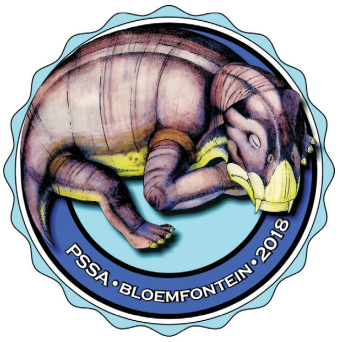
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# 20th Biennial Conference of the Palaeontological Society of Southern Africa Bloemfontein, 4–6 July 2018

## Organizers and acknowledgements

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**Editors**: Jennifer Botha-Brink, Kimberley Chapelle.

**Reviewers**: Marion Bamford, Paul Barrett, Julien Benoit, Emese Bordy, Jennifer Botha-Brink, Kimberley Chapelle, Jonah Choiniere, Adam Huttenlocker, Christian Kammerer, Robert Muir, Rose Prevec, Lloyd Rossouw, Bruce Rubidge, Lara Sciscio, Roger Smith, Christine Steininger, Pia Viglietti, Bernhard Zipfel.

**Organizing Committee Chairs**: Jennifer Botha-Brink, James Brink, Elize Butler, Kimberley Chapelle, Jonah Choiniere, Rose Prevec, Lloyd Rossouw.

**Pre-Conference Workshop**: This workshop on R was organized and presented by Kimberley Chapelle and Jonah Choiniere.

**Post-Conference Field Trip**: The field trip was organized and run by Jonah Choiniere and Pia Viglietti.

**Special Thanks to**: Elize Butler, Jonah Choiniere and Rose Prevec for all of the advice and support during the organization of this conference, without which this would not have been possible.

*The logo of the PSSA 2018 Conference depicts a curled up Lystrosaurus sleeping in a burrow. Lystrosaurus was a dicynodont therapsid and one of the few survivors of the Permo-Triassic mass extinction. It was designed by Jennifer Botha-Brink and Marelie van Rensburg.*

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# Programme

## Tuesday July 3

| | |
|---|---|
| 8:30 am–16:00 pm | Pre-conference Workshop: Introduction to R |
| 17:00 pm–19:00 pm | Ice Breaker & Registration |

## Wednesday July 4

| | | |
|---|---|---|
| 7:45 am | Prestart Coffee | |
| 8:15 am | National Museum Director, Ms Sharon Snell, **Opening Remarks** | |
| **Symposium: Palaeobiology of African Vertebrates** | | |
| 8:30 am | Plenary Talk: **Huttenlocker** | Synapsids inside out: perspectives on the origins of mammalian physiology from histology and computed tomography |
| 9:00 am | Talk: **Viglietti, G**. | The inner ear morphology of *Prolacerta broomi* and its significance for understanding basal archosaur evolution |
| 9:15 am | Talk: **Mdekazi** | Locomotory evolution in Crocodylomorpha: insights from *Litargosuchus leptorhynchus* |
| 9:30 am | Talk: **Chapelle** | The evolution of embryonic development in Archosauria |
| 9:45 am | Talk: **Neenan** | *Massospondylus* labyrinth geometry through ontogeny suggests a decoupled form–function relationship with locomotory performance in dinosaurs |
| 10:00 am | Talk: **Radermacher** | Novel postcranial features in a new specimen of *Heterodontosaurus* (Dinosauria: Ornithischia) revealed by synchrotron X-ray computed tomography: implications for ornithischian physiology, evolution, and systematics |
| Tea 10:15–10:45 am | | |
| 10:45 am | Talk: **Prondvai** | Meet medullary bone: functional and evolutionary considerations in extinct and extant archosaurs |
| 11:00 am | Talk: **Duhamel** | Juvenile biarmosuchians from the Karoo Beaufort Group shed new light on basal therapsid ontogeny |
| 11:15 am | Talk: **Botha-Brink** | Non-mammaliaform cynodont osteohistology and implications for the evolution of mammalian growth patterns |
| 11:30 am | Talk: **Benoit** | Is the infraorbital foramen homologous in non-mammaliaform cynodonts and mammals? Implications for the evolution of whiskers |
| **General Session:** | | |
| 11:45 am | Talk: **Gess** | New clues to the origins of tetrapods, from the South African Upper Devonian |
| 12:00 am | Talk: **Marsicano** | New early Permian tetrapod fauna from Namibia |
| Lunch 12:15–13:45 pm | | |
| 13:45 pm | Talk: **van den Brandt** | Understanding middle Permian pareiasaur diversity: the cranial morphology of *Nochelesaurus alexanderi* and *Embrithosaurus schwarzi* |
| 14:00 pm | Talk: **Viglietti, P.A.** | The first phytosaur from sub-Saharan Africa: implications for phytosaur distribution and regional correlation of Zimbabwe's mid-Zambesi basin |
| 14:15 pm | Talk: **Choiniere** | An unequivocal rauisuchian from the Elliot Formation of South Africa |
| 14:30 pm | Talk: **Dollman, K.N.** | The crocodylomorphs of southern Africa and their geographic and stratigraphic distributions |
| 14:45 pm | Talk: **Romano** | The first sphenacodontid synapsid from the Permian of Italy (Alghero, Sardinia): taphonomy and preliminary results |
| 15:00 pm | Talk: **Jirah** | Taxonomic revision of the Titanosuchidae (Therapsida, Dinocephalia) of the Karoo Basin, South Africa: a key to understanding middle Permian tetrapod diversity |
| Tea 15:15–15:45 pm | | |
| 15:45 pm | Talk: **Kammerer** | A new burnetiid from the mid-Permian of Zambia and its bearing on burnetiamorph phylogeny |
| 16:00 pm | Talk: **Butler** | Postcranial morphology of the Early Triassic epicynodont *Galesaurus planiceps* from the Karoo Basin, South Africa |
| 16:15 pm | Talk: **Tolchard** | A new cynodont from *Cynognathus* Subzone C and its implications on body size recovery in tetrapods following the Permo-Triassic mass extinction |
| 16:30 pm | Talk: **Hendrickx** | Evolution of the dentition in Gomphodontia (Therapsida: Cynodontia): disparity, rate of evolution and dental complexity |
| 16:45 pm | Talk: **Jakata** | Implications of computed tomography measurement errors in palaeoscience |
| **END OF DAY** | | |

18:15–19:15 pm: **Keynote Address**: **Paul Barrett** Dinosaur origins and their rise to dominance: an African perspective
19:15 pm: Opening Reception

**Thursday July 5**

8:00 am Prestart Coffee

## Symposium: African Palaeoenvironments

| | | |
|---|---|---|
| 8:30 am | Plenary Talk: **Suarez** | Multi-proxy approaches to elucidate chronostratigraphic and palaeoclimatic records of the end Triassic extinction event at low versus high latitudes |
| 9:00 am | Talk: **Harris** | Coombs Hill: a new Devonian fossil-bearing locality in the Witpoort Formation, Eastern Cape, South Africa |
| 9:15 am | Talk: **Rey** | Stable isotope record implicates aridification without warming during the late Capitanian mass extinction |
| 9:30 am | Talk: **Haupt** | Palaeoenvironmental change from the Hettangian to Toarcian in southwestern Lesotho |
| 9:45 am | Talk: **Head** | Sinemurian landscape changes in southern Gondwana: a new look at the Clarens Formation |
| 10:00 am | Talk: **Muir** | Long-lived Mesozoic palaeoenvironments nested in the Cape Fold Belt |

Tea 10:15–10:45 am

| | | |
|---|---|---|
| 10:45 am | Talk: **Mocke** | Age determination of fossil-rich cascade tufas in northwestern Namibia: palaeoclimatic and palaeoenvironmental implications |
| 11:00 am | Talk: **van Aardt** | Palynological reconstruction of middle Pleistocene environments at Florisbad, Free State Province, South Africa |
| 11:15 am | Talk: **Rossouw** | Direct evidence for $C_4$-grasslands from the ~1-million-year-old bone bed at Cornelia-Uitzoek, Free State province, South Africa |
| 11:30 am | Talk: **Singh** | A Holocene palaeoenvironmental reconstruction of the Okavango source wetlands in Angola |
| 11:45 am | Talk: **Adigu** | Palynological analysis of a short core from the Holocene of the Angolan highlands |
| 12:00 am | Talk: **Neumann** | Last Quaternary vegetation dynamics observed in a marine core from Maputo Bay, Mozambique |

Lunch 12:15–13:45 pm

## General Session:

| | | |
|---|---|---|
| 13:45 pm | Talk: **Browning** | Detailed sedimentology of the Soom Lagerstätte |
| 14:00 pm | Talk: **Smith** | Taphonomy and palaeoenvironments: a new Early Permian tetrapod fauna from Brazil |
| 14:15 pm | Talk: **Day** | Biesiespoort revisited: a case study on the relationship between tetrapod assemblage zones and Beaufort lithostratigraphy south of Victoria West |
| 14:30 pm | Talk: **Rubidge** | Middle Permian dicynodont stratigraphic ranges coupled with ID-TIMS dates from the Karoo Basin have implications for broad-scale stratigraphic correlation |
| 14:45 pm | Talk: **Groenewald** | Litho- and biostratigraphy of the Lower Beaufort Group in the northeastern part of the Main Karoo Basin–Preliminary results |

Tea 15:15–15:45 pm

| | | |
|---|---|---|
| 15:45 pm | Talk: **Cohen** | A new perspective on the taphonomy of the Langebaanweg vertebrates |
| 16:00 pm | Talk: **Bordy** | The Fire Walkers: tracking the last Karoo dinosaurs |
| 16:15 pm | Talk: **Sciscio** | The Roma Giant: large theropod tracks in the Lower Jurassic Upper Elliot Formation in Lesotho |
| 16:30 pm | Talk: **Abrahams** | Morphometric evaluation of Early Jurassic tridactyl dinosaur tracks at Lephoto, Lesotho |
| 16:45 pm | Talk: **Rampersadh** | Dinosaur footprints from a dynamic Early Jurassic aeolian palaeoecosystem, Clarens Formation, Ha Talimo, Lesotho |
| 17:00 pm | Talk: **Reid** | Dinosaur tail traces at the Lower Moyeni ichnosite of Lesotho |

**END OF DAY**

## Poster Session 18:00 pm

## Friday July 6

| | | |
|---|---|---|
| 8:00 am | Prestart Coffee | |
| **General Session:** | | |
| 8:30 am | Talk: **Matiwane** | A new approach to *Glossopteris* leaf taxonomy: embracing morphometric analyses |
| 8:45 am | Talk: **Prevec** | A missing link in *Glossopteris* evolution: new species of *Lidgettonia* from a middle Permian Lagerstätte in South Africa |
| 9:00 am | Talk: **Bamford** | Taxonomy and climate implications of Permian and Triassic fossil woods from Zambia |
| 9:15 am | Talk: **Anderson** | *Umkomasia:* does this megasporophyll (female fruit) have a worldwide distribution or is the genus restricted to the Gondwanan Triassic? |
| 9:30 am | Talk: **Esteban** | Recent advances in phytolith studies in the archaeological and palaeontological record: a review |
| 9:45 am | Talk: **Davids** | Insect fauna and associated plant–insect interactions at the Ouberg Pass and Onder Karoo locality: implications for the evolution of insect utilization of plants in the middle Permian of the Karoo Basin of South Africa |
| 10:00 am | Talk: **Moyo** | Preliminary report on the first mid-Permian ecosystem from South Africa, as revealed by a new Lagerstätte near Sutherland, Northern Cape |
| Tea 10:15–10:45 am | | |
| 10:45 am | Talk: **Kirkaldy** | The past meets the present: exploring the biogeography of extant Plecoptera of South Africa with reference to ancient middle Permian fossil forms from the Onder Karoo locality near Sutherland |
| 11:00 am | Talk: **Badenhorst** | The Equidae from Cooper's Cave, an early Pleistocene fossil locality |
| 11:15 am | Talk: **Tommy** | Trabecular structure in the distal tibia of *Australopithecus africanus* |
| 11:30 am | Talk: **Zipfel** | The first humans and the origins of endurance running–a review |
| 11:45 am | Talk: **Dollman, G.J.** | Raising future prospectors within rural communities |
| 12:00 am | Talk: **McKay** | Collaborative palaeosciences engagement: Grahamstown Science Festival as a case study |
| Lunch 12:15–13:45 pm | | |
| 13:45–16:00pm | | **Biennial General Meeting** |
| **END OF DAY** | | |
| 18:45 pm: **Conference Dinner** | | |

## POSTERS

| | |
|---|---|
| **Anderson** | Earth Alive! 101 Strategies towards stemming the Sixth Extinction: revised edition |
| **Cawood** | Palaeoenvironmental resconstruction of middle Permian ecosystems, inferred from insect fossils of ice crawlers Grylloblattodea) from the Onder Karoo, South Africa |
| **Harris** | *Archaeopteris*, the earliest tree in South Africa, makes its appearance in the Upper Devonian (Famennian) Witpoort Formation |
| **Kato** | Bone lesion in a gorgonopsian fossil from the Permian of Zambia: periosteal reaction in a premammalian synapsid |
| **Mataboge** | A microtomographic study of the StW 669 hominin molar from Milner Hall, Sterkfontein, South Africa |
| **Munyikwa** | New Triassic–Jurassic (Upper Karoo Group) fossil localities on the margin of Lake Kariba, Zimbabwe |
| **Nxumalo** | The phylogenetic classification and locomotion of a non-mammaliaform cynodont *Lumkuia fuzzi* (Probainognathia, Cynodontia) based on CT-tomography of the postcranial skeleton |
| **Robinson** | Taxonomic affinities of large-bodied sauropodomorph dinosaurs from the Elliot Formation of South Africa |
| **Stratford** | The complex taphonomic history of the StW 573 *Australopithecus* skeleton (Sterkfontein, South Africa as revealed by high-resolution computed tomography data |
| **Welman** | Origin and diphyly of theropod dinosaurs |
| **Zozo** | Phylogenetic relationships of the Permian 'cicada-like' family Pereboriidae (Insecta: Hemiptera: Pereborioidea) |

# Keynote address

## Dinosaur origins and their rise to dominance: an African perspective

**Paul M. Barrett**[1,2]

[1]*Department of Earth Sciences, Natural History Museum, London, U.K.*

[2]*Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa*

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Dinosaurs were the dominant terrestrial vertebrates for much of the Mesozoic Era, but their early history remains controversial. New work has questioned the veracity of fundamental splits within the dinosaur family tree and advances in geochronology suggest that the origin of the group might have been more rapid than previously supposed. Until recently, most of our information on the earliest dinosaurs and their immediate antecedents came from Ladinian–Norian deposits in southern South America, but new discoveries in southern and eastern Africa are starting to have a major impact on these debates. Fieldwork in the Manda Basin of Tanzania, in combination with reassessment of historical museum collections in London, has identifed a suite of Anisian-aged East African taxa that have a direct bearing on dinosaur origins. These include recognition of the new clade Aphanosauria, consisting of Teleocrater and other relatives from India and Russia, a group of quadrupedal(?) archosaurs that possess a number of dinosaur-like features and that demonstrate the earliest avemetatarsalians had a broad geographical distribution, which was not limited to southern Pangaea. In addition, the same beds have yielded the holotype specimen of *Nyasasaurus*, which is a contender for the title of earliest true dinosaur and increases the ages of many splits within the dinosaur tree. The Manda Beds and contemporary Ntaware Formation of Zambia have also provided information on silesaurids, the closest relatives of dinosaurs, including the observation that some of these animals convergently reached dinosaur-like body sizes. Inclusion of new information from a range of southern African dinosaur taxa also contributed to a fundamental revision of the dinosaur family tree – in particular the realization that ornithischians like *Heterodontosaurus* and *Lesothosaurus* share numerous features with theropods, which are absent in sauropodomorphs, led to the genesis of the Ornithoscelida hypothesis, in which theropods and ornithischians are sister-taxa, leading to the abandonment of Saurischia as a monophyletic group. Finally, new dating work on the Elliot Formation is showing that many of these sites might be Late Triassic, rather than Early Jurassic, in age, thus resetting the tempo of dinosaur evolution and their ascendancy to ecological dominance.

# Plenary talk

## Synapsids inside out: perspectives on the origins of mammalian physiology from histology and computed tomography

**Adam K. Huttenlocker***

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Synapsids are the tetrapod clade that includes mammals and their extinct forebears. Their lineage diverged from reptile-line tetrapods 320 million years ago and produced the wide-ranging ecological diversity of modern mammals, many of which have a remarkable capacity for sustained exercise. This ability has been linked to classic 'mammalian' traits – elevated thermometabolism, insulating hair, muscular diaphragm, respiratory turbinates – which might have evolved in nonmammalian therapsids before crown Mammalia. Key skeletal transformations almost certainly influenced athletic ability, and understanding how these changes were associated with adjustments in thermometabolism remains an active area in synapsid research. Trends in palaeophysiology have shifted from macro- to microstructural scales, and external to internal data with advanced imaging techniques. Bone tissue texture and remodelling, for example, have provided the strongest evidence for endothermic-like metabolism in some Permo-Triassic therapsids. Nevertheless, interpretations have been qualitative in nature, and belie the diverse continuum of tissues observed in ectotherms and endotherms alike. Quantitative histometry aims to use measurable tissue parameters to retrodict metabolism and other physiological attributes. For instance, it has been suggested that hypoxia and a broncho-alveolar lung limited some Triassic therapsids to small body size, precluding them from niches requiring high aerobic activity (cursors, powered-flyers). Histometric evidence suggests that an active, subterranean lifestyle in Triassic cynodonts may have presented conditions that favoured improved diffusive capacities through smaller, enucleated red blood cells and associated vasculo-lacunar networks as in mammals. High-resolution computed tomography (HRXCT) permits better access to internal anatomy, expanding baselines to test established notions. For example, recent HRXCT scanning has questioned whether Permian therapsids had respiratory maxilloturbinates, popularly believed to be a 'Rosetta Stone' of endothermy, but, apparently, a crown mammal feature. Emerging analytical approaches in biomedical imaging, biogeochemical congruence tests (biomarkers, clumped isotope palaeothermometry), and phylogeny-augmented retrodictive models are needed to further clarify the conditions under which canonic 'endothermic' traits arose, and how their evolution shaped the success and the resulting physiological landscape of synapsids and other athletic tetrapod groups.

