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Edited & Reviewed by Emese M. Bordy Reviewed by Miengah Abrahams

Golden Gate Highlands National Park, South Africa



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### Building a home: morphological description of clustered Middle Pleistocene termitaria, Calitzdorp (South Africa)

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Termite colonies are "superorganism", large-scale geo-engineers and soil-nutrients recyclers that modify the landscape and underlying substrates through their complex nest building efforts. These eusocial insects build some of the most intricate structures, consisting of impressive above and below ground extensions. The nest morphologies are the physical expression of the colony's behaviour and the specialised design innovations are aimed at protecting the colony against predation, and housing the queen's chamber and nursery galleries. Of the eusocial insects, termites exhibit the most organised and morphologically variable nest architectures that reflect their evolved, complex caste system. Nest architectures may be species specific, though species living in similar environmental conditions may have morphologically similar mound features. Given that termites themselves have a low preservation potential, their hardier fossil nests offer valuable insights into their evolution and palaeoenvironmental conditions at the time of nest building. Here, we describe eight distinct columnar boxwork features, preserved in a calcified palaeo-soil within an ancient fluvial terrace near Calitzdorp. The nests are ~ 1.5 m tall, cylindrical structures (~ 60 cm diameter) composed of horizontally shelved chambers, which are connected by inclined ramps and supported by partition walls. The nests are composed of freestanding boxwork walls that lack external covering and surround hollow centres. Some of the nests share walls or are connected by structures at the column bases. Pebble to cobble-sized clasts are incorporated at different heights throughout the nests, indicating that they are subterranean features that were excavated into the upward fining conglomeratic fluvial terrace sediments. The complexity of the nest architecture with its distinct micromorphological textures suggests that the nests were built through termite activity. These Middle Pleistocene fossil termite nests, dated using U-Th radiometric techniques, are macromorphologically distinct from known fossil and extant termite nests, and may be assigned to a new ichnogenus potentially attributed to extinct termites.

### Exploring the biodiversity of past floras – The Molteno Gondwana Triassic flora as a window into the past

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With the United Nations Decade of Biodiversity (2011-2020) completed and the Decade on Ecosystem Restoration (2021–2030) underway, it is timely to take stock of what we know about past floras. With the exponential loss of modern plants through human activity and the race to save those on the endangered list, one may ask: "Why study fossil plants?" But as palaeoscientists point out: "The past is also the key to the future". As a basis for prediction, a thorough understanding of fossil floras is necessary. Globally, through the Triassic, the most biodiverse and best documented macroflora known is that from the Molteno Formation of southern Africa - as elucidated here. The Molteno Formation has the most extensive geographic outcrop of productive plant horizons in the Gondwana Triassic. Comprehensive sampling has been undertaken from 100 localities totalling over 27200 fossiliferous slabs. These vary from preliminary collections to six sites with over 1000–3000 catalogued slabs. Our documentation of this flora has been underway for 50 years. The first published monograph in 1983 was a review of Dicroidium - a key index fossil in the Gondwana Triassic. This revealed that Dicroidium was complex and that numerous genera previously applied formed a continuum. A further four monographs have described most of the flora with one awaiting publication. Another two volumes investigating the Molteno flora within a local and global context, have likewise been published. The described vegetative biodiversity of the Molteno flora includes 61 genera and 211 species. A further 6 genera and 14 species of unassociated fertile organs are known. Unique discoveries include the female fruit Kannaskoppia, with leaves and fruit attached to the same stem and six further fruit genera new to science. Additionally, the Molteno flora has been reconstructed with illustrations of the plants occurring in seven primary habitats.

# New data on the origin of endothermy in therapsids: insight from the bony labyrinth geometry

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The evolutionary success of mammals is, in large part, due to their elevated metabolism, but pinpointing the origin of endothermy among their synapsid ancestors has proven difficult. This is mostly due to the absence of a reliable and accessible proxy to endothermy in the fossil record. The bony labyrinth not only houses the organ of audition, but also that of balance: the vestibule and semi-circular canals. The semi-circular canals of the inner ear are oriented in the three dimensions of space and are filled with a fluid (the endolymph) that flows to activate receptors as the head moves. These receptors tell the brain the exact three-dimensional position of the head and body. The viscosity of the endolymph is critical for the balance organ to work efficiently. As temperature influences fluid viscosity, it is expected that the onset of endothermy in archosaurs and synapsids would have altered endolymph viscosity, thus requiring adaptations to maintain a functional balance organ. We found that birds compensated for the shift in viscosity linked to endothermy by changing the chemical composition of their endolymph, thus keeping the geometry of the semi-circular canals mostly untouched. In contrast, mammals adapted to this shift by changing the shape of their semicircular canals. This change in canals geometry happened rapidly c. 233 Ma ago in the nonmammaliaform Probainognathia (the branch of the Cynodontia that gave birth to the Mammaliaformes). This is consistent with previous results that suggested that hair and lactation evolved in this group too. This supports that endothermy evolved c. 30 Ma prior to the origin of Mammaliaformes. More importantly, this new approach offers, for the first time, a gateway to the evolution of endothermy.

# Late Permian woods from Aberdeen, South Africa, and growth ring features

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Silicified wood is found in various age deposits in the main Karoo Basin but usually as fairly small, fragmentary pieces. Fossil "forests" are rare but offer the opportunity for studying a larger sample from one locality. Twenty-nine in situ trunks, up to 9 m long, partially enclosed in fine-grained sandstone surrounded by mudstone and siltstone, were discovered at Aberdeen in the Eastern Cape. They are preserved in horizontal position in the Upper Permian Middleton Formation, Adelaide Subgroup, Beaufort Group of the Karoo Supergroup. Sedimentological assessment indicates that the fossil wood was transported and deposited in a fluvial paleoenvironment, with sandstone representing in-channel deposits and the mudstone-siltstone unit being the products of overbank areas. The trees originally grew on the floodplains before being uprooted and transported within the river channels. Using standard petrographic methods, four taxa, Aqathoxylon africanum, Agathoxylon karooensis, Australoxylon natalense and Australoxylon teixeirae, were recognized in thin sections. All the samples show growth ring widths ranging from 1 to 11 mm. This wide range of widths has been interpreted as growth under favourable climatic conditions with adequate water supply, interspersed by very wet and warm periods. From detailed growth ring analysis, we interpret the felling of trees during catastrophic events followed by transport prior to deposition within the channel sediments. These paleoenvironmental signals are compared with other late Permian woods in Gondwana.

### Sauropodomorph dinosaur material from the Upper Triassic Pebbly Arkose Formation of Zimbabwe

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The Karoo-aged basins of Zimbabwe contain continental sedimentary strata that are generally recognised as lateral correlatives of Permian-Early Jurassic deposits in the main Karoo Basin of South Africa and Lesotho. However, the Zimbabwean basins have been less extensively explored than their southern counterparts. Consequently, their precise stratigraphic relationships to each other, and to other Karoo-aged basins in the region, as well as their palaeontological resources, are relatively poorly known. Here, we report on new dinosaur material collected from Spurwing Island, in Lake Kariba on the northern border of Zimbabwe. The specimen was collected from the Pebbly Arkose Formation (PAF) (Upper Triassic) and consists of an articulated partial hind limb. Various features of the specimen support its referral to Sauropodomorpha and cladistic analyses place it within a clade of Norian taxa from both South Africa (Eucnemesaurus) and Argentina (Riojasaurus), suggesting a wider distribution of this group ('Riojasauridae') in southern Gondwana and, potentially, further biostratigraphical evidence for the Norian age of this section of the PAF. Preliminary work suggests that the Spurwing sauropodomorph is distinct from these taxa, but the material is fragmentary and might not warrant the description of a new species at this time. However, other isolated sauropodomorph bones are common nearby and there is high potential for additional discoveries that will further clarify the species-richness and composition of these Zimbabwean dinosaur faunas. Moreover, this – and other discoveries along the Kariba shoreline – suggests that the PAF offers a window into several different, contemporaneous palaeoenvironments. Other localities in the PAF yield a predominantly freshwater fauna (phytosaurs, lungfish, amphibians) with few terrestrial reptile remains, whereas sauropodomorph material has not been found in association with these aquatic taxa so far.

#### Did a gorgonopsian survive the end-Permian Mass Extinction?

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Gorgonopsians were the dominant carnivores of the late Permian (Lopingian) and became extinct at the Permian–Triassic boundary, *c.* 252 Ma ago. However, three specimens of gorgonopsians have been reported from the Early Triassic *Lystrosaurus* Assemblage Zone which, if correctly interpreted, would be survivors of the end-Permian Mass Extinction. We used Synchrotron X-ray computed microtomography to confirm their identification and reconstruct the taphonomic history. In parallel, we relocated the original sites where these specimens were found to evaluate their stratigraphic provenance and determine whether they were reworked from underlying Upper Permian strata. Gross anatomical comparisons and synchrotron scanning support the identification of all three specimens as gorgonopsians, two of them belonging to the long-snouted genus *Cyonosaurus*. We found that only one of the three specimens comes from a locality devoid of any Upper Permian outcrop, and thus deserves more scrutiny. If the occurrence of Early Triassic gorgonopsians is confirmed, this would support the hypothesis of a protracted end-Permian Mass Extinction. If disproved, this would confirm the extinction of gorgonopsians at the Permian–Triassic boundary and remove these anomalous occurrences from the dataset.

#### Indigenous knowledge of Karoo fossils

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The Karoo-aged deposits of southern Africa are globally famous for their richness in vertebrate fossils and scientific significance. The first Karoo fossil was reportedly discovered in 1827 near Beaufort West, but such a wealth of conspicuous bones must have attracted some prior attention. Here, we review the literature on this indigenous knowledge of palaeosciences. In South Africa and Lesotho, dinosaur bones and trackways have long been assigned to mythical dragon-like creatures such as the Amagongqongqo and Kholumolumo according to local folklore. Some rock paintings in the Cederberg mountains that border the Karoo Basin seem to depict animals similar to what the discovery of a large and tusked dicynodont skull might inspire. In Kwazulu-Natal, a rich fossiliferous Early Triassic site is located on a hill known locally as Tambokhazi ("the hill of many bones" in IsiZulu). The seemingly widespread awareness of Karoo-aged fossil plants and bones by local communities all over southern Africa suggests an old traditional knowledge, but evidence supporting the antiquity of this fossil awareness remains elusive. The painting of a possible dinosaur footprint at Mokhale Cave in Lesotho and the discovery of the first Mesosaurus specimen near Kimberley in South Africa attest that at least localised discoveries of fossil vertebrates were made as early as the 1800s by communities without prior Western scientific education. In sharp contrast, chert originating from Karoo-aged, silicified wood, was collected and worked by hominins since the Early Stone Age, suggesting a much older exploitation of fossil resources for tool-making. Overall, this review offers compelling preliminary evidence that some indigenous knowledge and interpretation of fossils existed and still exist in southern Africa. This offers an opportunity for further exploration of this knowledge and its potential interface with modern science and challenges the status quo whilst promoting inclusivity.

# Analysis of an unidentified theropod skull, BP/1/8571, from the Stormberg Group of South Africa

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Theropod dinosaurs were the dominant large-bodied predatory vertebrates from the Jurassic until the end of the Cretaceous. Theropod specimens are disproportionately rare in the Late Triassic -Early Jurassic Elliot Formation of the upper Stormberg Group of South Africa, yet they are critical for understanding the phylogenetic relationships of major clades. All previously known theropod body fossils in the upper Elliot Formation represent only two nominal taxa (Megapnosaurus rhodesiensis and Dracovenator regenti). In contrast, theropod ichnofossil assemblages are far more diverse within the same strata, indicating that theropod diversity was much higher than the currently available body fossil material indicates. In early 2020, a fragmentary theropod specimen (BP/1/8571) was salvaged from Golden Gate Highlands National Park from exposures of the uppermost Elliot Formation. CT-scans and digital reconstructions reveal that this specimen is the near-complete skull of a small-bodied theropod dinosaur, with a distinctive pair of low nasal ridges and an exceptionally large subnarial gap. The specimen bears clear differences in its bones that overlap with the holotypes of Dracovenator and Megapnosaurus. Instead, it more closely resembles BP/1/5278, a now-missing snout of a theropod previously considered a juvenile *Dracovenator*. These observations suggest that BP/1/8571 (and by extension 5278) represents a new theropod taxon. Phylogenetic analysis of the specimen places it among early branching Neotheropoda, but outside of Coelophysoidea and Dilophosauria. These findings increase the diversity of theropods known from body fossils in the Jurassic part of the Elliot Formation and add information about the cranial anatomy of early neotheropods.

### Tracking in the southern African Jurassic Park

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The Karoo's world-famous rocks provide a record of environmental change in the deep past from land of ice during glacial conditions to a land of fire that was covered by extensive sheets of lava flows. The youngest Karoo rocks are Jurassic and document the early evolution of dinosaurs and mammals in form of skeletal remains and trace fossils, ichnofossils. These include trails, footprints, trackways, and burrows of animals, which are essentially the petrified behaviour of an organism. For example, vertebrate footprints preserved in the upper Stormberg Group (Upper Triassic – Lower Jurassic) of the main Karoo Basin of South Africa and Lesotho are powerful in reconstructing the living conditions of long-gone creatures, including some of the renowned dinosaurs of southern Gondwana. Collectively, the exceptional diversity of these Early Jurassic fossils allows not only the identification of unique prehistoric animals, but also a rare insight into the intricate behaviour of ancient communities that lived in the Karoo *c*. 200 Ma ago. In this brief review of our regional Jurassic Park-themed fossil footprint sites, I will focus on those locations that can serve as global geoheritage destinations because of their proven scientific and educational values. Being easily accessible, these footprint sites may also be cost-effectively targeted by the emergent palaeotourism industry in both South Africa and Lesotho.

