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Cover Image

The Active Okovanatje Cascade Tufa Complex, Kaokoland, Namibia

(Image: Martin Pickford)

Project Report: Grinding Through the Ediacaran-Cambrian Transition

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Abstract: The Neoproterozoic Era (1000 - 541 Ma) was one of the most dramatic in Earth history: metazoans evolved, the supercontinent Rodinia formed and broke apart, the global carbon cycle underwent high-amplitude fluctuations, oxygen concentrations rose and climate experienced at least two episodes of worldwide glaciation. However, the discontinuous and fragmented nature of outcrop-based studies has hindered developing quantitative models of Earth system functioning during that Era. The *Geological Research through Integrated Neoproterozoic Drilling* (GRIND) project will begin to rectify this scientific shortcoming by obtaining 13 cores, each between 150 to 600 m in length, through the archetype successions that record the environmental and biogeochemical context during which animals evolved. The specific targets are the Ediacaran-Cambrian transition (ECT; c. 560-530 Ma) strata of west Brazil (Corumbá Group), south China (Doushantuo, Dengying and equivalent formations) and south Namibia (Nama Group). Our objective is to create a core network of correlative ECT strata that will enable the construction of a high resolution, temporally constrained geobiological, stratigraphic and geochemical database, as well as to provide a legacy archive for future research. The goal is to understand the drivers of the Neoproterozoic Earth system revolution: it began with simple eukaryotes that populated Earth during the preceding billion years of the Mesoproterozoic, underwent multiple Snowball Earth events and emerged with the oxygenated, diverse ecosystems of the Cambrian. The excellent outcrops of the Nama Group in Namibia are central to the success of the GRIND project, as is the invaluable expertise and support of the Geological Survey of Namibia. The stratigraphy of these rocks is well-documented and is an archetype of the late Ediacaran to early Cambrian. Furthermore, the presence of abundant ash beds offers excellent opportunities for obtaining high-precision U-Pb geochronology, making the Nama Group an ideal target for acquiring precise temporally constrained and detailed geobiological and geochemical data to meet our research goals.

Key words: Corumbá Group, Doushantuo Formation, Dengying Formation, Ediacaran, International Continental Scientific Drilling Program, Nama Group, Neoproterozoic

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Introduction

The Neoproterozoic Era (1000 - 541 Ma) began with simple eukaryotes that populated Earth during the preceding billion years of the Mesoproterozoic and ended with the oxygenated and diverse ecosystems of the Cambrian. In the interim, some of the most dramatic changes in Earth history occurred (Fig. 1): animals appeared from a world of bacteria and algae (Cohen & Macdonald, 2015) the supercontinent Rodinia formed and broke apart (Evans, 2013; Li *et al*. 2008), the carbon cycle underwent high-amplitude fluctuations (Halverson *et al*. 2005), oxygen concentrations are thought to have risen (Lyons *et al*. 2014) and climate experienced at least two episodes of prolonged worldwide glaciation (Rooney *et al*. 2015). However, the fragmented nature of outcrop-based studies and lack of exact age constraints on the timing and durations of those episodes hinders the development of quantitatively constrained models of Earth system functioning during that Era.

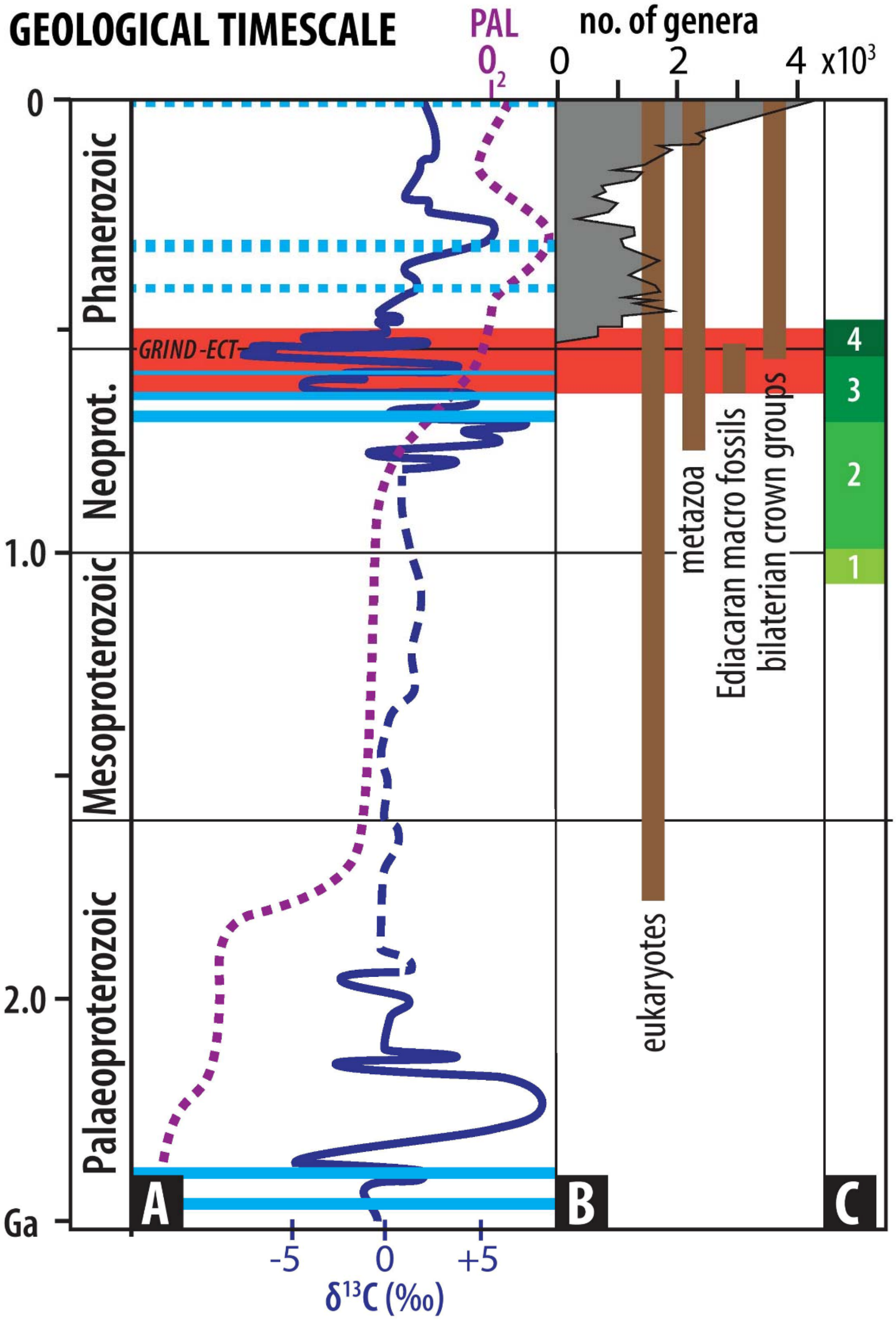

Figure 1. Selected secular trends revealing the distinctiveness of the Neoproterozoic. (A) C cycle and pO_2 (PAL - present atmospheric level). (B) Biospheric evolution. (C) Global tectonics: 1-Grenville orogeny; 2-Rodinia supercontinent; 3-Rodinia rift-to-drift phase; 4-Pan-African orogeny. Solid blue bands represent periods of global glaciations, dashed blue bands denote glaciations restricted to high-latitudes and the red band is the time interval to be targeted by GRIND-ECT.

The *Geological Research through Integrated Neoproterozoic Drilling* (GRIND) project (Condon *et al*. 2015) aims to address that shortcoming by creating a global core archive for the Neoproterozoic Era. Fresh, oriented cores will enable the construction of continuous high-resolution bio-, chemo- cyclo- and magnetostratigraphies integrated with geochemical and chronostratigraphic data. The project is an international, community-wide collaborative effort to understand better the nature and drivers of this pivotal time in Earth history and will be achieved via a series of coordinated drilling projects, undertaken sequentially, that target the key localities recording those Earth system transformations. The first phase of GRIND will focus on the Ediacaran-Cambrian transition (GRIND-ECT; Fig. 2, Time Slab C), with potential future phases targeting the remainder of the Neoproterozoic (Time Slabs A and B).

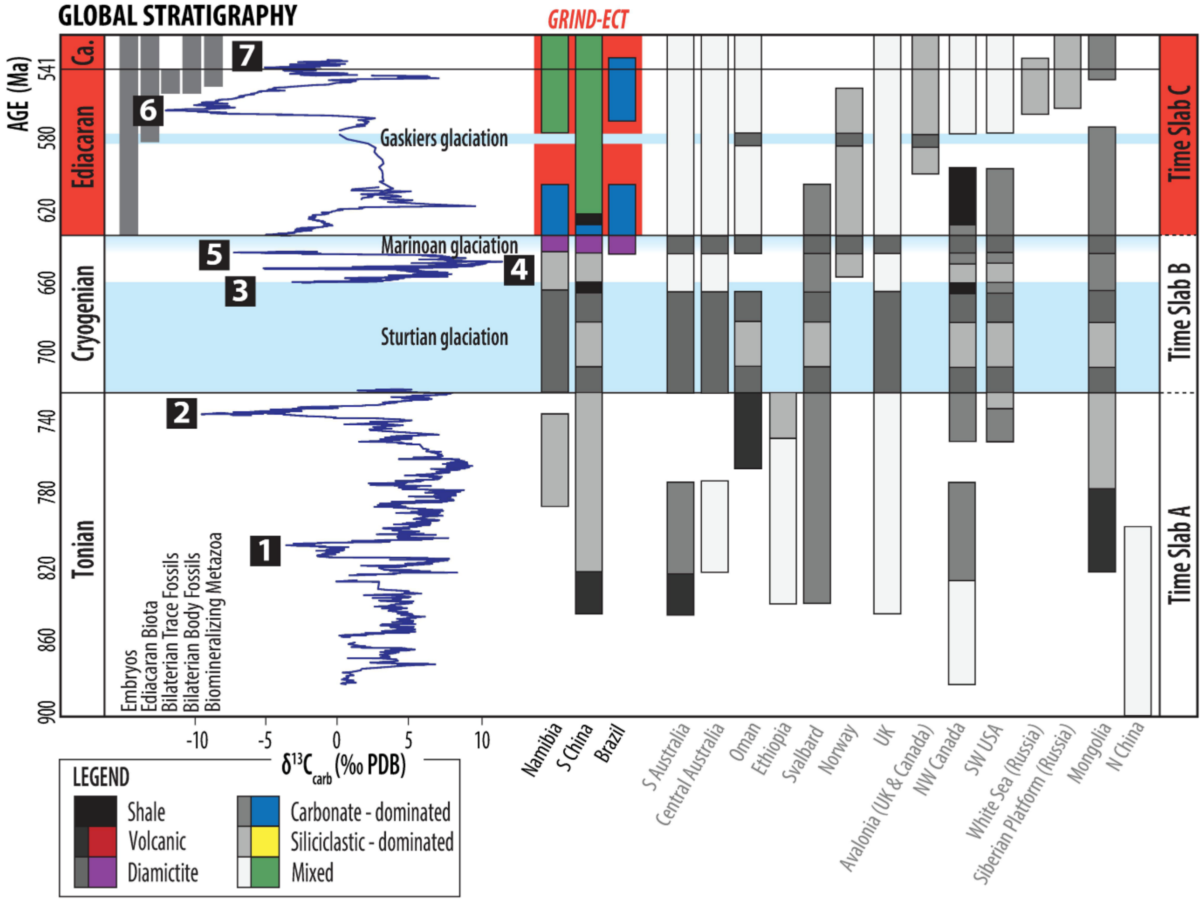

Figure 2. Neoproterozoic time slabs identified for drilling in the GRIND project and stratigraphy and major glacial periods for key successions worldwide. Red highlighted intervals denote the Time Slab C target of GRIND-ECT. Biospheric evolutionary trends are given to the left with a plot of the composite C-isotopic profile and excursions: 1-Bitter Springs; 2-Islay; 3-Keele Peak; 4-Taishir; 5-Trezona; 6-Shuram; 7-BASE. Ca - Cambrian. See text for references providing the sources of data.

Since Darwin's (1859) observation of the seemingly rapid appearance of fossils in Cambrian strata, resolving the causes and tempo of the 'Cambrian Explosion' remains one of science's great challenges (Erwin *et al*. 2011). GRIND-ECT will obtain sufficient temporal resolution and integration of geological, geochemical and biological data to address the following key questions:

- What were the timing and rates of the advent, expansion and extinction of Ediacaran biota?
- What were the environmental contexts and timing for changing skeletal mineralogy and diversification of biomineralising Metazoa?
- What was the pattern of oxygenation (globally and regionally) and how does it

relate to other geochemical patterns? Was there a Neoproterozoic oxygenation event?