# Plenary talk

## Multi-proxy approaches to elucidate chronostratigraphic and palaeoclimatic records of the end Triassic extinction event at low versus high latitudes

**Celina Suarez[1]*, Jonah N. Choiniere[2], Emese M. Bordy[3], Pia A. Viglietti[2], Glenn Sharman[1]**

[1]*Department of Geosciences, University of Arkansas, Fayetteville, AR, U.S.A.*

[2]*Evolutionary Studies Institute and School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa*

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Recent work on the end Triassic mass extinction (ETE) has greatly refined the climatic circumstances surrounding it. Biotic data suggest a degree of provinciality, with pseudosuchian archosaur-dominated fauna and small theropod dinosaurs thriving in the Late Triassic before the ETE in the low latitudes and a diverse derived fauna of early sauropods, theropods, and ornithopods at high latitudes. Besides latitudinal climatic gradients, global climate change due to the Central Atlantic Magmatic Province (CAMP) must have had a high impact on climate and habitat during this time and likely contributed to the extinction. The investigation of the relationship between latitudinal climate gradients, rapid global climate change caused by the CAMP, biotic provinciality, and extinction, requires a highly-resolved chronostratigraphic record. This project investigates the location/occurrence and characteristics of the ETE at low versus high latitude locations of the Moenave Formation, U.S.A., and Elliot Formation, South Africa and Lesotho. Here we present C-isotope chemostratigraphic records, detrital zircon geochronology, and palaeomagnetic data. For the Moenave Formation detrital zircon geochronology suggests that the upper part of the lower member of the formation, the Dinosaur Canyon Member, is earliest Jurassic; no older than 201.33 ± 0.07/0.12/0.25 Ma based on high-resolution CA-ID-TIMS U-Pb ages. A distinct negative C-isotope excursion (NCIE) of –5.5 occurs in the lowest part of the upper member, the Whitmore Point Member; however, its occurrence above the 201.33 Ma date precludes it from being the initial NCIE that marks the ETE. Magnetic reversals can be compared to the Newark-Hartford chronological record. Preliminary and published data from the Elliot Formation suggests a NCIE that may indicate that the ETE excursion occurs close to the contact between upper and lower members of the Elliot Formation. Preliminary detrital zircon U-Pb data (LA-ICP-MS) from sandstone within the Elliot Formation demonstrate the presence of age contemporaneous detrital zircons that indicate latest Triassic-earliest Jurassic maximum depositional ages. Additional grain analyses are needed to obtain a more robust set of young age clusters, and the youngest grains will be reanalysed using CA-ID-TIMS to increase the resolution of these dates.

# Conference Abstracts

## Morphometric evaluation of Early Jurassic tridactyl dinosaur tracks at Lephoto, Lesotho

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Footprints are products of the interaction between the trackmaker and substrate. Thus, track morphology is primarily influenced by the trackmaker's anatomy, locomotion style and substrate conditions. Consequently, track morphology can be highly variable and complex within the same palaeosurface and requires multidisciplinary analysis for understanding *why* a track presents in a particular way. Traditionally, track studies relied on two-dimensional descriptions, but with the availability of affordable software technology, rooted in photogrammetric methods, three-dimensional investigations of tracks have become vital in understanding the complexities of track formation. While the quest to standardize track and trackway documenting methodologies is ongoing, recent focus has shifted to quantifying the variability in track morphology. Herein, we present the preliminary findings of a novel landmark-based geometric morphometric approach for the analysis of the tridactyl tracks from the upper Elliot Formation at Lephoto in Lesotho. To minimize intricacies associated with variable trackmakers, locomotion styles and substrate conditions, only four trackways on the Lephoto palaeosurface were included in this comparative study. Omitting individual tracks enhanced the robustness of the comparisons, because a given trackway is made by a single trackmaker, therefore morphological variation is unlikely to result from the trackmaker's anatomy. Furthermore, trackways provide insight into locomotion, which can be used to explain morphological variation within and between trackways. Three trackways are attributed to ichnogenera of the *Eubrontes–Grallator* plexus, which are generally accepted to have theropod affinities. The fourth trackway is assigned to the ichnogenus *Trisauropodiscus*. Digital pad impressions, claw marks and the lack of a merged proximal region in the theropod tracks collectively indicate a uniform, firm substrate across the palaeosurface aiding inter-trackway comparisons. Using a combination of principal component analysis and multivariate analysis of variance, this study aims to address the following: 1) which features contribute significantly to intra-trackway variability? 2) how similar are the tracks that lie on a single ichnogenus spectrum? and 3) how well can morphometrics assign and distinguish ichnogenera? The answers will contribute to our understanding of track morphological variation with implications for reconstructing more accurate vertebrate biodiversity patterns in the Early Jurassic of southern Africa.

## Palynological analysis of a short core from the Holocene of the Angolan highlands

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Many of the studies conducted in most Quaternary environments are aimed at tracking climate change in order to understand the accelerating pace of the changing environment. This has led to robust data archived from various proxies (e.g. phytoliths, pollen, tree rings among others) that have aided effectively in the reconstruction of past environments across southern Africa. However, some parts of southern Africa still have little or no records available for tracking environmental change. This project provided one such data set for the Angolan highlands where a palynological study was conducted. A short core housed at the Evolutionary Studies Institute retrieved from the highlands of Angola and covering the Late Holocene was used for this study. To enable us to provide this data, fossil pollen was retrieved from the samples labelled CC1. These pollens were identified using reference collections from published literature across southern Africa. More than 250 pollen grains that were counted from each sample of the short core were entered into Microsoft Excel and graphs were used to identify the dominant taxa. Selected pollen taxa were further subjected to Principle Component Analysis in R 3.2.1 to evaluate the co-varying taxa. Stratigraphic diagrams showing the important pollen taxa were plotted using C2 program version 1.7.7 for analysing the pollen composition. From our results the selected pollen taxa reveal slight changes in vegetation that alternated between wet and dry periods of deposition. There was a strong presence of some characteristic taxa (Asteraceae, Cyperaceae and Typhaceae) that were associated with these

environments. The results from this study provide an ample basis for further studies on the environment to validate if these changes resulted from climate change or if they were influenced by local disturbance.

## *Umkomasia:* does this megasporophyll (female fruit) have a worldwide distribution or is the genus restricted to the Gondwanan Triassic?

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It is now over 90 years since Hamshaw Thomas suggested that the origin of angiosperms may lie in the ancient pteridosperms (seed ferns) such as *Caytonia* from the Yorkshire Jurassic and *Umkomasia* from the Triassic of South Africa. Since then many new early angiosperm fossils have been documented and our understanding of plants has progressed from morphological and anatomical studies to exploration of their phylogenetics using DNA and RNA blueprints. The hypotheses of Thomas have generally not been supported in subsequent studies. However, the origin of angiosperms in their probable seed fern ancestry remains an enigma. Therefore, ancient plants such as *Umkomasia* with seeds enclosed in cupules should be studied and analysed from a modern perspective. As a first step the megasporophyll genus *Umkomasia* was reassessed comprehensively worldwide. *Umkomasia* is rare in the fossil record and most localities in Gondwana have only one or two specimens recorded, with a few collections of up to 20 specimens. An exception is the Molteno Formation, which is by far the best sampled in terms of volume and stratigraphic occurrence, yielding eight species and 503 specimens from 22 localities. The two specimens of *Umkomasia* reported from the Upper Permian of India were incorrectly identified, and to date there are no other records of *Umkomasia* from the Triassic *Dicroidium* flora of India. A whorled fertile structure from Antarctica named *Umkomasia uniramia* is re-evaluated. The *Umkomasia* species described from the Triassic of China is shown to belong to another genus. The Lower Cretaceous record of *Umkomasia* from Mongolia has been renamed by other researchers as *Doylea mongolica*. The Lower Jurassic record from Germany and another two non-Gondwana *Umkomasia* records are shown to be incorrect. Following a re-evaluation of reports of this taxon, *Umkomasia* is here shown to be restricted to the Triassic of Gondwana, and is clearly affiliated to the microsporophyll genus *Pteruchus* and the vegetative leaf genus *Dicroidium*. By the removal of material previously incorrectly assigned to *Umkomasia*, a deeper understanding of this important Gondwanan genus can be gained, informing the development of more constructive and accurate phylogenies.

## The Equidae from Cooper's Cave, an early Pleistocene fossil locality

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Cooper's Cave is an early Pleistocene fossil locality in the Cradle of Humankind, close to Sterkfontein and Kromdraai, Gauteng Province, South Africa. The fossil deposits at Cooper's Cave date to between 1.5 and 1.4 million years ago and comprise a diverse faunal assemblage that includes hominins. Here, we report on the Equidae remains. The sample contains specimens from the extinct *Equus capensis* and one specimen may possibly be attributed to the small extinct hipparion *Eurygnathohippus* sp. The relevant specimen identified as hipparion, is smaller than the plains zebra. Previous research suggested that the contribution of Equidae to the total fossil assemblage of Cooper's Cave is low. However, we suggest that the ratio of Equidae to Bovidae is similar at Cooper's Cave to other similarly-aged deposits in the Cradle of Humankind. Equidae were either not common on the landscape, they effectively defended themselves against predators thereby reducing their predation rates, or predators utilizing the caves may not have selected larger prey sizes.

## Taxonomy and climate implications of Permian and Triassic fossil woods from Zambia

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Although the Karoo sequence in southern Africa is better known for its vertebrate fauna a large collection of Permian and Early Triassic silicified woods from South Africa, Zimbabwe, Namibia, Botswana and

Zambia is housed in the Evolutionary Studies Institute. By far the most common genus of secondary xylem woods is *Agathoxylon*, with at least two species, *A. africanum* and *A. karooensis*. This genus has the typical araucarian alternate bordered pitting on the tracheid walls and has been called *Dadoxylon* and *Araucarioxylon* in the past. Other genera include *Australoxylon* with clusters of pits on the tracheid walls, and *Prototaxoxylon* with spiral thickenings on the tracheids, from the early Permian. *Podocarpoxylon* with abietinian tracheid pitting and *Rhexoxylon* with lobes of xylem separated by parenchyma, each with only a few species, have been collected from Triassic strata. In upper Carboniferous and lower Permian strata there are a few woods with piths preserved such as *Megaporoxylon*. This apparent lack of diversity in the woody plants is investigated. With a focus on the new collections of woods from Zambia where trunks with diameters greater than 2 m occur at several sites, their identification, growth rings and estimated height and spacing are presented as well as the environmental implications.

## Is the infraorbital foramen homologous in non-mammaliaform cynodonts and mammals? Implications for the evolution of whiskers

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In mammals, the infraorbital foramen (IOF) and canal are located in the maxilla rostral and ventral to the orbit and provide a passage for the infraorbital nerve (i.e. the infraorbital branch of the trigeminal nerve). The infraorbital nerve (ION) ensures sensitivity of the upper teeth and face between the eye and upper lip. Noticeably, the innervation of the facial vibrissae (whiskers) is ensured by the ION. Homology of the IOF across mammals is based on the fact that it gives passage to the ION. For example, the IOF is located dorsal to the orbit in odontocetes (Cetacea) and can only be recognized as such because it gives passage to the ION. In most non-mammalian synapsids the IOF is replaced by the maxillary canal, which completely encloses the ION and its branches. Remarkably, the pattern of ramification of the branches of the maxillary canal can be homologized with that of the ION in modern mammals, which strongly supports the idea that the two structures are homologous. In contrast, a conspicuous foramen present below the orbit on the maxillo-lacrimal suture in Probainognathia (the non-mammaliaform Cynodontia more closely related to mammals than to *Cynognathus*) and early Mammaliaformes (e.g. *Morganucodon*), has in the past been homologized to the IOF by most authors. Using $\mu$CT-scanning and 3D modelling to reconstruct the evolution of the maxillary canal from the primitive synapsid condition to the modern mammalian condition in Probainognathia, it is here suggested that this foramen did not provide a passage for the ION. According to our observations, this pseudo-IOF might, in fact, have been for the zygomatic nerve and/or a blood vessel. In addition, this study shows that the transition from a maxillary canal to a mammal-like IOF was gradual, which imposes a reassessment of the evolutionary origin of the associated whiskers.

## The Fire Walkers: tracking the last Karoo dinosaurs

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Over fourteen vertebrate footprints, forming three distinct trackways, have been identified on a sandstone interbed within the lowermost Drakensberg Group lava flows in the northern main Karoo Basin. The ichnosite is on farm Highlands 1239 near Bethlehem in the Free State (South Africa), and ~45 m above the contact between the Clarens Formation and Drakensberg Group, which have local thicknesses up to ~140 and ~125 m, respectively. The sandstone interbeds in the lava flow succession consist of silty very fine- to medium-grained sandstones that are either massive, horizontally laminated, ripple cross-laminated, planar or trough cross-bedded. The interbed units range in thickness from a few 10s of cm to ~15 m. The track-bearing, fine-grained, massive sandstone layer is ~5 cm thick and forms part of a ~1.2 m thick interbed unit. The tracks are among desiccation cracks and low-amplitude, asymmetrical ripple marks, implying deposition in low energy, shallow, ephemeral water currents. All tracks are tridactyl pes prints attributable to animals of assorted sizes based on their track lengths. The largest footprints are just over 14 cm long with locomotion parameters of a fast running individual. The other footprints vary in length from ~2 to ~4 cm, and indicate much smaller individuals (? juveniles) that moved at a slower

speed. Based on the morphological parameters, the tracks are tentatively attributed to *Grallator* and considered to have been made by bipedal theropod dinosaurs, like *Coelophysis*, a common Early Jurassic genus in southern Africa. Based on K-Ar and $^{40}Ar/^{39}Ar$ dating of lava flows, the dinosaur footprints at Highlands 1239 were generated around the Pliensbachian–Toarcian transition. This not only suggests that the theropod trackmakers lived after the onset of the Drakensberg volcanism, but also that these dinosaurs were among the last animals that inhabited the Karoo Basin some 183 Ma ago. Although these vertebrates survived the first Karoo volcanic eruptions, their rapidly dwindling habitat was turned into a land of fire as it was covered by the outpouring lavas in one of the largest flood basalt events (by volume) on Earth and in one of the most dramatic geological episodes in southern Africa.

## Non-mammaliaform cynodont osteohistology and implications for the evolution of mammalian growth patterns

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Non-mammaliaform cynodonts appeared during the late Permian about 256 million years ago and radiated into a diverse array of body sizes and ecological niches before evolving into the first mammals some 37 million years later during the Late Triassic. The acquisition of an increasingly mammalian skeletal morphology during the Triassic indicates that many features required to facilitate homeothermic endothermy were in place prior to the appearance of crown group mammals. The bone tissues of non-mammaliaform cynodonts reflect the diversity of this clade, but do they follow the acquisition of mammalian characteristics and show increasingly mammalian growth patterns during their evolution? During the Early Triassic, non-mammaliaform cynodonts were relatively small and showed growth attenuation within one to two years. Two major lineages diverged at this time, the Cynognathia and Probainognathia. The Middle Triassic Cynognathia evolved into large-bodied taxa that exhibit high growth rates and multi-year growth to somatic and presumably reproductive maturity, similar to large extant mammals (e.g. ruminants). The Probainognathia includes the smaller bodied prozostrodontians, which themselves evolved into the tiny mammaliaforms during the Late Triassic. The Prozostrodontia also exhibit high growth rates, despite progressively smaller body sizes. They exhibit increasingly mammalian characteristics such as more efficient locomotory and masticatory structures allowing for increased activity levels and energy assimilation, maxillary vibrissae indicating improved sensory capabilities and improved thermoregulatory and reproductive controls (implied from the loss of a pineal foramen). However, despite being similar in size to small, extant placental mammals that typically reach reproductive maturity within one year, early prozostrodontians still took more than one year to reach growth attenuation, even the brasilodontids, the sister taxa to Mammaliaformes. Thus, although the small Early Triassic non-mammaliaform cynodonts matured within one year, this strategy was abandoned when the lineage diverged into larger body sizes and appears to have taken a relatively long time to be regained. It is likely that future investigations will reveal a diverse array of life history patterns amongst the Mesozoic mammals and, despite their rodent-like body plans, the extremely rapid growth attenuation typical of small placental mammals may not necessarily reflect the plesiomorphic state of this clade.