### A new giant Late Triassic crocodylomorph from the Elliot Formation, South Africa and the transition to decreased growth rates in crocodilians

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Today's crocodilians grow slowly but evolved from a faster-growing ancestor and may even be secondarily ectothermic. Supporting evidence for this comes from rapid growth rates preserved in the osteohistology of basal archosauromorphs and early crown group archosaurs. The transition from fast to slow growth rates along the crocodilian stem lineage is hypothesized to coincide with evolutionary body size reduction. However, the exact timing of this transition remains unknown, obscuring its relationship with the dynamics of body size evolution. Recently, the osteohistology of Batrachotomus revealed that rapid growth was still present at the base of Loricata. Here, we present the osteohistology of a tibia and fibula of a new, giant species (estimated body mass 250–400 kg), from the Upper Triassic lower Elliot Formation at Qhemegha, Eastern Cape. The new species exhibits highly vascularized parallel-fibred bone tissue with a laminar vascular arrangement. The bone tissues are interrupted by lines of arrested growth, which become closer together towards the subperiosteal surface, showing that the individual was at least a sub-adult. Although there is no external fundamental system, it is unlikely that this individual would have grown significantly larger. The combination of highly vascularized parallel-fibred bone with a laminar arrangement has not previously been found in other pseudosuchians. High vascularity indicates the taxon was growing relatively quickly to reach large adult size. This contrasts with the lamellar-zonal bone that indicates slower growth in smaller-bodied early crocodylomorphs such as Hesperosuchus. Nevertheless, woven bone is completely absent in the new species, indicating slower maximum growth rates, whereas abundant woven bone in Batrachotomus indicates rapid growth rates. The new specimen is tentatively placed at the base of Crocodylomorpha, suggesting that the transition to decreased growth rates occurred early in the history of this clade via a loss of woven bone deposition.

#### Why is the enamel of Microgomphodon oligocynus orange?

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Many extant rodents and shrews have iron-enriched tooth enamel making their teeth more resistant to wear and staining them orange. Here, we present a recent discovery of a Microgomphodon oligocynus specimen with orange-coloured enamel from Lemoenfontein, an Early-Middle Triassic locality near Aliwal North in South Africa. Our preliminary analyses of this individual's teeth were aimed at determining whether iron enrichment can account for the colour. SEM images confirm that the white portion of the tooth has the diagnostic porous microstructure of dentine, whereas the orange-coloured enamel is distinguished by a smooth microtexture. SEM EDS analysis of these fossil teeth confirms the expected ratios of oxygen, calcium, phosphorus, and carbon that geochemically distinguishes enamel from dentine. However, the orange-coloured enamel does not contain any significant elemental (i.e., iron) enrichment that might explain the different colour. No enrichment of iron was detected using RAMEN spectrography either. Because both RAMEN spectrography and SEM EDS analyses measure surface chemistry, subsurface enrichment is undetectable using these methods. Some modern shrews have three zones of enamel: an outer clear zone, a middle iron-rich zone, and an inner clear zone. If the M. oligocynus specimen enamel is similarly structured, it would account for the lack of surface enamel elemental enrichment. Destructive analysis would make it possible to determine the sub-surface chemistry; however, non-destructive analyses (e.g., synchrotron scanning) could also indicate either microstructural variations in the tooth (e.g., prismatic microstructures), or peaks in the grey-scale range that may indicate elemental variation. Ongoing research, including microwear analysis, aims to determine whether there is indeed enrichment of the enamel of *M. oligocynus* and if this possible enrichment could have afforded this species a competitive advantage for exploiting hard-food sources (e.g., arthropods, molluscs, tough plants) and thus thrive in the aftermath of the end-Permian Mass Extinction.

### Late Ordovician, mid-latitude Gondwanan palaeoenvironments under the microscope: Cedarberg Formation, Cape Supergroup, South Africa

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The c. 440-Ma-old Soom Shale Lagerstätte (Cedarberg Formation, South Africa) records a rich assemblage of exceptionally well-preserved fossils. These ancient organisms lived in an unusually cold-water ecosystem in the aftermath of the Hirnantian glaciation and associated, pulsed, extinction event, which may account for the low diversity of the fauna and occasional gigantism of the conodont taxa. Although most of the Soom Shale fossils are remains of pelagic organisms, benthic brachiopods also occur, but individuals are small and relatively rare. Supported by the geochemical results, the pelagic-benthic size disparity is attributed to adverse benthic conditions. Compared to the palaeontology, the sedimentology of the Soom Shale is relatively understudied, despite the unit containing some unusual lithofacies with aggregates of out-sized clay and quartz clasts that is intimately associated with organic matter and fossils. The aggregates have been tentatively interpreted as marine snow of aeolian origin, but this hypothesis required further testing. Here, we present a detailed account of the Soom Shale lithofacies including millimetre-scale core logs, thin-section analyses, scanning electron microscopy, and micro-CT imaging. Regional studies reveal that the unusual lithofacies with clast aggregates occurs at multiple localities along a strike of 200 km. Preliminary field observations suggested that this unusual lithofacies was restricted to the lowermost Soom Shale Member. However, we found that this lithofacies extends from the Soom Shale into the lower Disa Member (~ 17 meters of core) and that there is no temporal change in the texture, composition, or size of lithofacies components, including the grain size characteristics of the aggregated clasts. This indicates that a regionally pervasive and temporally persistent sedimentary process operated throughout the deposition of the Soom Shale and lower Disa Members. We discuss various controlling factors, including depositional processes, to elucidate the origin of this lithofacies and contextualize it within the unusual taphonomic conditions that led to the exceptional preservation of the Soom Shale Lagerstätte.

# Small bodied sauropodomorph from the upper Elliot Formation of South Africa

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The earliest sauropodomorphs were small omnivores (< 10 kg) that first appeared in the Carnian (233–231 Ma). By the Early Jurassic (190–199 Ma), early branching sauropodomorphs (EBSMs) were globally distributed, had a range of postures, and evolved masses exceeding ten tonnes. Smallbodied EBSMs like Massospondylus (< 500 kg) persist at least until the Pliensbachian at nearly all dinosaur-bearing localities worldwide but are comparatively low in alpha diversity. One potential reason for the paucity of smaller EBSM species is competition at this body size from other amniote groups, including gomphodont cynodonts (e.g., Scalenodontoides) in the Late Triassic, and early branching ornithischian dinosaurs (e.g., Heterodontosaurus) in the earliest Jurassic. Extant herbivorous mammals show a range of body masses from < 10 g to 7000 kg, with considerable sympatry of phylogenetically distantly related species at smaller body masses. By this comparison, our understanding of the phylogenetic distribution of body mass classes in the Elliot Formation, and its explanatory power for the lower thresholds of body mass in EBSMs, is clearly in need of more data. During our recent investigations of EBSM growth strategies, we osteohistologically sectioned a small humerus, BP/1/4732, from the upper Elliot Formation of the eastern Free State of South Africa. Careful consideration of its comparative morphology and characterization of its osteohistology clearly show that this specimen represents a skeletally mature individual of a new sauropodomorph taxon with an adult body mass of 69 kg. This makes it among the smallest-known sauropodomorph taxa ever to live on Earth, and the smallest ever reported from the Early Jurassic.

#### Computed tomography image reconstruction using the ASTRA toolbox

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Computed tomography equipment is usually supplied with proprietary reconstruction software that is not customizable and has limitations such as prolonged reconstruction times. We report the implementation of the ASTRA toolbox, a customizable open-source tool which can be used with python or MATLAB. Additionally, we have used iterative algorithms for 3D reconstruction that are not yet available in most proprietary software and make use of the FBP algorithm. This will also give us additional capabilities such as customizing the reconstruction process and developing phase retrieval reconstruction methods that can be used to enhance contrast. The ASTRA toolbox uses graphics processing units (GPUs) to allow for parallel processing of CT data and thereby reducing the reconstruction time. We will demonstrate reconstructions of a few samples using the simultaneous iterative reconstruction technique (SIRT).

# Palaeobiological implications of the bone histology of the Pleistocene dromornithid, *Genyornis newtoni*

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During life, the bones of vertebrates record various aspects of their life history and biology. Since fossilisation preserves the integrity of the bone microstructure, histological studies of the bones of extinct animals can provide substantial information about their overall biology. Genyornis newtoni was a giant flightless galloansere bird that belonged to the Dromornithidae. It was fairly widespread in the mid-late Pleistocene of Australia but went extinct c. 50000 years ago (together with other contemporary megafauna). Genyornis is estimated to have weighed c. 180–260 kg and was c. 2–2.5 m tall. Although its skeletal remains are reasonably well studied in terms of their anatomy and taxonomy, little information is known about its biology. Here, we investigate the histology of fifteen long bones (tibiotarsi, tarsometatarsi and femora) of Genyornis to deduce information about its growth dynamics and life history. Thin sections of the fossil bones were prepared using standard petrographic methods, and the histology of the bones were studied under polarised and ordinary transmitted light microscopes. Our analyses demonstrated that of the three elements studied, the tibiotarsus preserved the best track record of its growth. Our findings suggest that unlike most modern birds, Genyornis took more than a single year to reach sexual maturity, and several years to reach skeletal maturity. Thus, sexual maturity and skeletal maturity were asynchronous, with the former preceding the latter. Furthermore, we found that Genyornis responded to prevailing environmental conditions by changing its growth patterns, which suggests that it retained the plesiomorphic, flexible growth strategy of its nonavian dinosaurian ancestors.

#### The first body fossil evidence of aetosaurs in southern Africa

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Aetosaurs are medium-sized, quadrupedal pseudosuchians with heavy body armour. They are among the most ubiquitous vertebrate fossils of the Upper Triassic, easily recognized from their dermal scutes, and known from continental deposits in Europe, India, the Americas, and northern Africa. The lower Elliot Formation and its lateral equivalents in southern Africa are world-class Upper Triassic successions, but surprisingly have yet to produce aetosaur body fossils. The absence of aetosaurs in southern Africa and Antarctica has been explained by various hypotheses, including exclusion of aetosaurs from cooler, high-latitude climate zones. South African strata do, however, record ichnofossils sometimes attributed to aetosaurs, providing tentative evidence of their presence in the Upper Triassic. In 2018, our research group recovered a badly broken, 30-cm-long skull from the uppermost lower Elliot Formation (Rhaetian) at Qhemegha Village, Eastern Cape Province (BP-1-8384; field log ID of "cynodont?"). The poor nature of its preservation precluded manual preparation. High-resolution (42 µm isotropic voxel size), propagation phase-contrast micro-CT scans on BM18 at the European Radiation Synchrotron Facility revealed many features of the cranium, including numerous closely packed teeth, a partially edentulous premaxilla, and a large external naris. These features allow us to identify the specimen as a likely new taxon of aetosaur, positioning BP-1-8384 as one of the latest-surviving, most southerly occurring members of the clade. It also indicates that incomplete sampling, rather than latitudinal exclusion, is a better explanation for the scarcity of aetosaur fossils in southern Africa. Because BP-1-8384 occurs closer to the presumed position of the end-Triassic Extinction Event than other aetosaur taxa, it provides evidence that the lineage persisted until this biotic crisis, strengthening the evidence for the dynamics of faunal turnover at that time.

# A potential new tetrapod assemblage in the lower Abrahamskraal Formation, Beaufort Group

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The tetrapod biostratigraphy of the Beaufort Group of the main Karoo Basin, South Africa, is the best documented and chronologically constrained for the late Guadalupian (mid-Permian) to the Middle Triassic. The oldest part of the Beaufort Group, the Guadalupian-aged Abrahamskraal Formation, comprises two assemblage zones: the older Eodicynodon Assemblage Zone (AZ) and younger Tapinocephalus AZ. Our research programme has improved our understanding of the Tapinocephalus AZ, but it also revealed an unsampled gap of several hundred metres which obscured the transition to this assemblage zone from the underlying Eodicynodon AZ. Over the past few years our team has been collecting fossils from the middle Abrahamskraal Formation in the southwestern Karoo Basin to explore this transition, which has revealed an unexpected assemblage comprising novel and rare or geographically-restricted taxa from the lower Abrahamskraal Formation to the north and east. This suggests that these occurrences may represent temporal rather than geographic diversity phenomena, resulting from the established diachroneity of the lower contact of the Abrahamskraal Formation. The assemblage seems to lack the dicynodonts Eodicynodon and Eosimops, which characterize the adjacent assemblage zones, and thus likely represents a new biostratigraphic unit. Its discovery contributes to the emerging realisation that mid-Permian tetrapod faunas experienced higher levels of turnover than previously supposed and highlights the constraints of sampling on reconstructing diversity patterns in the oldest rocks of the Beaufort Group.

### Permian magnetostratigraphy in the southeast Karoo Basin, South Africa: implications for Ecca-Beaufort contact diachronocity

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The contact between the Ecca and Beaufort groups represents a change from marine to continental deposition and has long been interpreted as diachronous and younging from the southwest to the north based on sedimentology and biostratigraphy. Here, we calibrate the magnitude of that diachronicity, for the first time, by using magnetostratigraphy. Palaeomagnetic results from a ~ 2353-m-thick section of undeformed Middle to Upper Permian rocks in the south-eastern Karoo Basin are presented. A dual-polarity high-stability magnetization is interpreted as the record of the Permian geomagnetic field. This timing is further constrained by the effect of Jurassic dolerite intrusions. During the Permian, the Kiaman Reverse Polarity Superchron (end-Kiaman) is a prominent c. 318–265 Ma magnetostratigraphic interval of reverse polarity that is followed by an interval of mixed polarity. An astronomically calibrated age model at Ouberg Pass in the southwestern Karoo Basin constrains the end-Kiaman to  $266.5 \pm 0.26$  Ma. The base of the Beaufort Group at Ouberg Pass occurs 138.9 m below this and can be dated at 267.4 ± 0.26 Ma, assuming a constant sedimentation rate of 16 cm/kyr. In KWV-01 borehole in the south-eastern Karoo Basin, the same lithological boundary falls within the middle part of a normal polarity zone, which is correlated to a corresponding horizon at Ouberg Pass (i.e., 266.3 ± 0.26 Ma middle of polarity zone N2, ~ 27 m above the end-Kiaman). This reveals diachronicity of the Ecca-Beaufort Group boundary to be on the order of 1.1 Ma across 900 km of the E–W extremes of the southern Karoo Basin.