- What were the timing, duration, genesis and implications for the global C cycle and the large amplitude C-isotope excursions in late Ediacaran to Cambrian strata?
- Is the Ediacaran-Cambrian boundary a synchronous worldwide biological event or a lengthy episode of biological innovation?

The ECT strata in west Brazil, south China and southern Namibia were chosen to answer these questions because their geological record from the Marinoan glacial to the early Cambrian is excellent, well understood and will guide drilling and supplement core data (Fig. 3). In addition, each country has expertise and infrastructure for drilling and coring. GRIND-ECT will be coordinated around three research foci (RF).

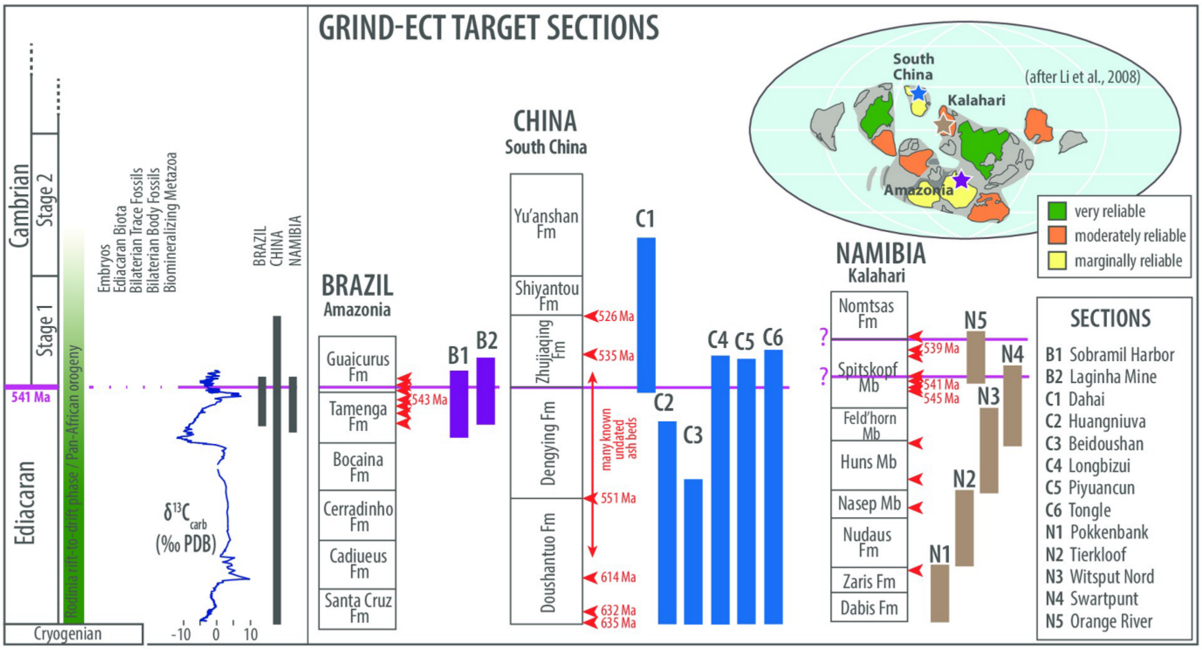

Figure 3. Schematic showing GRIND-ECT target sections in Brazil (B1-2), China (C1-6) and Namibia (N1-5), and their temporal relationship to key evolutionary, C-isotope and tectonic events. Red arrows represent ash beds. Inset map shows locations of drill sites (marked by stars) on a palaeocontinent reconstruction for the formation of Gondwana during the late Ediacaran. See text for references providing these data.

Research Focus 1: A highly resolved temporal framework

The goal of RF1 is to obtain precise dates on tuffs and organic-rich shales using U-Pb zircon CA-ID-TIMS and Re-Os geochronology and integrate those with palaeomagnetism and physical stratigraphy to construct age models for the ECT. ECT strata preserve the earliest known phosphatised Metazoa embryos, the first appearance datum of *Treptichnus pedum* and an increase in diversity of Metazoa, trace fossils and phytoplankton (Landing, 1994; Yin *et al.* 2007; Narbonne, 2005; Grotzinger *et al.* 1995; Cohen *et al.* 2009; Marshall, 2006). These evolutionary milestones are associated with C-isotope excursions (amplitudes of ≥8‰; e.g. Maloof *et al.* 2010; Smith *et al.* 2016; Zhu *et al.* 2017) and, although temporal coincidence is often assumed, their timing and duration remain to be constrained precisely. These data will underpin the work being done in RF2 and RF3.

Research Focus 2: Fossil record of early animal evolution

The goal of RF2 is to refine the patterns of biotic evolution of organic-walled and mineralised microfossils, metazoans and trace fossils and integrate those data with RF1 and RF3 to assess the links between and test hypotheses about biological evolution and environment. Documenting changes in morphology and skeletal mineralogy integrated with age data and geochemical and palaeoenvironmental data using the new cores, in conjunction with existing outcrop studies along with CT scanning to reveal ichnofossil assemblages, will yield ideas about the causes of increasing body size and ecological complexity vis-à-vis oxygen levels and biological innovation (e.g. Butterfield, 2017), such as structural defences against predation. Where appropriate, biomarkers will also provide insight into the late Ediacaran and early Cambrian communities (Love *et al.* 2009; Brocks *et al.* 2017) using drilling and sampling protocols established during Agouron-funded drilling to recover Archaean hydrocarbons (Brocks *et al.* 2008; Jarrett *et al.* 2013; Schinteie & Brocks, 2014; see French *et al.* 2015 for details).

Research Focus 3: Palaeoenvironmental conditions and the rise of oxygen

The goal of RF3 will be to determine palaeoenvironmental conditions using facies interpretations, geochemistry and elemental and stable isotope data integrated into the age model of RF1 and fossil record of RF2. This work will distinguish cause-and-effect relationships and basin-specific versus global-scale secular trends in geochemical and stable isotope patterns. Trace metal abundances, Fe speciation and a suite of traditional and non-traditional isotopes will be used to guide hypotheses on weathering and nutrient fluxes (e.g. Sr, Os, Li isotopes, P), ocean redox (e.g. Mo, δ^{238}U, Fe speciation) and biogeochemistry (e.g. δ^{34}S, δ^{15}N, δ^{98}Mo, δ^{13}C isotopes). Perturbations in C and S cycles and studies of redox-sensitive elemental ratios (e.g. Fe, U) have been used to link the advent of animals with a putative global rise in oxygen, the Neoproterozoic Oxygenation Event (Och & Shields-Zhou, 2012). Ediacaran oceans are postulated to have had spatially and temporally varying oxygenation, with ferruginous and anoxic deep waters and variably oxic surface waters but oxic everywhere by the end of the Ediacaran (Lyons *et al.* 2014). Other workers question this scenario (Butterfield 2009; Sperling *et al.* 2015). Hence, although temporal coincidence between the advent of skeletonisation and animals, and the inference for a rise in oxygen hints at causality, the precise role of oxygen in driving biological evolution remains uncertain. New core data will be compared to, and incorporated with, published geochemical and isotopic data from equivalent outcrop-based studies to create and test ideas linking changing ocean-atmosphere conditions and compositions to the evolution of animals.

Assessing diagenesis

The potential overprinting of original signals by diagenesis is a critical issue for assessing geochemical proxies that are used to yield information about ancient environmental conditions. Fresh cores are crucial because they recover rocks that have been minimally influenced by surface weathering. To identify samples in which geochemical and isotopic signals are preserved, screening protocols will be used that have been applied successfully to Neoproterozoic strata in many areas worldwide (e.g. Fantle & Higgins, 2014; Kasemann *et al.* 2005). Screening will first use basic observation (e.g. presence/absence of veins, recrystallisation textures, colour alteration), then petrography, SEM and cathodoluminescence imaging, followed by a battery of geochemical tests to assess for diagenetic overprints and to distinguish those from primary signals via patterns and trends in selected elements and their ratios (e.g. Al, Ba, Ca, Fe, Mg, Mn, P, S, Si, Sr) as well as stable isotope ratios and patterns (C, O, B, Ca, Mg).

In summary, RF1-3 will enable integration of new core data with published and in-progress outcrop-based studies worldwide. This approach will provide high-resolution sedimentological, geochemical, palaeobiological, palaeomagnetic, geochronological and cyclostratigraphic data to determine rates of change of biogeochemical processes, evolutionary tempos, and the spatio-temporal record of oxygenation across a spectrum of environmental settings.

Need for multi-craton, multi-site Neoproterozoic scientific drilling

Pristine cores recover complete intervals typically unattainable from outcrops that often have limited continuity of exposure and have been modified by weathering. Cores are crucial for evaluating diagenesis and for reducing uncertainty in proxy records, and the value of core networks has been demonstrated by the International Ocean Discovery Program (IODP). In contrast, few core archives exist for Neoproterozoic strata, exceptions being the South Oman Salt Basin and Australia's Centralian Basin which yielded benchmark works on biospheric evolution (Amthor *et al.* 2003; Bowring *et al.* 2007; Fike & Grotzinger, 2008; Fike *et al.* 2006; Pisarevsky *et al.* 2001; Walter *et al.* 2000). We expect a similar impact and value for the GRIND-ECT core network. Creating a worldwide, integrated network of cores through Neoproterozoic strata will yield unrivalled 3-D and 4-D stratigraphies for differentiating global from regional phenomena and for creating and testing hypotheses about, as well as advancing understanding of, the Neoproterozoic Era for scientific as well as natural resource perspectives. Previous experience with the International Continental Drilling Program (ICDP) FAR-DEEP (Melezhik *et al.* 2013) and NASA Agouron Deep Time drilling projects (Schröder *et al.* 2006) confirms that a continental scientific drilling programme would be decisive in delivering knowledge of the environmental and biogeochemical episodes that record how the Earth system transformed from simple eukaryotes through the ECT to the Cambrian Explosion. GRIND-ECT targets that important transition in Earth history: the advent of animals and the change to a well-oxygenated planet. Each of the three chosen localities has distinct, yet complementary records: fossiliferous organic-rich limestone and shale in west Brazil, microfossil-rich carbonate-dominated strata in south China, and macro- and trace fossil-rich carbonate-siliciclastic rocks in Namibia. Further, all sections have datable ash beds and organic-rich rocks for high-resolution U-Pb and Re-Os geochronology that will permit age models and correlations at high temporal resolutions to enable quantitative assessments of the mechanisms and rates-of-change leading to and culminating in the Cambrian Explosion.

Drilling and drill site selection

Despite the scientific importance of the ECT and years of detailed and meticulous mapping in the target locations, the fragmented nature of the outcrop, and its susceptibility to surface weathering, has hindered the development of quantitative models of Earth system functioning during that Era. These limitations will be overcome through the GRIND-ECT drilling programme. Existing detailed geological maps and outcrop-based datasets, structurally simple geology, industry-generated drilling data and in-country skill for drilling and coring provide a solid framework for identifying drill hole locations in west Brazil, south China and south Namibia. The strategy is to core correlative strata within and between nations to test models on the genesis, synchronicity versus diachronicity and global versus regional aspects of early animal evolution and its environmental context. Combined, the core archives will obtain a level of resolution that surpasses all current datasets and will offer rich opportunities for future research. Most cores will be between 150 – 400 m in length, with several approaching 600 m lengths; such shallow drilling depths combined with the well-understood geology of the drill sites maximise confidence that target strata will be recovered and structural problems avoided. Further, the existing and detailed knowledge from outcrop-based studies will help guide the drilling and supplement the core data. Drilling logistics are also straightforward: drill sites are in relative proximity to necessary infrastructure, roads and access to water, which will reduce costs and maintain a low drilling-operation-cost to post-drilling-research-cost ratio. The first phase of drilling will target the Nama Group in Southern Namibia.

Nama Group, Southern Namibia

Five cores, 200 – 450 m in length, will target the lower and middle Nama Group (Figs. 4 and 5; Table 1) with its diverse record of the ECT including the type *Nama assemblage* of Ediacaran rangeomorphs, erniettomorphs, calcified macrofossils and complex trace fossils (Wood & Curtis, 2014; Vickers-Rich *et al.* 2012; Penny *et al.* 2014). The Kuibis and Schwarzrand Subgroups are the drilling targets (the latter is dated between 547 ± 1 Ma and 540.61 ± 0.67 Ma; recalculated from Grotzinger *et al.* 1995) and consist of mixed carbonate-siliciclastic strata that define outer ramp through nearshore and fluvial-deltaic settings (Germs, 1983).