## Detailed sedimentology of the Soom Lagerstätte

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The Ordovician Soom member is a <28 m laminated shale unit at the base of the Cedarberg Formation, Table Mountain Group (South Africa). The unit was deposited just after the Hirnantian glaciation, during which major climatic shifts lead to the second most devastating mass extinction event on Earth. It is of palaeontological importance not only because it contains an exceptionally well-preserved, yet largely undocumented faunal assemblage, but because it provides a unique glimpse of a post-glacial refugium in southwestern Gondwana. We have studied freshly drilled core from the lower Cedarberg Formation using detailed petrography, millimetre-scale logging, standard surface microtexture analysis, SEM, TEM

and nano-CT and synchrotron scanning in order to interpret the lamina-by-lamina scale palaeoclimatic information and determine the origin of a unique sedimentary facies recorded in the Soom member. One microfacies in particular is remarkable; within claystone, abundant clusters of multiple quartz and clay grains occur, closely associated with fossil algae. The quartz grains are all similarly sized and resemble those from modern loess (wind-blown dust). This microfacies is temporally and spatially persistent. It occurs in boreholes drilled 200 km apart and throughout 25 metres of core, although it becomes less abundant as the Cedarberg Formation gradually coarsens upwards, suggesting that the source and processes forming this sediment remained consistent throughout deposition. There are neither temporal variations in grain size, nor in the relative proportions of the components of this microfacies. Preliminary results from nano-CT and synchrotron scans have shown that framboids, closely associated with this microfacies, appear to record lamina-scale variations in palaeo-redox conditions. To explain the origin and palaeoenvironmental context of this unique facies, we explore hypotheses, including: 1) loess-derived sediment possibly associated with marine algal blooms, 2) an algal mat bound seafloor trapping quartz grains, and 3) episodic binding and transport of sediment originally deposited in water bodies on land. Through our detailed study we hope to fully realize the immense potential of the Soom member to provide significant insights into the precise course of climate change as major ice-sheets retreated – and a greatly improved understanding of the climate dynamics of Early Palaeozoic icehouse climates.

## Postcranial morphology of the Early Triassic epicynodont *Galesaurus planiceps* from the Karoo Basin, South Africa

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The South African Karoo Basin is well-known for its extraordinary preservation of Permo-Triassic therapsids, the extinct relatives of mammals, which include non-mammaliaform cynodonts. The Early Triassic non-mammaliaform epicynodont, *Galesaurus planiceps*, formed an important part of the recovery ecosystem following the Permo-Triassic Mass Extinction, the greatest mass extinction in Phanerozoic history. Here, we re-examine the postcranial skeleton of *Galesaurus* and present data that provide valuable information on its biology and ecology. Two morphotypes are recognized, a gracile and a robust morph, which are interpreted to be stages in an ontogenetic series, due to differences in size. The principal differences between the morphs are in the girdles with additional slight changes in the fore- and hind limbs. Our results also reveal postcranial differences between *Galesaurus* and the contemporaneous *Thrinaxodon liorhinus*, permitting these taxa to be distinguished in the absence of cranial material. The first evidence of intraspecific variation in the presence and distribution of disc-like phalanges in a non-mammaliaform cynodont is also reported. An analysis of the osteohistology of *Galesaurus* reveals rapid growth to skeletal maturity within one to two years, thereafter transitioning to slow intermittent growth. This growth pattern is comparable to that of *Thrinaxodon*, which also grew rapidly and continuously to skeletal, and possibly reproductive, maturity within its first year of life. Characteristics such as thick, robust forelimbs and stout unguals, a strong, reinforced pelvis and elongated ilium suggest that *Galesaurus* was capable of actively excavating burrows. The combination of rapid maturation and fossoriality may have aided in its survival during the harsh, unpredictable post-extinction Early Triassic environment.

## The evolution of embryonic development in Archosauria

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Birds are the sole living dinosaur lineage and are therefore often used as a modern analogue when studying dinosaurian evolution. Embryology has revealed, however, that dinosaurs display both plesiomorphic developmental characteristics present in non-avian saurians (such as a long incubation period) as well as derived developmental characteristics of birds (such as skeletal anatomy and egg macro- and microstucture). Little is known, however, about the cranial ossification sequence of dinosaurian embryos, and how this sequence compares to other archosaurians. Here we make a primary inquiry into the *in ovo* cranial ossification sequences of Archosauria, using data from synchrotron microtomography

scans of the world's oldest known dinosaur embryos and comparing these to extant exemplar study systems. The three dinosaur embryos are from a single clutch of eggs associated to the southern African basal sauropodomorph dinosaur *Massospondylus carinatus* Owen 1854. Our results are novel for non-avian Dinosauria and include: 1) previously unknown patterns in the onset of the postcranial and cranial ossification sequence revealing, for example, that the lateral bones of the face and the palate ossify before braincase bones; and 2) differences in the ossification stages of braincase bones, such as the presence/absence of basipterygoid processes and the quadrate bone. Previous research has shown that braincase bones grow the least during ontogeny. This would imply that within the third portion of embryonic development, these bones ossify and reach a size closer to full size than other cranial bones, or that they grow at high rates during the initial post-hatching development. Comparison to extant model systems shows that ossification sequences in dinosaurs are most similar to those of birds. Although caution is warranted because of the large phylogenetic distances involved in our study and because of high variability of ossification sequences in other tetrapod groups, our data suggest that aspects of avian *in ovo* development likely evolved before the origins of powered flight.

## An unequivocal rauisuchian from the Elliot Formation of South Africa

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'Rauisuchia' is a paraphyletic assemblage of primarily large-bodied, carnivorous, non-crocodylomorph pseudosuchian archosaurs whose members were relatively common components of Triassic terrestrial faunas. As they went extinct at the end of the Triassic, 'rauisuchians' can be useful biostratigraphic markers for discerning the position of the Triassic–Jurassic boundary. Surprisingly, the Late Triassic (Norian–Rhaetian) lower Elliot Formation of South Africa has never produced a definitive rauisuchian fossil, although several jaw fragments and isolated teeth have been referred to this group. The productive Elliot Formation locality Heelbo (Free State Province, South Africa) has yielded abundant remains of Early Jurassic sauropodomorph dinosaurs, including *Aardonyx*, *Pulanesaura*, and *Arcusaurus*. Excavations at Heelbo by our research team in 2016 recovered the articulated sacrum of a large archosaur that we initially identified as a sauropodomorph. However, preparation of the specimen revealed derived features of the ilium, including a large, dorsolaterally projecting buttress dorsal to the acetabulum, that are diagnostic for 'Rauisuchia'. Furthermore, the ilium bears strong anatomical similarities to that of *Postosuchus*, a member of the Late Triassic, monophyletic rauisuchian group Rauisuchidae. The new material represents the first unequivocal 'rauisuchian' from South Africa, and one of the most southerly known records for this group (~55 degrees South in the Late Triassic). The strata at Heelbo are poorly dated, but intriguingly the new fossil comes from a layer previously thought to be Early Jurassic (this level also contains *Aardonyx*). This means either that our find represents the only Jurassic 'rauisuchian' or that the relative age of the Heelbo strata and its fossils needs to be reassessed.

## A new perspective on the taphonomy of the Langebaanweg vertebrates

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The world-renowned Mio-Pliocene vertebrate locality at Langebaanweg has been studied for over 60 years. However, many questions remain regarding the palaeoenvironmental dynamics and palaeoecological reconstructions of the site. Langebaanweg has been interpreted as an estuary that formed during a transgressive phase with associated marine flooding of the coastal regions. Many of the fossil

remains, which include a staggering diversity of animals, have been recovered from palaeoestuarine channels and associated floodplain deposits. Taphonomic research investigating the depositional history of these fossil remains is limited and little has been published to date. Excavations and research have focused on remains from the channel and the bonebed deposits; however, other fossiliferous strata, like the underlying stratigraphic units, have not been investigated since the 1970s. We present results from a taphonomic analysis of remains recovered from test pit excavations in three areas of the Langebaanweg E-Quarry, including the bonebed, the river channel and a previously unstudied area. Two of these excavations sampled both the Muishond Fontein Phosphatic (MPPM) Sand Member and the Langeberg Quartz Sand Member (LQSM). The MPPM consists of fine- to medium-grained sands and preserves channel structures containing highly fossiliferous deposits including the bonebed. The underlying LQSM unit consists of fluvio-estuarine quartzose sands. Our results show a predominance of small or fragmented remains throughout the Langebaanweg deposit, including within the bonebed. Tortoise shell fragments were the most commonly recovered bones. Possible reasons for the abundance of tortoise remains will be discussed. The most commonly observed bone surface modifications were trampling and abrasion. Evidence for carnivore activity was rare (<5%), whereas burning was observed on approximately 10% of remains. The ecological implications for these findings are discussed. We show how the taphonomic patterns of the deposits in conjunction with their sedimentological properties indicate deposition in a low energy environment. These new results show a profound need for expanding research at Langebaanweg beyond the bonebed into the wider area of the quarry.

## Insect fauna and associated plant–insect interactions at the Ouberg Pass and Onder Karoo locality: implications for the evolution of insect utilization of plants in the middle Permian of the Karoo Basin of South Africa

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The study of plant–insect interactions has been an integral part of many modern biodiversity studies. However, the study of the interactions evident in the fossil record is a relatively new and emerging field. Here, two study sites are considered, Ouberg Pass and Onder Karoo, which are located near Sutherland, Northern Cape. They lie within the Abrahamskraal and Waterford formations, respectively, and date back to the middle Permian (Guadalupian). These sites offer a rich record of excellently preserved leaves (mostly *Glossopteris*), seeds, insect wings and body fossils, which provide further insight into the plant life as well as the insects that utilized them. Little work has been published on Gondwanan plant–insect interactions in general and studies that have been done have focused mainly on the lower and upper Permian deposits of the northern and eastern parts of the Karoo Basin, respectively. The sheer lack of both plant and insect fossils from the middle Permian has severely impacted the study of the evolution of these plant–insect interactions through time. Many of these studies have taken qualitative approaches, while the few quantitative studies remain unpublished. This study has adopted a more quantitative and detailed approach to describing these interactions, incorporating intensity, frequency and detailed accounts of interactions, allowing a more in depth and high-resolution assessment of plant–insect interactions during this critical time period. Of particular interest to this study are the patterns of host specificity, interaction diversity and feeding preferences that are present in the fossilized material. The proposed data aims to bridge the current gap in the fossil record and provide insight into the coevolution of plant–insect utilization prior to the end-Guadalupian extinction.

## Biesiespoort revisited: a case study on the relationship between tetrapod assemblage zones and Beaufort lithostratigraphy south of Victoria West

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The relationship between the lithostratigraphic units and the vertebrate assemblage zones of the lower Beaufort Group in the Main Karoo Basin of South Africa is considered to be consistent. This is based mostly

on collecting efforts in areas surrounding the Great Escarpment, where lithostratigraphic units are well exposed. However, in the district of Victoria West some anomalies were observed when attempting to determine the stratigraphic provenance of middle Permian fossil tetrapods across the Karoo Basin. One such locality, Biesiespoort, was famously explored by Broom in the 1920s and a number of specimens discovered there are holotypes. Here, historically collected fossils suggested the presence of the upper Permian *Tropidostoma* and *Cistecephalus* assemblage zones (AZs) in strata mapped as belonging to the Poortjie Member of the Teekloof Formation, a unit which is usually associated with the middle Permian *Pristerognathus* AZ. In order to resolve this, we visited Biesiespoort and collected 57 fossil vertebrates that corroborated the findings of previous palaeontologists and established that the strata were indeed late Permian. This suggests that either the constituent members of the lower Teekloof Formation are diachronous, younging in a northeasterly direction, or that the geological maps are inaccurate. No diachrony for the contact of the Abrahamskraal and Teekloof formations is suggested from historical collections, in which case the presence of the *Tropidostoma* AZ in the Poortjie Member would imply the absence or reduced thickness of the *Pristerognathus* AZ. Further work is required to test if the *Pristerognathus* AZ is present in the vicinity of Victoria West.

## Raising future prospectors within rural communities

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South Africa has access to a rich and varied fossil record with a long history of important discoveries. One of the key outreach goals of the palaeosciences, which is funded via the National Research Foundation, is to develop young researchers' skills and promote a career in palaeontology in order to ensure a promising future for the science within South Africa. QwaQwa campus, a rural campus in the Phuthaditjaba municipality area belonging to the University of the Free State, is an excellent institution of higher learning for reaching demographic groups that are underrepresented in the palaeontological community. The campus is geographically positioned within the upper Elliot Formation and is in close proximity to the Golden Gate National Highlands Park, an area which has already been identified for the development of a palaeontological museum. Currently, there is little to no active palaeontologically-based research on the campus. Students who complete a geography-based education have no palaeontology modules and are not aware of the importance of the fossil record available to them. To meet this shortcoming, the Evolutionary Studies Institute of the University of the Witwatersrand in collaboration with the University of the Free State Afromontane Research Unit has begun an annual workshop and field trip for undergraduate students. In our first iteration of this workshop, we presented a series of lectures and trained students in palaeontological field methods (including drone surveys) during a field trip to an upper Elliot locality within the Phuthaditjhaba, QwaQwa campus area. We assessed our performance using a questionnaire designed to test awareness among students about opportunities within geography, sedimentology, palaeontology and applied computer science. Students have been introduced to the benefits of collaborative science projects and post-graduate applications are expected to improve within the fields of geography, palaeontology and applied computer science.

## The crocodylomorphs of southern Africa and their geographic and stratigraphic distributions

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Currently there are seven known crocodylomorph taxa from the upper Elliot Formation of southern Africa, including the 'sphenosuchians' *Sphenosuchus* and *Litargosuchus*, and 'protosuchians' *Protosuchus*, *Lesothosuchus*, *Orthosuchus*, *Notochampsa* and *Clarencea*. Although not as numerous as their dinosaurian contemporaries, there are still many unidentified or poorly diagnosed crocodylomorph fossil remains within collections across the country. Taxonomic identifications of these specimens have been haphazard, particularly with regard to the protosuchians *Notochampsa* and *Protosuchus*. Furthermore, this taxonomic

confusion prevents an understanding of their geographic and temporal distributions, and hinders their use as biostratigraphic markers. In this study, we review all crocodylomorph material in the Evolutionary Studies Institute, the Iziko South African Museum and the National Museum Bloemfontein to provide testable, apomorphy-based diagnoses for all valid genera and species, and present full geographic and stratigraphic provenance information that has been ground-truthed where possible. Results from this study show that there are additional diagnostic features within the mandible, frontal and osteoderms allowing for correct identification of many misdiagnosed specimens. It appears that *Protosuchus* and *Orthosuchus* are much more numerous than previously thought, and that *Notochampsa* is a valid genus. Review of their stratigraphic and geographic distributions shows that crocodylomorphs were constrained to the uppermost Elliot and lower Clarens formations, which supports the age of these strata as Jurassic. Furthermore, it supports the use of basal crocodylomorphs as relatively precise stratigraphic markers that may represent a localized recovery fauna following the end-Triassic extinction, or perhaps reflect the changing environments of the upper Elliot Formation.

## Juvenile biarmosuchians from the Karoo Beaufort Group shed new light on basal therapsid ontogeny

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The Beaufort Group of the South African Karoo Supergroup is internationally celebrated as one of the richest sources of vertebrate fossils chronicling the Permo-Triassic evolutionary radiation of Therapsida. This clade includes modern mammals as well as their non-mammalian ancestors and relatives. Biarmosuchia is the most basal clade of the Therapsida and an important group for understanding their origin and early evolution. Unfortunately, it has a very poor fossil record with only thirty known specimens. Most of these specimens come from the highly fossiliferous mid-late Permian lower Beaufort Group of South Africa. Fifteen monotypic genera have been described, of which only *Biarmosuchus* from Russia and *Hipposaurus* and *Lemurosaurus* from South Africa are represented by more than one specimen. As a consequence, very little is known of their ontogeny and intraspecific variation. The best represented biarmosuchian subclade, both in terms of number of specimens and quality of preservation, is the Burnetiamorpha, comprising ten genera of which *Lemurosaurus pricei* is the most basal. Here, we discuss two new burnetiamorph specimens recovered from the *Pristerognathus* Assemblage Zone of the Beaufort Group. Both specimens (CGP MJF 22 and SAM-PK-K11126) show typically juvenile characteristics, such as a large orbit relative to the skull length, an un-ossified braincase, and well defined sutures. Interestingly, both have several bones present in the position expected to be occupied by the parietal, suggesting that this bone was formed from several centres of ossification. SAM-PK-K11126 preserves postcranial material, including a complete pelvic girdle, making it the most complete burnetiamorph specimen to date. Using CT-microtomography to virtually render these specimens, we describe the internal anatomy of the skull and the histology of some of the cranial bones. Description of these well-preserved specimens sheds light on biarmosuchian ontogeny.