# Harnessing palaeontological expert knowledge for use within a deep learning model to prospect remotely

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The successful identification of a fossiliferous site requires expert knowledge of palaeontology, geology, and a degree of luck. The development of a machine learning model to help prospect for new fossil sites is a challenge that has been met with limited success to date. One hurdle that had to be overcome is how to train a model to recognize a suitable area to prospect. Existing known sites are far too sparse, resulting in a small training dataset that cannot be used to train a deep learning model. The solution was to undertake a fossil site annotation study using expert knowledge. Within this study, two phases were performed. Within the first phase, three palaeontological experts annotated areas within an orthomosaic drone map covering approximately 0.5 km<sup>2</sup> that they thought should be prospected for fossils. In the second phase, the experts annotated areas within the same drone map marked as prospectable by at least one expert within phase one. If both experts agree that an area is prospectable, the area is added to the training dataset for the model. Annotation was performed within QGIS Desktop 3.10.3 (https://www.qgis.org/en/site/) by drawing a polygon on a drone orthomosaic model which has a ground resolution of 2.86 cm/pix with a resolution of 52634 x 32383. After processing the data, the resulting training dataset resulted in 34512 patches. This training dataset is sufficient to train a high-performance deep learning model to prospect for fossils using orthomosaic drone maps.

#### Implications of non-ammocoete larvae in the earliest known lampreys

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Since the late nineteenth century biologists have commonly utilized the ontogeny of extant lampreys to model a scenario for the origin of vertebrates. Thus, metamorphosis from an invertebrate-like ammocoete larva (resembling a cephalochordate) into an apparently simple cartilaginous adult was held up as a recapitulation of the macro-evolutionary change from invertebrates to vertebrates. Consequently, the unknown last invertebrate ancestor of vertebrates was portrayed as Amphioxuslike and the earliest form of vertebrate as lamprey-like. This scenario rested on several assumptions and prerequisites. One of these was that throughout their history lampreys had conserved this ontogeny, and that both lampreys and ammocoetes extended back to the dawn of vertebrates, c. 500 Ma ago. Publication in 2006 of Priscomyzon riniensis, a 360-Ma-old lamprey from the Witpoort Formation (Witteberg Group, Cape Supergroup) of South Africa potentially added credibility to this scenario - the world's oldest exemplar of a lamprey, it already exhibited the distinguishing characteristics of extant adults. Further excavation and analysis of material from the Waterloo Farm lagerstätte, from which Priscomyzon was recovered, subsequently permitted reconstruction of an ontogenetic series for Priscomyzon. Importantly the smallest member of this series, a mere 14-mmlong, exhibits a yolk sac bulge (indicative of recent emergence), but already has adult lamprey characteristics, such as a sucker disc and well-developed eyes. In brief, there was no ammocoete phase. Comparison with more fragmentary ontogenetic evidence from slightly younger (Carboniferous) lampreys has added robustness to the finding (published in 2021) that Palaeozoic lampreys did not have an ammocoete phase, it being first evidenced in the Cretaceous. Conclusions that ammocoetes are a derived evolutionary 'add-in', rather than a conserved form, collapses their value in reconstructing vertebrate origins. Indeed, other evidence suggests that the apparently simple, boneless, form of lampreys is likewise derived.

Reconstruction of the high-latitude Late Devonian (Famennian) Waterloo Farm lägerstatte from the Witpoort Formation (Witteberg Group, Cape Supergroup) of South Africa

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The Waterloo Farm lagerstätte, on the outskirts of Makhanda (Rhini) in the Eastern Cape, provides the only comprehensive window into a diverse high-latitude marginal marine or continental ecosystem of the Late Devonian. This time interval is of macro-evolutionary importance for several reasons, because it preserves the earliest body fossils of tetrapods (four-footed animals); represents the time when the first woody trees are known to have reached a global distribution and showcases conditions and diversity of life immediately prior to the finale of the end-Devonian Mass Extinction (second of the Big 5 extinction events). Waterloo Farm was home to two of the three Devonian tetrapods known from Gondwana and provides the world's best understood ecological setting of any early tetrapod. Anoxic bottom water conditions in an estuarine setting most likely account for frequent episodes of exceptional preservation, and left evidence of soft tissue, in addition to bone and woody material. As a result, it evidences an entire broad ecological system, from diverse aquatic vertebrates (fish and early tetrapods) to seaweeds, fresh to brack water waterweeds, aquatic invertebrate fauna, and plants and invertebrates from the adjacent terrestrial environment. To make this South African palaeoheritage treasure more accessible to the public a project, funded by SANRAL (the South African National Road Agency Limited), included production of paintings by the renowned South African palaeo-illustrator, Maggie Newman. Recent completion of a 3.5-m-long triptych, largely focussed on underwater diversity and ecology, is the culmination of c. 4 years of on and off collaboration between RG and Maggie Newman, as well as discussions with numerous specialist international collaborators. It incorporates 30 of the better understood taxa from Waterloo Farm, including 23 of the 25 taxa so far diagnosed from the locality, and two taxa assigned to existing species.

#### Millipede-tetrapod associations from the Karoo Basin, South Africa

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Millipedes, which have a trackway record extending from the Ordovician and body fossil record going back to the middle Silurian, were among the first animals to colonise Early Palaeozoic continental ecosystems. However, millipede fossils of late Permian to Early Triassic age are exceptionally rare worldwide and only ten or so genera have been described to date. Although it is best known for tetrapod fossils, the main Karoo Basin also boasts a rich diversity of insect fossils. Most of the insect fossils recovered from Upper Permian to Lower Triassic Beaufort Group are found in close association with abundant well-preserved plant impressions. Exceptions to this are a handful of millipede body fossil specimens that occur in close association with articulated tetrapod fossils. Two multitaxic tetrapod aggregations that contain Triassic millipedes have been reported from the main Karoo Basin. Here, we briefly describe two new millipede-tetrapod associations from the Early Triassic Lystrosaurus declivis Assemblage Zone. The first includes two millipedes associated with an articulated small therocephalian Scaloposaurus, whereas the second comprises an articulated skeleton of the dicynodont Lystrosaurus murrayi. The high degree of skeletal articulation in both specimens, coupled with preservation of delicate bones *in-situ*, suggest rapid burial soon after death, or that they died in a place protected from weathering and agents of dispersal. Possible hypotheses to explain the presence of millipedes closely associated with articulated tetrapod skeletons include: shelter sharing, predator-prey accumulations, and post-mortem scavenging by the millipedes. Of these, our taphonomic interpretation favours the latter. Within the Karoo Supergroup, the appearance of millipede fossils in the uppermost Balfour and lower Katberg formations suggests that the scarcity of plant detritus on the Karoo floodplains in the aftermath of the end-Permian Mass Extinction may have contributed to millipedes switching to a more scavenging feeding strategy.

# The Permo-Triassic boundary in the KwaZulu-Natal Province of South Africa

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Middle-to-late Permian deposits of the Beaufort Group in the Stoffelton and Bergville districts (KwaZulu-Natal, South Africa) have yielded numerous tetrapod fossils but have been overlooked in recent biostratigraphic revisions. This is largely because many of the collected specimens from this part of the basin remain unprepared. Furthermore, the limited locality data associated with the specimens muddled the stratigraphic context for many of the fossils and restricted their use for biostratigraphy. What is certain is that faunas from both the late Permian and Early Triassic are represented and there is the possibility that the Permo-Triassic boundary, which in the southern parts of the basin fully preserves the effects of the end-Permian Mass Extinction, may also be present. Here, we present preliminary results from our recent palaeontological and sedimentological studies in the Balfour Formation in KwaZulu-Natal. Historically productive and newly identified localities were visited, enabling us to provide a better stratigraphic context for all collected specimens. Palaeontological data from the field, supplemented by data from Karoo Fossil Collections, reveal that at least 18 fossil tetrapod taxa are represented and confirm the presence of both the latest Permian Lystrosaurus maccaigi-Moschorhinus Subzone of the Daptocephalus Assemblage Zone and the Early Triassic Lystrosaurus declivis Assemblage Zone in surface outcrops. The contact of these two assemblage zones in other parts of the basin coincides with the radiometrically dated Permo-Triassic boundary. Future fieldwork targeting the fossils and any radioisotopically datable layers at this contact will determine how complete the Permo-Triassic boundary succession is in KwaZulu-Natal.

#### Golden Gate: geologists' dream, palaeontologists' paradise

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The Golden Gate Highlands National Park, first proclaimed in 1963, remains one of the, if not the only, national park in South Africa established specifically to preserve the scenic beauty of the area with special aim to conserve the integrity of the Clarens Formation, the stratigraphic unit that forms the towering sandstone cliffs that gave the park its name. Outcrops of the Upper Triassic – Lower Jurassic Elliot and Clarens formations and the conformably overlying Drakensberg Group are most prominent but older strata from the Burgersdorp and Molteno formations also crop out within the boundaries of the Park. Although all of these are rich in fossils, including bones, eggs, plants, burrows, and footprints, most of the palaeontological work in the Park during the past decades has focused on the Elliot and Clarens Formations. One of the most notable, and famous sites, is the locality at Rooidraai where Massospondylus eggs with embryos were first reported by James Kitching in the 1970s. In addition to the rich palaeontological heritage, several sites within the Park also record more recent heritage. Dozens of sandstone overhangs are decorated with rock art and there are also several important sites from the Anglo-Boer War. Here, I briefly showcase some of the lesser known geological and palaeontological sites within the park, including a vertebrate burrow locality, an outcrop with well-preserved Dicroidium plant remains, dramatic examples of exudation, cave formation and outcrops of in situ basaltic lava flows. All these sites further cement the status of the Golden Gate Highlands National Park as geologists' dream and palaeontologists' paradise and can be used to expand the geotourism potential of the region.

## Digitally reassembling a gorgonopsian skull from the drawings of serial sections made by Denise Sigogneau-Russel

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Before the development of computed tomographic methods, studying the internal anatomy of fossils was challenging. The most widespread way to proceed was through serial grinding and sectioning. These destructive methods consisted in grinding or sectioning a specimen at evenly spaced intervals and drawing the resulting polished surfaces. Serial sectioning was performed on a well-preserved gorgonopsian skull (BP/1/277) referred to Gorgonops torvus by Denise Sigogneau-Russell. The sections were used for her publication on gorgonopsian inner ear in 1974, but the rest of the sections of the skull were not included. The drawings were then kept and curated at the Museum National d'Histoire Naturelle (Paris, France). Here we used the over one thousand drawings made by Sigogneau-Russell to build a 3D model of the skull of BP/1/277. The drawings were aligned and then treated using VGSTUDIO MAX 3.1. This model enabled access to details of the cranial anatomy such as the trigeminal innervation, palate bones and inner ear. The specimen was also included in a recent phylogenetic analysis of gorgonopsians. The skull exhibits a similar pattern of innervation to what was recently described in gorgonopsians. The palatal anatomy reveals an unexpected contact between the vomer and pterygoid, a feature only described in basal gorgonopsians (though this can be due to deformation or the coarse resolution of the tomographic method). The phylogenetic analysis placed the specimen closest to G. torvus, even though some of its traits do not match what has been described elsewhere for this taxon. This highlights the need for a complete revision of the genus Gorgonops. This study also demonstrates that data produced almost 50 years ago are still relevant and that many Karoo fossils studied using serial grinding/sectioning may still help improve knowledge in the field of vertebrate evolution.

### The farm Driefontein 11: type locality of the *Langbergia-Garjainia* Subzone of the *Cynognathus* Assemblage Zone and key to understanding terrestrial recovery following the Permo-Triassic boundary crisis

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Fossil collecting on the farm Driefontein 11 over the past 30 years has documented a macro- and micro-fauna dominated by actinopterygian, chondrichthyan and sarcopterygian fish, mastodonsaurid temnospondyls, archosauriforms, non-mammalian synapsids, the enigmatic diapsid Palacrodon, and undescribed procolophonoids. The significance of the site is shown by its designation as the type locality of the Langbergia-Garjainia Subzone of the Cynognathus Assemblage Zone. Thousands of vertebrate coprolites of various morphologies have also been collected, which contain vertebrate and invertebrate remains. Recent and ongoing investigations of these coprolites using advanced imaging methods has reinvigorated their study and shown their importance in reconstructing trophic networks. Other recent work has focused on the microfauna, particularly the chondrichthyans, and three hybodont taxa, including new species of Lissodus and Polyacrodus, are now documented from the site. Hybodontid material comprises hundreds of extremely small (< 4 mm maximum dimension) tooth crowns from multiple tooth positions. The Lissodus species differs from Lissodus africanus from the overlying Trirachodon-Kannemeyeria subzone and shows that even isolated Lissodus teeth may be useful in a biostratigraphic context. Isolated diapsid reptile teeth from the microvertebrate assemblage provide evidence of several morphotypes, and a higher diversity of diapsids than is documented by the macro-faunal remains. An important aspect of the site is that it preserves a mixture of large specimens and diminutive forms. The dichotomy is that all large forms are piscivorous, however all recovered chondrichthyan, actinopterygian and sarcopterygian (dipnoan) fossils are diminutive in size. Given the large sample size this cannot be an artefact of sampling. Their diminutive nature may represent an ongoing Lilliput effect amongst these taxa following the end-Permian Mass Extinction.

# Fossil Bovidae (Mammalia: Artiodactyla) from South Africa and their significance for hominin evolution

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Bovidae is usually the most common large mammal family encountered in Plio-Pleistocene (5.33–0.78 Ma) deposits of Africa. Moreover, bovids are primary consumers and are often the preferred prey of large carnivores, including hominins. Thus, they can be used as a proxy for studying palaeoecology, taphonomy as well as early hominin subsistence behaviours. However, despite their dominant statue in bone assemblages, there are proportionally very few taxonomic studies of the southern African material. Nowadays, as more material is available for study, it is possible to study the taxonomic composition of bovid assemblages across the Plio-Pleistocene of South Africa and here, I provide the first updated overview of this bovid fossil record. Using updated systematics, I question the validity of certain bovid taxa (e.g., *Tragelaphus pricei, Parmularius vrbae*) and highlight the need for taxonomic revision. This review permits the proposal of a new bovid-based biochronology and a simple biozonations approach that defines four biozones ("Standard Bovid Units") with potential for estimating the geological age of future deposits. Moreover, the gap in the fossil record between 5.0 and 3.5 Ma shows the importance of additional fieldwork and systematic taxonomic analysis of bovid bone assemblages.