The stratigraphy of the Nama Group is well-documented and is an archetype of the late Ediacaran - early Cambrian (e.g. Grotzinger & Miller, 2008). Several C-isotope and redox-sensitive element ratio studies have been done on the Nama rocks, including those that archive the C-isotope excursions and fauna typical of the ECT. In addition, these rocks are central to models that postulate patchy ocean oxygenation and for ideas that the evolution of animals was driven by varying oxygenation of late Ediacaran oceans (e.g. Wood *et al.* 2015). Furthermore, the presence of abundant ash beds (e.g. Saylor *et al.* 2005) offers excellent opportunities for obtaining high-precision U-Pb geochronological data, making the Nama Group an ideal target for acquiring precise temporally constrained and detailed geobiological and geochemical data to meet the goals of Research Foci 1-3.

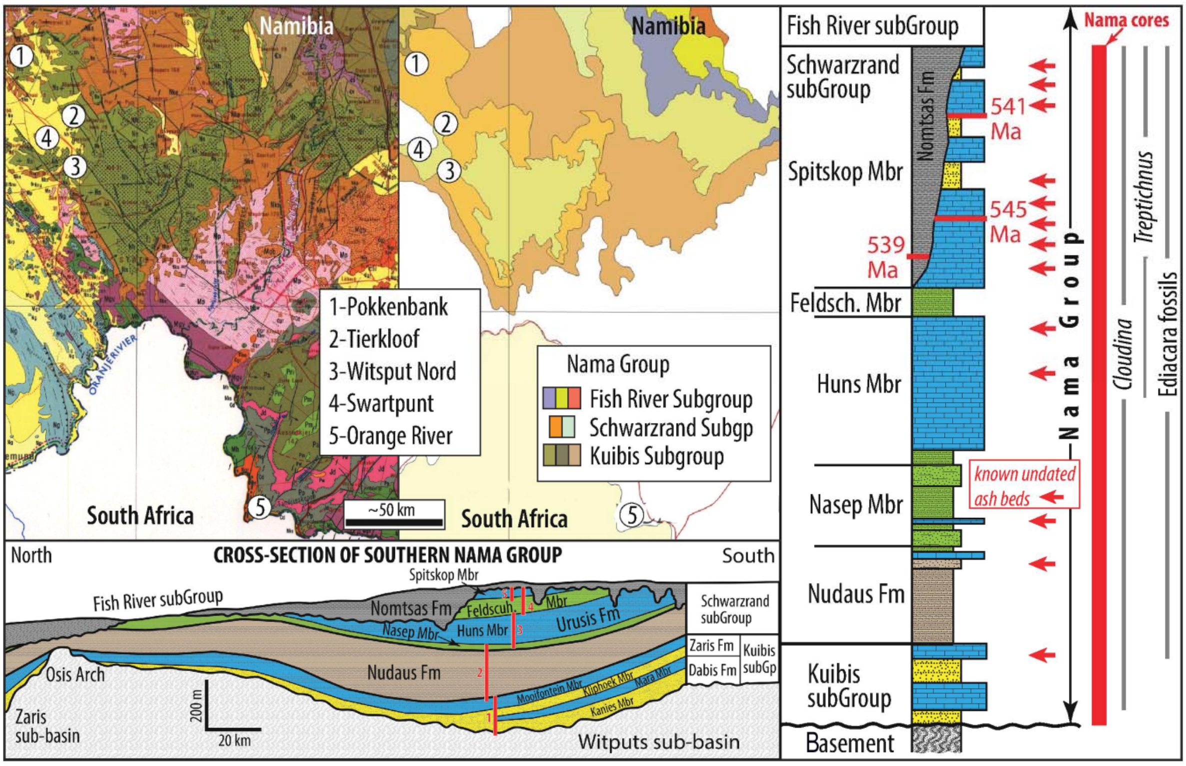

Figure 4. Geological map of southern Namibia (left) and Nama Group outcrop belt (right) showing drill site locations. Cross section of southern portion of Nama basin (Witputs sub-basin) shows the geological simplicity of the basin. Stratigraphic column shows positions of dated ash beds, including many known undated ash beds (red arrows). Red vertical bar indicates targeted coring interval, which captures the entire Ediacaran-Cambrian transition as recorded in the Kuibis and Schwarzrand Subgroups (Nama Group). Data obtained from references cited in text.

Site selection

Five sites were chosen in geologically well-understood areas near to roads and water sources thus mobilisation-demobilisation logistics are simple: Pokkenbank, Tierkloof, Witputs Nord, Swartpunt and Orange River (Figs. 4 and 5; Table 1). Exposure is excellent and the stratigraphy of the Nama rocks has been established by decades of detailed mapping. The rocks are flat-lying or dip at low-angles (<20°), there are few faults, none at the target sites, and most are sub-vertical and occur in clearly identifiable narrow zones (hundreds of metres in width); the frontal thrusts of the Gariep Orogen are to the west of the drilling sites and their subsurface projections are already known. Previous drilling confirms that the Nama rocks retain a layer-cake geology in the subsurface but those cores failed to capture the oldest stratigraphy that GRIND-ECT is targeting. Reconnaissance surveys of the sites corroborate the accuracy of the existing geological mapping, providing strong confidence that the stratigraphic intervals targeted for coring will be recovered.

Table 1. Summary of core details for the south Namibia drilling sites.

drill site	location; elevation	target interval	core length	geology	access	water
Pokkenbank	27.160737S 16.545447E 1145 m	Dabis and Mooifontein Fms (Kuibis Subgroup)	c. 275 m	flat lying, mixed siliciclastic-carbonate sedimentary rocks	24.6 km along farm track off and NE of C13	water will be trucked in
Tierkloof	27.403949S 16.739627E 980 m	Nudaus Fm and Nasep Mbr (lwr Schwarzrand Subgp)	c. 300 m	flat lying, mixed siliciclastic-carbonate sedimentary rocks	6.4 km along farm track off and E of C13	access to nearby farm well
Witputs Nord	27.558859S 16.689447E 977 m	upper Nasep and Huns Mbrs (mid Schwarzrand Subgp)	c. 360 m	flat lying, mixed siliciclastic-carbonate sedimentary rocks	1 km along farm track off and N of C13	access to nearby farm well
Swartpunt	27.473417S 16.690464E 1011 m	Feldschuhhorn and Spitskop Mbrs (upr Schwarzrand Subgp)	c. 425 m	flat lying, mixed siliciclastic-carbonate-chert sedimentary rocks	6.8 km along farm track off and NW of C13	water will be trucked in
Orange River	28.685900S 17.494231E 243 m	top Spitskop Mbr (top Schwarzrand Subgp)	c. 200 m	flat lying, mixed siliciclastic-carbonate-chert sedimentary rocks	6.5 km along farm track off and W of C13	access to nearby farm well

Drilling

Günzel Drilling will do the drilling and coring, obtain permits, provide core boxes and temporary on-site core storage, multi-sensor logging equipment to enable initial characterisation of the cores, and core transportation. The Namibian Geological Survey will assist with all customs and shipping permits. *Günzel Drilling* has operated for almost two decades in Namibia and has ample experience in meeting the drilling and coring requirements of GRIND-ECT: core diameter of ≥56 mm, high drill core recovery, minimal or no contamination and low cost.

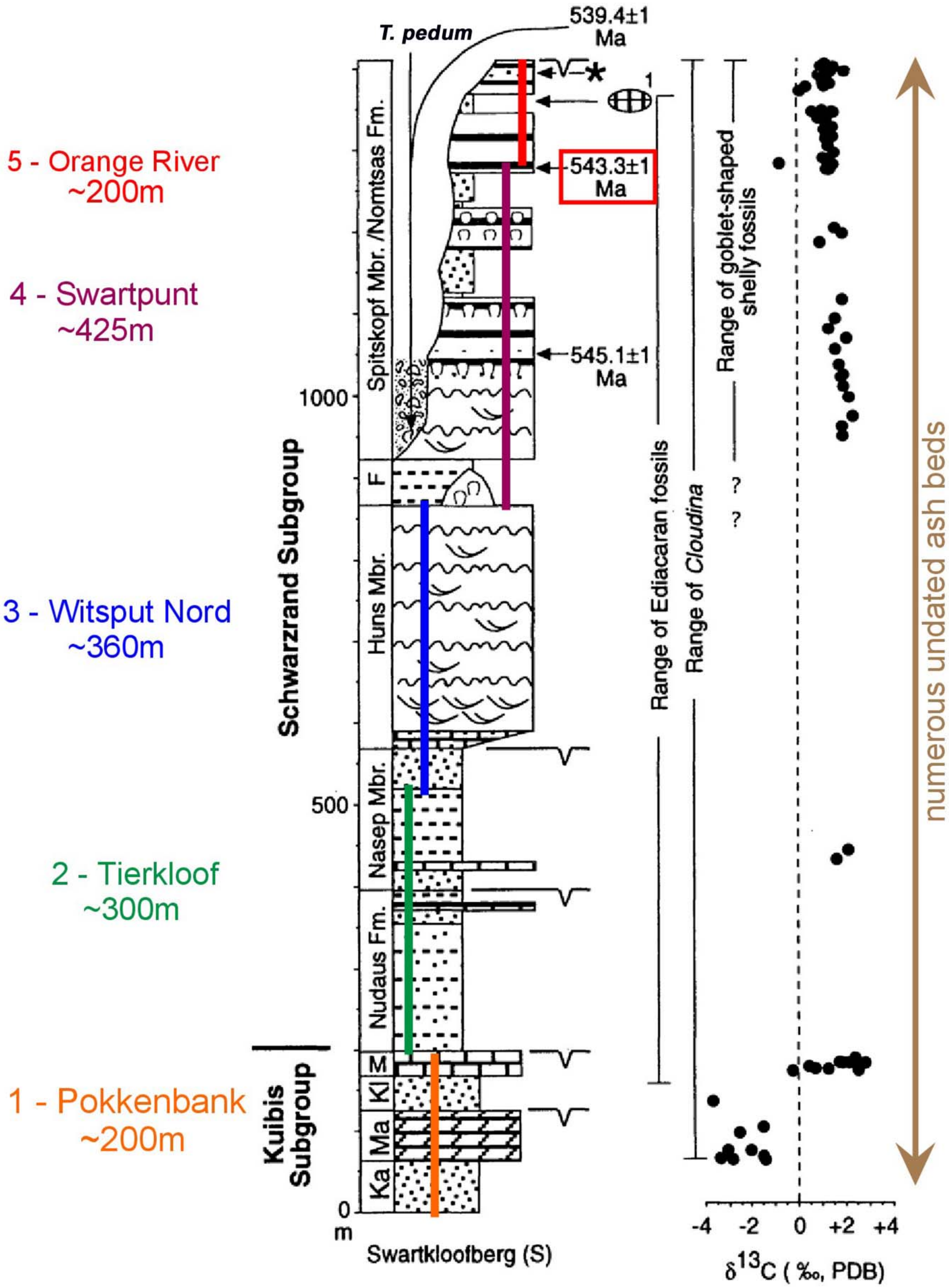

Figure 5. Schematic showing GRIND-ECT drilling target sections in Namibia and their stratigraphic context.

Core handling: characterisation, archiving and sampling

Drilling Information System data acquisition

Core data acquisition will use the ICDP Drilling Information System (DIS) for real-time capture of information at the drill site and for all subsequent data-gathering activities.

DIS will form a reference framework for use by all project scientists and the platform for integrating the varied data (lithological, palaeobiological, geochemical, geochronological, palaeomagnetic) to ensure that a consistent and uniform data management-integration-recording protocol is maintained and coordinated across GRIND-ECT.

Core archiving and repositories

The three-nation drilling programme will be undertaken sequentially: drilling will commence in Namibia in 2019, with subsequent drilling in Brazil and China. A total of c. 0.4, c. 2.6 and c. 1.5 km of core will be obtained for the Brazilian, Chinese and Namibian targets, respectively. Once on-site and initial core characterisation work is completed, cores will be transported to core repositories. One half of all cores will be retained in-country for research and educational training purposes and the other half will be shipped to the Federal Institute for Geosciences and Natural Resources (BGR) in Berlin-Spandau, Germany, for permanent archiving (Fig. 6). The BGR repository has technical staff and a suite of analytical equipment including multi-sensor and high-resolution XRF and CT scanners that will be available for use by project scientists. In Namibia, the core repository will be at the Ministry of Mines and Energy, Namibian Geological Survey, Windhoek. At each core repository, accessing the cores is free-of-charge. When the agreed GRIND-ECT moratorium restrictions end (three years from the drilling start date), the cores at both the in-country and BGR repositories will become freely available to the Earth Science community for study and educational training purposes. Importantly, having centralised, open access and easily accessible repositories will mark the first step towards meeting the goal of creating a global core archive for onshore continental scientific drilling that will match in scope and scale that of the IODP.