## Recent advances in phytolith studies in the archaeological and palaeontological record: a review

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South Africa continues to receive substantial attention from scholars researching a variety of plant forms from the late Devonian period to the present. Biological micro-remains are invaluable data sources for improving our capacity to reconstruct past climatic and environmental conditions. The reconstruction of past environments can also help us to shed light on survival strategies of hunter-gatherers. Phytoliths are microscopic particles of amorphous silica formed in plant tissues. Phytolith studies have been widely used to identify plants exploited by past humans as foodstuffs, medicines, fuel-wood and for shelter, as well as

for palaeoenvironmetal and palaeoclimatic reconstructions. Previous studies have shown the potential of phytoliths to be preserved in Cenozoic deposits and even in Late Cretaceous dinosaur coprolites. Here, a review of the high diversification of phytolith research topics and the advantages and disadvantages of phytolith studies in the palaeontological and archaeological record, with particular emphasis on South Africa, is presented. New directions and recent advances in phytolith research such us the characterization of new plant taxa and extant habitats, the use of morphometric analysis, radiocarbon dating and isotope analyses are highlighted and may be used to inform the design of new research.

## New clues to the origins of tetrapods, from the South African Upper Devonian

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The fish to tetrapod transition is one of the most crucial macroevolutionary events in the history of vertebrates, which moreover had unparalleled ecological consequences. Description over the last three decades of a small number of well-preserved transitional forms, such as the Late Devonian tetrapod, *Acanthastega* and the pre-tetrapod *Tiktaalik*, have significantly advanced our understanding of the morphological and probable habitat changes involved in this transition. Furthermore, these discoveries have permitted identification of a larger set of related taxa on the basis of isolated skeletal elements, some of which had long languished in collections as unidentified specimens. All of these specimens are derived from rocks deposited in the Devonian palaeotropics, the majority of which are from Laurussia ('the Old Red Sandstone Continent'). The only known Gondwanan taxon, *Metaxygnathus*, represented by a single lower jaw ramus from eastern Australia, was recovered from sediments deposited on the tropical rim of Gondwana, adjacent to Laurussia. This has led to an assumption, entrenched within the literature, that pre-tetrapods and tetrapods were solely the denizens of tropical water bodies and probably arose in Laurussia. The Waterloo Farm Lagerstätte near Grahamstown, a Famennian (Late Devonian) aged deposit preserved in strata of the Witpoort Formation (Witteberg Group, Cape Supergroup), by contrast supplies unique evidence for a lagoonal setting within the palaeoantarctic circle. Systematic collection of material from this site over three decades has provided a large sample of vertebrate remains. Analysis of this material reveals the remains of taxa nested within the fish to tetrapod transition, establishing that theories regarding the latitudinal and palaeogeographic setting of the transition largely result from collection bias.

## Litho- and biostratigraphy of the Lower Beaufort Group in the northeastern part of the Main Karoo Basin – Preliminary results

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Guadalupian to Lopingian aged strata of the Beaufort Group in the distal, northern parts of the Main Karoo Basin have received much less palaeontological attention than in the proximal, southern portions, predominantly due to poor outcrop and flat topography. To date, no concerted fossil collecting has been done between Kroonstad and Frankfort, although isolated finds have been made by farmers or field geologists during the production of geological maps. In the eastern Free State, the last intensive fossil collecting efforts undertaken in the lower Beaufort Group rocks was during the 1980s. As such, our understanding of the biostratigraphy in the distal part of the Karoo Basin is relatively poor, relying heavily on assumptions based on limited fossil collections and lithostratigraphic correlations. In addition to the biostratigraphic uncertainties, the definition and placement of the Ecca-Beaufort contact has been a contentious subject amongst different researchers over the years, with workers using differing criteria for its placement in the north and south of the basin. Recent and ongoing work is, however, showing that the Waterford Formation (Ecca Group) is present in the northern sector of the basin, and the same lithological criteria used for the placement of the Ecca-Beaufort contact in the southern parts of the basin can now be applied to the northern sector as well. Recent fossil collecting excursions targeting the lowermost

Beaufort Group in the northeastern Free State during 2017 and 2018 yielded several tetrapod fossils (including rhinesuchid temnospondyls, large and medium-sized dicynodonts, and a therocephalian) stratigraphically lower than any previously discovered in that area. In addition to the fossils collected during fieldwork for this study, the sample size was augmented by using data from the Karoo Fossil Database, and by revisiting existing collections. Our initial results show that, although the strata are thinner than in the south, the Ecca-Beaufort contact can be placed at the top of the Waterford Formation. The lowest Beaufort Group rocks may record the lower *Daptocephalus* Assemblage Zone, or perhaps even older biozones in some places.

## Coombs Hill: a new Devonian fossil-bearing locality in the Witpoort Formation, Eastern Cape, South Africa

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Extensive rock cuttings generated in 2015 and 2016 expose a number of fossiliferous shale strata interbedded in quartzites of the Upper Devonian Witpoort Formation (Witteberg Group, Cape Supergroup) on Governors Kop, near Grahamstown. Intensive palaeontological sampling of the shale horizons recovered an array of Late Devonian fossil plants and invertebrates. The fossil biota is characterized in 10 plant, two algal and three invertebrate morphotypes. Discoveries at Coombs Hill include exquisitely preserved vegetative and fertile material of *Archaeopteris* (progymnosperm tree), new lycopod taxa, phaeophyte algae and *in situ* bivalves. The fossil biota and sedimentology suggest lagoonal deposits with both freshwater and marine inputs. To the east, on a parallel ridge, the 'Rabbit's Ear' mudstone horizon contains abundant autochthonous lingulid brachiopod shells associated with fragmentary, transported plant remains. Together with *Kinneya*-like algal mats and the trace *Spirophyton*, these indicate a shallow, marine dominated lagoonal environment for this horizon. The intensity of structural deformation in this part of the Cape Fold Belt hindered stratigraphic work in this study, as it has in the past 80 years of research. However, analysis of way-up features, stratigraphic logging and mapping of strata with the aid of satellite imagery were used to 'unfold' the stratigraphy. These data suggest that the Rabbit Horizon underlies the Coombs Hill succession. Thus, a trend of increasing proximity to the vegetated habitat is recorded up-succession. This study allows for comparison with other known localities in the Witpoort Formation such as at Waterloo Farm and Howison's Poort. The Coombs Hill succession therefore provides a rare new window into high latitude Late Devonian ecosystems of southern Gondwana.

## Palaeoenvironmental change from the Hettangian to Toarcian in southwestern Lesotho

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The upper Karoo Supergroup of southern Africa encompasses the record of the Late Triassic-Early Jurassic geobiological evolution of Gondwana. The environment is known to have shifted from wet swamps to a semi-arid fluvio-lacustrine and then to an aeolian system before the outpouring of the Karoo continental flood basalts. The Moyeni study area in South West Lesotho exposes the highly fossiliferous Lower Jurassic upper Elliot and Clarens Formations and the lowermost Drakensberg Group. We used integrated geological methods (e.g. field mapping, sedimentology, ichnofacies analysis) to document the palaeoenvironmental and tectonic changes in the Early Jurassic in Moyeni. The upper Elliot Formation contains very fine to fine-grained sandstone with either massive or with ripple cross-lamination, low-angle cross-bedding and sandy siltstone with *in situ* carbonate nodules, desiccation cracks, bone fossils and ichnofossils of invertebrates and vertebrates (e.g. tracks of theropods, ornithischians, amphibians, crocodylomorphs). Sedimentological evidence indicates that during the Hettangian the area was prone to flash floods and drying in a low energy depositional system with small rivers and shallow lakes. The bulk of the Clarens Formation comprises very thick, tabular, fine- to medium-grained, massive to large-scale cross-bedded arenites. However, the lower part of the unit preserves not only massive sandstones and rare, thin-bedded mudstones, but also theropod tracks (at Phahameng). This suggests a

change in the Sinemurian from a wet to a dry desert with large, down-wind migrating sand dunes. Within the lowermost Drakensberg Group, interbedded with lava flows and pillow lavas, massive to cross-stratified sandstone units are common. These beds typically thin and fine upward, and at least locally, terminate in surfaces that are covered by symmetrical ripple marks. These suggest that by the Toarcian the land surface was again covered by temporary lakes and streams into which the lavas outpoured during the early stages of the Karoo volcanism. The study area was structurally deformed by ~east-southeast–west-northwest trending normal faults, some of which appear to have been already active during Clarens Formation times. This syn-sedimentary faulting is interpreted as evidence for the changeover from a compressional to extensional tectonic regime during the Early Jurassic, and may represent the first signs of the Gondwana break-up.

## Sinemurian landscape changes in southern Gondwana: a new look at the Clarens Formation

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The Lower Jurassic Clarens Formation is the youngest sedimentary unit of the Stormberg Group within the Karoo Supergroup. Dominated by thick to very thick, massive and large-scale cross-bedded sandstones, the unit has a striking lithological uniformity across southern Africa and frequently forms impressive cream- to buff-coloured sandstone cliffs. Compared to the underlying Elliot Formation, fossil occurrences are diverse, but less abundant in the Clarens Formation. Fossils are also limited mainly to the lower part and include crocodylomorphs, sauropodomorph and ornithischian dinosaurs, cynodonts, insects, freshwater fish (*Semionotus capensis*), freshwater crustaceans and various trace fossils. To date, no published geochronological study is available for the Clarens Formation; however, it is generally assumed to be mainly Sinemurian based on the bio- and chronostratigraphic constraints of the adjacent formations. Nearly five decades ago, this sandstone-dominated sedimentary rock succession was subdivided into three facies assemblages, which were related to complex interactions among aeolian, ephemeral fluvial and lacustrine processes, and cyclic wet–dry climatic changes. Although the overall aeolian depositional setting is relatively well established, the complexity of the depositional processes within it are still poorly understood and so is the applicability of the tripartite facies subdivision across the main Karoo Basin and in the rest of southern Africa. The aim of this ongoing study is to achieve a high-resolution modern facies analysis integrated with geochronology and biostratigraphy. With the advancement in remotely controlled aerial vehicle technology, these previously inaccessible Clarens Formation cliffs can now be extensively studied at close range to map sedimentary architecture on a finer scale and across large areas. This multidisciplinary approach will aid in developing a deeper understanding of the Sinemurian palaeoenvironmental and climatic changes in southern Gondwana and the relationship of the local climate to the global Early Jurassic climate trends.

## Evolution of the dentition in Gomphodontia (Therapsida: Cynodontia): disparity, rate of evolution and dental complexity

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Gomphodont cynodonts were close relatives of mammals and one of the two Mesozoic lineages of cynodont therapsids that became extinct at the end of the Triassic. Members of this clade were small to medium-sized (0.3 to 2 m in body length), quadrupedal animals characterized by labiolingual expansion of the upper postcanines (gomphodont morphology) allowing crown-to-crown occlusion. Such morphology of the postcanines suggests that gomphodonts were omnivorous or possibly exclusively herbivorous animals, feeding on hard plant material. Three clades, mainly differentiated by the postcanine morphology, are currently recognized among Gomphodontia, the Diademodontidae, Trirachodontidae and Traversodontidae. This project investigates morphological diversity and rates of anatomical innovation in the dentition of gomphodonts based on a data matrix of 109 dentition-based characters coded in 36 gomphodont taxa. Postcanine complexity through time is also explored using three-dimensional crown surface reconstructed from photogrammetry in 32 taxa and orientation patch count (OPC) methods.

Results of these analyses reveal: i) fast rates of dental evolution with the emergence of gomphodonts and neogomphodonts (i.e. Trirachodontidae and Traversodontidae) in the Early Triassic, traversodontids in the Olenekian, and gomphodontosuchian traversodontids in the early Ladinian; ii) slow rates of dental evolution in derived gomphodontosuchians in the late Ladinian; iii) a limited morphospace occupation of the dentition of trirachodontids throughout the Olenekian and Anisian, and a widespread morphospace occupation of the dentition of traversodontids, which increases up to the early Carnian then decreases throughout the rest of the Late Triassic; iv) a slight increase in dental complexity in gomphodonts from the late Anisian to the early Norian, and a drop in dental complexity at the end of the Triassic. This shift in dental disparity, evolutionary rate and postcanine complexity in gomphodont cynodonts, all decreasing in the Late Triassic, is likely due to increasing competition with other clades of emerging terrestrial herbivorous tetrapods (e.g. tritylodontids, dinosaurs), leading to the disappearance of gomphodonts at the end of the Triassic.

## Implications of computed tomography measurement errors in palaeoscience

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The computed tomography (CT) scanning technique assists reseachers in palaeosciences with taking dimensional measurements of stuctures in fossils, which can be useful for morphometric analyses. It is therefore necessary to devise a method to determine the limits of reliability of the values obtained from such measurements. There are a number of factors that can lead to measurement errors including the X-ray focal spot, the geometry used for CT scanning such as the cone beam geometry, alignment of the detector-specimen and X-ray source and positioning of the specimen on the stage. These sources of error contribute to the overall error in the final result. The uncertainty can be determined experimentally with the use of measurement standards or with computer simulations. CT dimensional values are typically obtained in imaging software such as VGStudio and Avizo. I used a 200 mesh transmission electron microscopy (TEM) grid as a measurement standard for comparison with trabecular bone measurements. The TEM grid has specifications of a 35 $\mu$m bar width, 90 $\mu$m hole width, 0.225 mm rim width and a 20 $\mu$m thickness. I investigated the errors obtained from edge detection and positioning of the specimen by CT scanning trabecular bone at a resolution of 10 $\mu$m and the scanning parameters of 70 kv and a current of 120 $\mu$A using a Nikon XT H 225/320 LC dual source industrial computed tomography system. An estimate of the uncertainty in the edge detection of the result was found to be approximately half a voxel. A 1.8% error results in the determination of the morphometric index TbTh showing that this measurement is reliable.

## Taxonomic revision of the Titanosuchidae (Therapsida, Dinocephalia) of the Karoo Basin, South Africa: a key to understanding middle Permian tetrapod diversity

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Dinocephalians are a group of therapsids that constitute a significant part of middle Permian tetrapod biodiversity worldwide. The group is known from middle Permian basins in Russia, Central Asia, China, Brazil, Tanzania, Zambia and Zimbabwe, but is best represented in the Abrahamskraal Formation of the South African Beaufort Group. Three dinocephalian families have been found in South Africa: the Anteosauridae, Titanosuchidae and Tapinocephalidae and of these only Anteosauridae have recently undergone a comprehensive taxonomic revision. Tapinocephalidae are currently undergoing a taxonomic revision by a PhD student, but the family Titanosuchidae has been neglected, and its current taxonomy has not changed since 1969. Currently the family Titanosuchidae comprises two genera and nine species (*Titanosuchus ferox*, *Jonkeria boonstrai*, *J. haughtoni*, *J. ingens*, *J. koupensis*, *J. parva*, *J. rossouwi*, *J. truculenta* and *J. vanderbyli*). This project is an investigation into the validity of these species and involves first hand examination of the majority of the known specimens of the group to evaluate the morphological

features that have been used to characterize the different members of the Titanosuchidae. In addition, aspects relating to ontogenetic development and sexual dimorphism are also examined. This study, together with the recent taxonomic work on anteosaurids, and tapinocephalids, will give a comprehensive picture of dinocephalian diversity in the middle Permian of South Africa. Taxonomic clarification of groups represented in the South African Karoo fauna is a basic prerequisite for any project aiming to explore diversity changes and the extinction of middle Permian terrestrial faunas throughout Pangaea.

## A new burnetiid from the mid-Permian of Zambia and its bearing on burnetiamorph phylogeny

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Recent fieldwork in southern Zambia has yielded a diverse therapsid fauna from the middle calcareous member of the Madumabisa Mudstone Formation. Based on the presence of tapinocephalid dinocephalians in these deposits, this fauna is considered Guadalupian (middle Permian) in age. Here, we present a new taxon from this fauna: a burnetiamorph biarmosuchian represented by a partial cranium (missing the anterior portion of the snout). The new taxon can be diagnosed by its autapomorphic cranial boss morphology: the bosses are exceptionally discrete and bulbous and the median nasal boss is situated on a 'stalk' (i.e. transversely narrow at base and then expanding dorsally to form a bulbous tip). Although boss morphology in this taxon is unique, the general number and positioning of these bosses match those of *Burnetia* and *Bullacephalus*, notably including two pairs of supraorbital bosses. Indeed, the new taxon shows many characters intermediate in morphology between those of *Burnetia* and *Bullacephalus* (and to a lesser extent *Pachydectes*), necessitating reevaluation of the recent hypothesis that these taxa are only distantly-related within Biarmosuchia. We present a new phylogenetic analysis for Biarmosuchia, reformulating and recoding a number of characters of uncertain homology in previous analyses and presenting a new scheme for burnetiamorph cranial boss homology. Inclusion of the new Zambian taxon in this revised analysis recovers it within Burnetiidae, in a subclade Burnetiinae also including *Burnetia*, *Bullacephalus*, *Pachydectes*, and possibly *Niuksenitia*. We suggest that the stratigraphic incongruence reflected by this tree topology is likely an artefact of poor sampling in the South African fossil record. Burnetiamorph fossils are rare in the Main Karoo Basin, but are proving to be among the most commonly-found fossils in the mid-Permian of the Mid-Zambezi Basin and the upper Permian of the Ruhuhu Basin, suggesting that much of the diversification of this clade occurred outside of the Karoo.