#### Ecomorphology of South African crocodylomorph mandibles

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Crocodylians are the only living descendants of Pseudosuchia, a diapsid lineage that originated in the Early Triassic. Living crocodylians are all semi-aquatic ambush hunters with limited functional diversity, but extinct crocodylomorphs show a variety of ecomorphologies including a range of dietary specializations. The ecomorphological diversity of extinct pseudosuchians are hypothesized to be comparable to that of living mammals based on the reported instances of herbivory occurring in pseudosuchian groups and subsequent studies hypothesizing that derived pseudosuchians have food processing mechanisms similar to those of mammals. Craniodental anatomy is an excellent source of evidence for inferring the ecology of extinct animals, particularly functionally informative craniodental features such as the shape of the mandible. Investigating the diversity of mammals statistically and studying it comparatively with pseudosuchians could provide a methodology for predicting the diet and ecology of extinct pseudosuchians. Here, the ecomorphological disparity of pseudosuchians and mammals are assessed by studying the mandibular morphology using geometric morphometrics. A sample comprising 44 living and extinct pseudosuchian species and 56 extant mammal species was used to compute a phylogenetically corrected principal component analyses and two-way ANOVA tests. The results indicated that mammals are a poor analogue to use in pseudosuchian comparative studies due to the biomechanical differences between the groups. Mandibular shapes were poorly indicative of ecology as there were minor differences between the mandibular shapes of carnivores and herbivores in the sample.

# *Zoophycos* (*'Spirophyton'*) trace fossils from marginal marine settings in the Witpoort Formation (Witteberg Group)

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*Zoophycos* is a trace fossil of marine deposit feeding invertebrates and comprises systematic probes (spreite), helically constructed around a central axis. It is one of the most geologically widespread and long-lived ichnotaxa, ranging from the Cambrian until the Holocene. Many aspects of the trace are still debated despite dozens of studies over the past *c*. 170 years, including the identity of the tracemaker(s), the mode and rate of construction, the purpose of the structure and taxonomic classification within the '*Zoophycos* group', among which these characters may vary. *Zoophycos* may comprise a helicoidal architecture. This morphology is common in Late Devonian strata of the Witteberg Group and is usually referred to '*Spirophyton*' with an architecture comparable to *Z*. *brianteus*. Occurrences within well-constrained depositional settings in the Witpoort Formation (Eastern Cape) indicate that *Zoophycos* formed in oxygen-poor estuarine and lagoonal muddy sediments. This supports contentions that the archetypal *Zoophycos* ichnofacies, widely considered to represent shelf settings below wave base, is not applicable for Palaeozoic strata. Our analysis of the traces indicates that they are built from the bottom upwards in contrast to some of the constructional models previously proposed.

# Evolution of an Early Jurassic desert system: erg dynamics and geochronology of the Clarens Formation, southern Africa

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The Lower Jurassic Clarens Formation represents the youngest sedimentary succession of the Stormberg Group in the Karoo Supergroup of southern Africa. The unit is dominated by thick to very thick beds of massive and very large to large-scale cross-bedded sandstones, which were interpreted as deposits of aeolian origin with intermittent wet conditions throughout. Its Early Jurassic age is deduced from the biostratigraphy and geochronology of the underlying Elliot Formation, and radioisotopic ages of the overlying Drakensberg Group. Despite extensive work on the sedimentary facies, a detailed understanding of small to large-scale processes remains elusive, while a systematic regional geochronological framework has not yet been conducted. Utilising field-based facies analysis and U-Pb radioisotopic age dating of detrital zircons, this study confirms the dominance of Massive and Aeolian Dune Facies Associations and establishes a broad chronostratigraphic framework for the Clarens Formation. The spatiotemporal distribution of the facies can be explained by a typical zoned-erg depositional model controlled by short- and long-term drivers, where shortterm water table fluctuations controlled the spatial expression of the lateral facies distribution, whereas vertical facies changes are attributable to erg expansion/contraction dynamics through time. Maximum depositional ages suggest a Late Sinemurian age for the lower zone, an Early Pliensbachian age for the middle zone and a Late Pliensbachian age for the upper zone. This trend is particularly prevalent in the south of the basin, where these signals are incorporated into each zone, respectively, and towards the north and northeast, they appear in the subsequent younger zone, which may demonstrate that sediment was primarily supplied from the south and southwest towards the north and northeast. The reported facies distributions and geochronology therefore confirm the validity of the zonation of the Clarens Formation, which is consistent with climatic trends reported from the Tethyan margin of Gondwana during the Sinemurian and Pliensbachian. The results thus suggest that the temporal facies changes in the Clarens Formation in southern Gondwana resulted from global climatic fluctuations during the Early Jurassic.

## Quaternary termitaria as proxy for palaeoclimate and vegetation in western South Africa

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Fossil termite nests (termitaria) are commonly preferentially overprinted by calcium carbonate precipitates and preserved as hardy, calcretized material. A typical process for pedogenic carbonate precipitation is the downward migration of saturated carbonate solutions from the upper soil levels. Consequently, the precipitates may be used as proxies for the palaeoenvironment at the time of formation. Termitaria carbonates have previously been used to infer palaeo-vegetation and palaeoclimate trends using carbon (C) and oxygen (O) stable isotope ratios. Here, we evaluate the  $\delta^{13}$ C values of two calcretized, Quaternary termitaria preserved in a well-developed soil profile near Calitzdorp, South Africa. The fossil nests comprise 27 wt% of carbonate minerals, specifically calcite and dolomite. The carbonate horizons, which can be identified macroscopically as cream-coloured layers amongst beige-coloured sands, have  $\delta^{13}$ C values ranging between -3.45‰ and -0.69‰ , based on 33 samples for the two termitaria. This  $\delta^{13}$ C signature is comparable to calcretized termite mounds studied in Worcester (South Africa), which are interpreted to have C4 characters, a proxy commonly associated with vegetation adapted to warmer, drier climates. Whether the C4 character observed in the Calitzdorp termitaria is related to preferential harvesting of plants by the ancient termites or related to soil respiration rates is still under investigation and needs to be considered in conjunction with our ongoing  $\delta^{18}$ O palaeoclimate assessments.

#### 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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Titanosuchidae are a group of derived herbivorous, long-snouted dinocephalians currently only known from the South African Karoo Supergroup. This project, focused on the taxonomic revision of the titanosuchids, enabled, for the first time, the recognition of only two genera each represented by a single species. These are *Titanosuchus ferox* and *Jonkeria truculenta*. Previously recognised Jonkeria species, J. vanderbyli, J. ingens, J. haughtoni, J. parva, J. rossouwi and J. boonstrai, are here, synonymized with J. truculenta. The species J.koupensis is a nomen dubium only identified as Titanosuchid indet. Cranial characters, which modified during ontogenetic development, were recognized, and for the first time, an ontogenetic growth series is presented for Jonkeria. The project also produced a phylogenetic analysis of the two titanosuchid taxa with their deuterosaurid, estemmenosuchid, anteosaurid, styracocephalid and tapinocephalid counterparts confirming the sister group relationship between Styracocephalidae, Estemmenosuchidae, Titanosuchidae and Tapinocephalidae. This phylogenetic analysis manifests a long ghost lineage extending over most of the Guadalupian. The first extensive stratigraphic analysis of the Titanosuchidae shows that the South African Karoo Supergroup hosts both genera in the upper levels of the Abrahamskraal Formation (Moordenaars Member) with a single specimen (Titanosuchid indet) recovered in the lower levels of the overlying Poortjie Member of the Teekloof Formation.

### Spiriferids and SQL statements: databasing lessons learned from the CGS palaeontology collections at Bellville

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Institutional palaeontology collections are valuable repositories for natural heritage objects and are important resources for biostratigraphic, evolutionary and palaeo-environmental studies. Functional management of the metadata associated with these heritage objects is a basic yet essential curation practice. Modern digital databasing systems are a powerful tool for managing and conserving collections metadata, especially when these databases are tailored to the requirements of specific collections. In its efforts to curate South African geoscientific information, the Council for Geoscience (CGS) has developed an MS Access based relational database tailored specifically to the palaeontology collections housed at the CGS Bellville Regional Office. The database comprises data associated with approximately 20000 specimens from this small yet diverse collection and relates them to other geoscientific datasets through SQL-based field relationships. The use of Access SQL as the main database coding language allows for complex query building and cross-platform compatibility to Specify, Oracle, and MySQL. This enables easy integration with other institutional databases and compatibility with multiple GIS software packages such as ArcMap and QGIS. MS Access form builders and VBA coding were used to create custom database interfaces for easy data querying and capturing. Furthermore, the built-in interfaces and query structures allow users to graphically track various metrics including the geographic, stratigraphic, and taxonomic representation of the collection. Access to data and database functions is controlled through multilevel security protocols, thereby securing sensitive data and unauthorized data editing. Finally, long-term data conservation is achieved through automated backup processes to remote server locations. This database represents a useful collection management tool that will be used to curate the historic CGS palaeontology collections according to local and international best practices. Ultimately, this will enable the CGS to be a continued resource for palaeoscientific information whilst ensuring the long-term conservation and development of our incredible palaeoheritage.

### Palaeoclimatic signatures of southern Africa Permo–Triassic fossil woods

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The rocks of the Karoo Basin hold great value in Southern Hemisphere palaeoenvironmental studies due to the extensive and almost uninterrupted fossil record that they host, along with the important palae-ecological and climatic events that they archived (e.g., the end-Permian Mass Extinction, progressive warming from Carboniferous to Triassic). Karoo palaeoenvironmental studies have rarely focused on the palaeoclimatic signatures of fossil woods, choosing to use stratigraphy, vertebrate fossils, macrofloral fossils and palynomorphs as their proxies. This study will focus on the palaeoclimatic signatures of the Permian-Triassic southern African fossil woods found in Mozambique, Namibia, South Africa, Zambia, and Zimbabwe. These palaeoclimatic signatures will be used to create a robust late Permian to Early Triassic palaeoclimatic reconstruction for southern Africa. Each fossil wood sample will undergo a comprehensive growth ring analysis for determining the trees' habits, seasonality of the past climate, favourability of the growing conditions, occurrence of environmental stresses and extreme climate conditions. Along with the growth ring analysis, the following parameters will be calculated for each fossil wood sample (i.e., each represented tree): vulnerability index, mesomorphy ratio, conductivity capability and estimated tree height. Preliminary growth ring analysis results of the South African fossil woods will be presented.

#### A new specimen of *Hewittia albanensis* (Brink 1958) from Cradock, Eastern Cape, South Africa

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Therocephalia is an extinct suborder of synapsids and is currently accepted as the sister taxon to the cynodonts that gave rise to modern mammals. This close relationship means that the origin of several characteristics that are now used to define the order Mammalia can be studied in Therocephalia that lived across Pangea (e.g., southern Africa, China, Russia and Antarctica) during the Permo-Triassic. The most famous region of these fossil occurrences is the main Karoo Basin of South Africa. Hewittia albanensis (Brink 1958) was first described based on a skull that was missing its braincase. Due to various reasons, *H. albanensis* has been largely ignored in subsequent research. The first aim of this project was to describe a new specimen that is attributed to H. albanensis and was collected from the mudstones of the late Permian Daptocephalus Assemblage Zone (c. 255.2– 252 Ma) southeast of Cradock. The new description used non-destructive techniques including illustrations, µ-CT scanning, and digital visualization, including digital 3D models of the skull. The µ-CT scanning and the visualization of the scans were conducted at the RADTOM Department of NECSA at Pelindaba and the 3D models were generated in VG Studio. Using the original fossil remains and digital 3D models, comparative studies were conducted on other closely related therocephalian fossils that are curated at various institutions. The new specimen can be confirmed as *H. albanensis* based on the generic diagnosis by Brink with just a couple of proposed changes. Having successfully completed the first aim by attributing the newly described skull to H. albanensis, further work will be conducted on the braincase and the taxonomic revision of the group using phylogenetic analyses.

### New gorgonopsian species from the middle Permian of South Africa supports early radiation of Gorgonopsia (Therapsida, Synapsida)

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Gorgonopsia is an iconic group of carnivorous synapsids known from the middle and late Permian. They were the dominant predator in the late Permian, whereas in the middle Permian, only two species are recognised, namely Eriphostoma microdon (with many species synonymised to it) and the recently described Phorcys dubei. These two species differ by their relative size, with Eriphostoma being small (i.e., dog-sized), and Phorcys being the largest known middle Permian gorgonopsian (comparable to some large late Permian taxa). This complicates the understanding of the Gorgonopsia body size evolution and suggests that the ecological niche of the middle Permian gorgonopsians overlapped with that of basal therocephalians. The recent discovery of a new gorgonopsian specimen from the lower Abrahamskraal Formation, much larger than Eriphostoma, but twice as small as *Phorcys*, adds to this diversity of middle Permian gorgonopsians. The specimen BP/1/8260 is a complete skull with an articulated lower jaw and arguably does not belong to any previously known gorgonopsian species. Moreover, its strongly laterally compressed dentition, particularly the caniniforms, contrasts sharply with most other gorgonopsians and suggests a hypercarnivorous diet. This supports the hypothesis that the middle Permian gorgonopsians were more diverse taxonomically and ecologically than previously thought. Moreover, reassessment using CTscanning of some genera currently synonymised with Eriphostoma suggests that Galesuchus may be resurrected, which would add to this, hitherto unrecognised diversity.

## A new middle Permian Burnetiamorph (Therapsida: Biarmosuchia) from the Karoo

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Biarmosuchia is the most recently recognised major clade of therapsids. They are among the basalmost therapsids and cranial ornamentation is an important feature distinguishing Burnetiamorpha among biarmosuchians. Biarmosuchian phylogeny has recently become contentious, especially the internal relationship of burnetiamorphs. A new burnetiamorph biarmosuchian (SAM-PK-12118A) from the Abrahamskraal Formation (Beaufort Group) in middle Permian of South Africa shows an almost complete snout preserved in three-dimensions but limited to the pre-orbital region. This specimen originated from the Diictodon-Styracocephalus subzone of the Tapinocephalus Assemblage Zone (c. 261 Ma), a subzone known for its relative scarcity of Biarmosuchia (only 2% of the fauna). To place this new specimen among the middle Permian burnetiamorphs of South Africa, it has been compared to the holotype Bullacephalus (BP/1/5735), Pachydectes (BP/1/5387), Lemurosaurus (BP/1/816), and Lende Chiweta (MAL 290). The phylogenetic relationship of biarmosuchians is assessed using cladistic analyses carried out on the pre-existing character matrices. The character scoring is updated using Mesquite and TNT (Tree analysis using New Technology). The hypothesis of this project is that SAM-PK-12118A is a new species of the middle Permian Burnetiamorpha and the addition of this specimen to pre-existing phylogenetic analyses will refine the phylogeny of burnetiamorphs and incidentally, the origin of mammals. This specimen has the potential to solve the controversy about burnetiamorph relationships, expand the middle Permian fossil record of burnetiamorphs, and shed some new light on the middle Permian ecosystems.