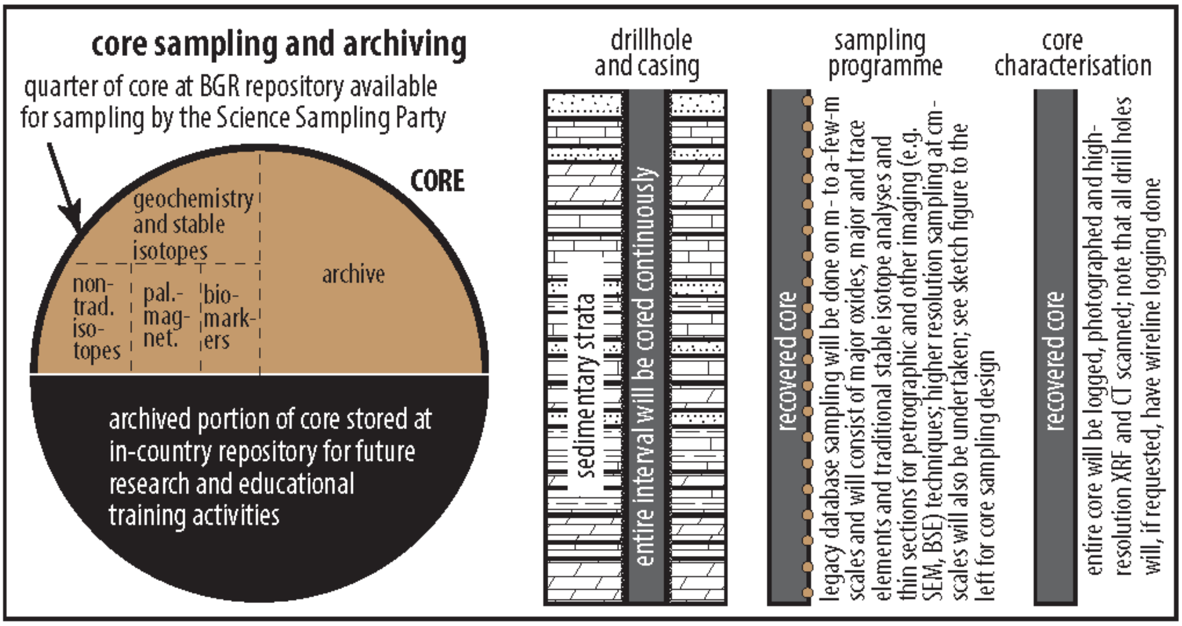

Figure 6. Core sampling and archiving design. Cores will be shipped to the BGR core repository in Berlin-Spandau, Germany, where cores will be slabbed in half. One half of the core will be for use by the Science Sampling Party and for archiving and future studies. The other half will be returned to the country of origin for research, educational training and capacity-building purposes. Prior to sampling, cores will be photographed and undergo high-resolution XRF and CT scanning. Samples will be for geochemical, isotopic, biomarker and palaeomagnetism analyses.

Science sampling party

Research will be via five Science Themes (Depositional Frameworks, Geobiology, Geochemistry, Geochronology, Palaeomagnetism), each with a designated Coordinator. Each Theme is designed to address the three Research Foci defined in

Section 1. It is estimated that within 3 months of the cores being transferred to repositories, the Science Sampling Party (SSP) will begin detailed core description and sampling; this will require several weeks (depending on the amount of core) to complete for each nations' cores. The SSP will consist of representatives from each Science Theme. A legacy dataset will be obtained at several m-scale sampling density in order to characterize the cores geochemically, to identify intervals of interest (isotope excursions, changes in faunal trends, extinctions, first occurrences) and to sample for thin-sections and imaging analyses (e.g. SEM, BSE). Sampling at higher-resolution, commonly at cm-scale spacing, will then be needed to characterise any high-frequency isotopic and biogeochemical patterns. In addition to standard geochemical analyses (major and trace oxides and elements), all samples will be analysed for $\delta^{13}C_{bulk}$, $\delta^{18}O_{bulk}$, $\delta^{13}C_{org}$, organic C/N, TOC and $CaCO_3$. Biogenic carbonate $\delta^{18}O$, $\delta^{13}C$ and Sr isotopes will also be measured on carbonate rocks. ICP-MS and automated mineral analysis calibration of core-scan XRF will be undertaken on selected samples. Sampling of ash beds for U-Pb geochronology and organic-rich intervals for Re-Os dating will be done jointly with the geochemistry sampling. Samples will initially be available for use by GRIND-ECT scientists. Once the GRIND-ECT moratorium ends, cores (both in-country and at the BGR) will be made available for study to any researcher worldwide.

Summary

The goal of GRIND-ECT is to deliver a worldwide network and archive of time-calibrated cores for open-access sharing and state-of-the-art research. This three-nation drilling programme will be undertaken sequentially: drilling will commence in Namibia in 2019, with subsequent drilling in Brazil and China. The identified drill sites will sample shallow-to-deeper marine rocks across shelf-to-basin transects. The work aims to 1) construct a highly resolved temporal framework that will lead to the development of age models for the ECT; 2) refine the patterns of biotic evolution of organic-walled and mineralised microfossils, metazoans and trace fossils, and identify the links between as well as test hypotheses about biological evolution and environmental change, and 3) determine the palaeoenvironmental and biogeochemical conditions that led to the rise of oxygen and distinguish cause-and-effect relationships and basin-specific versus global-scale secular trends in geochemical and stable isotope patterns.

All cores will be split into halves with one-half being archived in repositories within each of the target nations and used for research purposes by GRIND-ECT scientists and for education and training for national capacity building and outreach activities. The other half of all cores will be permanently archived in the Federal Institute for Geosciences and Natural Resources in Berlin-Spandau. The cores at all the repositories will be available for future research and education activities and will mark the first step towards creating an on-shore continental scientific drilling archive that will match in stature that of the IODP. Central to GRIND-ECT's success is the geology of the Nama Basin, which is known in exceptional detail owing to outstanding 3-D surface exposure, enabling the creation of a highly resolved age model integrated with the palaeontological record of Ediacaran early Cambrian biospheric evolution, oxygenation and biogeochemical cycling.

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Tiny Tenrecomorpha (Mammalia) from the Eocene of Black Crow, Namibia

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Abstract: The 2019 campaign of acid treatment of Eocene freshwater limestone from Black Crow, Namibia, resulted in the recovery of a minuscule mandible of an insectivoran-grade mammal representing a new genus and species of Tenrecomorpha. The specimen is the smallest mammal described from the fossil record from Africa. From the incisor alveoli to the rear end of the angle, the jaw measures a mere 8.6 mm. The jaw is relatively complete, but has lost the incisors, canine and p/2. It shows several characters that link it to the suborder Tenrecomorpha. In some morphological features it recalls Tenrecidae, in others Potamogalidae. The new genus and species throws doubt on the homogeneity of the order Afroinsectiphilia, which in its turn renders doubtful the concept of Afrotheria as currently understood.

Key words: Tenrec, Ypresian/Lutetian, Mandible, Namibia

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Introduction

This paper is devoted to the description and interpretation of a minuscule mammalian mandible from the middle Eocene limestones at Black Crow, Namibia. The freshwater limestone at Black Crow in the Sperrgebiet, Namibia, first yielded vertebrate fossils a decade ago (Pickford *et al*. 2008a, 2008b). The primitive aspect of the arsinoithere (*Namatherium*) and the hyracoid (*Namahyrax*) from the site suggested an age significantly older than any of the Fayum, Egypt, deposits (Pickford *et al*. 2014; Pickford, 2015a) an inference borne out by subsequent studies of the small and medium-sized mammals (Mein & Pickford, 2018; Morales & Pickford, 2018; Pickford, 2018b, c, d, e, f).

Each year the Namibia Palaeontology Expedition has visited the locality to search for blocks of limestone showing the presence of bones and teeth on their surfaces and these have been developed in the laboratory to extract the fossils. During 2019, as a blind test, the NPE decided to treat 150 kg of limestone that showed no signs of fossils on the surfaces of the blocks. The exercise was a success, with the recovery of several significant fossils including an adult mandible of *Namahyrax corvus*, several maxillae and mandible fragments of tenrecoids and chrysochlorids, along with over 110 crocodile teeth, several scincid jaws and vertebrae, bird postcranial bones, gastropod steinkerns and fruits of the Hackberry, *Celtis* (Pickford, 2018g).

Geological context

The geological context and age of the freshwater limestone at Black Crow have been mentioned on several occasions (Pickford *et al*. 2008a, 2014, 2015a). In brief, the locality comprises a small, shallow basin eroded into PreCambrian dolomites and infilled by a series of well-bedded limestone layers (probably of carbonatitic ash origin) overlain by freshwater limestone that accumulated in a low-energy aquatic environment in which plants were growing, probably a shallow swamp or a sluggish backwater in a slow-flowing river (Fig. 1). The dominant gastropods in the limestone are landsnails of the genus *Dorcasia* (an indicator of a summer rainfall climatic regime, contrasting with the present day winter rainfall regime of the Sperrgebiet) and an elongated small subuliniform snail. No freshwater snails are known from this site. There are many small crocodile teeth in the deposits and freshwater fish teeth are quite common, although none were found in the 2019 sample.

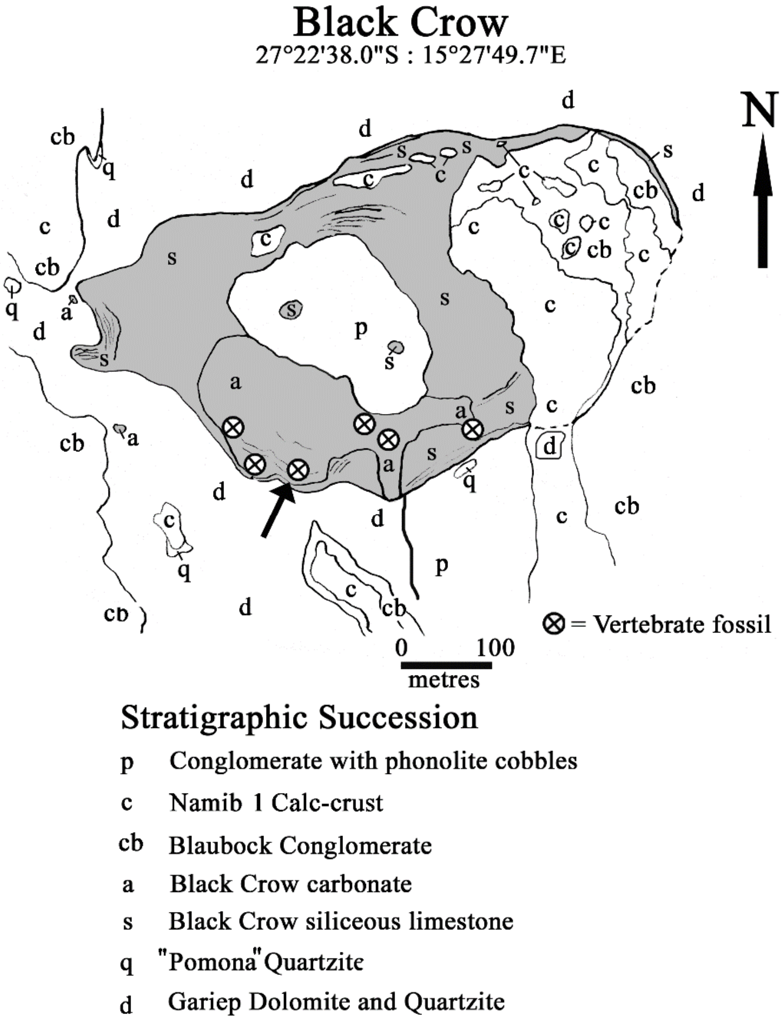

Figure 1. Geological sketch map of the freshwater limestone outcrops at Black Crow, Sperrgebiet, Namibia, showing the locality from which the limestone blocks discussed in this paper were collected (large black arrow).

Material and methods

150 kg of limestone were collected from Black Crow (Fig. 1) and delivered to the laboratory in Paris for acid treatment. The blocks were bathed in formic acid (7%) without buffer (previous attempts to use calcium triphosphate buffer resulted in a precipitate covering the fossils which rendered it difficult to pick out from the insoluble residue and almost impossible to clean without damaging the fossils). Once the fossils had been released from the limestone they were washed in fresh water for 24 hours, dried and then consolidated with a solution of plexigum dissolved in acetone. Images were obtained using a Sony Cybershot camera by placing the lense over the eyepieces of a stereo microscope and treating the images with Photoshop Elements15 to increase contrast and remove unwanted background. Scales were added manually.

Abbreviations

BC - Black Crow
DPC - Duke Primate Center
GSN - Geological Survey of Namibia, Windhoek
TM - Transvaal Museum (now the Ditsong National Museum of Natural History), Pretoria

Systematic Palaeontology

Suborder Tenrecomorpha Butler, 1972

Genus *Nanogale* nov.