## The past meets the present: exploring the biogeography of extant Plecoptera of South Africa with reference to ancient middle Permian fossil forms from the Onder Karoo locality near Sutherland

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The Onder Karoo locality near Sutherland, Northern Cape, recently yielded an unprecedented diversity of middle Permian insects, which were preserved in deposits of an aquatic lake margin system, in the Waterford Formation. These specimens are exceptionally well preserved in fine-grained mudrock, suggesting that they are either autochthonous or at least parautochthonous. This extraordinary material will produce crucial data for a fauna that has never been documented previously in southern Africa. A large number of Plecoptera (stonefly) specimens were found, which include fragmented wings along with a number of full body impression fossils. The Plecoptera are some of the earliest Neoptera, a large group, which includes the vast majority of extant winged insects. This makes stoneflies particularly interesting in the context of insect evolution, and their study is likely to contribute vital information for understanding the development of modern winged insects. An extensive study of these specimens is being conducted, which has already resulted in the discovery of several new species. Careful attention has been paid to the functional morphology of the specimens, which is helping to reconstruct the ecology of

this site. Initial surveys of the site suggest a large diversity and abundance of Plecoptera, which coincides with recent evidence that the stoneflies underwent a major radiation in Gondwana during the Permian Period. Modern Plecoptera mostly consist of cold-adapted species that prefer running shallow water, although some species also live in lake habitats. These latter conditions are probably analogous to those present at the Onder Karoo locality during the middle Permian. Further comparisons between ancient and modern diversity of Plecoptera may also allow for a better understanding of the relatively low diversity of stoneflies in southern Africa today, as only two modern families are present. Here we present preliminary findings regarding the taxonomy and palaeontological context of the new middle Permian plecopteran collection from Onder Karoo.

## New early Permian tetrapod fauna from Namibia

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The earliest tetrapods in Western Gondwana are the mesosaurs, a group of specialized endemic aquatic parareptiles known only from Artinskian strata of Namibia, South Africa, Uruguay, and Brazil. Recent finds from early Permian beds in northern Brazil revealed a new freshwater fauna from tropical Gondwana. However, it was not until the Guadalupian (middle Permian) that diverse temnospondyl amphibian and amniote faunas became widespread across south-central Gondwana. A new source of evidence lies in the Carboniferous-Permian continental strata from the Huab Basin (Tsarabis, Huab and Gai-As formations) of northwestern Namibia. These strata have yielded scattered tetrapod remains (temnospondyls, *Mesosaurus*) reported several years ago. The Gai-As Formation was deposited in a freshwater rift valley lake at approximately 60°S palaeolatitude. The lake opened westwards into the Parana Basin and eastwards it was closed off by river deltas. It is in this transition between aquatic and terrestrial environments that most of the fossils are preserved. To date, we have collected 75 fossils of mainly fishes (actinopterygian and chondrichthyan) and temnospondyl amphibians from a single lower Gai-As locality just above the *Mesosaurus*-bearing levels. Absolute zircon dates from ash beds in the upper Gai-As (265.5 ± 2.2 Ma), and the underlying *Mesosaurus*-bearing beds (270 ± 1 Ma) constrain the new fauna to the Roadian. At least three different temnospondyl taxa are represented by partial remains of a long-snouted form, and a short-snouted (parabolic) one with a highly vaulted skull-roof. The third taxon, which includes near-complete large (3 m long) skeletons, presents character states that place it in the edopoid clade, a basal temnospondyl group only previously known from the Carboniferous-early Permian of Euroamerica and the uppermost Permian of Niger. These include exclusion of the vomers and palatines from the interpterygoid vacuities, which themselves are relatively small and taper strongly anteriorly, and the presence of intertemporal ossification in the skull table. This new Namibian fauna that lived in and around saline to brackish water lakes and fjords, helps to fill a crucial *c*. 10 Ma gap in the fossil record of tetrapods in the southern hemisphere and presents a previously unknown radiation of Laurasian lineages into the region during the Roadian.

## A new approach to *Glossopteris* leaf taxonomy: embracing morphometric analyses

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*Glossopteris* leaves are one of the most common and easily recognized Permian fossils across Gondwana, but they are morphologically conservative and taxonomic approaches to species differentiation have been varied, relying on visual estimations of relatively plastic characteristics such as shape, length, etc. Species identification in the past has therefore proven to be subjective, inconsistent and extremely challenging. To address these taxonomic challenges, we have produced the first morphometric study

using *Glossopteris* leaves from two localities in the Karoo Basin of South Africa: a new site on the Ouberg Pass (Northern Cape Province) and Kwa-Yaya (KwaZulu-Natal Province). The Ouberg Pass lies in the southern Karoo Basin, in a region rich in fossils of terrestrial vertebrates of the *Tapinocephalus* Assemblage Zone. A detailed biostratigraphic framework, together with multiple ash dates in the immediate area, provided excellent context for this study of a well-preserved, middle Permian parautochthonous flora. The Kwa-Yaya locality, in the late Permian Emakwezini Formation of the Lebombo Basin in the eastern Karoo Basin, has yielded a superbly preserved and diverse, parautochthonous flora. For this study, 43 quantitative leaf features were measured and analysed to identify morphological characteristics that could produce well defined specimen clusters. The morphometric analysis included: leaf length, width, vein angles (proximal, medial, and marginal), mesh areas and width, and leaf area among other features. Fifteen qualitative features were also considered. Our results suggest that the use of the medial portion of the leaf produced the most discrete clusters; and that a combination of features (vein angles, mesh width, mesh area, and leaf area) provided the most reasonable grounds for morphologically defined taxonomic discrimination of species. This work has been used for the development of a standardized leaf characterization template that we hope will facilitate more reliable and consistent typification of glossopterid leaves in South Africa and other regions of Gondwana.

## Collaborative palaeosciences engagement: Grahamstown Science Festival as a case study

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Most funding platforms require palaeoscientists to do more public engagement while simultaneously escalating their publication output. Additionally, a small number of palaeoscience researchers in South Africa must meet an exponentially increasing demand for engagement, partly due to fundamentalist anti-evolution, anti-climate change sentiments as well as the inclusion of palaeosciences in the formal school curriculum. One solution to the problem is that palaeoscientists work as a collective. A model for such cooperation is the 'Maze of Time' exhibit of the Albany Museum Earth Science Department, Evolutionary Studies Institute, and the Origins Centre at the Grahamstown Science Festival. The exhibit consists of a 10 × 30 m maze constructed from shade cloth and press boards, with posters illustrating various stages in Earth history ranging from the Big Bang to the Middle Stone Age, as well as themes such as climate change, jobs in palaeosciences, palaeotourism and the geological time scale. Scattered within the maze are exhibits of real fossils from the Devonian Period at Waterloo farm and the Permian of the Karoo Basin. Worksheets and puzzles provide an interactive aspect. By combining forces, the partner organizations are able to provide a team of 'explainers' including students, educators, and technical staff who communicate to the science festival public at different levels and in several languages. The framework of the exhibit is flexible and other palaeoscientists are invited to join the initiative by offering information, exhibits, and activities in their own fields of study. The Maze has won prizes at the Science Festival, and its appearance at other events such as the Rand Show, has increased its reach exponentially. One concern under investigation is the use of language in the Maze, which needs to be at the correct level and include explanations in other indigenous languages.

## Locomotory evolution in Crocodylomorpha: insights from *Litargosuchus leptorhynchus*

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Extant crocodilians have sprawling postures and rarely engage in cursorial locomotion, but extinct members of Crocodylomorpha (the clade that includes extant members and all their closest fossil relatives) include many animals that exhibit a wide variety of locomotory habits, including marine and terrestrial forms. The earliest branching members of this group, non-crocodyliform crocodylomorphs, are hypothesized as being terrestrial; however, the hind limb and locomotory strategies of these animals are understudied. *Litargosuchus leptorhynchus* is a non-crocodyliform crocodylomorph from the uppermost Elliot Formation of South Africa. *Litargosuchus* is a monotypic taxon (BP/1/5237) with a highly gracile

appendicular structure, but its postcranial anatomy has never been described in detail. This study investigates the hind limb anatomy of *Litargosuchus* and compares it to other extinct and extant crocodylomorphs. To do this, we CT scanned the hind limb of *Litargosuchus* at the Wits microfocus CT facility, then digitally reconstructed these scans using VG Studio Max 3.0. We measured the tibia, femur and the longest of the metatarsals and using principle component analysis in R 3.2.1, we evaluated varying states of cursoriality across sampled crocodylomorph specimens which consists of 20 extinct and three extant taxa. Our results show that the ankle of *Litargosuchus* differs dramatically from extant species and other basal crocodylomorphs in morphology. The main differences include an elongated calcaneal tuber in *Litargosuchus*, an astragalus with a double tibial articular surface and a medial malleolus on the medial, distal end of the tibia. *Litargosuchus* was a terrestrial crocodylomorph with a highly cursorial habit, which is markedly different to extant crocodilians, which exhibit a semi-aquatic ecology. The results of this study provide a basis for further evaluating crocodylomorph ankle morphology and locomotory habits.

## Age determination of fossil-rich cascade tufas in northwestern Namibia: palaeoclimatic and palaeoenvironmental implications

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Tufa deposits, many of which are Quaternary in age, have not been formally mapped in the past and thus do not feature on geological maps of Namibia. However, in recent years, field surveys in northwestern Namibia, including Damaraland and Kaokoland, have resulted in the discovery of several fossil-rich cascade tufas at Otjikondavirongo, Otjitaime, Omatapati, Okongotirwa, Okongwe (near Okozonduno), Okapiku, Orutjene, Okovanatje, Okomutati, Ongongo SE and Ongongo SW. These new tufa occurrences can now be formally added to the geological maps. Many of the sites preserve visible impressions and casts of floral structures and invertebrate remains such as snails. Treatment of breccia samples collected from several of these sites has yielded an unexpectedly rich biodiversity, which includes frogs, lizards, chameleons, snakes, birds, and mammals (rodents, hares, shrews, macroscelidids, bats, bovids, equids, giraffids, papionines). These faunas shed light on the age of the cascade tufas, some of which are Late Pliocene to Early Pleistocene and others Pleistocene to Recent. Okongwe is the same age as Makapansgat, i.e. Middle to Upper Pliocene, on the basis of rodents, and Otjitaime and Omatapati are younger, probably Early Pleistocene. In addition to the fossil fauna and flora, stone tools and burnt bone have also been discovered in some of these deposits, in association with the remains of large and small mammals. The cascade tufas in northwestern Namibia have palaeoclimatic and palaeoenvironmental implications, indicating a somewhat cooler and more humid climate than the current arid climate. Furthermore, the results also show that the area was home to Miombo woodland or a transitional zone between Miombo and Mopane woodlands, in contrast to the Mopane woodland that exists there today.

## Preliminary report on the first mid-Permian ecosystem from South Africa, as revealed by a new Lagerstätte near Sutherland, Northern Cape

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The fossil record of terrestrial invertebrates from the mid-Permian (Guadalupian) is very poor, especially in Gondwana; furthermore, the few known fossils generally do not preserve soft tissue. Here we present preliminary details of a recently discovered and exceptionally well-preserved assemblage of freshwater and terrestrial invertebrates and plant fossils, from a Lagerstätte near Sutherland, South Africa. The locality represents a lacustrine environment and includes a very high density of insect fossils and associated plants, in a very fine-grained mudrock. To date the site has yielded impression fossils of insects (>200 specimens), some potentially containing organic residues and evidence of soft tissues, fine details such as setae, and even patterns of wing colouration. Many completely articulated insect bodies have been found, mostly aquatic nymphs, which are typically rare in the Permian fossil record. Specimens of arthropod

groups such as the Hydrachnidia (water mites), Odonatoptera, Hemiptera, Coleoptera, Archaeorthoptera, Palaeodictyoptera, Dictyoptera, Grylloblattodea, and Plecoptera have been found so far. This assemblage shows some parallels with those from the middle Permian of Russia and Brazil and has the potential to contribute significantly to our understanding of insect biodiversity and biogeography during the mid-Permian in Gondwana. Also recovered from the site are numerous, very well-preserved plant impressions (>2000 specimens), including *Glossopteris* leaves and three new glossopterid fertile organs. Many of the leaves show evidence of insect interactions (traces of predation and reproductive platforms). This highly diverse fossil biota shows complex inter-relationships of organisms that once lived in and along the margins of a lake during the mid-Permian. Along with input from regional studies of the coeval vertebrate fossils, these fossils capture an exceptional glimpse into the palaeodiversity of the ecosystem at that time. Refined studies of the site will offer new insights into possible trophic connections, palaeoenvironment and palaeoclimate of the southern Karoo Basin during the mid-Permian.

## Long-lived Mesozoic palaeoenvironments nested in the Cape Fold Belt

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The Jurassic–Cretaceous Uitenhage Group outcrops within the Cape Fold Belt of South Africa in a series of rift basins, which formed during the fragmentation of Gondwana. Each basin contains varying thicknesses of continental syn-rift sedimentary successions deposited in fluvio-lacustrine and alluvial fan settings, with rare marine and intermittent volcaniclastic interbeds. The rich continental and shallow marine fossil biota of the Uitenhage Group are insufficiently age-diagnostic with the exception of the foraminifera-bearing marine interbeds, which are rare and localized. However, the evolution of the rifting margin, and spatio-temporal changes in the palaeoenvironment within these intermontane basins can only be reconstructed if the chronostratigraphy of the Uitenhage Group is improved. This study thus established a new geochronological framework of the unit by integrating data used to reconstruct palaeoenvironments with U-Pb zircon ages from primary and reworked volcaniclastic deposits. The volcaniclastics range in age from 172.37 +0.3/–0.82 Ma[a] to 140.21 ± 0.35 Ma[b] (Aalenian–Berrisian) and indicate that deposition of the Uitenhage Group lasted a minimum ~30 million years. The oldest part of the unit is Lower–Middle Jurassic and comprises laterally extensive lacustrine and intermittent fluvial deposits within the Heidelberg and Mossel Bay Basins. To the northeast and northwest, in the Oudtshoorn, Robertson and Worcester Basins, the Uitenhage Group mostly consists of Upper Jurassic fluvial red-beds and alluvial fan conglomerates. These Jurassic deposits are separated from the overlying lithologically similar Lower Cretaceous succession by a regional angular unconformity. However, the Knysna, Gamtoos, and Algoa Basins do not exhibit this two-stage history of tectonically-controlled rift-sedimentation and instead contain a relatively uninterrupted succession of Upper Jurassic–Lower Cretaceous fluvial and alluvial fan deposits, with minor lacustrine and marine influences. The Uitenhage Group illustrates the complexity of long-lived, diachronous rift-basin sedimentation and highlights the importance of high-resolution chronostratigraphy when investigating the palaeontological, biogeographical, tectonic and palaeoenvironmental records from the final moments of a unified Gondwana.

[a]TuffZirc age calculated using U-Pb zircon ages from LA-ICPMS.
[b]Weighted mean age of U-Pb zircon ages acquired from TIMS

## *Massospondylus* labyrinth geometry through ontogeny suggests a decoupled form–function relationship with locomotory performance in dinosaurs

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The inner ear, or labyrinth organ, is an important structure that controls balance and orientation in all vertebrates, and plays a vital role in head stabilization. The morphology of the semicircular canals is generally hypothesized to be heavily influenced by sensory inputs imposed by locomotor styles and behaviour, and is thus an important subject for form-function studies. However, it is still not understood how semicircular canal geometries respond to locomotory changes during ontogeny within a single species. The dinosaur *Massospondylus* was relatively common during the Early Jurassic in southern Africa,

and is hypothesized to have undergone a pronounced gait change from a quadrupedal juvenile mode to a bipedal adult one, making it an ideal palaeontological study system in which to examine this issue. We used micro-computed tomographic ($\mu$ CT) scanning to reconstruct the endosseous labyrinths (endocasts of the bony canals that house the inner ear) of eight specimens of *Massospondylus*, ranging in age from near-hatchling to adult. Labyrinths scale isometrically with skull size throughout ontogeny. Geometric morphometric analyses using a sliding semi-landmark approach show that, despite the hypothesized gait change, no significant morphological differences occur to the semicircular canals of the endosseous labyrinth during growth. This indicates that changing functional input from disparate gaits does not affect the geometry of the labyrinth after braincase ossification. Possible explanations for this are: i) *Massospondylus* did not undergo a gait change during ontogeny after all; ii) geometries may have changed in the membranous labyrinth organ, but these changes are not reflected in the bony canals housing it; iii) adult labyrinth geometries reflect ossification at ontogenetically earlier, quadrupedal locomotory stages and do not record the shift to bipedalism. These results also indicate that, in Dinosauria at least, the maturity of an individual may have no impact on palaeoecological or phylogenetic interpretations ascertained from labyrinth geometries, and are thus important for future studies.