#### TimeTripSA a travelling exhibition marketing geoheritage in South Africa Ian J. McKay<sup>1,2</sup> \*

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South Africa's extraordinary geoheritage wealth has globally significant, geological, paleontological, geomorphological, and related cultural significance. The geoheritage sites are often situated in beautiful landscapes and cover a time-period of 3.6 Ga ranging from life's origins to human origins. In South Africa, the concept of conservation is intimately linked to the need for public participation and engagement and is essential for creating awareness of/and support for preserving our geoheritage wealth. Stimulating public engagement requires the creation of geoheritage experiences in visitors' centres, guided and self-guided tours and museum exhibitions. In turn, these create jobs that grow the local and national economy and stimulate museum visitorship. Even before the Covid-19 pandemic, however, it was clear the geoheritage industry was struggling to attract visitors and provide sustainable and meaningful employment. The TimeTripSA project aims to market geoheritage by designing several A0 geoheritage posters. The posters create interest by using striking images and, where relevant, recreate for visitors, the experience of being present in the past as events at that site unfolded. They also describe the excitement of the geoheritage experience and other tourist attractions in the area. The posters were made in collaboration with subject experts and efforts were made in providing technically correct descriptions while keeping the text exciting and attractive for the public. Ten more posters are planned, and good progress is being made with a complimentary website. The target audience is families, and the aim is to encourage them to take a week's holiday to participate in the geoheritage experience. The TimeTripSA project is especially beneficial for geoheritage sites in remote locations and will be showcased during tourism industry events (e.g., as an exhibit at "Tourism Indaba").

### You cannot judge a turd by its cover: micro-CT characterization of South African Early Triassic coprolites

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Direct evidence for trophic interactions and feeding behaviour rare in the fossil record. Coprolites, fossilised faeces, are one of the few fossils that document these interactions and behaviours and can thus provide unparalleled insight into palaeoecology. In addition to trophic interactions and feeding behaviour, coprolites provide direct information on the diet, parasitism, and digestive systems of extinct organisms. Moreover, because coprolites can selectively preserve the remains of tiny prey items, like arthropods and microvertebrates, they address specific taphonomic and taxonomic deficiencies in the fossil record. Surprisingly, coprolites remain understudied, despite their potential utility in reconstructing ancient ecosystems. The farm Driefontein 11, a fossiliferous Early Triassic locality in Free State, has yielded an exceptional collection of coprolites, currently estimated to exceed 30000 specimens. We provide a preliminary report, based on non-destructive microtomography (micro-CT), on the coprofabrics and contents of ~ 50 coprolites from this collection. Fish remains (scales, teeth, unidentified skeletal fragments) are the most common inclusions found in the coprolites. Other significant inclusions are bivalve molluscs and represent the second occurrence of freshwater bivalves of any kind in the Early Triassic of southern Africa. Terrestrial vertebrate remains, notably jaws and other postcranial fragments, are sporadically present. These coprolites represent the leavings of vertebrates inhabiting terrestrial and freshwater ecosystems that developed in the wake of the end-Permian Mass Extinction and are therefore a key component of understanding how trophic networks respond to biodiversity crises.

### South Africa's earliest giant: systematics and palaeobiology of a new species of sauropodomorph

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The Elliot Formation (EF) of South Africa preserves a diverse archosauromorph fossil record spanning the Late Triassic to Early Jurassic. The most common dinosaurian clade preserved within the EF are sauropodomorphs, with representative taxa displaying a range of body sizes and postures. However, the lower EF (LEF; Upper Triassic) is depauperate in well-provenanced and skeletally, wellrepresented sauropodomorph specimens in comparison to the upper EF (UEF; Lower Jurassic). This discrepancy contributes to global issues in studying taxonomy, phylogeny, and evolution of early Sauropodomorpha. A quarry discovered in 2016, by a local shepherd in Qhemegha, Eastern Cape, provides LEF sauropodomorph specimens that can assist in addressing this issue. Here, we present the anatomy and systematics of an associated postcranial skeleton on one of these sauropodomorphs, BP/1/8469. Comparative anatomy and phylogenetic analyses suggest that this specimen is a new lessemsaurid with a unique combination of plesiomorphic and derived features. Osteohistological analysis of the femur suggests an animal approaching adulthood and indicate growth patterns similar to other large-bodied sauropodomorphs such as Ledumahadi. Estimates of body mass and posture for BP/1/8469 using recently developed methods indicate a 2.6-tonne quadrupedal sauropodomorph. This specimen confirms the presence of gigantic lessemsaurids in both South America and South Africa during the Norian, supporting the hypothesis that postural experimentation and gigantism preceded the end-Triassic Extinction Event. It provides critical anatomical and biostratigraphic information needed for addressing the historical shortage of specimens from the LEF.

### From grains to tracks: role of substrate on morphological preservation quality of dinosaur tracks (Stormberg Group, southern Africa)

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Footprints result from the interaction between the animal's foot and the sediment conditions in which the tracks are formed. For example, difference in sediment grain size (e.g., mud vs coarsegrained sand) and water content often cause dramatic variations in track morphology from high to extremely low anatomical fidelity. The upper Stormberg Group of the main Karoo Basin in South Africa and Lesotho is rich in Triassic–Jurassic dinosaur tracks, and the highly variable abundance and anatomical fidelity of the tracks between and within ichnosites are well documented. To quantify the role of substrate in the track preservation potential and morphological quality at selected ichnosites, we examine the petrographic properties (e.g., grain size, grain shape, composition) of the host sedimentary rock to complement the established macro-sedimentary observations. Our preliminary findings suggest that from the Upper Triassic lower Elliot to the Lower Jurassic Clarens formations the: (1) maximum and average grain size decreases; (2) grain roundness increases; (3) morphological quality increases (i.e., tracks have higher anatomical fidelity in substrates with finer, more rounded grains). Some of these trends fit well with the earlier interpretation of changing palaeoenvironments in the investigated stratigraphic interval. This, in addition to a boom in dinosaur populations, could explain the increase in track and tracksite abundance across the Triassic–Jurassic boundary, however quantifying the role of the substrate on track registration and preservation can facilitate disentangling the apparent from real macro-evolutionary trends.

### Intensive re-curation: A case study on the faunule at the CGS Bellville regional office

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The palaeontological collections of the Council for Geoscience (CGS) at the Bellville Regional Office are a stratigraphic reference collection with taxa present from virtually all known fossil-bearing stratigraphic units in South Africa. These range from the Ediacaran (Nama/Vanryhnsdorp Group trace fossils) to Palaeozoic fossils from the Cape and Karoo supergroups. The collection is associated with catalogue books, miscellaneous documents as well as several figured and/or mentioned specimens in peer-reviewed publications. There is unfortunately little indication of the true extent of this collection owing to its apparent dormancy. Effective management of this and similar collections are obligatory for the CGS, requiring that procedures are put in place to curate these unique resources, in line with both national and international standards. Curation efforts began in earnest in 2020 with the implementation of a three-phase approach that includes: (1) the migration of analogue to digital datasets; (2) auditing and verification of all specimens including updating fossil descriptions, and (3) the construction of an interlaced and integrated database of all fossils in the repository. Efforts by previous staff in the well-documented storage map assists greatly in the verification phase. To date, these methods have resulted in the creation of relational datasets that can be integrated with standing CGS databases, maps as well as faunal lists. During this ongoing process, numerous type and figured specimens, including one culturally significant specimen that was thought to be lost, have been "rediscovered" in the collection. The palaeontology team continues to generate management documents to ensure the continued safeguarding of this collection so that the CGS achieves and maintains its mandate as the custodian of all geoscientific information in South Africa whilst enabling geoscientific research. The prominence of this seemingly small collection as scientific and heritage resource is only just about to emerge.

#### Geomorphology, sedimentology and preliminary radioisotopic age of Middle Pleistocene termitaria near Calitzdorp, South Africa

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Termites are keystone organisms, capable of modifying the physical structure of the landscape and recycling important soil nutrients. Their soft bodies are not commonly preserved in the fossil record and often the only evidence of their existence are their intricate nest structures. In Calitzdorp, Western Cape, eight interconnected fossil termite nests (termitaria) are described, which may represent a new ichnogenus and potentially records the presence of a termite species that is now locally extinct. The sediments that host the termitaria have not been previously studied in detail, nor dated, and therefore the termitaria lack geological constraints. In this on-going research, we describe the geomorphological and sedimentological contexts of the fossil termitaria and provide preliminary uranium-series radioisotopic age constraints on their construction. By building a digital elevation model (DEM) using an aerial photograph database and undertaking field investigations, we show that the termitaria are situated on an alluvial terrace along the Gamka River within calcified gravel-rich palaeo-soils. The fluvial terrace and associated deposits are exposed elsewhere in the vicinity, which aids future prospecting efforts. Both the alluvial host sediments and the termitaria themselves are strongly affected by secondary pedogenic carbonate precipitation that solidifies the nest structures, enhancing their preservation. A geochemical pre-screening procedure was followed using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) to identify high U/Th carbonate layers suitable for uranium-series dating. Subsequently, selected layers were hand-drilled and dated using solution multi-collector inductively coupled mass spectrometry (MC-ICP-MS). Preliminary results indicate that the carbonates formed in the Middle Pleistocene (Chibanian), around 320 ka, which provide a tentative minimum age constraint for the construction of the nests and carbonate precipitation. This research exemplifies the usefulness of multi-disciplinary methods when studying the largely overlooked Quaternary geology and ichnology of the Western Cape.

#### Diet of Early Triassic therocephalian *Olivierosuchus parringtoni* revealed by fossil stomach contents: implications for habitat and feeding behaviour in a post-extinction ecosystem

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Two specimens of Early Triassic therocephalian *Olivierosuchus parringtoni* present masses in the abdominal region. The anatomical position of the mass, tooth marks and acid degradation observed on the surface of bone elements support the interpretation of the mass as stomach contents. Fossilised stomach contents are rare in the fossil record and fundamentally provide direct information about the ecology of ancient organisms. Analysis of the stomach contents reveals vertebrate matter, including bone elements conceivably belonging to a procolophonid reptile and other bone elements that could not be identified to species level due to their advanced degradation. For the first time, the diet of an Early Triassic therocephalian is inferred from direct evidence and a possible prey species is identified. The body mass of the identified prey is only 3% of the therocephalian's body mass. This compared to modern animals of approximately the same mass is low. At least two feeding events were identified in each therocephalian as different elements were degraded to different levels. This pattern is not observed in their modern analogues, instead complete digestion will occur before the next meal. Both these observations reinforce the harsh environmental conditions after the end-Permian Mass Extinction.

### Insight into the morphological disparity in the rarely preserved soft tissue portion of antiarch placoderm fish, *Bothriolepis africana*

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The loss of squamation on the tail has been hypothesized to have occurred in multiple placoderm lineages, including antiarch placoderms. Placoderm fossils are the most commonly preserved early vertebrate remains in most Devonian deposits, because of their robust cephalic and trunk armour, preserved either articulated or, more commonly, as disarticulated plates. Placoderm range in size from a few mm to over 6 m in length, and although the head and trunk are often fossilized, the tails of placoderm fish are rarely preserved. Placoderm fossils from the Late Devonian (late Famennian) Waterloo Farm Lagerstätte (Eastern Cape Province, South Africa) include remains of several placoderm taxa. Exhibiting exceptional preservation including soft tissue impressions, these rare fossils are represented by micaceous minerals, partially altered to clay. Caudal fin and epidermal impressions are present in three juvenile Bothriolepis africana (antiarch placoderm fish) specimens. Only two other species of Bothriolepis are known to have exceptional tail impressions. These are B. canadensis, from the Late Devonian Frasnian deposit at Miguasha, and B. gibbslandiensis, from the Frasnian deposit at Mt Howitt, Victoria. Tails of both above-mentioned taxa evidence soft tissue morphology different from that of B. africana. B. gibbslandiensis has squamation on the tail with a spine-bearing dorsal fin, whereas B. canadensis has a naked tail with an elongated dorsal fin. The tail morphology of the latter is similar to B. africana, however, the dorsal fin of B. africana is low and rounded. The current revision of B. africana and its subsequent inclusion in a phylogenetic matrix will reveal the relationships between these three species, thereby shedding light on the sequence of character acquisition in antiarch placoderms.

### The completeness of the fluvial record: a case study from Old Lootsberg Pass

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The Beaufort Group of the Karoo Supergroup (South Africa) provides an unrivalled record of the evolution of life in the continental realm from the middle Permian to the Middle Triassic. It is generally considered to represent a relatively continuous record across this time interval. While most likely an appropriate description at coarse scale, little data exists on the completeness of the sedimentary record for shorter stratigraphic intervals. Fluvial depositional systems, more so than other sedimentary systems, are known not only to represent periods of sediment accumulation, but also capture long periods of stasis and erosional events. Yet the temporal relationships between these processes are difficult to quantify in deep time. While some efforts have been made to calculate the time captured by fluvial sediments through the application of crudely estimated accretion rates, these attempts are, by necessity, dependent on multiple assumptions and suffer from an absence of empirical data. Any attempt to quantify the completeness of the stratigraphic record requires a high-resolution dataset that utilises all available sources of data. Such a dataset has been established during a recent high-resolution stratigraphic investigation at Old Lootsberg Pass in the Eastern Cape Province. Here, a stratigraphic framework was established based on the detailed sedimentological logging of > 850 m of rock record, obtained from twelve, physically correlated localities, across a distance of > 4 km. This framework was placed into a magnetostratigraphic context and constrained by U-Pb ID-TIMS radioisotopic dating. The integrated dataset represents the best proxy to-date for the completeness of the sedimentary record for shorter stratigraphic intervals in this critical part of the Beaufort Group that is renowned for containing evidence for the end-Permian Mass Extinction.