Diagnosis: Minute tenrecomorph with mandibular foramen in a very posterior position close to the termination of the angle of the jaw. Clear separation between the lingual and buccal parts of the alveolar process distal to the tooth row, the coronoid part rising at an angle of ca 70°, the lingual part (endocoronoid crest) extending horizontally and forming a strong lingual wall for a deep coronoid fossa. Mandibular condyle low down, in line with the cheek teeth. Mental foramen beneath the p/3. Lower permanent dental formula 3-1-3-3. Smaller than *Eochrysochloris* Seiffert *et al*. 2007, *Dilambdogale* Seiffert (2010), *Jawharia* Seiffert *et al*. (2007), *Qatranilestes* Seiffert (2010), *Widanelfarasia* Seiffert & Simons (2000), *Namagale* Pickford, (2015b), *Sperrgale* Pickford (2015b), *Arenagale* Pickford (2015b) ; *Protenrec* Butler & Hopwood (1957), *Erythrozootes* Butler & Hopwood (1957) and *Promicrogale* Pickford (2018a).

Etymology: The genus name is a combination of the Greek word 'nano' in refererence to the its tiny dimensions, linked to the word 'gale' meaning 'weasel', a suffix commonly used when naming potamogalids, tenrecids, other insectivorans and small carnivores.

Type species *Nanogale fragilis* nov.

Diagnosis: As for genus. Length of mandible from incisor alveoli to angle ca 8.6 mm; length m/1+m/2+m/3 = 2.29 mm.

Etymology: The species name refers to the extremely fragile nature of the specimen referred to it.

Holotype: GSN BC 3'19, left mandible containing p/3-m/3 and alveoli of i/1-i/3, c/1 and two alveoli of p/2.

Description

The mandible of *Nonogale fragilis* possesss some peculiar characteristics, among which figures a deeply concave coronoid fossa bordered lingually by a strong mandibular buttress, the endocoronoid crest (Seiffert *et al*. 2007). The sheet of bone between the coronoid process and the condylar process is reduced to a low wall on the lateral side of the coronoid fossa, expanding slightly as it approaches the condyle. This part of the mandible superficially resembles the morphology in *Dasypus hybridus* (Abba & Superina, 2016) but the rest of the jaw and the teeth of the two genera are completely different. The mandibular foramen is positioned close to the posterior end of the jaw and lower than the tooth row. Unlike most mammals, the lingual and buccal parts of the alveolar process do not coalesce distal to the m/3, but the buccal part rises at an angle of ca 70° to form the coronoid process, while the lingual part extends directly distally as a strong ridge, the endocoronoid crest, which forms the lingual wall of the deep coronoid fossa and terminating distally as the condylar process.

The ramus is long, slender and shallow. In lingual view, the ventral margin of the ramus is observed to be gently curved, deepest beneath the molars and rising gently anteriorly and posteriorly where it flexes gently ventrally towards the posterior end of the angle (Fig. 2, 3). The symphysis is unfused and short, ending beneath the canine alveolus. It has an elongated central depression. The alveolar margin is straight from m/3 to p/3 then rises gently towards the incisors. The endocoronoid crest is a straight horizontal bony ridge behind the m/3 which extends posteriorly towards the condyle, forming the lingual wall at the base of the coronoid fossa. The condyle is at the same level as the occlusal surface of the cheek teeth. The mandibular foramen opens far back in the re-entrant between the condylar process above and the posterior end of the angle below (Fig. 4). As such it is well beneath the level of the alveolar process and the mandibular canal courses in almost a straight line from its origin at the foramen to the level of the p/3. The angle of the jaw itself is short and slightly recurved medially.

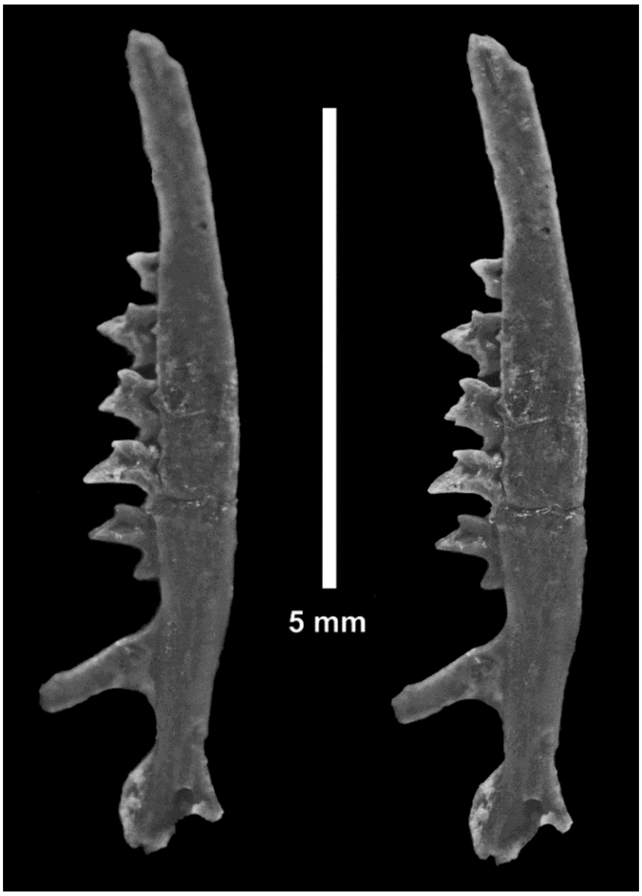

Figure 2. Stereo lingual view of GSN BC 3’19, mandible of *Nanogale fragilis*, after repair. The coronoid process is slightly out of position. Note the groove in the symphyseal surface and the extremely low and posterior position of the mandibular foramen (scale : 5 mm).

In lateral view, the coronoid process is seen to rise well behind the m/3 at an angle of about 70° (Fig. 3, 5, 6). Posterior to the coronoid process there is a large space bordered ventrally by the thin lateral margin of the coronoid fossa. The edge of the thin bone forming the lateral margin of the coronoid fossa descends gently from the base of the coronoid process then rises gently as it approaches the condyle to form a lamina of bone which then curves in the opposite sense before blending into the condylar process near the distal end of the jaw. There is a single mental foramen, opening at mid-height of the ramus between the roots of the p/3.

In dorsal view the entire jaw is remarkably straight (Fig. 6, 7).

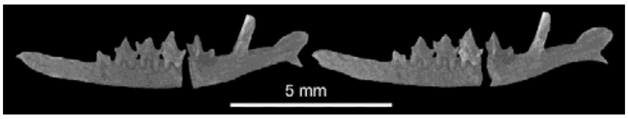

Figure 3. Stereo image of the buccal side of GSN 3’19, left mandible of *Nanogale fragilis* with the coronoid process in position prior to breaking off (scale : 5 mm).

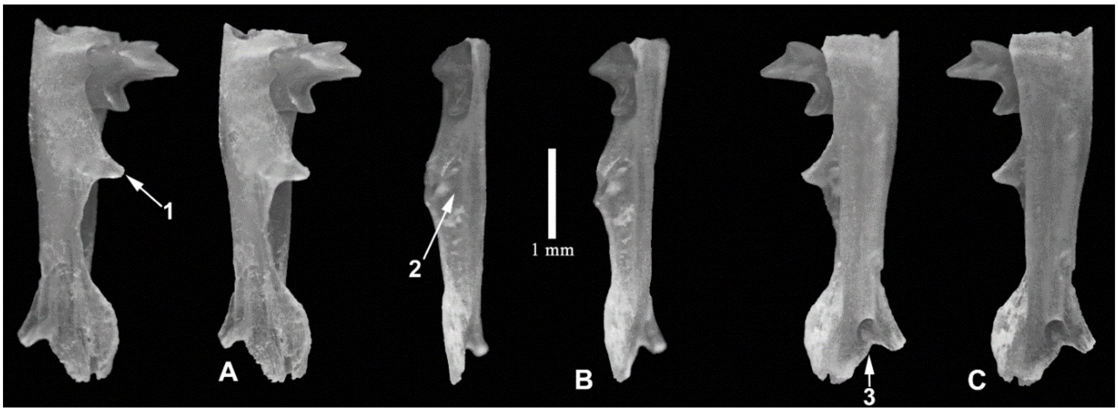

Figure 4. Stereo images of the posterior part of GSN BC 3'19, holotype left mandible of *Nanogale fragilis* gen. et sp. nov. from Black Crow, Namibia. A) buccal view, B) occlusal view, C) lingual view to show details of the condylar process, the angle and the posteriorly situated mandibular foramen. 1 - base of the coronoid process, 2 - coronoid fossa, 3 - mandibular foramen (scale : 1 mm).

There are three procumbent incisor alveoli but they are damaged ventrally, the one for the second incisor is seemingly slightly bigger than those for the i/1 and the i/3. The canine alveolus is close behind that of the i/3 and is ovoid in outline with a slight undulation on the lingual side suggesting that the root of the tooth possessed a shallow longitudinal groove. This alveolus slants disto-ventrally. There is a short diastema behind the canine alveolus followed by two alveoli close together which slope disto-ventrally, sub-parallel to the alveolus of the canine. These alveoli are interpreted to correspond to a two-rooted p/2 rather than representing alveoli for single-rooted p/1 and p/2. The diastema behind the alveolus for the p/2 is somewhat longer than the one in front of it. The two roots of the p/3 are splayed apart, the anterior one slanting slightly antero-ventrally, the posterior one slightly disto-ventrally. The roots of the p/4 and the three molars are almost vertical.

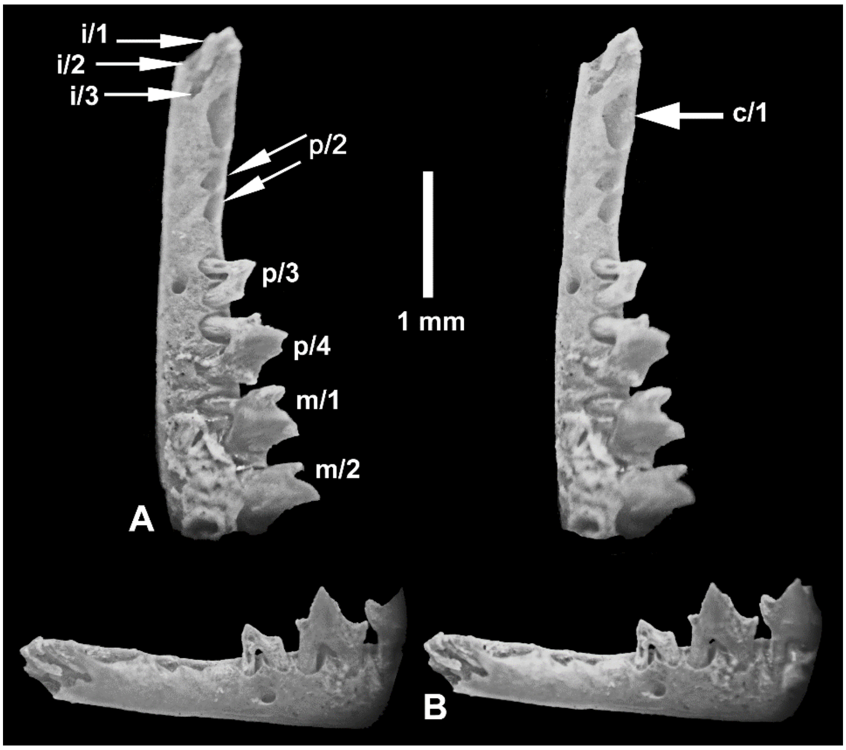

Figure 5. Close-up stereo images of the anterior part of the ramus of GSN BC 3'19, the holotype mandible of *Nanogale fragilis* gen. et sp. nov. from Black Crow, Namibia, to show details of incisor and post-incisor alveoli. A) and B) buccal views (scale : 1 mm).

Table 1. Measurements (in mm) of GSN BC 3'19, the holotype mandible of *Nanogale fragilis* gen. et sp. nov. from Black Crow, Namibia.

Length of mandible from incisor alveoli to posterior end of angle	8.6
Greatest depth of ramus beneath m/2	0.8
Depth of ramus beneath p/3	0.6
Distance from rear of m/3 to posterior end of angle	2.63
Length p/3 to m/3	3.45
Length p/4	0.70
Length m/1	0.73
Length m/2	0.78
Length m/3	0.78

There are three incisor alveoli, but the teeth are missing. Judging from the remnants of the alveoli, the i/2 was probably slightly larger than the i/1 and i/3.

The canine is single-rooted and much larger than the incisors. Its root and the two roots of the p/2 descend disto-ventrally into the ramus.

The p/2 was a two-rooted tooth with the roots sub-parallel to each other and close together, but not coalescent. The p/3 is damaged by corrosion, but it is possible to infer that it was significantly smaller than the p/4.