## Last Quaternary vegetation dynamics observed in a marine core from Maputo Bay, Mozambique

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A marine core (BMBF SPACES project RAiN (03G0862) and MA-RAiN (03F0731)) from Maputo Bay, Mozambique, reveals vegetation fluctuations since the last *c*. 18000/19000 years. Until *c*. 16 ka Before Present (BP) high percentages of fynbos elements, especially Ericaceae, prevailed whereas forest or woodland taxa were low or absent. From *c*. 14ka BP onwards savanna taxa, e.g. *Spirostachys* and *Burkea*, gradually increased and showed a warming of the atmosphere. The mid Holocene altithermal between *c*. 8.5 and 4.4 ka BP is characterized by high percentages of *Podocarpus* pollen pointing to humid and warm environmental conditions. From *c*. 2 ka BP the *Podocarpus* values decline, either due to human disturbances or, more likely, slightly more arid conditions as shown by the increase of Chenopodiaceae and Asteraceae. The last *c*. 250 years show the impact of the European colonialists; when pollen from pines, a typical neophyte, appeared and the indigenous *Alchornea*, a disturbance indicator, increased. In addition to vegetation fluctuations due to climate shifts, effects of sea level fluctuations on palynomorph composition are evident. High sea levels lead to an increase in mangrove pollen and foraminifera linings whereas low sea levels, e.g. at the bottom of the profile, are signalled by high pollen concentrations and abundant fungal spores. The core allows a comparison with marine cores from offshore the Zambezi river catchment and terrestrial cores from the Mfabeni peatlands and Lake Eteza in KwaZulu-Natal, South Africa.

## A missing link in *Glossopteris* evolution: new species of *Lidgettonia* from a middle Permian Lagerstätte in South Africa

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South Africa is renowned for its unparalleled collections of seed-bearing structures of the widespread Gondwanan fossil plant taxon, *Glossopteris*. These have been collected from either lower Permian coal-associated deposits (Artinskian) in the northeastern Main Karoo Basin (MKB), or late Permian (Lopingian) localities in the eastern parts of the country. Two new localities near Sutherland in the southern MKB, have yielded an exceptional flora in association with an unprecedented abundance of

insect fossils, and represent the first conclusively dated middle Permian fossil plant sites in South Africa. A Guadalupian (Roadian) age has been determined through proximity to dated ashes, vertebrate biostratigraphy and stratigraphic correlations. In addition to a low diversity of *Glossopteris* leaf species, a new species of *Lidgettonia* has been identified, along with the first record of *Squamella*, the pollenate cone of *Glossopteris*, outside of Australia. To date, *Lidgettonia* has only been found in the late Permian of KwaZulu-Natal and at one site in the Eastern Cape. This occurrence expands the temporal range of this fertile organ into the middle Permian, and provides an exciting glimpse of a plesiomorphic form of the genus. *Lidgettonia* taxa comprise a scale leaf with one to three pairs of campanulate organs, each homologous with the larger dictyopteridiacean forms typically found attached singly to a *Glossopteris* leaf. The scale leaves lack a midrib, have flabellate venation and are coriaceous. The new taxon from Sutherland is approximately 30% larger than previously recognized forms, and up to eight pairs of large cupules are attached to the extended pedicel of the scale. The scale leaves have a well-developed midrib and venation that more closely resembles that of a vegetative leaf than a typical scale, forming a narrow morphological continuum with associated *Glossopteris* leaves. This form represents an evolutionary link between the Dictyopteridiaceae and the Lidgettoniaceae that has been long hypothesized, with the reduction of fructification size coincident with an increase in number of fructifications per *Glossopteris* leaf, with the subtending leaf closer in morphology to a vegetative leaf than the highly reduced scale typical of more derived species.

## Meet medullary bone: functional and evolutionary considerations in extinct and extant archosaurs

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Medullary bone (MB) is a special, rapidly mobilizable calcium store that is deposited endosteally in the bones of female birds during the egg-laying period to assist in building the rigid eggshell. In the last few decades, several studies reported MB or similar tissues to be present in extinct vertebrates, including non-avian dinosaurs, birds, and pterosaurs, albeit with sometimes different biological interpretations. Whereas studies considering the presence of MB as the incontestable evidence of sexually mature females being in their reproductive period have gained broad acceptance, other studies questioning the conventional reproductive role of MB in some fossils drew much less attention. These opposing views originate from important but readily unnoticed uncertainties related to the functional significance and evolution of MB in birds and non-avian fossils and from the biological interpretation of reconstructed fossil growth curves. Looking deeper into avian and fossil MB, several questions emerge: What are the characteristics of 'true' MB? Is distribution of MB restricted to long bones in avian skeletons? Do birds use MB exclusively for providing calcium for eggshell formation? Is the evolutionary drive of MB formation the same in non-avian archosaurs and birds? How does MB formation relate to hormonal regulation and ontogeny? Is apparent MB in juvenile fossils pathological? Are MB and related growth trajectories comparable between non-avian and avian archosaurs? Studies and observations on modern avian MB imply diverse histological characteristics, skeletal distribution beyond limb bones, and utilization of MB also during molting. Flight-related selection pressure suggested for the evolution of MB formation in birds does not explain the presence of MB in non-volant dinosaurian lineages. MB in histologically juvenile fossils without any osteological abnormalities indicates a healthy condition and a potentially non-reproductive role of MB in these specimens. Finally, modern avian and fossil non-avian growth trajectories most likely reflect different life history strategies with possibly disparate functional significance of MB. Further investigation of MB in modern birds is vital to resolve the apparent controversies and unknown aspects of avian MB and MB-like tissues in fossils and to explore the origin, evolution, and functional significance of this intriguing bone tissue.

## Novel postcranial features in a new specimen of *Heterodontosaurus* (Dinosauria: Ornithischia) revealed by synchrotron X-ray computed tomography: implications for ornithischian physiology, evolution, and systematics

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*Heterodontosaurus tucki* is a basal ornithischian dinosaur that was an abundant member of Early Jurassic southern African dinosaur faunas. Fieldwork led by the Albany Museum in the Eastern Cape recently recovered a nearly complete, three-dimensionally preserved specimen of this taxon. Manual preparation showed that the specimen preserves important new anatomical features for Ornithischia, such as gastralia, but also revealed that these enigmatic features are extremely delicate. To fully document the anatomy of the specimen, we CT-scanned the fossil at high resolution on the European Synchrotron Radiation Facility in Grenoble, France. Our results confirm that the specimen preserves gastralia, as well as sternal plates and sternal ribs with a unique spatulate morphology. These features are either completely unknown (gastralia) or poorly known (paired sternal plates and sternal ribs) in other ornithischians. When scored in two recent phylogenetic analyses, we infer that paired sternal plates and sternal ribs are plesiomorphic for Ornithischia, possessing markedly different morphologies at the base of this clade. Additionally, we present unambiguous evidence that gastralia were not only present in basal ornithischians, but that they potentially possess morphology that differs from the saurischian condition, with crocodilian gastralia providing a closer analogue to the condition now found in heterodontosaurids. A hypothetical myological reconstruction is presented that seeks to provide a model for how gastralia would have functioned with the retroverted pubis of ornithischians and what their subsequent loss in this clade suggests about their physiology, and how it likely differed, fundamentally, from their saurischian sister taxon.

## Dinosaur footprints from a dynamic Early Jurassic aeolian palaeoecosystem, Clarens Formation, Ha Talimo, Lesotho

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The Lower Jurassic 'Cave sandstones' (i.e. Clarens Formation) of southern Africa are well-known to have been deposited in the overall semi-arid to arid, resource-limited continental interior of southern Gondwana. We present evidence that these generally harsh conditions were alleviated by wetter periods capable of supporting more abundant life (e.g. fish, dinosaurs, trees). As a result, the rocks of the Clarens Formation preserve key insight into the biotic adaptations in this dynamic aeolian palaeoecosystem in the Early Jurassic. Vertebrate trace fossils are formed *in situ* by the direct interaction of the tracemaker and the substrate. They are thus valuable tools for interpreting palaeoenvironments and the animal behaviour within them. This is a sedimentological and ichnological investigation of a Lower Jurassic dinosaur footprint site in the lowermost Clarens Formation at Ha Talimo (Butha-Buthe District) in northern Lesotho. Over 40 tracks, some of which form part of the several trackways at the site, were recorded. All tracks are pes prints made by tridactyl theropod dinosaurs, with foot lengths ranging from 15 to 38 cm. Most of the tracks are natural casts in the roof of a shallow cave, with the exception of three isolated foot impressions on two detached, broken slabs. Tracks were made in two different mud layers, both of which were overlain by sandy deposits. The well-preserved three-dimensional nature of the footprint casts, which often show unequivocal digital pad impressions and claw marks, allow for detailed observations and inferences on the trackmakers' foot anatomy and locomotion style as well as substrate saturation. The overall palaeoenvironmental analysis indicates that the dinosaurs were walking on soft muddy substrates that dried out before being buried by the sand bed. These fine- to medium-grained silty sandstone beds, show evidence for high energy, upper flow regime sedimentary structures, and are interpreted as the deposits of fast flowing ephemeral streams. The evidence for intervals of wetting and drying observed at Ha Talimo is consistent with the episodically wet aeolian desert environment documented from the Lower Jurassic equivalents of the Clarens Formation in southern Africa.

## Dinosaur tail traces at the Lower Moyeni ichnosite of Lesotho

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Although dinosaurs are not considered habitual tail-draggers, there have been rare descriptions of dinosaur tail traces from the Jurassic and Cretaceous. Of the 38 globally reported dinosaur tail trace

ichnosites, over 14 have been lost from the global stratigraphic record due to natural and anthropogenic factors. Most remaining occurrences of tail trace sites in the southern hemisphere are found in Lesotho and only one in the Eastern Cape of South Africa. Arguably the most important is the Lower Moyeni ichnosite found within the Lower Jurassic Elliot Formation. This is unequivocally the best preserved and diverse vertebrate tracksite of southern Africa, and thus the ideal candidate for a modern ichnological reinvestigation focusing on tail traces. To date, the most detailed account of this site was given by Paul Ellenberger in the 1970s, and more recently, it was studied by Roger M.H. Smith and co-workers. The tracksite originally preserved >450 footprints and a variety of trackways attributed to theropod (*Neotrisauropus* morphotype) and ornithischian (*Moyenisauropus* morphotype) dinosaurs, basal crurotarsal archosaurs (chirotheroid morphotype), and a short-legged basal tetrapod (*Episcopopus* morphotype). Preliminary results of the current investigation suggest over 10 tail drag marks and approximately three tail impressions attributable to ornithischians. Many originally reported tail drag marks are in fact toe drag impressions. All tail trace marks were assessed with modern ichnological techniques, which involved high-resolution digital photography followed by photogrammetric assessment with the software Agisoft Photoscan Professional and the generation of colour depth maps in the software Paraview. Our documentation is in accordance with an established set of ichnological criteria, which are crucial in distinguishing between tail impressions, tail drag impressions and toe drag traces. At Lower Moyeni, there is plausible evidence for an unusual array of ornithischian behavioural patterns such as resting traces with both metatarsal impressions and tail impressions as well as reactions to a change in substrate consistency, resulting in tail drag marks. Along with their associated footprints, these tail traces allow for the examination of specific recurring ichnotaxa and provide new insights into locomotion, behaviour and ecology of tetrapods in the Early Jurassic of southern Africa.

## Stable isotope record implicates aridification without warming during the late Capitanian mass extinction

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The mid-Permian, late Capitanian, mass extinction event (~260 million years ago) represents one of the greatest biotic perturbations of the Phanerozoic and was the earliest mass extinction to affect terrestrial tetrapods and ecosystems. In the past, this extinction event has been largely associated with taxonomic loss and ecological restructuring in marine environments, but more recently it has also been recognized in terrestrial ecosystems. Though various environmental mechanisms have been proposed for the former, little evidence has yet been presented for the cause of terrestrial extinctions. We focused our research on the dicynodont therapsid *Diictodon feliceps*, a relatively abundant herbivorous therapsid that occurred above and below the extinction event. We determined the stable oxygen and carbon isotope compositions of dentine apatite from 28 specimens of this species, to investigate the potential role of climate in driving terrestrial tetrapod extinctions in southern Gondwana. Studied specimens were recovered from a 270 m thick stratigraphic section that constrains the mass extinction event and post-extinction recovery period in the uppermost Abrahamskraal Formation in the well-sampled main Karoo Basin of South Africa. Our results demonstrate a positive excursion of $\delta^{13}C$ values coinciding with the interval of maximum extinction that is followed by a return to pre-extinction $\delta^{13}C$ values, and this suggests a local increase in aridity at the time of the extinction event. For the same time interval, the $\delta^{18}O$ values did not statistically demonstrate any change suggesting constant temperature in the South African palaeoenvironment. This unusual increase in aridity without any change in temperature has been interpreted as the possible result of orogenic events within the Cape Fold Belt that spanned the southern margin of Gondwana.

## The first sphenacodontid synapsid from the Permian of Italy (Alghero, Sardinia): taphonomy and preliminary results

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The Torre del Porticciolo fossil locality is notable for producing the first osteological material of a basal non-mammalian synapsid from Italy, the giant herbivore *Alierasaurus ronchii*, which likely represents one of the largest non-therapsid synapsids (6–7 m total length). Recently, a new productive site was discovered approximately 100 metres from the *Alierasaurus* type locality, but roughly at the same stratigraphic level. The fragmentary nature of most of the recovered bones prompted a taphonomic analysis in order to define the type of finding, the kind of burial and the mode of preservation. The data set and derived inferences allowed the reconstruction of a multiphase entombment process to be done: i) after death, the corpse was lying on a medium-proximal flood plain and was rapidly buried by a flood(s) carrying heavy suspended-loads; ii) the carcass was subjected to early diagenesis; iii) subsequently, was re-exhumed and transported by a strongly energetic current during a new flooding event, generating a crevasse-splay. Bone remains and embedding sediments were carried on by a high density flow transported for a short distance and finally re-deposited, after a levee breakage, in a peaceful small lake in the vicinity of the main channel. The preliminary study of recovered osteological material, especially the diagnostic structure of the maxilla and of preserved teeth, allows the referral of the new finding to a medium-sized sphenacodontid synapsid. This finding represents the second basal non-mammalian synapsid from Sardinia and from Italy. Whereas most of the sphenacodontid material described is from North America, the European record for the clade is far more lacunose and limited, with just a few sphenacodontid genera reported from this continent. Thus the new specimen referred to Sphenacodontidae indet. from Torre del Porticciolo will shed new light on the occurrence of this faunivorous clade of non-mammalian synapsids on the continent. In addition, with a late early Permian to early middle Permian age for the Cala del Vino Formation, the specimen would represent, to date, the youngest occurrence of sphenacodontids in Europe, with a possible equivalency of this assemblage to that of the San Angelo and Flower Pot formations in North America, both characterized by huge caseids, varanopids and sphenacodontids.

## Direct evidence for $C_4$-grasslands from the ~1-million-year-old bone bed at Cornelia-Uitzoek, Free State Province, South Africa

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The antiquity of open, Highveld-type grasslands in South Africa, as reflected by tooth enamel $\delta^{13}C$ values of southern endemics present in the grazing component of the Cornelian faunal suite, is corroborated by the presence of $C_4$-grass phytoliths. These were recovered from a ~1-million-year-old bone bed at the Cornelia-Uitzoek type site locality that previously also yielded a hominine tooth and several Acheulean artefacts. The occurrence of $C_4$-morphotypes at this locality reflects a more localized environmental signal related to local edaphic conditions, whereas a predominance of saddle morphotypes suggests that the bone bed was accumulated under summer rainfall conditions with lower than present soil moisture availability. Primarily concentrated within the Chloridoideae, the saddle morphotype is mainly produced by NAD-ME and PCK photosynthetic types, which are most abundant in open habitats in summer rainfall areas receiving less than 500 mm of rainfall per year. This suggests that species turnover at Cornelia together with the presence of early *Homo* on the central plains of southern Africa occurred under conditions of increased aridity.

## Middle Permian dicynodont stratigraphic ranges coupled with ID-TIMS dates from the Karoo Basin have implications for broad-scale stratigraphic correlation

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The Karoo Supergroup preserves the most continuous record of continental Permian to Jurassic tetrapod biodiversity, which has enabled a 10-fold biostratigraphic subdivision of this sedimentary succession. The three mid-Permian (Guadalupian) Beaufort Group biozones (*Eodicynodon*, *Tapinocephalus* and *Pristerognathus* assemblage zones) comprise half the total thickness of the Karoo tetrapod-bearing sedimentary pile in the proximal part of the basin. Achieving biostratigraphic refinement of the Lower Beaufort Abrahamskraal Formation has been challenging, and has been exacerbated by the relative paucity of tetrapod fossils in the lowermost Beaufort Group, the difficulty in extracting them from very hard matrix, the thickness of this sedimentary succession, and the complex folding of these rocks over much of their exposure. Compilation of tetrapod fossil locality data resulting from more than three decades of stratigraphic collecting, combined with an improved understanding of the lithostratigraphic subdivisions of the Abrahamskraal Formation has enabled a dicynodont-based biostratigraphic subdivision of the middle Permian succession. A lower *Eodicynodon* range extends through much of the Combrinkskraal Member, the overlying *Eosimops* range extends from the upper Leeuvlei Member to the base of the Poortjie Member, and a *Diictodon* range extends from the base of the Moordenaars Member up into the late Permian *Daptocephalus* Assemblage Zone. A major hindrance for studies on the vertebrate record has been the lack of reliable radiometric dates for Permian assemblages and age determination for the Beaufort Group has been largely dependent on faunal correlation with other Pangaean tetrapod successions, where palaeomagnatism and marine biostratigraphy have provided some time constraints. Recognition of these dicynodont range zones in the main Karoo Basin has significance for understanding temporal patterns of tetrapod diversity in the mid-Permian and potentially for correlation with the rift basins of southern Africa. These correlations are enhanced by recent U-Pb zircon isotope dilution-thermal ionization mass spectrometry (ID-TIMS) dates for volcanic layers in the lower Beaufort.