#### Fossil wood diversity from Karoo-equivalent sites of Mozambique

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Discoveries of fossil wood from Mozambique date back to the 1800s, and samples were collected during various expeditions of the Geological Survey in Mozambique. For example, Dadoxylon nicoli (Silva et al. 1967), which is now in invalid name, was the first Karoo-aged fossil wood identified in Mozambigue. Subsequently, Australoxylon teixeirae (Marguerier 1973) and Zalesskioxylon zambesiensis (Maithy 1977) were also described and later amended to Australoxylon zalesskioxylon. More recent studies revealed that Agathoxylon is the most abundant fossil wood genus of Karoo age in Mozambique, as it is in the main Karoo Basin of South Africa. The two species of Agathoxylon (A. africanum, A. karooensis) are found in the Upper Karoo of Mozambique and are differentiated by having mostly biseriate or triseriate tracheid radial pitting, respectively. The fossil wood diversity increases with Australoxylon teixeirae, a taxon with irregular radial pitting, being identified for the first time in Mozambique. Other wood taxa, such as Prototaxoxylon uniseriale and P. africanum characterised by spiral thickening, also appear for the first time in the Karoo-aged formations of Mozambique. Even more remarkable is the novel occurrence of two new Prototaxoxylon species in the Mozambican Karoo, namely P. metangulense and P. verniersi. These taxa are mainly characterised by mixed radial pitting and taxodioid pits in the cross fields. This study presents the implication of these Mozambican fossil wood taxa for the Karoo-age palaeogeography of southern Africa.

## Using X-ray microtomography to determine the number of upper canines in the smallest individuals of *Thrinaxodon liorhinus* (Therapsida, Cynodontia)

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Utilisation of X-ray microtomography (µCT) to study Karoo fossils has allowed for novel information to be obtained from re-analysing specimens that were described several decades ago. One of the main findings from these studies was that canine replacement in Galesaurus and Cynosaurus seemingly ceased with the attainment of maturity, whereas replacement continued well into adulthood in *Thrinaxodon*. Additionally, the functional and replacement upper canines in juvenile and subadult specimens of Cynosaurus were positioned in a manner suggesting the presence of double canines in the maxilla. The presence of two canines in the maxilla is assumed to be the ancestral condition for cynodonts, as it is present in basal synapsids (e.g., sphenacodont pelycosaurs), basal therapsids (e.g., Raranimus), Gorgonopsia, and lycosuchid therocephalians. The presence of paired upper canines has previously been hypothesised in the smallest individuals of Thrinaxodon, but none of these specimens have previously been subjected to µCT-scanning. For this study, we expanded the previous sample (n = 5) of  $\mu$ CT-scanned individuals of *Thrinaxodon* to include three of the smallest 'early juveniles', and an additional juvenile specimen that shows the unusual condition of the replacement upper canine erupting distal to the functional canine. We found that the early juvenile specimens of Thrinaxodon had two replacement canines developing simultaneously—a small replacement lingual to the functional canine, and a second more developed replacement distal to the functional canine. This condition closely resembles that described in lycosuchid therocephalians, supporting the hypothesis that paired upper canines were plesiomorphic in Cynodontia.

### The evolutionary origins of the trunk in Proboscidea (Mammalia, Afrotheria) based on osteology

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The proboscideans originated in the late Paleogene of the Afro-Arabian landscape, and are named after their single-most diagnostic feature, the trunk. The elephant trunk is composed of soft-tissue, and is not readily preserved in the fossil record. To date, no quantitative assessment of the evolution of the trunk in elephant ancestors has been undertaken, and there is no systematic approach for determining whether a trunk was present or not in fossil species. This study aims at quantifying the dimensions of the infraorbital canal (volume and surface area of the infraorbital foramen) and retraction of the naris, to test how these metrics correlate with the dimensions of the nose/trunk in some selected modern mammals, and apply these assessments to the fossil record to determine the evolutionary origin(s) of the trunk in Proboscidea. The gross morphology of the infraorbital canal in mammals is described in detail for the first time. The results indicate that there is a significant and strong correlation between the surface area of the infraorbital foramen and the dimensions of the snout. There is no correlation between the degree of narial retraction and dimension of the snout in extant taxa. The application to fossils suggests that among basal proboscideans, Numidotherium had a trunk shorter than that of a tapir, and Deinotherium possessed a more tapir-like trunk. Gomphotheres, Anancus and Palaeoloxodon had an elephant-like trunk. The trunk did not originate as a single event at the root of Proboscidea but rather resulted from a long evolution that spanned the proboscidean phylogenetic tree for at least 60 Ma, between the last common ancestor of Proboscidea and that of Sirenia.

#### Some aspects of micropalaeontology in South Africa

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Microfossils are an essential biostratigraphic tool due to their small size, widespread distribution, rapid evolution and abundance in rocks. Many groups of microfossils – calcareous, siliceous, phosphatic or organic-walled - are crucial for high resolution biostratigraphy of various time intervals and types of sedimentary rocks. Moreover, microfossils are instrumental for reconstructing depositional history of sedimentary basins, palaeoenvironments, past climates and even sedimentary ores. Yet, the full potential of microfossils is underutilized in South Africa. Calcareous nannofossils, or calcareous nannoplankton, have been proved particularly helpful in resolving some key geoscientific problems. The analysis of nannofossil assemblages from a core retrieved from the Durban Bight facilitated reconstruction of the late Holocene shoreface evolution over the last 250-300 years, pointing to fluctuations in nutrient supply and sea water temperatures driven by the Agulhas Current and by flood and storm events. Calcareous nannofossils from cores or encrustations of manganese nodules dredged at the Mozambique Ridge and in the Mozambique Basin allowed to establish the age of samples, as well as the mode of Fe-Mn oxide precipitation rates in the basin, with far reaching implications for palaeo-oceanography. Nannofossil dating suggested bi-modal ages for the samples, the late Zanclean–Piacenzian (Pliocene) and the Calabrian (Pleistocene)–Holocene. The calculated rates of manganese precipitation range from 4.7 to 248.3 mm/Ma, which are mostly typical for hydrothermal manganese accretion. The Pliocene manganese precipitation may reflect the closing of the Panama Isthmus, while the terminal Pleistocene–Holocene accretion may result from oceanic fluctuations caused by glacial and interglacial periods. Calcareous nannofossils identified in phosphate samples dredged offshore Ggeberha (previously Port Elizabeth) help constrain the genesis and ages of the phosphorites along the south-eastern African margin. Calcareous nannofossil dating suggests that the samples are Bartonian-Priabonian (Middle-Late Eocene) and Calabrian (Pleistocene)-Holocene.

#### The rise and fall of the Malvinoxhosan (Malvinokaffric) bioregion: Evidence for Early-Middle Devonian biocrises at the South Pole

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The Devonian Period is punctuated by numerous biocrises (extinctions; turnovers), intimately intertwined against a backdrop of bioevents and revolutions (colonization of land, 'Age of Fishes', Nektonic Revolution). These events mediated feedback loops that forever changed terrestrial and aquatic ecosystems. Most of our knowledge of Devonian bioevents and biocrises are disproportionately known from low-intermediate latitudes (30-60°) with little recorded from high (polar) latitudes (60–90°). South Africa is advantageous in understanding high-latitude regions as it comprises a relatively complete and fossiliferous record for most of the Devonian, represented by the uppermost Table Mountain, Bokkeveld, and lower Witteberg groups. Fauna of the Malvinoxhosan (Malvinokaffric) bioregion included South Africa, as well as most of West Gondwana, during the Early–Middle Devonian and are the focus of this study. The rise and fall of this lowdiversity, endemic marine fauna is largely undocumented seemingly correlating with changes in sealevel and global temperature. Biostratigraphic data from publications as well as from collections at the Council for Geoscience and Iziko SA Museum suggest that this bioregion persisted as a cohesive unit during Rietvlei-Baviaanskloof to Waboomberg depositional phases. Few endemic faunas continued during the deposition of the upper Bokkeveld and Witteberg groups, disappearing entirely by the deposition of the Blinkberg Formation. A stepped decline in diversity with little origination of new taxa is observed, correlating with third-order sea-level changes. Trace fossil assemblages also change from diverse to disparate in post-Waboomberg strata. A trend in epifaunal and semi-infaunal taxa and behaviours being disproportionately affected with respect to infaunal, deep infaunal and nektonic taxa is observed not only in South Africa, but also in the age-equivalent strata of South America. Although a linkage between sea-level changes and fauna decline is noted, there is no obvious temporal change in the palaeo-environment. This suggests that the extinction mechanism is complex and can be possibly linked to sea-level changes.

### Comparative palaeohistological analysis of extant and extinct samples of *Rhea americana* (Linnaeus, 1758)

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Osteohistology is a reliable source of information to elucidate important aspects of vertebrate biology, including life history, growth rates and longevity. Bone microstructure in modern species, supported by biological information (anatomical and ecological), is the framework to evaluate fossil taxa. In order to recognize the morphological transformations throughout the ontogeny of Rhea americana (Linnaeus, 1758), a comparative osteohistological analysis of extant and extinct specimens was carried out. For this purpose, thin-sections of postcranial bones of fossil and modern specimens of *R. americana* were performed. The fossil samples came from different Argentine localities of Upper Pleistocene–Lower Holocene and Miocene and are housed in the paleontological collection of Museo de La Plata and Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina. Extant specimens were a priori assigned to different ontogenetic stages based on their maximum length and the degree of bone fusion (published data). Transverse crosssections of the sample here studied revealed the cortex formed by highly vascularized fibrolamellar bone. The vascular canals are organized in primary osteons and arranged in laminar, plexiform, longitudinal, radial, and reticular patterns. Throughout ontogeny, an increase in the organization of intrinsic fibers, a decrease of the vascularization, and an increase of the secondary remodelling were observed. These results suggest a similar osteohistology in both fossil and modern forms and showed a fast growth rate at the first ontogenetic stages that decreases as the individuals grow. The variation of the bone microstructure observed in the extant sample allows to identify the ontogenetic stage of the fossil specimens. For all the cases, the inferences made from osteohistology was consistent with the osteological information derived from published data. In this way, the bone microstructure applied to modern specimens provides valuable information for the determination of ontogenetic stages in fossil remains.

### Phylogenetic ancestral character state reconstruction using maximum likelihood of hominin encephalization

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Unravelling the evolutionary pattern that characterizes hominin brain evolution is critical for understanding what is neurologically distinctive about modern humans and what cognitive underpinnings humans share with their ancestors and relatives. Studies on the evolution of human brain have long focused on brain size changes and contributed to support the hypothesis of a gradual size increase over human evolutionary history. Due to recent discoveries of relatively lateappearing small-brained hominin species, such as Homo floresiensis and Homo naledi, this view is no longer tenable. Here we propose to use a phylogenetic approach to provide a robust framework for the inclusion of outliers in the study of human brain size evolution. Six cladistic hypotheses were time-calibrated and subjected to phylogenetically controlled statistical tests to obtain the most likely tree given the data and brain and body mass evolution. We considered Lambda, Brownian Motion, Ornstein Uhlenbeck, and ordinary least squares as candidate model structures, using Akaike information model selection criterion. Then, we investigated changes in the tempo of hominin brain evolution by subjecting the best fitting hypothesis to maximum likelihood and Markov-chain Monte Carlo rate shift tests. Finally, we performed an ancestral character state reconstruction of absolute brain mass, encephalisation quotient (EQ) and body mass to interpret the pattern of changes that occurred during hominin brain evolution. The results of the ancestral character state reconstruction on brain size, body size, and EQ show general plasticity of brain mass during the Pleistocene, with decrease in brain size in some small-brained Homo species along with increase in other Homo species. We thus conclude that a phylogenetic framework is best suited for capturing these oscillating changes during the evolution of hominin brain size.

### Dimensions of *Diictodon*: exploring ontogeny and sexual dimorphism with geometric morphometrics

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The South African Karoo Basin is renowned for the abundance and diversity of the Permian dicynodont taxa. Among the most ubiquitous and persistent of these is the small-bodied Diictodon, which is sometimes associated with helical burrows. Associated aggregations of young specimens of Diictodon as well as different sized specimens, including tusked and tuskless forms, spark interest in the reproductive ecology and ontogeny of the species. Here, we revisit the historically confounding issue of intraspecific variation and examine 93 Diictodon crania to investigate the association between cranial shape, size and sexual dimorphism. Using a MicroScribe digitiser, the present study explores dorsal and lateral landmark configurations within the framework of 3-D geometric morphometry. Our results show a significant relationship between shape and allometry, with juveniles having relatively shorter snouts, enlarged orbits, and a wider, more rounded skull profile, while the adult skulls tend to become slenderer, with a longer snout and larger temporal fenestrae. Functionally, these changes in morphology are accounted for by the development of the jaw musculature for feeding on volumetrically larger, tougher material. Non-allometric variation between tusked and tuskless specimens was found to be negligible but a marked difference is observed between allometries, expressed in the variable development of the caniniform process. Despite this, a large component of non-allometric variation still cannot be accounted for, and our analysis suggests that this likely represents natural population variation rather than being an artefact of taphonomic deformation. This study of Diictodon is an example of how advances in the digitisation of morphological data have enabled historical palaeobiological questions to be revisited and explored with better resolution, and how current research in the field of geometric morphometrics continues to highlight new avenues for improvement and innovation.