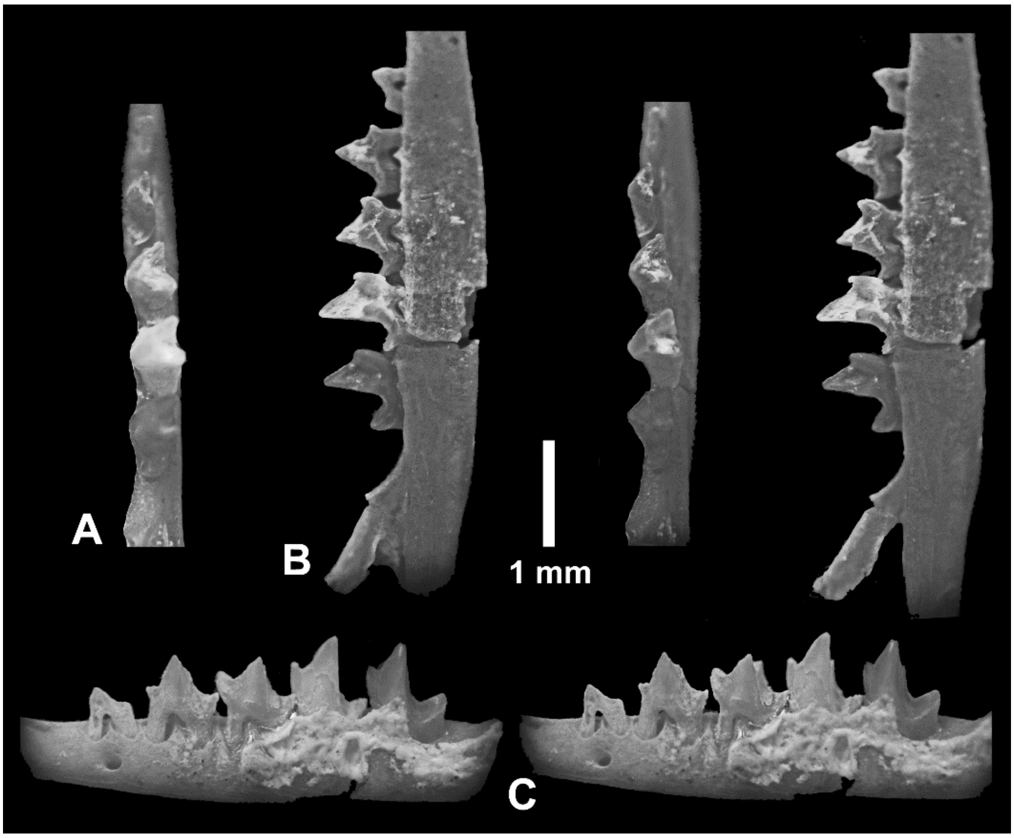

Figure 6. Close-up stereo images of the cheek teeth of GSN BC 3'19, the holotype mandible of *Nanogale fragilis* gen. et sp. nov. from Black Crow, Namibia. A) occlusal view, B) lingual view, C) buccal view (scale : 1 mm).

The crown of the p/3 is too corroded to provide any useful details of crown morphology, but it is possible to surmise that it was appreciably smaller than the p/4 and that it has two roots. It is separated from the p/4 by a short gap, but this could be due to the loss of the talonid of the tooth rather than signifying the presence of a diastema between the two teeth.

The p/4 is molariform, but with the trigonid less well-defined and more bucco-lingually compressed than in the molars. The paraconid is low and projects anteriorly, the metaconid is tall, being only slightly lower than the protoconid and slightly behind it. The precingulid slopes downwards gently towards the buccal side of the tooth. The talonid is very low and positioned more towards the buccal side of the midline of the tooth.

The m/1 is a larger version of the p/4, but with the trigonid more inflated bucco-lingually. The postprotocristid is slightly oblique extending disto-lingually at a small angle towards the premetacristid. The paraconid is about half the height of the protoconid and the metaconid is slightly lower than the protoconid and is positioned slightly behind it. There is a low-relief precingulid. The talonid is low and its hypoflexid is tilted slightly buccally.

The m/2 and m/3 are similar to each other and both are slightly larger than the m/1. The precingulid is low down on the mesial edge of the tooth, well beneath the paraconid and protoconid. The paraconid and metaconid are subequal in dimensions and are 2/3rds the height of the protoconid and are well separated at their apices with a deep gulley between them on the lingual aspect of the crown representing the lingual opening of the trigonid basin. The postprotocristid and premetacristid form a transverse wall to the trigonid basin. The talonid is bucco-lingually narrow and the hypoflexid is relatively expansive comprising about half the occlusal area of the talonid. The hypoconulid is 1/3rd the height of the protoconid and the cristid obliqua slopes forwards and downwards towards the base of the metaconid and, as a result, the talonid basin is small and shallow.

Discussion

The mandible of *Nanogale fragilis* shows some peculiar features concentrated in the posterior part of the jaw. The coronoid fossa is deeply excavated and has a robust lingual wall and a thin, low lateral wall. The condylar process is low down, such that the condyle is at about the same level as the occlusal surface of the cheek teeth. The angular process is short and medially recurved and bends ventrally and between it and the condyle there is a prominent mandibular foramen which is located below the level of the tooth row. The mandibular canal runs directly anteriorly, emerging at a mental foramen between the roots of the p/3.

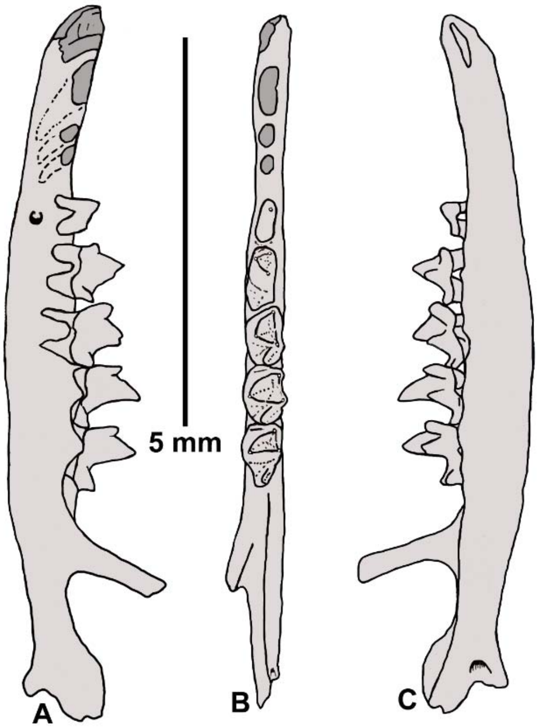

Figure 7. Interpretive sketch of GSN BC 3'19, the holotype left mandible of *Nanogale fragilis* from the Eocene limestone at Black Crow, Namibia. A) buccal, B) occlusal, C) lingual views (scale : 5 mm).

There are three procumbent incisors, a slanting canine, the p/1 is absent and the p/2 has two sub-parallel roots which are inclined ventro-distally in the ramus. The canine is separated from the incisors and the p/2 by short diastemata and there is another diastema between the p/2 and p/3.

The molars of *Nanogale fragilis* have prominent trigonids and somewhat reduced and low talonids, which are slightly bucco-lingually compressed.

Comparison of this jaw with those of various mammals is a challenge. Many of the fossil afrosoricid mandibles described do not preserve the distal parts of the jaw. The post-dental part of the jaw of *Nanogale* differs from the corresponding part of mandibles of many tenrecoids and potamogalids, as well as those of most other mammals. The dentition, however, most closely recalls those of tenrecomorphs.

For this reason, *Nanogale* is included in the Tenrecomorpha, but with the understanding that it is a peculiar member of the suborder. Whether it is closer to Tenrecidae or to Potamogalidae is a moot point, with the balance slightly in favour of it being a tenrecid.

Nanogale differs from *Todralestes* Gheerbrant (1991) by the short retromolar space and the steeper coronoid process in the latter genus. It is also smaller (length m/1-m/3 in *Todralestes variabilis* is 3.9 mm, in *Nanogale fragilis* it is 2.9 mm).

There are some dental similarities between *Eochrysochloris* Seiffert *et al*. (2007) and *Nanogale fragilis* but the latter genus is considerably smaller and the talonids of the molars are more bucco-lingually compressed such that the cristid obliqua is positioned lingual to the midline of the crown, unlike the situation in *Eochrysochloris* in which it is largely buccal of the midline of the tooth. The distal part of the jaw is unknown in *Eochrysochloris*, so no comparisons can be made.

Dilambdogale Seiffert (2010) from the Fayum, Egypt, is much larger than *Nanogale*. The morphology of the jaw in the vicinty of the coronoid process is different, in particular concerning the presence of a deep masseteric fossa in *Dilambdogale* (only the base is preserved in DPC 23783B, from BQ-2, Birket Qarun Formation, Fayum, Egypt). Both the Namibian and Egyptian jaws have long retromolar spaces between the m/3 and the base of the coronoid process. The talonids of the m/2 and m/3 in *Dilambdogale* appear to be taller relative to trigonid height than they are in *Nanogale*.

Jawharia Seiffert *et al*. (2007) from Quarry E, Jebel Qatrani Formation, Egypt, is larger than *Nanogale*. The rear of the mandible of *Jawharia* is almost complete and it reveals major differences from that of *Nanogale*. In *Jawharia* there is a sheet of bone between the coronoid process and the condylar process on the lateral surface of which is a well-developed masseter fossa. The corresponding area is devoid of a sheet of bone in *Nanogale*. The mandibular condyle is slightly above the level of the tooth row in *Jawharia* but is lower in *Nanogale*. Finally, the coronoid fossa in *Jawharia* is shallow, whereas in *Nanogale* it is deep and is bordered by a robust lingual ridge, the endocoronoid crest.

Qatranilestes Seiffert (2010) from Quarry L, Jebel Qatrani Formation, Egypt, is larger than *Nanogale*. Poorly known due to the fragmentary nature of the available sample, it is difficult to make detailed comparisons, but it is noted that it also has a long retromolar space.

Widanelfarasia Seiffert & Simons (2000) from the Jebel Qatrani Formation, Egypt, is larger than *Nanogale* and the trigonids in the lower molars are more mesio-distally compressed, with the paraconid closer to the metaconid than in *Nanogale*. The protoconid of p/4 is appreciably taller relative to tooth length in *Widanelfarasia* than it is in *Nanogale*.

Nanogale differs from *Namagale* Pickford (2015b) by its considerably smaller dimensions. The rear of the jaws are morphologically divergent, with *Namagale* from Eocliff possessing a well-developed sheet of bone between the coronoid process and the condylar process with a shallow masseteric fossa on its lateral aspect. *Namagale* has an exceedingly shallow coronoid fossa, unlike the deep and capacious fossa that occurs in *Nanogale*. The mandibular condyle is missing in the *Namagale* sample but it was at about the same level as the occlusal surface of the cheek teeth and thus higher than it is in *Nanogale*. The molar talonids of *Namagale* are broader bucco-lingually than those of *Nanogale*.

Sperrgale Pickford (2015b) is slightly larger than *Nanogale*. The rear of the jaw in *Sperrgale* is well-represented and it shows a number of differences from that of *Nanogale*. The mandibular condyle is above the level of the cheek teeth in *Sperrgale*, below it in *Nanogale*. There is a clear masseteric fossa and a shallow coronoid fossa in *Sperrgale* and interestingly, the sheet of bone between the coronoid process and the condylar process is quite small, but not nearly as reduced as it is in *Nanogale*. There is a strong bony margin to the coronoid fossa in *Sperrgale*, as in *Nanogale*, but the fossa is not as deeply excavated. Like *Sperrgale*, there is no p/1 in *Nanogale*, but the mental foramen is beneath the p/2 rather than the p/3. The mandibular foramen is at the same level as the cheek teeth in *Sperrgale*, but is lower than them in *Nanogale*. However, of all the fossil tenrecomorphs described, *Sperrgale* is closest morphologically to *Nanogale*.

The mandible of *Arenagale* Pickford (2015b) is rather poorly represented, so comparisons with *Nanogale* are limited to the lower dentition. The talonids of the lower molars of *Arenagale* are almost as broad bucco-lingually as the trigonids unlike the narrower talonids in *Nanogale*. *Arenagale* is the smallest of the Eocliff tenrecomorphs, but it is larger than *Nanogale*, which is currently the smallest known fossil representative of the suborder Tenrecomorpha.