## The Roma Giant: large theropod tracks in the Lower Jurassic upper Elliot Formation in Lesotho

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Theropod dinosaur body fossils are scarce in the Lower Jurassic rocks of southern Africa. To date, there are only two known valid theropod genera: the small, lightly built *Coelophysis* (*Syntarsus*) *rhodesiensis* and the slightly larger *Dracovenator regenti*. In South Africa, both *C. rhodesiensis* and *D. regenti* are known from the upper Elliot Formation (Stormberg Group, Karoo Supergroup). Whereas body fossils are uncommon, the density and diversity of tracks and trackways that can be attributed to theropod dinosaurs within the Stormberg Group is world renowned. Here we present new findings on a tracksite on the outskirts of Roma in the Maseru District of Lesotho. Stratigraphically, the tracksite is within the uppermost Lower Jurassic upper Elliot Formation and represents a palaeosurface with >20 tridactyl theropod tracks. The easternmost sector of the palaeosurface contains two very large theropod pes impressions with an average length and width of 57 cm and 50 cm, respectively. These unusually large tracks have no southern African equivalent in terms of size, but share several morphological similarities with the North American ichnogenera *Kayentapus* (Lower Jurassic) and *Irenesauripus* (Upper Cretaceous). These tracks have been placed within the ichnogenus *Kayentapus*, but are described as a new ichnospecies (*Kayentapus*

*ambrokholohali*). Morphological characteristics of *K. ambrokholohali* suggest that the tracks were made by a relatively gracile, allosaurid-like carnivorous dinosaur with an estimated body length of >8–9 metres. Extremely large theropod tracks, and by extension large carnivorous dinosaurs, within the Lower Jurassic are unexpected, with large theropod tracks and trackmakers typically occurring from the Middle Jurassic onwards. In southern Africa, these tracks add to the general diversity of tridactyl theropod tracks and hint at the great taxonomic breadth of theropod dinosaurs in southern Gondwana during the Early Jurassic.

## A Holocene palaeoenvironmental reconstruction of the Okavango source wetlands in Angola

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Pollen is a useful proxy record of past vegetation that enables us to reconstruct past climates and determine their drivers. This is a necessity in this day and age as humans are affected by changes in their surrounding environment. Tracking climate change enables us to predict future climatic models by looking at the dynamics of past ecosystems and how they dealt with change. It applies to Recent studies and as far back in time as the Permian. This study was initiated to reconstruct the Holocene palaeoenvironmental history of the source wetlands to the Okavango Delta in Angola. The primary focus is to use fossil pollen and AMS radiocarbon dating to record dominant shifts in vegetation during the given time period, as well as establish the likely drivers of such change. Sediment core samples ranging in depths from 40 to 100 cm were extracted from Cuito Cuanavale, one of the source wetlands located in Angola. Pollen deposited in the sediment layers were extracted using a variety of chemical and physical techniques. Statistical analysis on the data enabled a quantitative analysis to be done and provided a means of determining any samples contaminated by contemporary pollen. Current analysis of the pollen counts from these high-resolution cores shows that Cyperaceae, Poaceae, and Typhaceae are the dominant types and are typical of wetlands. Varying input of savanna elements, such as Malvaceae and Fabaceae, as well as a variety of herbs, indicate alternating wet and dry periods. Core sediments that were AMS C14 dated reveal that the cores range in age from 3000 years ago to recent times.

## Taphonomy and palaeoenvironments: a new Early Permian tetrapod fauna from Brazil

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The Lower Permian Pedra de Fogo Formation of northeastern Brazil accumulated in a large intracontinental sag-basin (Parnaíba Basin) located in subtropical Gondwana approximately 20°S (palaeolatitude). With progressive climatic drying, palaeoenvironments changed from a large, shallow lake to expansive exposed mudflats surrounding a shrinking lacustrine wetland, culminating in isolated playas fed by ephemeral streams, which finally became an aeolian dune field. Our team has collected over 500 fossils from this formation including actinopterygians, dipnoans, chondrichthyans, two fully articulated coelacanths, at least four temnospondyl taxa (the archegosaurid *Prionosuchus*, trimerorhachid *Procuhy*, dvinosaur *Timonya*, and a rhinesuchid), small-to-medium-sized captorhinid reptiles (*cf. Captorhinus*/*Captorhinikos*), a small parareptile, and numerous fish-scale-bearing spiral coprolites. Three gradationally

superimposed sedimentary facies associations are recognized in this formation: offshore lacustrine, shoreline/carbonate mudflats and finally an ephemeral stream/dune complex. The taphonomic style varies with depositional facies reflecting different modes of post mortem burial. Offshore facies comprise thick beds of massive siltstone and finely-laminated siltstone/mudstone couplets showing algal crenulations, but no infaunal burrowing, indicative of an anoxic lake bed. Scattered actinopterygian fish skeletons with scales are rare, but some fine sandstone turbidites contain more fully-articulated aquatic tetrapods, with rare soft tissue preservation, indicative of death and burial by storm-induced density underflows. The carbonate mudflats facies association contains silicified algal-laminated limestones displaying stromatolite mounds, tepee and desiccation structures typical of alkaline lake shorelines. Clusters of coprolites and fish-hash lenses comprising masses of isolated teeth and scales are suggestive of heavy predation within drying ponds and channels. The ephemeral stream/dune facies contains most of the plant material, mainly tree trunks and in places at the top of the Formation rare 3-D petrifications of leaves and fructifications. This previously unknown diversity of early Permian (~280 Ma) tetrapods in Gondwana shares faunal aspects (e.g. captorhinids, trimerorhachids) with the Permian redbeds (Clear Fork Group) of the southwestern United States, however, the presence of taxa such as rhinesuchids suggest that the Gondwanan tropics were an important cradle of later Permo-Triassic biodiversity.

## A new cynodont from *Cynognathus* Subzone C and its implications on body size recovery in tetrapods following the Permo-Triassic mass extinction

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In tetrapods, body mass is an important proxy for many ecological variables. Mass extinction events have been hypothesized to have a 'Lilliput Effect' on vertebrate taxa, i.e. a dramatic, but short-lived decrease in average body mass in survivor species. Work in the Triassic *Cynognathus* Subzone C of South Africa during 2014 and 2017 recovered a partial cranium of a cynodont of enormous size with an estimated basal skull length exceeding that of any non-mammaliaform cynodont specimen yet described. Taxonomic and phylogenetic analysis show that the new specimen, BP/I/7976, is a new taxon representing a late-branching trirachodontid. Using a regression equation based on original measurements to infer body mass from basal skull length, we conducted an extensive study of body size evolution throughout the Triassic of cynodonts, dicynodonts, and archosauriforms. The presence of the new cynodont in subzone C indicates that the late Anisian represents the body mass peak in non-mammaliaform cynodonts and, along with evidence from other lineages, the point of maximum recovery in body size following the Permo-Triassic mass extinction.

## Trabecular structure in the distal tibia of *Australopithecus africanus*

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Trabecular fabric in the distal tibia has been shown to be sensitive to subtle variation in ankle sagittal plane kinematics during locomotor-related loading in both mammals and birds. Differences or similarities within hominoid trabecular structure can be insightful for interpreting gait kinematic experimentation in the hominin lineage leading to the evolution of obligate bipedalism. This study tested the hypothesis that trabecular structure in the distal tibiae of *Australopithecus* from Sterkfontein Member 4 is more human-like than ape-like in structure, reflecting bipedality. High-resolution computed tomography (micro-CT) images (25–48 $\mu$m voxels) were acquired to quantify trabecular bone structure deep to the tibial plafond in extant comparative species attributed to modern human hunter-gatherers (*Homo sapiens*), *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus* and *Papio hamadryas*, as well as four fossil hominin individuals from

Sterkfontein Cave (Member 4). Nine trabecular sub-regions were isolated beneath the articular surface of the tibial plafond and further segmented into spherical volumes for quantification of localized structure. Descriptive statistics were used to visualize variation followed by an analysis of variance (ANOVA) ($P < 0.05$). A further stepwise discriminant function analysis (DFA) was conducted to assess the capability of trabecular structure to discriminate between species with divergent locomotor behaviours based on trabecular structural properties. Trabecular structure of *A. africanus* distal tibiae was highly variable, which could suggest the presence of two potentially different morphs in Sterkfontein Member 4. One morph resembled a baboon-like structure, composed of numerous thin trabecular struts that were highly oriented (i.e. anisotropically distributed), whereas the other resembled a mixture of human-like and ape-like traits. We conclude that trabecular structure in the distal tibia is effective at distinguishing species based on locomotor behaviour repertoires, provided that homologous regions are sampled, and that trabecular bone structure and organization mirrors kinematic indicators of ankle loading regimes. When these criteria are met, trabecular fabrics may be a useful tool for reconstructing behaviour in fossil hominin specimens in order to corroborate external morphological studies.

## Palynological reconstruction of middle Pleistocene environments at Florisbad, Free State Province, South Africa

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In a global earth system with regular long-term climate oscillations, palaeobotanical reconstructions of environments associated with fossil faunas, are difficult because they come from deposits that are often not dated precisely. This review of the palynology of Florisbad, helps to estimate prevailing grassland conditions in the Free State during the Middle Pleistocene when '*Homo helmei*' (a local intermediate form between *H. heidelbergensis* and *H. sapiens*) and associated fauna existed there *c.* <259 ka ago as well as during the subsequent Middle Stone Age occupation of the site from *c.* 157 ka onwards. Van Zinderen Bakker's pollen study of 1989, based on samples that, according to his laboratory notes, were mainly derived from sections in the vicinity of the great western spring eye in the northern extension of excavations, is reconsidered here in an updated palynological reconstruction. His pollen data are combined with more recent pollen analyses from the younger Holocene levels, hyaena coprolites associated with the old spring deposit and organic-rich soil layers from Test Pit 2. Although there is evidence for regional climatic cycles, the results suggest that part of the variation in pollen composition may be related to the changing spring landscape which in turn determined local vegetation patterns and depositional facies within the study area. The most likely environment in which '*H. helmei*' and the associated spring fauna lived, was cool, moist and grassy. While the Middle Stone Age layers encompass the Last Interglacial period, there are indications of more shrubs and cool conditions as characterized by upland fynbos pollen-types. These possibly occurred shortly before MIS 5e, and immediately afterwards at the time of the 121 ka MSA occupation.

## Understanding middle Permian pareiasaur diversity: the cranial morphology of *Nochelesaurus alexanderi* and *Embrithosaurus schwarzi*

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Pareiasaurs were abundant, large, herbivorous parareptiles of the middle and late Permian with a global distribution. During the middle Permian they comprised 25% of the terrestrial tetrapod fauna, making them important stratigraphic markers for biodiversity turnover. The most basal pareiasaurs known are from the middle Permian of South Africa, suggesting a Gondwanan origin for the group. Despite their abundance, the large middle Permian South African taxa are poorly known. Unabated naming of new

species, often using doubtful characters, created taxonomic confusion, which persisted for more than 100 years until Lee conducted an alpha-taxonomic reorganization of all pareiasaurs. Lee reduced the middle Permian South African taxa from 11 to four species (*Bradysaurus baini*, *B. seeleyi*, *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi*). However, Lee's revision did not include detailed anatomical descriptions or diagnoses of the 262 million year old *Tapinocephalus* Assemblage Zone forms. Here, we present the first detailed cranial description and diagnosis of *Nochelesaurus alexanderi* and a comparative analysis to the other middle Permian pareiasaurs. *Nochelesaurus alexanderi* is distinguished from the other co-occurring taxa by several unique features of the dentition and cranial ornamentation, such as: mandibular teeth with a unique very low, very small, horizontally-oriented cusp at base of the mesial margin; quadratojugal corner boss large, elongated, and covered with distinct rugose ridges; posterior edge of quadratojugal (cheek flange) with distinct pointed bosses, and with a vertical embayment above the highest quadratojugal boss; and maxilla lacking a central maxillary boss. We recognize *Embrithosaurus* and *Nochelesaurus* as valid and distinctly separate taxa, and find dentition and cranial ornamentation the most useful regions for species identification.

## The inner ear morphology of *Prolacerta broomi* and its significance for understanding basal archosaur evolution

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*Prolacerta broomi* Parrington 1935 is a small archosauromorph of debated phylogenetic affinity from the Lower Triassic of South Africa and Antarctica. Although its braincase is partially known, descriptions of the inner ear morphology and specific braincase bone morphologies of *Prolacerta* have not previously been undertaken due to the small size and nodular preservation of most specimens. We used high-resolution X-ray computed tomography (CT) and digital reconstruction methods in VG Studio Max 3.0 to reassemble the morphology of the braincase bones and partial osseous labyrinth of *Prolacerta* specimen BP/1/5066. We were able to recover the morphology of most of the osseous labyrinth of the specimen, as well as visualize the anatomy of the basioccipital, exoccipital, parabasisphenoid, prootic, opisthotic, and supraoccipital braincase bones. Comparisons of *Prolacerta*'s inner ear with a broad array of archosauromorphs, turtles, amphibians, *Youngina capensis*, and modern squamates show that *Prolacerta* exhibits features consistent with early branching taxa such as the archosauriform *Euparkeria capensis* and the phytosaurs *Parasuchus augustifrons* and *Ebrachosuchus neukami*. These include a dorsally elevated anterior semicircular canal, the posterior end of the lateral semicircular canal joining the posterior semicircular canal, a small and antero-posteriorly elongate vestibular apparatus, and possibly an inferred elongate common duct between the anterior and posterior semicircular canals due to the shape of the vestibular apparatus. In addition, lifestyle adaptations deduced from the angles of the semicircular canals to the ampullae, and the shape of the vestibular apparatus support that *Prolacerta* was a terrestrial generalist. Finally, compelling observations of the state of preservation of BP/1/5066, the pneumatic features of its bones, and a lack of labyrinth preservation on its medial and ventral sides support the hypothesis that the specimen is a juvenile. The similarities in shape and size of the inner ear morphology of *Prolacerta* to that of the archosauriform *Euparkeria* and other archosauriforms support close phylogenetic affinities with archosauromorphs.

## The first phytosaur from sub-Saharan Africa: implications for phytosaur distribution and regional correlation of Zimbabwe's mid-Zambesi basin

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Phytosauria are an extinct semi-aquatic group of archosaurs, superficially resembling, but not directly

related to, modern crocodiles (Eusuchia). A distinctive clade consisting of approximately 30 genera, phytosaurian characteristics include long snouts comprising an elongated premaxilla with no secondary palate, and the external nares lie in the posterior half of the skull, close to the orbits. Although considered reasonably cosmopolitan in their time, they are almost strictly known from late Carnian-Rhaetian deposits on ex-Laurasian continents, are surprisingly rare in Gondwanan faunas, and completely absent in sub-Saharan Africa. No phytosaurs are known to cross the Triassic/Jurassic boundary, making them important biostratigraphic markers. We present new unquestionable phytosaur fossil material, including hundreds of teeth and several sections of the rostrum, from the Mid-Zambesi basin of Zimbabwe, within the upper Karoo Group's Pebbly Arkose unit (Tashinga Formation). This material represents the first official documentation of this group in sub-Saharan Africa and widens the geographic distribution of this group in Gondwana. Because phytosaurs are important index fossils for Upper Triassic deposits, this finding also allows for local correlation to the lower Elliot Formation (Stormberg Group) of South Africa's main Karoo Basin. Globally, the Pebbly Arkose unit now represents an important Late Triassic unit temporal to the upper Chinle Formation, the Newark Basin, and other well-known Laurasian Upper Triassic deposits. Sedimentological data also suggests a palaeoenvironmental analog to the Chinle and Bull Run formations, perhaps pointing to palaeoclimatic patterns formed by latitudinal climate belts for which phytosaurs show some preference.

### The first humans and the origins of endurance running – a review

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Endurance running (ER) in modern humans is a unique capability among primates. Among other mammals, only horses and some dogs are capable of ER. Although bipedal gaits include walking and running, in the past, running has generally not been considered to play a major role in human evolution. Early human relatives did not appear to have the ability to run for prolonged periods of time, at least not to the extent of modern humans, who have the inherent capability to run endurance distances. Did we develop this capability as part of our evolution through natural selection, or did it occur as a natural 'spin-off' as a result of our evolving physiology for other reasons? A review of the capability of humans to run long distances, skeletal correlates, thermoregulation, respiration, hunting strategies and evolutionary hypotheses partially answer these questions. Today, ER is primarily a form of sport and recreation, but may have origins as ancient as the *Homo* genus. The fossil evidence of these features suggests that ER is a derived capability of the genus *Homo*, originating about 2 million years ago, and may have been instrumental in the evolution of the human body form. The uniquely specialized anatomy of the human foot is a product of barefoot bipedalism, which is still practiced in parts of the world. This coupled with longer hindlimbs, shorter toes and a fully arched foot are part of a suite of features; the evolution of which is probably linked directly to barefoot running as an integral part of an adaptive strategy for pursuit hunting. A recent study has found that the skeleton of humans since the advent of agriculture (over the last 12 000 years) have become 'lighter' than those of early humans, chimpanzees and fossil hominins. This reduction in trabecular density in recent humans has been attributed to an increase in sedentary lifestyle, even in the presence of recreational long distance running and exercise. Clearly, ER is an integral part of our evolutionary history, and the presence or absence thereof may be reflected in modern day human health and disease.