# Exploring the Dinosaur Cave: palaeoecological implications of unique footprints in the Lower Jurassic Clarens Formation of the Maloti-Drakensberg

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Vertebrate tracks are considered rich archives of palaeoenvironmental and palaeoecological information, yet palaeontological attention in southern Africa has primarily focused on the vertebrate body fossils. This is despite the fact that the first fossil footprints ever reported in Sub-Saharan Africa were described as early as 1885 from the Lower Jurassic Clarens Formation at Morija in Lesotho. A cliff-forming sandstone-dominated succession across southern Africa, the Clarens Formation was deposited in the prevailing southern Gondwanan aeolian system c. 192–183 Ma ago. The Formation preserves a diverse faunal record, including remains of sauropodomorphs, ornithischians and crocodylomorphs, but is still considered body fossil scarce. In contrast, fossil footprints are more abundantly preserved in the Clarens strata but are characterized by a low ichnodiversity, almost exclusively dominated by theropod tracks. Herein, we report the findings of a unique and diverse dinosaur track site from the Clarens Formation in the scenic Maloti-Drakensberg mountains of KwaZulu-Natal in eastern South Africa. The footprints are preserved as true tracks on sandstone blocks that are shielded from weathering in a rock shelter, aptly named 'Dinosaur Cave'. Over 60 tracks, comprising several trackways, were identified and assigned to five distinct morphotypes attributable to theropod, sauropodomorph and guadrupedal ornithischian trackmakers. Additionally, footprints of a large biped (track length ~ 39 cm) are tentatively assigned to a new ichnogenus and provisionally attributed to a large ornithischian, currently not represented in the skeletal record of the upper Karoo Supergroup in southern Africa. Although this new ichnogenus shares resemblance to other large ornithischian tracks from the Lower-Middle Jurassic of China and Poland, it lacks manus impressions and is much larger in comparison. Ultimately, the Dinosaur Cave footprint site not only presents a diverse dinosaur-dominated ecosystem but also provides new insight into the palaeogeographical and palaeoecological distribution and evolution of bipedal ornithischians in the Early Jurassic of southern Gondwana.

#### Grass phytoliths from Pliocene terrace sediments of the Sand River, Free State Province, South Africa

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This study pertains to the grass silica short-cell phytolith content of a fossil bearing, ~ 40 m alluvial terrace on the Sand River in the Free State Province. Phytoliths were extracted from river-deposited sediments that represent the only well-documented, late Neogene locality in the province. Results based on several phytolith indices offer an independent record of early Pliocene climatic conditions in the central interior of southern Africa.

### Establishing a Karoo palaeontological research, exhibition and outreach centre

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Knowledge of the paleontological wealth of the Karoo is the result of more than a century of work by scientists and amateurs, resulting in curated fossil collections that form the backbone of Karoo paleontological research. The Rubidge fossil collection, amassed through the enthusiasm of farmer Sidney Rubidge with the help of Robert Broom, Croonie Kitching and his sons (James, Ben and Scheepers), is one of South Africa's pioneering Karoo fossil collections. Since inception, the collection has been on the farm Wellwood, Graaff-Reinet and is visited by scientists and the public. This collection resulted from the question "Daddy, what are fossils?" posed to Sidney Rubidge in 1934, by his ten-year-old daughter Peggy. In response, Sidney took his family on a picnic to rocky outcrops. This resulted in the discovery of a large gorgonopsian skull, which was described as a new species by Broom, then at the Transvaal Museum. He encouraged Sidney Rubidge to collect more fossils and a productive partnership began with Rubidge collecting the fossils and Broom undertaking the scientific description. To utilize this collection for societal benefit, it will be relocated to Graaff-Reinet to form the nucleus of a self-supporting Karoo-based palaeontological centre. The business is being set up, and the centre will operate on four fronts: (1) Research - with national and international research collaborations and running field-based research programmes for scientists and students; (2) Display and exhibition - showcasing the collection with the message to preserve biodiversity and to encourage young people into a scientific career; (3) Palaeotourism - giving visitors the opportunity to experience the thrill of "finding" a fossil in the field; and (4) Educational outreach - offering curriculum-based scientific programmes to learners. This undertaking will be in collaboration with the University of the Witwatersrand and partnerships with other organisations are encouraged.

### Dinosaur body size evolution across the Triassic–Jurassic boundary: insights from South Africa's Elliot Formation

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The end-Triassic Extinction Event (ETE) took place c. 201 Ma ago and was triggered by the breakup of the supercontinent Pangaea. The Elliot Formation in South Africa's main Karoo Basin is one of the few continental strata with a rich vertebrate fossil record that spans the ETE. Currently, the ETE is hypothesized to lie between the litho- and biostratigraphically distinct lower Elliot (IEF) and upper Elliot (uEF) formations. Ecosystem upheavals from mass extinction events like the ETE may be captured by ecological proxies such as animal body size, e.g., the "Lilliput effect" where extinctions select for smaller body sizes. To examine these effects, we investigated the body-size distribution of dinosaurs across the Elliot Formation by assembling a skeletal measurement dataset of 373 vertebrate specimens (114 from the IEF, 253 from the uEF) from 20 genera. We also collated metadata on geographic occurrences, osteological representation, and taphonomic properties. We inferred masses of individual specimens using skeletal scaling methods, assessed geographical fossil collection biases using spatial autocorrelation metrics, and tested for taphonomic biases. Body-size distribution is generally similar across the Elliot Formation, with more small-bodied than large-bodied taxa being present throughout. However, IEF faunas have lower body-size maxima and mass variance compared to the uEF, where sauropodomorph body-size minima (notably the ~ 500 kg bipedal Massospondylus carinatus) and maxima (the 12-tonne quadruped Ledumahadi mafube) are present. Dinosaur collections in the Elliot Formation are spatially autocorrelated, with some clustering of localities that bear fossils of similar body mass. Our results find no support for a "Lilliput effect" in sauropodomorphs after the ETE, suggesting either that sauropodomorphs were unaffected by it or rebounded rapidly. They also counter anecdotal statements in the literature suggesting IEF taxa are larger than the uEF taxa, and that preservational style reflects temporal changes in palaeoenvironments.

#### Is the pattern of the maxillary canal apomorphic to synapsids?

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Varanopidae have long been classified as part of the basal grade of synapsids called the pelycosaurs. However, there have been some controversies on the position of varanopids in the tetrapod phylogeny. The morphology of the maxillary canal can bring some insight into this debate. As the maxillary canal of varanopids looks like that of other synapsids, this character has been proposed as supporting the position of varanopids among synapsids; however, their similarity could be plesiomorphic for tetrapods. This project documents the morphology of the maxillary canal in nonamniote tetrapods to aid in polarising this character. With the use of digital reconstruction, the condition of the maxillary canal of the amphibian group Temnospondyli (*Lydekkerina huxleyi* and *Lydekkerina* sp.) is compared with those of Diapsida, Synapsida and Varanopidae (*Heleosaurus scholtzi*), to trace the character history of the maxillary canal across tetrapods. The results suggest that the primitive condition of the maxillary canal in tetrapods conforms to the diapsid condition; i.e. it is simple, tubular, and runs horizontal to the dental margin of the maxilla. This supports that the maxillary canal condition shared by varanopids and therapsids (i.e., it is complex and ramified into branches that are homologous with those of the mammalian trigeminal nerve) is synapomorphic, which is consistent with the classification of varanopids among Synapsida.

### The postcranial skeleton of the therocephalians (Synapsida: Therapsida) *Moschorhinus kitchingi* and *Theriognathus microps*

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The Therocephalia are a diverse and widely distributed clade of non-mammalian therapsids that lived from the middle Permian to the Middle Triassic. They are the monophyletic sister-group to the Cynodontia (the therapsid lineage that gave rise to mammals). Importantly, the Therocephalia survived two mass extinction events, the Late Capitanian and the most devastating biotic crisis in Phanerozoic history, the end-Permian Mass Extinction. Although their success is evident through their global distribution, long stratigraphic range, and inferred ecological diversity based on their cranial morphology, their postcranial morphology remains poorly understood. With the aim of providing a modern framework and standard of postcranial descriptions, an extensive morphological and comparative analysis was conducted on the postcranial skeletons on two of the most abundant therocephalians, Moschorhinus and Theriognathus. This study provides novel data on the postcranial morphology of two of the most well-known therocephalians with the results showing the presence of postcranial and ontogenetic variation in postcranial elements of both taxa. The comparison of the postcranial morphology of both taxa with historical and more recent therocephalian descriptions reveals that fundamental limitations in our knowledge of therocephalian postcranial morphology and variation are present. A more detailed assessment investigating the postcranial morphology of multiple therocephalian taxa that span a broad phylogenetic and temporal range is needed to elucidate postcranial trends and phylogenetic relationships within the Therocephalia.

## Long-bone histology of *Melanorosaurus readi*: insights into the growth of a basal Sauropodiforms

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Multiple sauropodomorph dinosaurs have been recovered from the Upper Triassic – Lower Jurassic Elliot and Clarens formations of the Karoo Basin in southern Africa. These dinosaurs are renowned for spanning a range from basal bipedal Sauropodomorpha to more derived quadrupedal forms, and thus they provide significant insight into the evolution of the Sauropoda. Specimens of Melanorosaurus readi, the immediate out-group to Sauropoda, are represented amongst these sauropodomorph dinosaurs, and although they have been studied anatomically and taxonomically, their biology is not fully understood. This study assesses the long bone osteohistology of Melanorosaurus to derive information about aspects of its biology, such as ontogenetic status, growth dynamics and intraskeletal variation. Analysis of serial sections of a femur and tibia of Melanorosaurus (NMQR-1551) from Bloemfontein National Museum was conducted. Embedded sections of the bone, originally mounted on Perspex slides, proved highly problematic and were remounted to glass slides using standard petrographic methods. The histology of both long bones are similar but notable differences exist. Both skeletal elements comprise moderately vascularised parallel-fibred bone within the outer to mid-cortical regions, whereas well-vascularised fibrolamellar bone tissue, without any growth marks, dominates the inner cortex. Large resorption cavities occur in the perimedullary regions with secondary osteons commonly located within the inner and mid regions of the compacta. In the outer cortex of both bones, 5–6 lines of arrested growth are visible. The compacta of the femur and tibia differ from one another in a few ways: elongated radial vascular canals traverse large parts of the compacta of the tibia; a distinctive periosteal pathology is evident in the femur along with areas of excessive secondary reconstruction and bone remodelling. Overall, the growth dynamics of *Melanorosaurus* shows more similarity to the more derived Antetonitrus than to basal sauropodomorph dinosaurs such as Massospondylus and Plateosaurus.

#### A re-evaluation of the evolution of diet in terrestrial tetrapods

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"Carnivory" and "herbivory" are end-members of a multidimensional dietary spectrum, spanning varying types and proportions of plant and animal food. Evolution across this spectrum has profoundly impacted the evolution of amniotes and their ecosystems. To examine interactions between position on the dietary spectrum and other life history traits, we compiled new, broadly sampled datasets of diet, body size, and foraging strategy for most extant turtles (268) and lizards (5265), and integrated existing datasets for birds (9993) and mammals (5242). We use cluster analyses of these data to develop new, more nuanced, dietary guilds and existing, large amniote phylogenies to test the following hypotheses and assumptions: (1) the nature of the relationship between body size and dietary strategy; (2) the frequency and prevalent direction of evolutionary transitions between different feeding guilds; (3) the plasticity of feeding strategies (i.e., which dietary guilds most "easily" transition into others, and which tend to specialisation). We find that: (1) increased consumption of vegetative plant structures or carnivory, when considered independently of other variables, have little predictive power for body mass in extant amniotes, though different dietary guilds tend towards different body size optima, (2) transitions into specialized herbivory and carnivory occur more frequently than out of them, (3) feeding strategies involving arthropods are more plastic than other food categories and frequently transition into omnivorous and herbivorous feeding strategies. We compare these findings to an analysis using a dataset of 402 extinct nonmammalian synapsids, with dietary data expressed in a traditional faunivore-omnivore-herbivore classification system. We find that (1) herbivores and carnivores tend to have larger body sizes than omnivores, and (2) that transitions occur in and out of omnivory but not between herbivory and carnivory. By comparing the results of these analyses and their differing resolutions, we find new complexities to the evolution of diet in amniotes.

## Growth history, phylogenetics and taxonomy of a new armoured archosaur from the lower Elliot Formation of South Africa

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The Elliot Formation in the main Karoo Basin of southern Africa has made a significant contribution to vertebrate biostratigraphy across the Triassic–Jurassic interval. The Elliot Formation preserves fossils of most vertebrate lineages, particularly archosaurs in the guise of Dinosauria and Crocodylomorpha. There is strong bias in the distribution of the vertebrate fossils in the Elliot Formation, with dinosaurs being found throughout, and crocodylomorph fossils being so far only found in the Jurassic upper Elliot Formation. This is despite information from ghost lineages indicating that they should have been present in the Triassic lower Elliot Formation as well. Osteoderms are one of the most conspicuous features of archosaurs and have been hypothesised to aid in defence, thermoregulation, and sexual display. Osteohistology has been used to support or dispute these hypotheses and to determine the life history of different species. This study analyses the morphology and histology of a new collection of archosaur osteoderms from the lower Elliot Formation by using comparative morphology, osteohistology and phylogenetic analysis. The study will help refine the biostratigraphy of the Elliot Formation and the palaeoecology in the main Karoo Basin during the Late Triassic, before the end-Triassic Extinction Event.

#### Taxonomy, phylogeny and stratigraphic ranges of middle Permian pareiasaurs from the Karoo Basin of South Africa

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Pareiasaurs were relatively abundant, globally distributed, herbivorous parareptiles of the mid to late Permian. The basal-most forms, all members of the Bradysauria, are restricted to the Guadalupian (mid-Permian) of South Africa and went extinct in the late Capitanian near the top of the Tapinocephalus Assemblage Zone. Currently four species are recognised in this clade: Bradysaurus seeleyi, B. baini, Embrithosaurus schwarzi and Nochelesaurus alexanderi. Those taxa have historically been poorly defined and based on a limited number of specimens, leaving the taxonomic diversity of the group open to doubt and limiting their utility in biostratigraphy. Here we present a comprehensive review of the Bradysauria. Bradysaurus seeleyi is synonymised with Bradysaurus baini, resulting in three valid mid-Permian pareiasaur taxa: B. baini, E. schwarzi and N. alexanderi. Our cladistic analysis of cranial and postcranial characters supports the monophyly of Bradysauria with five synapomorphies. E. schwarzi is recovered as the sister taxon to a clade containing B. baini and N. alexanderi. By identifying 157 pareiasaur specimens in fossil collections, we show that the Bradysauria are stratigraphically restricted to the Abrahamskraal Formation of the Beaufort Group and suggest a staggered appearance. B. baini is first to appear in the upper Koornplaats Member, followed by N. alexanderi. E. schwarzi first appears in the lower Moordenaars Member. All three taxa have their highest occurrences near the top of the Karelskraal Member. B. baini and N. alexanderi thus begin their range in the Eosimops-Glanosuchus Subzone of the Tapinocephalus AZ and also occur in the Diictodon-Styracocephalus Subzone, whereas *Embrithosaurus* is restricted to the latter subzone.