Protenrec Butler & Hopwood (1957) from the early Miocene of Songhor, Kenya, is appreciably larger than *Nanogale* (length m/1-m/3 is 4.9 mm in *Protenrec* versus 2.9 mm in *Nanogale*). *Protenrec* resembles *Nanogale* in the low position of the mandibular foramen and the presence of an endocoronoid crest (albeit much weaker) but it differs from it by the somewhat more anteriorly positioned mandibular foramen, by the presence of a well-developed sheet of bone between the coronoid process and the condylar process, by the shallow coronoid fossa and by the presence of a mental foramen beneath the m/1 (Butler & Hopwood, 1957; Butler, 1984). The lower molars of *Protenrec* are comparable in morphology to those of *Nanogale* with the talonid somewhat narrower bucco-lingually than the trigonid.

Erythrozootzes Butler & Hopwood (1957) from the early Miocene of Kenya and Uganda, is much larger than *Nanogale*. The retromolar space is relatively short in *Erythrozootes* and the coronoid process rises at a steeper angle than in *Nanogale*.

Nanogale differs from *Promicrogale* Pickford (2018a) from the basal Miocene of Elisabethfeld, Namibia, by its slightly smaller dimensions (the length of m/1-m/3 in *Promicrogale* is 3.2 mm) by the lack of diastemata between the canine, the p/2 and p/3. The symphysis in *Promicrogale* is elongated, terminating posteriorly at the level of the anterior root of the p/4, and its surface is corrugated, unlike the short, relatively smooth symphyseal surface in *Nanogale* which ends beneath the root of the canine (indistinctly it must be admitted). The posterior part of the jaw of *Promicrogale* curves more steeply upwards behind the m/3 but the distal part is broken off. However, what remains suggests that the condyle would have been at about the level of the occlusal surface of the cheek teeth or slightly above it, because the entocoronoid crest rises dorso-posteriorly rather than running horizontally as in *Nanogale*. The paraconid and metaconid in the molars of *Promicrogale* are taller relative to the protoconid than in *Nanogale*.

Comparisons with extant tenrecs reveals several similarities in the dentition to forms such as *Microgale*, but few in details of the rear of the mandible. Like *Nanogale*, in *Microgale* the mental foramen lies beneath the p/3, there is no p/1, the p/2 has two roots that are inclined in the jaw and the symphysis is unfused. *Microgale* has a coronoid fossa bordered lingually by a ridge of bone that terminates distally as the condylar process, but the fossa is shallower than in *Nanogale*, and there is a sheet of bone between the coronoid process and the condylar process. Furthermore, in *Microgale*, the posterior part of the jaw bends upwards at the level of the m/3 which makes the coronoid process steeper, and lifts the mandibular condyle upwards so that it is above the occlusal surface of the cheek teeth. Thus, even though *Nanogale* has some dental resemblances to *Microgale*, its mandible is divergent, especially the posterior part.

Comparisons between the mandibles of potamogalids and *Nanogale* reveal few similarities except in the low positions of the condyle, the mandibular foramen and the angle. In *Potamogale* the coronoid process is almost vertical, the distal part of the jaw has a well-developed sheet of bone between the coronoid process and the condylar process, the condyle is at the same level as the occlusal surface of the cheek teeth, and there is a greater distance between the condyle and the angle, all of which are different from the condition in *Nanogale*. Furthermore, in *Potamogale* there is a mental foramen beneath the p/2 in addition to the ones beneath the p/3 and m/1.

Discussion and Conclusion

An almost complete micromammalian mandible from the middle Eocene Black Crow limestone, Namibia, is interpeted to belong to a new genus and species of Tenrecomorpha, herein named *Nanogale fragilis*. The fossil jaw shows several peculiar features including a large and deep coronoid fossa bordered lingually by a well-developed endocoronoid crest but the sheet of bone between the coronoid process and the condylar process is low, only increasing in height as it approaches the condyle. The condyle is low down, below the level of the occlusal surface of the cheek teeth and the mandibular foramen is far back.

Despite these differences from mandibles of Tenrecomorpha, the dentition of *Nanogale* shows affinities with some members of this sub-order, especially *Microgale* and to some extent *Protenrec*. The permanent lower dental formula is the same as that of *Microgale* (3, 1, 3, 3) and the p/2 is two-rooted, with the roots sub-parallel to each other and inclined in the jaw.

The most striking aspect of *Nanogale*, as its name implies, is its minuscule size. The entire jaw is a mere 8.6 mm long. This is as small as the lower jaw of a female *Suncus orangiae orangiae* (T.M. 2564 from Bothaville, Orange Free State, in Roberts, 1951) one of the smallest extant non-chiropteran African mammals.

No attempt is made to discuss the phylogenetic relationships of the new genus, *Nanogale*, partly because only the mandible is currently known and partly because many recent phylogenetic analyses of Afrotheria seem to be incompatible with each other (Asher, 2001; Seiffert *et al.* 2007). Most of them are heavily biassed towards molecular evidence and the few analyses that include fossils rely on fragmentary specimens which yield only a few characters, some of which are of doubtful value for phylogeny reconstruction.

The focus needs to be on the recovery of additional fossil material in an effort to obtain improved evidence of Palaeogene mammalian diversity rather than producing phenograms that obscure relationships rather than clarifying them.

The lower jaw of *Nanogale fragilis* is morphologically remote from those of Paenaungulata and many Tenrecomorpha (Afroinsectiphilia) to the extent of throwing doubt on the hypothesised homogeneity of the Superorder Afrotheria (Stanhope *et al.* 1998). This conclusion agrees with the results of the analysis by Averianov & Lopatin (2016).

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Adapisoriculidae from the Southern Hemisphere

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Abstract: Adapisoriculidae is a family of primitive small mammals known from India, Europe and Northern Africa ranging in age from Late Cretaceous to early Eocene. The 2019 sample of limestone from Black Crow, Namibia, yielded an upper molar which is interpreted to belong to this enigmatic family, thereby greatly extending the geographic range of the group. The specimen is described and illustrated but is left in open nomenclature, pending recovery of more complete remains.

Key words: Adapisoriculidae, Ypresian/Lutetian, Upper molar, Namibia

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Introduction

This paper reports the discovery of an upper molar interpreted to belong to Adapisoriculidae, the first record the family in the Southern Hemisphere. The specimen was collected from the middle Eocene limestones at Black Crow, Namibia. The systematic and phylogenetic relationships of this family of mammals remain enigmatic (De Bast *et al*. 2012; Kapur *et al*. 2017a, 2017b). Until the Black Crow discovery, the geographic distribution of the family was restricted to India, Western Europe and Northern Africa, and its known stratigraphic range spanned the Late Cretaceous to Early Eocene.

The fossil from Black Crow therefore greatly enlarges the geographic range of the family and extends its stratigraphic record upwards into the Ypresian/Lutetian.

Geological context

The geological context and age of the freshwater limestone at Black Crow have been mentioned on several occasions (Pickford *et al*. 2008a, 2008b, 2014, 2015a) (Fig. 1).

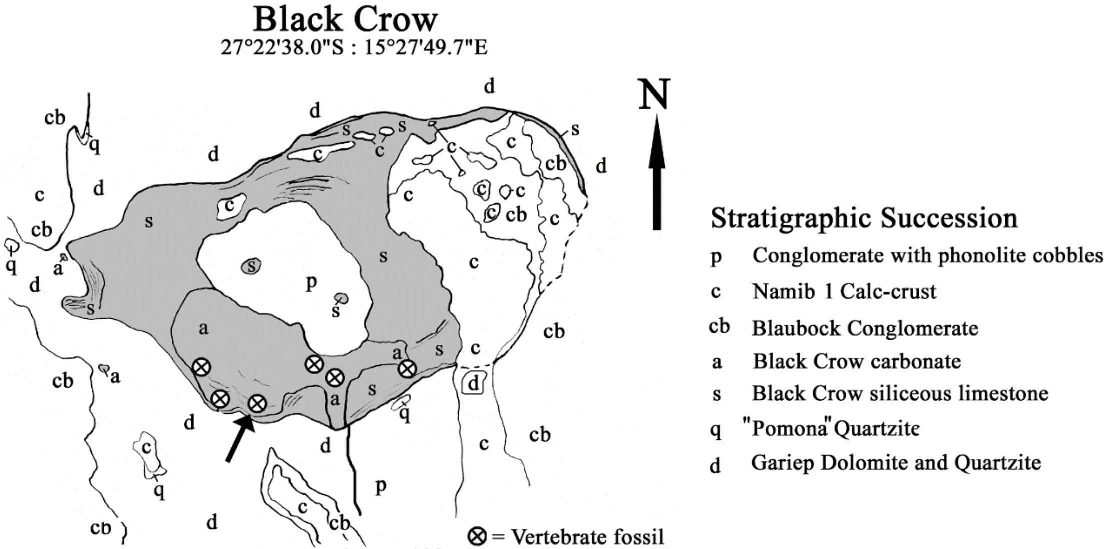

Figure 1. Geological sketch map of the freshwater limestone outcrops at Black Crow, Sperrgebiet, Namibia, showing the locality from which the adapisoriculid tooth discussed in this paper was collected (large black arrow).

Material and methods

The fossil tooth discussed herein was recovered from the insoluble residue left after acid treatment of limestone from Black Crow. It was consolidated in plexigum dissolved in acetone. Photographs were taken by placing the lense of a Sony Cybershot Camera over the eyepieces of a stereo microscope.

Dental nomenclature (Fig. 2) follows the system of Williamson *et al*. 2014.

Comparisons were made with illustrations of *Afrodon* Gheerbrant, 1988; *Adapisoriculus* Lemoine, 1885; *Bustylus* Gheerbrant & Russell, 1991; *Deccanolestes* Prasad & Sahni, 1988; *Garatherium* Crochet, 1984; *Bharatlestes* Kapur *et al*. 2017b; *Proremiculus* De Bast *et al*. 2012; and *Remiculus* Russell, 1964.

Abbreviations

BC - Black Crow
BSIP - Birbal Sahni Institute of Palaeontology, Lucknow, India
GSN - Geological Survey of Namibia, Windhoek
MNHN - Muséum National d'Histoire Naturelle, Paris
NHMUK - Natural History Museum of the United Kingdom, London

Systematic Palaeontology

Class Mammalia Linnaeus, 1758

Infraclass Eutheria Gill, 1872

Order *Incertae sedis*

Family Adapisoriculidae Van Valen, 1967

Genus and species indet.

Description

The upper molar of the Adapisoriculidae from Black Crow (GSN BC 6'19) is in light wear, with small dentine exposures at the apices of the main cusps and wear facets on the subsidiary cusps and along the crests.

Table 1. Measurements (in mm) of GSN BC 6'19, left upper molar of Adapisoriculidae from Black Crow, Namibia, compared to the M2/ of *Proremiculus lagnauxi* from Belgium (De Bast *et al*. 2012).

M2/	GSN BC 6'19	*Proremiculus lagnauxi*
Mesio-distal length	1.49	2.02
Bucco-lingual breadth	1.91	2.64

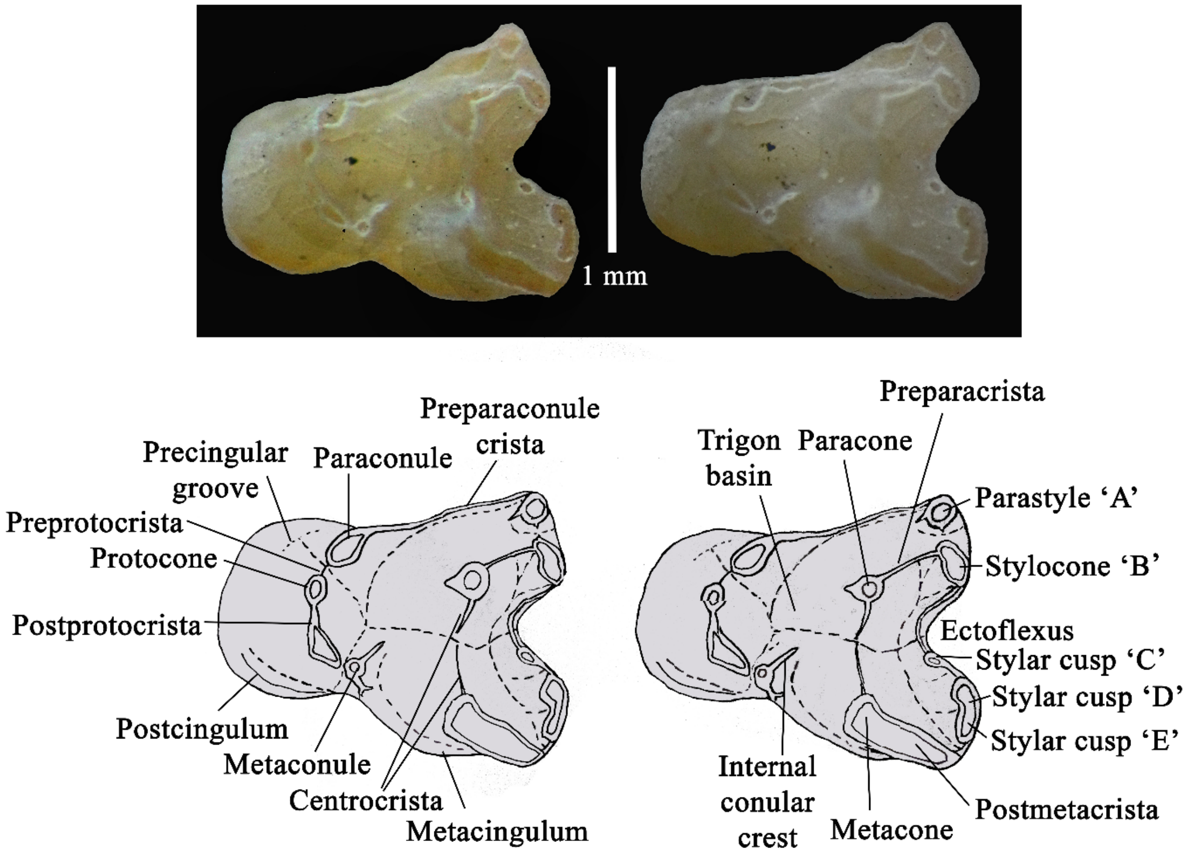

Figure 2. Stereo occlusal view of GSN BC 6'19, upper left molar (likely M2/) of Adapisoriculidae. The stereo drawing defines the nomenclature used in this paper based on Williamson *et al.* 2014 (scale : 1 mm).