## Posters

### Earth Alive! 101 Strategies towards stemming the Sixth Extinction: revised edition

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Our '***Earth Alive Strategies***' along '***Africa Alive Corridors***' project – a board game with 101 strategy cards towards stemming the Sixth Extinction and global warming – was launched at the IYPE (International

Year of Planet Earth) Conference in Arusha, Tanzania, in May 2008. Participating in the game were 10 scholars, from 14–17 years of age, from schools across South Africa and a further 10 from Tanzania. The strategies cover a holistic spectrum, from global governance to our individual contribution; from a love of nature to a sense of community. The 20 scholars competed in pairs through the 5–6 days of the event, with delegates from across Africa and beyond passing back and forth on their way to presentations. The feedback from the scholars was overwhelmingly enthusiastic: with comments such as, '*The card game exceeded my expectations. I enjoyed the way [it] allowed us to think laterally, holistically and to go beyond what we usually do. It was intellectually stimulating and I feel extremely proud of the ideas we came up with.*' President Kikwete of Tanzania took a keen interest and offered his support. It is now 10 years later, and the Sixth Extinction has deepened considerably across all fronts. The human population continues exploding in numbers, now up to 7.4 billion, and our impact on the other 10 million or so species sharing our world (number unknown) deepens beyond control. Climate change is worsening. We have let down those Arusha scholars, and we are severely failing all '*the children of today's world and the children of tomorrow's world*' (Nelson Mandela, 1998, in his endorsement for our project '***Gondwana Alive***'). We are planning to launch a revised edition of the '*101 Strategies*' game at the Mandela University, Port Elizabeth, later this year. Some 10 new strategies – with titles such as '*A Forest of Timetrees*', '*The Whole-brain Human*' and '*Half Earth*' – will replace earlier ones. The aim is to bring together as many of those Arusha scholars as we can find, along with a number of new ones, to rerun the game – in celebration of Mandela's 100th Anniversary.

## Palaeoenvironmental reconstruction of middle Permian ecosystems, inferred from insect fossils of ice crawlers (Grylloblattodea) from the Onder Karoo, South Africa

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Grylloblattodea (ice crawlers) are amongst the smallest insect orders, confined to cold, humid and extreme habitats of North America and North East Asia. The most noticeable attribute of extant grylloblattids is their lack of wings, quite unlike their winged fossil ancestors. The earliest grylloblattid insect fossils are known from the late Carboniferous, with their fossil record reaching a peak in species richness, abundance and diversity in the Permian. To date, Grylloblattodea have been found at many South African Lopingian (upper Permian) localities, with the South African grylloblattids representing 35% of the insect fauna at that time. Grylloblattodean fossils have been found in a recently excavated site near Sutherland in the Northern Cape and are the first recorded from the middle Permian of South Africa. This study addresses an important gap in our understanding of palaeoenvironment and ecosystem structure during this time interval. Wing vein patterns were used to identify grylloblattid fossils in the collections as comprehensively as possible, and these were compared to other Grylloblattodean fossils in South Africa and elsewhere in the world, both taxonomically and in terms of the palaeoenvironments they occupied. Factors such as physiology and climate were considered as part of a larger project aimed at reconstructing the ecological relationships between all the organisms identified from this middle Permian lake margin environment. Taken together, the findings from our study will contribute to the field palaeoentomology and Gondwana research.

## *Archaeopteris*, the earliest tree in South Africa, makes its appearance in the Upper Devonian (Famennian) Witpoort Formation

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The Late Devonian witnessed emergence of the first large woody trees, in the form of the cosmopolitan genus *Archaeopteris*. These formed the dominant species in the pioneering lowland forests that would ultimately lead to a complete reset of global environmental systems. The original description of *Archaeopteris notosaria* in 1995 was from the upper part of the Famennian aged Witpoort Formation (Witteberg Group, Cape Supergroup). It was particularly significant as all previously described *Archaeopteris* had come from

tropical to warm temperate palaeoenvironments, principally in Laurussia and the northern continental blocks. By contrast, the Waterloo Farm Lagerstätte, from which *Archaeopteris notosaria* was described, was situated in southern Gondwana at high palaeolatitude (currently reconstructed as being within the Devonian Antarctic Circle). This was the first evidence that cosmopolitan lowland forests had achieved a truly global distribution by the end of the Devonian. The environmental implications of this vegetative explosion have been explored by subsequent authors, particularly with regard to climate change and possible causes of the End Devonian Mass Extinction. The original description relied on portions of leafy 'fronds', and a single poorly preserved fertile fragment. New material has been provided by excavation of a stratigraphically lower site discovered during roadworks in the mid portion of the Witpoort Formation. Not only does this provide a slightly earlier record for the arrival of *Archaeopteris* in southern Africa but is also significant in that the new material provides additional anatomical information. It includes impressions of two whole 'fronds', one infertile and one fertile, as well as a fragment in which the structure of the fertile cones is clearly apparent, revealing the type material to have been incomplete.

## Bone lesion in a gorgonopsian fossil from the Permian of Zambia: periosteal reaction in a premammalian synapsid

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Gorgonopsians are an iconic group of sabre-toothed synapsids that were only distantly related to mammals, and were among the dominant terrestrial predators during the late Permian (*c.* ~260–252 million years ago). Whereas their external morphology has shed light on their evolutionary relationships and the origins of classic 'mammal-like' anatomical traits, surprisingly little else is known of their palaeobiology, including their behaviour and physiology. Study of an extraordinary bone lesion hence provides insights into the role of gorgonopsians in reconstructing the palaeobiological context in which the diversity of mammalian healing responses emerged. Here, we describe the first nonmalignant lesion in the forelimb of a large gorgonopid from the upper Permian Madumabisa Mudstone (Luangwa Basin, Zambia). High-resolution X-ray computed tomography and histological sectioning permit detailed description and analysis of the lesion and its healing response. The solitary lesion is localized on the anterodorsal edge of the radius shaft. The reactive bone is a thickened, disorganized layer comprising a homogenous meshwork of fine cancellous bony spicules with few radial spicules. Distally, near the metaphysis, there is some internal remodelling of perimedullary bone. The lesion was 'finished' by a dense layer of poorly vascularized periosteal bone during final phases of healing. However, evidence of infection, pyogenic abscess, or malignancy is lacking. Periosteal reactions have a range of differential diagnoses, including trauma, infection, and malignancy. We suggest this instance of periostosis could be attributed to a post-traumatic subperiosteal haematoma ('bone bruise'). The rapidity of the healing response – evidenced by its disorganized texture and localization to a single growth period – is unexpected for an ectotherm, but such haematomas are occasionally documented in surveys of extant reptiles (crocodylids, varanids). This report adds to a list of putative disease entities recognized in early synapsids, broadening comparative baselines for the evolution of pathologies in the forebears of mammals and in tetrapods more broadly.

## A microtomographic study of the StW 669 hominin molar from Milner Hall, Sterkfontein, South Africa

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The Sterkfontein Caves, South Africa are one of the richest hominin fossil-bearing sites in the world. Fossil hominin remains from Sterkfontein have been attributed to the genera *Paranthropus*, *Australo-*

*pithecus* and *Homo*. Recent excavations have revealed the potential of the Milner Hall locality to contribute to the Sterkfontein hominin fossil record through the discovery of one upper right molar (StW 669). The description and metrical analyses of this specimen suggests an enigmatic mix of primitive and derived morphological traits. StW 669 combines quantitative and qualitative similarities with the first upper molars of *Homo*. However, for now, the taxonomic status of StW 669 remains uncertain. Micro computed tomography allows the accurate visualization and analysis of internal dental surfaces. Tissue proportions, enamel thickness and the morphology of the enamel–dentine junction (EDJ) are key features in hominid evolution and the internal morphology of molars has been successfully used to distinguish between hominin taxa. The stratigraphy of Milner Hall is complex and StW 669 was excavated from the STK-MH1 site in Milner Hall from the T1 deposit, which consists of a mixture of Member 2 and Member 5 Oldowan sediments. Within deposit T1 we could potentially find *Australopithecus*, *Paranthropus* and/or *Homo*. The aim of this project is to clarify the taxonomic attribution of StW 669 by analysing its tissue proportions, enamel thickness and morphology of the EDJ in conjunction with comparisons to previously reported data.

## New Triassic–Jurassic (Upper Karoo Group) fossil localities on the margin of Lake Kariba, Zimbabwe

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A collaborative field project in 2017 and 2018 between the National Museums and Monuments of Zimbabwe, the University of the Witwatersrand, and the Natural History Museum, London resulted in the first systematic palaeontological and stratigraphic review of the southern margin of Lake Kariba, Zimbabwe in over 40 years. We identified nine new fossiliferous sites that harbour the potential to reveal new insights into the biodiversity of Gondwana during the Triassic–Jurassic interval. Investigations into the Pebbly Arkose unit of the Tashinga Formation (Bumi Hills, Matusadona Lake Shore, Musango, Spurwing Island) and Forest Sandstone (Namembere, 126/127, and other Sibilobilo islands) identified typical early dinosaurian faunas consisting largely of sauropodomorphs. However, in the lower Pebbly Arkose, dinosaurs are absent and instead a largely aquatic vertebrate assemblage is present, which includes the first known phytosaur material from sub-Saharan Africa and a rich fossil wood flora (various sites in Matusadona National Park various sites in Matusadona National Park and the Omay Communal Land). Stratigraphic and palaeontological data gathered on this trip provide new evidence of how the sediments within the Mid-Zambezi Basin correlate with those in the main Karoo Basin, and more broadly with other Upper Triassic and Lower Jurassic strata. It also potentially provides insights into climate belt shifts across the Triassic–Jurassic Boundary, which may have acted as a biogeographic barrier for some vertebrate taxa.

## The phylogenetic classification and locomotion of a non-mammaliaform cynodont *Lumkuia fuzzi* (Probainognathia, Cynodontia) based on CT-tomography of the postcranial skeleton

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*Lumkuia fuzzi* is a small-bodied non-mammaliaform cynodont from the South African early Middle Triassic *Cynognathius* Assemblage Zone of the Karoo Supergroup. It is known by only one specimen,

BP/1/2669, a complete skull associated with postcranial material. The phylogenetic position of *Lumkuia* is unresolved and has been widely debated. *Lumkuia* has been traditionally placed at the base of Eucynodontia or within the Probainognathia, based on cranial features. Probainognathia is an important clade in the study of mammalian evolution as its derived members gave rise to Mammaliaformes. Previous studies on *Lumkuia* focused only on cranial morphology since the associated postcranial skeleton was poorly prepared and considered to provide no additional value. This research investigates the postcranial skeleton of *Lumkuia* using Synchrotron scanning in order to resolve its position within Eucynodontia. This will be performed on CT-scanned material through segmentation and 3D reconstruction in the software Avizo 9.0. Phylogenetic analysis to assess the evolutionary relationship of *Lumkuia* with other non-mammaliform cynodonts will be performed using the software TNT. Preliminary results indicate preservation of hitherto unrecognized skeletal material, including manual phalanges and numerous vertebrae concealed within the matrix, which may help to elucidate the posture of *Lumkuia fuzzi*.

## Taxonomic affinities of large-bodied sauropodomorph dinosaurs from the Elliot Formation of South Africa

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The Elliot Formation of South Africa and Lesotho is one of the world's richest areas for fossils of early sauropodomorph dinosaurs. This formation has been studied by palaeontologists over the last 150 years. Sauropodomorphs are a key biostratigraphic marker for the Late Triassic and Early Jurassic deposits in Gondwana. Moreover, sauropodomorphs survived the end-Triassic extinction and were one of the few terrestrial taxa to cross this boundary and flourish during the Early Jurassic. Recent reviews have shown that many sauropodomorph taxa thought to be from the lower Triassic portion of the Elliot Formation were either misprovenanced or based on non-diagnostic material, and that the lower Elliot Formation has fewer sauropodomorph taxa than the upper Elliot Formation. However, these reviews did not consider all sauropodomorph material collected from South Africa. This project analyses five previously overlooked sauropodomorph specimens from the lower Elliot Formation housed at the University of the Witwatersrand in Johannesburg, South Africa. Using comparative anatomical techniques and phylogenetic analyses, we identify each specimen to its lower taxonomic level (including genus). Our results show that they represent an unappreciated diversity of Triassic Sauropodomorpha. Our preliminary work shows that at least one of the specimens represents a new taxon and that one of the specimens has a body mass approaching that of *Antetonitrus*. These new data have important implications for sauropodomorph diversity prior to the Triassic/Jurassic boundary. This research will provide valuable information as to what effect the end-Triassic extinction had on sauropodomorph evolution. It may also provide evidence regarding sauropodomorph diversification and body size increase during their early evolution.

## The complex taphonomic history of the StW 573 *Australopithecus* skeleton (Sterkfontein, South Africa) as revealed by high-resolution computed tomography data

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StW 573, 'Little Foot', represents the most complete *Australopithecus* specimen yet found and has been attributed to the species *Australopithecus prometheus*. Over the last 3.67 million years since its deposition, a complex taphonomic history has resulted in the extremely fragile condition of the bones. Meticulous exca-

vation of the specimen within and outside of the Silberberg Grotto has preserved the skeleton in the best possible condition for morphological description and analysis. X-ray microtomography (microCT) has come to the fore as a valuable tool in the palaeosciences, allowing non-destructive *in silico* fossil extraction, reconstruction and analysis. This method is particularly useful where fossils are fragile, fragmented or difficult to remove from the host sediments without damaging them. Scanning of the StW 573 lower limbs, using the MicroCT facility at the Wits Palaeosciences Centre, has revealed significant and localized variability of both superficial and internal structural modification of the fossil elements. This fossil modification can now be correlated with the identified complex depositional processes acting within the vicinity of the specimen – providing, for the first time, cross-disciplinary corroboration of the complex depositional history of Sterkfontein and its impact on the preservation of this important hominid specimen.

## Origin and diphyly of theropod dinosaurs

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Here we: i) discuss variation in the theropod braincase; (ii) review the published phylogenetic analyses of theropod dinosaurs including the idea that theropods are derived from early ornithischians; and (iii) conduct a braincase-based phylogenetic analysis of the earliest birds, early archosauromorphs and a range of theropods. The derivation of the highly diagnostic crista tuberalis in early ceratosaurs could have happened from a model based upon sauropodomorphs such as *Adeopapposaurus*. This conclusion is contentious and could be based upon plesiomorphies of early dinosaurs following the ideas of Baron (2017). The formation of the cristra tuberalis took place when the pterotic bone, an element described in the braincase of birds in classical literature, moved from the inside of the brain cavity to a position near the top of the crista tuberalis. Investigation now shows that the braincase elements of early ornithischian dinosaurs such as *Heterodontosaurus* and *Lesothosaurus* could equally well serve as models for this transition. A crista tuberalis *sensu stricto* is not formed in coelurosaurs. Coupled to the evolution of the crista tuberalis it further seems that in the theropods, either a fenestra pseudorotunda or alternatively an avian fenestra rotunda is present. The condition of the middle ear of *Tyrannosaurus* is now clear and from published illustrations an avian-like fenestra rotunda is present in this Cretaceous coelurosaur. This contrasts with the condition in early theropods where a fenestra pseudorotunda is present. There seems to be a break in the phylogeny between *Allosaurus* and coelurosaurs as far as the characters defining the structure of the wing behind the middle ear is concerned. Analysis of numerous braincase characters suggests that coelurosaurs and ceratosaurs are independently rooted in dinosauromorphs. Resolving theropod relationships needs a renewed effort in the light of questions posed in the current work about the possible diphyly of the more derived groups.

## Phylogenetic relationships of the Permian 'cicada-like' family Pereboriidae (Insecta: Hemiptera: Pereborioidea)

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The Onder Karoo fossil locality near Sutherland has yielded some fascinating insect specimens over the past two years. Recently, two well-preserved wing fossils belonging to members of the Hemiptera were excavated from this middle Permian site. Initial investigations of the specimens revealed that these are 'cicada-like' insect fossils within the family Pereboriidae. We investigated the phylogenetic relationships within this family. We undertook an extensive review of existing literature on Pereboriidae, and subsequently described the fossil specimens. Based on published wing descriptions (e.g. wing venation) and comparisons with other members of this family in the literature, the two wings will be described to species level. These 'cicada-like' fossil specimens are the first known, definitive representatives of the

family in South Africa. This finding suggests that the Pereboriidae were widely distributed in the world during the Permian – prior to these findings they were only known from Siberia and Brazil. Some Triassic taxa previously attributed to this family are excluded, rendering the family strictly from the Permian. Finally, the extant Cicadidae, which are closely related to the Pereboriidae, will be considered in the search for trends to determine the phylogenetic relationships between extinct and extant taxa. Based on these observations, we discuss possible scenarios that led to the diversity we observe today. These findings will have a bearing on our understanding of Hemiptera diversity in the Permian and will ultimately contribute to Gondwana research.