#### Network-based biostratigraphy for the late Permian–Middle Triassic Beaufort Group (Karoo Supergroup) in South Africa enhances biozone applicability and stratigraphic correlation

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The Permo-Triassic vertebrate assemblage zones (AZs) of South Africa's Karoo Basin are a standard for local and global correlations. However, temporal, geographical and methodological limitations challenge the reliability of the Karoo AZ framework. We analyse a unique fossil dataset comprising 1408 occurrences of 115 species grouped into 19 stratigraphic bin intervals from the *Cistecephalus*, Daptocephalus, Lystrosaurus declivis, and Cynognathus AZs. Using network science tools, we compare six frameworks: Broom, Rubidge, Viglietti, Member, Formation, including a framework suggesting diachroneity of the Daptocephalus-Lystrosaurus AZ boundary (Gastaldo). Our results demonstrate that historical frameworks (Broom, Rubidge) still identify meaningful AZs, and can be useful in corroborating frameworks that identify more unique Karoo Basin AZs. None support the Cistecephalus AZ, and it likely comprises two discrete communities. The Lystrosaurus declivis AZ is traced across all frameworks, despite many shared species with the underlying Daptocephalus AZ, suggesting the extinction event across this interval is not a statistical or methodological artifact. A community shift at the upper Katberg to lower Burgersdorp formations may indicate a depositional hiatus with important implications for regional correlations, and Mesozoic ecosystem evolution. The Gastaldo model still identifies a Daptocephalus and Lystrosaurus AZ community shift, does not significantly improve recent AZ models (Viglietti), and highlights important issues with some AZ studies. Localized bed-scale lithostratigraphy (sandstone datums), and singleton fossils cannot be used to reject the patterns shown by hundreds of fossils, and regional chronostratigraphic markers (i.e., subaerial unconformities, index fossils) of the Karoo foreland basin. Meter-level occurrence data also suggest that 20–50 m sampling intervals capture Karoo AZs. This unifies the use of meterlevel placements of singleton fossils to delineate biozone boundaries and improves Karoo AZ applicability for correlations across southern and eastern Africa, and globally.

### Bone microanatomy of Anomodontia (Synapsida: Therapsida) from the Karoo Basin of South Africa

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The Anomodontia were a successful clade of Permo-Triassic therapsids (non-mammalian synapsids). Bone microanatomy (internal structure of bone) reflects the biomechanical constraints that organisms experience and usually records strong ecological signals. In turn, this relationship allows microanatomy to be used to estimate an extinct animal's lifestyle as well as adaptions to graviportality. Here, we investigate the limb bone microanatomies of 18 anomodont taxa to predict lifestyle habits. Relationships between bone microanatomy and body size were examined using linear regressions, and phylogenetic signal was measured using Bloomberg's K. A normalised principal components analysis was then conducted on the humeri and radii separately to visualise the differences within each of these elements. Results obtained from all limb bones studied indicate an aquatic (or amphibious) lifestyle in anomodonts (due to the infilling of the medullary cavities by bony trabeculae) regardless of body size or phylogeny. Robertia is the only exception as the inference model predicted a terrestrial lifestyle. Because the gross morphology of the anomodont clade and other evidence indicates a fully terrestrial lifestyle (including fossoriality in some cases), this is an unexpected result and suggests that other factors caused this microanatomical pattern. For example, this pattern may have been caused by biomechanical constraints associated with their semi-erect gait, which is unique to therapsids (the forelimb is abducted, and the hind limb is semiadducted). Body size appears to play a major role in the inner organisation, where the limb bones of larger taxa show a surprisingly thin cortex, which might also be linked to their semi-erect gait. Kannemeyeria is an extreme example of this pattern, where the bone microanatomy is most similar to extant pelagic mammals, despite the gross morphology suggesting a terrestrial lifestyle. This study shows that bone microanatomy should only form part of the assessment when investigating the lifestyle of extinct vertebrates.

#### Rediscovery of the *Euparkeria* bonebed locality (Middle Triassic) in Aliwal North, South Africa with an update on its taphonomy and depositional environment

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Euparkeria capensis is a Middle Triassic archosauriform reptile widely regarded as phylogenetically close to the base of the Archosauria. More recently, however, its status as a stem-archosaur has become a matter of considerable debate. Fossils of this species are only known from a single locality in the townlands of Aliwal North in South Africa. The exact location was, until now, uncertain due to misreading the field notes of the collector Mr Alfred "Gogga" Brown and conflicting anecdotal information gleaned from local townsfolk. Careful transcription of the voluminous hand-written fieldnotes, followed by archival research in the town museum, and ground-truthing of the targeted area, has led to the re-discovery of the Euparkeria type locality. Sedimentary facies analysis of the locality combined with taphonomic observations of the 38 fossil-bearing rock slabs collected by Brown, now housed in Iziko South African Museum reveal the origin of the Euparkeria–Mesosuchus bonebed. The bones are preserved within the base of two tabular massive sandstone beds. The stratigraphic position, sedimentology, and geometry of the sandstone layers and interbedded floodplain mudrocks allow their interpretation as part of an infilled chute-channel that cross-cut a point-bar in a high-sinuosity river channel. The taphonomic analysis of the main bonebed suggests that the initial concentration of tetrapod remains was controlled by a combination of a mass mortality event of a pack of Euparkeria, and a few Mesosuchus becoming overwhelmed by a flash flood, and the hydrodynamics of the small floating carcasses getting trapped in the chute-channel.

#### Vertebrate palaeontology of a tetrapod fossil accumulation in the Triassic Burgersdorp Formation of the Karoo Basin

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Field investigations on the farm Lemoenfontein, near Aliwal North in the southern Free State, recovered a diverse amniote fauna from exposures of the Burgersdorp Formation assigned to the lower part of the early Middle Triassic Trirachodon-Kannemeyeria Subzone of the Cynognathus Assemblage Zone (AZ). In total, 140 skulls and articulated skeletons of seven tetrapod taxa were collected along with details on their palaeoenvironmental setting. Trace fossils including three different burrow casts, each with distinctive geometries, were also collected and documented. The amniotes include both juveniles and adults of the procolophonids Teratophon spinigenis and Thelephon contritus; trirachodontid cynodonts Trirachodon berryi and Cricodon kannemeyeri; probainognathid cynodont Lumkuia fuzzi; bauriid therocephalian Microgomphodon oligocynus; and the rhynchosaur Eohyosaurus wolvaardti. Specimens include the holotypes of T. spinigenis and E. wolvaardti, and potential paratypes of M. oligocynus and E. wolvaardti, and only the second specimen of L. fuzzi. The diverse fauna is dominated by herbivorous tetrapods, mainly procolophonids, all with dental adaptations for browsing fibrous plant material. The only carnivore present is the small probainognathian cynodont L. fuzzi. Several of these taxa have previously been proposed as burrowers. The diversity and profusion of well-preserved fossils has provided new insight into how palaeoenvironmental and behavioural factors combined to produce this hyperaccumulation of tetrapod fossils. Whilst the herbivorous dicynodont Kannemeyeria simocephalus and carnivorous erythrosuchid archosaur Erythrosuchus africanus are common components of the middle Cynognathus AZ Trirachodon-Kannemeyeria Subzone elsewhere in the basin, they are absent from the lower exposures at Lemoenfontein. This insight increases the biostratigraphic resolution of the Cynognathus AZ. Another interesting aspect of the site is that all the tetrapod remains are of animals with small body size. This apparent Lilliput effect supports the view that full faunal recovery after the end-Permian Mass Extinction in the Karoo Basin was only achieved later in the Middle Triassic.

### Vertebra spinous process deviation in extant hominids and fossil hominins

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This study compared the asymmetry of the spinous processes and articular facets of the upper thoracic spine (T1–T6) in extant hominids and fossil hominins to determine if any structural or functional differences could be identified. A sample group of extant hominids with varying locomotor propensity, including chimpanzees (Pan troglodytes), gorillas (Gorilla gorilla), baboons (Papio ursinus), contemporary human and fossil hominins were compared. In addition, Late Stone Age (LSA) and contemporary humans were compared to evaluate potential effects of lifestyle on the morphologic features. Measurements of photographed specimens were made utilizing ImageJ software (as a metric measurement or a non-metric visual determination). Comparisons of extant species demonstrated statistically significant differences between species and sex. Spinous process deviations demonstrated a low overall incidence, with classification of five presenting patterns. Fossil hominins showed similarities between samples utilized (as would be expected, as all samples were Australopithecus). The comparisons of LSA and contemporary humans showed little evidence of differences, suggesting a limited impact from lifestyle. No significant correlations were identified relating to spinous process deviation as a feature. The study demonstrated a novel approach to photography and measurement of vertebrae. We conclude that spinous process deviations appear not to be related to functional (in this case locomotor or lifestyle) differences and may be associated with numerous factors that are possibly interrelated, or simply as the result of normal variation between individuals.

### Destructive sampling of fossils – scientific research versus preservation

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In recent years, there have been remarkable technical advances in palaeontology. Sophisticated imaging techniques have reduced the need to access original specimens and require no directly destructive procedures. However, direct dating, isotopic studies, and the study of ancient DNA, proteins, and microstructures have also advanced with great technical improvements, and still require a degree of physical invasive sampling. The power of these invasive approaches for answering important questions in palaeontology and evolutionary anthropology poses the question of how to balance preservation of fossil remains for the future against the advances in scientific analyses and their ability to answer more nuanced scientific questions. Requests to carry out destructive sampling are common. Many of these requests have been granted in the past, however, with a substantial number of fossils having been sampled, the wisdom of when to permit such sampling has been questioned. With reference to the literature and institutional guidelines, the following summarized principles are recommended in making decisions: (1) a ranking system of the uniqueness of specimens: For example, holotypes and fossil hominins are considered more critically. Specimens are required to have been published, imaged, and open access for study; (2) a standardized formal application procedure: The scientific question addressed should be important enough to justify invasive sampling of fossil remains. (3) an impartial Access Advisory Panel and list of referees make an informed decision and take collective responsibility. SAHRA destructive permits are applied for. It is hoped that by employing sound procedures in vetting destructive sampling requests, the delicate balance can be better achieved between preservation of precious fossils for future generations and the use of such remains for gaining further insights into evolution of life.

#### The age of the Mpandi Formation in the Tuli Basin of Zimbabwe

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The Mpandi Formation is the only vertebrate fossil-bearing unit in the upper Karoo Supergroup in the Zimbabwean part of the Tuli Basin. Historically, these fossils were assigned to the Massospondylus and the now invalid "Euskelosaurus," but recent taxonomic revision of sauropodomorph dinosaurs in the main Karoo Basin necessitates reconsideration of the Mpandi material. We investigated historically and recently collected Mpandi fossils and identified specimens potentially referrable to the earlybranching sauropodomorphs Massospondylus, Melanorosaurus, and Pulanesaura, and theropod material potentially representing Megapnosaurus ("Syntarsus rhodesiensis"). Biostratigraphic correlation to the Norian–Sinemurian Elliot Formation from South Africa and Lesotho suggests that the Mpandi Formation also spanned the Late Triassic and Early Jurassic. The overlying Forest Sandstone Formation is correlated with the Sinemurian–Pliensbachian Clarens Formation of the main Karoo Basin. Borehole data show that the 60-m-thick-succession of outcropping Mpandi strata represents only the upper third of the red beds in the Tuli Basin. To test these correlations, we collected detrital zircon samples from the fossiliferous Mpandi outcrop, near the middle of the exposed section. Laser Ablation Inductively Coupled Plasma Mass Spectrometry U-Pb radioisotopic dating resulted in three reliable maximum depositional age estimates, each indicating a Rhaetian-Hettangian age. The combination of our detrital zircon age data and our biostratigraphic work suggests that: (1) the upper third of the Mpandi Formation was deposited around the time of the end-Triassic Extinction Event, (2) Melanorosaurus (or a closely related genus) persisted until the end of the Triassic, and (3) the upper part of the Mpandi Formation is temporally best-correlated with the uppermost lower Elliot Formation in South Africa. Furthermore, our results suggest that the ~ 1-m-thick silcrete unit marking the top of the Mpandi Formation and other red beds in the Tuli Basin could represent a significant amount of time, which can only be resolved by reliably dating the overlying Forest Sandstone Formation, for which samples have been collected.

Notes

Notes

## Schedule of the talks at the 21<sup>st</sup> PSSA Biennial Meeting

Talk Slot	Tuesday, September 13	Wednesday, September 14		Thursday, September 15
8:45	Welcome: Prof Bruce Rubidge, Genus	Harris, C		Ovechkina
9:00 AM	Welcome: Paddy Gordon, GGHNP Manager	Botha		Roussouw
9:15	Zipfel	Benoit: Indigenous		Stuart
9:30 AM	Chinsamy-Turan	Hanon		Harris, W
9:45	Rampersadh	Day		Van Den Brandt
10:00 AM	Tolchard	Nel		Bordy
10:15	Wolvaardt: Euparkeria	Mukwevho		Zondo ( <i>TBD</i> )
10:30 AM	Теа	Теа		<b>T</b>
10:45				Теа
11:00 AM	Macungo	Wolvaardt: Tetrapods		Penn-Clarke
11:15	Sibiya	Head		Choiniere
11:30 AM	Abrahams	Dollman, G		Genus: Steininger
11:45	Peyreyra	Rabe		Genus: Steininger
12:00 PM	De Kock	Seerane		
12:15	Kock, S	Browning: Enamel		
12:30 PM	Viglietti	Barrett		
12:45	Yelverton	Nhamutole		
1:00 PM		Lunch		Lunch
1:15	Lunch			
13:30 PM				
1:45				
14:00 PM	Norton	Anderson, H		AGM
2:15	Benoit: Gorgon Survival	Toefy		
14:30 PM	Browning: Ordovician	Groenewald, G		
2:45	Rubidge	Hancox		
15:00 PM	Weiss	Gess: Larvae		
3:15	Montgomery	Neveling		
15:30 PM	Теа	Теа	Preparator's	Теа
3:45			Workshop	rea
16:00 PM	Bolton	Lloyd		AGM
4:15	Jirah	Chapelle		
4:30 PM	Moopen	Bamford		
16:45		Araujo: Presented by Benoit		
5:00 PM				