The Black Crow adapisoriculid tooth, an upper molar (probably M2/) is bucco-lingually appreciably broader than its mesio-distal length. It has a deep ectoflexus and the paracone and metacone are widely separated from each other, the centrocrista from each cusp not quite joining in the midline of the crown, meaning that the bases of the paracone and metacone are separated from each other. The paraconule and metaconule are clearly expressed and the metaconule has an internal conular crista. The buccal margin of the tooth sports five cusplets, from mesial to distal, the parastyle ('A'), Stylocone (stylar cusp 'B'), Stylar cusp 'C', Stylar cusp 'D' which is accompanied by a small accessory cusplet ('E' in Fig. 2) (unnamed by Williamson *et al.* 2014). There is a well-developed metacingulum and a sharp preparaconule crista. The protocone has a short, shallow groove on its mesial surface, probably corresponding to a precingulum, and it has a clear postcingulum (a structure that was not illustrated by Williamson *et al.* 2014, but which is present in the upper molars of the larger genus *Proremiculus* De Baast *et al.* 2012).

The trigon basin in GSN BC 6'19 is capacious and the buccal shelf quite broad.

Discussion

The morphology of GSN BC 6'19, an isolated upper molar from the middle Eocene limestone of Black Crow, Namibia, accords in most pertinent details to those of most genera of Adapisoriculidae, with one exception, the presence of a cingular structure on the distal surface of the protocone (present, however, in *Proremiculus*). Comparison with illustrations of upper molars of diverse genera of this family indicate that it is closest in overall morphology to the genus *Proremiculus* De Bast *et al.* 2012, from the early Paleocene of Hainin, Belgium. Like his genus, the Black Crow specimen has a horizontal mesial groove on the protocone and a postcingulum, two structures which also resemble the situation in the todralestid *Todralestes variabilis* from Morocco (Gheerbrant, 1991, 1994) but the buccal shelf of the latter species is narrower than in the Black Crow tooth, the ectoflexus is not as deep and there are no signs of stylar cusplets 'B', 'C' and 'D'.

The historical review of the Adapisoriculidae by De Bast *et al*. 2012, indicates an extremely diverse series of interpretations by the various authors who have studied the fossils, with little consensus emerging about the suprafamilial (and even the familial) affinities of the group. This is fuelled to a great extent by the plesiomorphic condition of the teeth attributed to this family, members of which historically have been linked to Lipotyphla, Dermoptera, Nictitheriidae and even to Marsupialia among others.

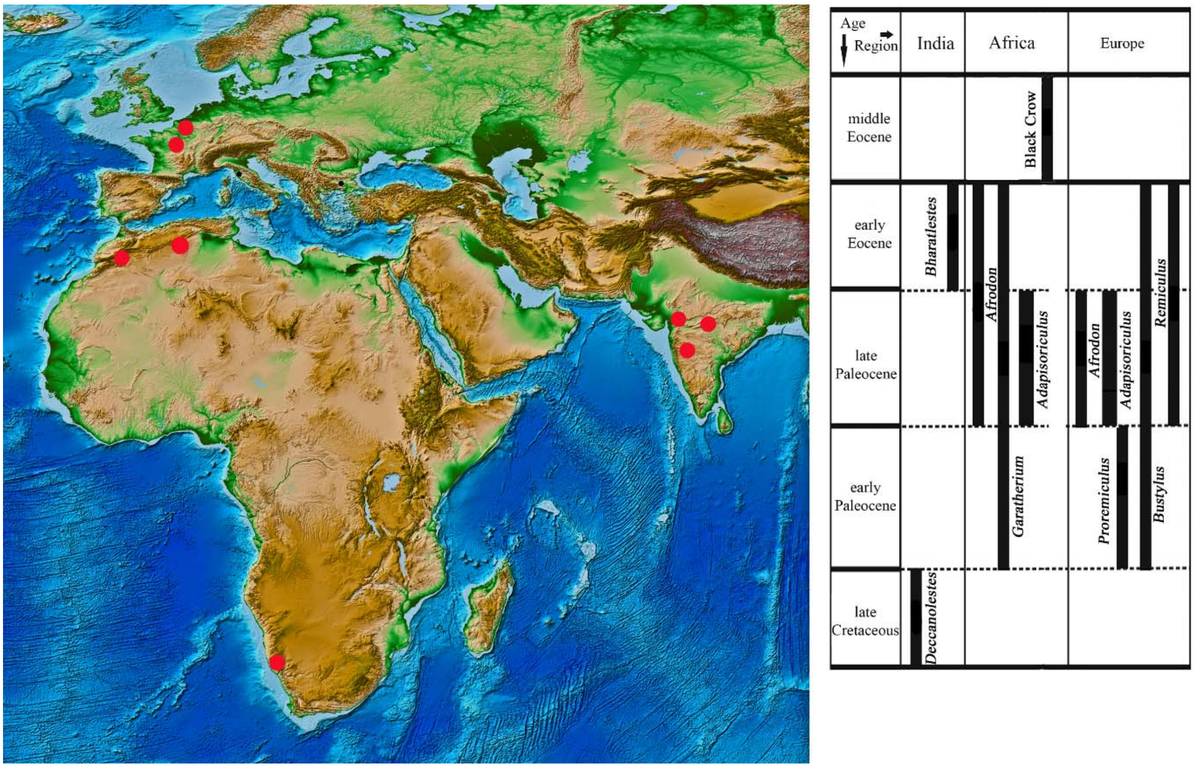

Figure 3. Geographic and stratigraphic distribution of Adapisoriculidae. Data from Kapur *et al*. 2017a and Crochet, 1984, with addition of the Black Crow specimen.

Given that the Black Crow tooth is isolated and with the exception of *Proremiculus*, differs from most other adapisoriculid upper molars in respect of the presence of a cingulum on the distal surface of the protocone, the genus and species to which it belongs are left in open nomenclature, in the hope of recovering more informative specimens.

Nevertheless, the presence of an adapisoriculid or a close relative of this family in the Ypresian/Lutetian of Namibia is of great interest, not just because of the great geographic extension of the distribution of the family and a stratigraphic extension upwards into the Middle Eocene, but also because, being quite plesiomorphic it could have given rise to more derived mammals, including tenrecomorphs or todralestids, for example.

The relationships of the Black Crow adapisoriculid to other groups of mammals from the same locality are enigmatic, but there could be some link to the genus *Nanogale* (Pickford, 2019) which is considered to be a primitive tenrecomorphan, but direct comparisons are not possible because *Nanogale* is known only from a mandible. However, against this possibility is the fact that the hypoconid of the lower molars of *Nanogale* is not in line with the paraconid and metaconid, unlike the situation in adapisoriculids in which these three cuspids are disposed in almost the same line (De Bast *et al*. 2012; Kapur *et al*. 2017a) along the almost straight lingual margin of the crown.

Conclusion

A tiny isolated mammalian upper molar from the Ypresian/Lutetian of Black Crow, Namibia, is compatible in morphology and its minute dimensions to fossils attributed to the family Adapisoriculidae, previously known only from India, Western Europe and the northern extremities of Africa. This discovery, even though limited to a single tooth, indicates that the geographic range of the family was likely considerably greater than previously reported, and that it may have persisted into the Middle Eocene. Its affinities to other adapisoriculids remain to be established, but it seems to be closest in overall morphology to *Proremiculus* from the early Paleocene of Europe.

The Black Crow fossil is left in open nomenclature, pending the recovery of more complete specimens, this report being a preliminary announcement of the presence of the family in Southern Africa and of the extension of its stratigraphic range into the middle Eocene.

Acknowledgements

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Mandible of *Namahyrax corvus* from the Eocene Black Crow Limestone, Namibia

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Abstract: In 2019 an adult mandible of *Namahyrax corvus* was discovered during acid treatment of limestone blocks from Site A at Black Crow (Ypresian/Lutetian) Namibia. The specimen confirms the peculiar morphology of the symphysis already observed in a juvenile specimen from the same site and it reveals a reduced dental formula (tendency to suppress i/3, suppression of the permanent lower canine) and the presence of elongated diastemata between the i/2 and the p/1. The long gap between the incisors and the anterior cheek tooth indicates that food acquisition was distinct from mastication. The symphysis is weakly fused posteriorly despite the fact that in this individual the m/3 is fully erupted and in light wear.

Key words: Hyracoidea, Mandible, Palaeogene, Namibia, Dental morphology.

To cite this paper: Pickford, M. 2019. Mandible of *Namahyrax corvus* from the Eocene Black Crow Limestone, Namibia. *Communications of the Geological Survey of Namibia*, **21**, 32-39.

Introduction

In May-June 2019, the Namibia Palaeontology Expedition processed 150 kg of limestone from Black Crow in the hope of obtaining additional fossils from these Eocene deposits.

The exercise was successful, with the discovery of several mandibles, a maxilla, isolated teeth and postcranial bones of tiny mammals, over 110 crocodile teeth, abundant scincid jaws and vertebrae and some bird bones, snail steinkerns and fruits of *Celtis*.

Among the larger fossils recovered is an adult mandible of *Namahyrax corvus*. The specimen shows several features which indicate that the genus is remote from most other described hyracoids, showing several characters in the symphyseal parts which are unique in the order, and which in some ways suggest morphofunctional convergence towards sirenians. Among these is the presence of several prominent mental foramina with anterior grooves, a down-bending of the symphysis, retarded fusion of the symphysis, and the tendency to lose the i/3 and suppression of the permanent lower canine.

Geological and faunal contexts

The geological context of the Black Crow Limestone was described by Pickford *et al.* (2008a) and Pickford (2015a). The deposits comprise almost pure calcium carbonate : after acid attack of 150 kg of limestone the insoluble residue, including fossils, weighs less than 1 kg. This sample was collected at site A (Pickford, 2018a, fig. 1).

The abundance of crocodile teeth (112 specimens in 150 kg of raw material) and the presence of silicified plant root systems indicates deposition in a freshwater swamp or a low energy fluvial backwater.

The associated fauna consists of freshwater fishes and crocodiles (Pickford, 2018b), land snails (Pickford, 2018a) squamates, birds and mammals (Pickford *et al.* 2008b; Pickford, 2015b, 2015c, 2015d, 2015d, 2018c).

The limestones are considered to date from the late Ypresian or early Lutetian (Pickford, 2018a, 2018b, 2018c).

Material and methods

150 kg of limestone were collected at Site A, Black Crow (Pickford, 2018a, fig. 1). Blocks were selected at random, and none of them showed evidence of fossils exposed on the surface.

After transport to Paris, the blocks were dissolved in formic acid (7%) without buffer (addition of calcium triphosphate buffer results in the formation of an insoluble residue that greatly complicates subsequent search for fossils).

Once treated the insoluble residue was washed in freshwater for 24 hours and then dried. Fossils were then picked out using a low power stereo microscope and consolidated in plexigum dissolved in acetone. Broken fossils were fixed with cyano-acrylate.

Images were obtained with a Sony Cybershot camera and treated with Photoshop Elements15 in order to improve contrast and eliminate unwanted background. Scales were added during treatment.

Dental nomenclature

Nomenclature of the lower cheek teeth of Hyracoidea is based on Rasmussen & Simons (1988) (Fig. 1).

The anterior premolars possess reduced trigonids, but many of the same morphological features that occur in the molars can be recognised, but are in vestigial states.

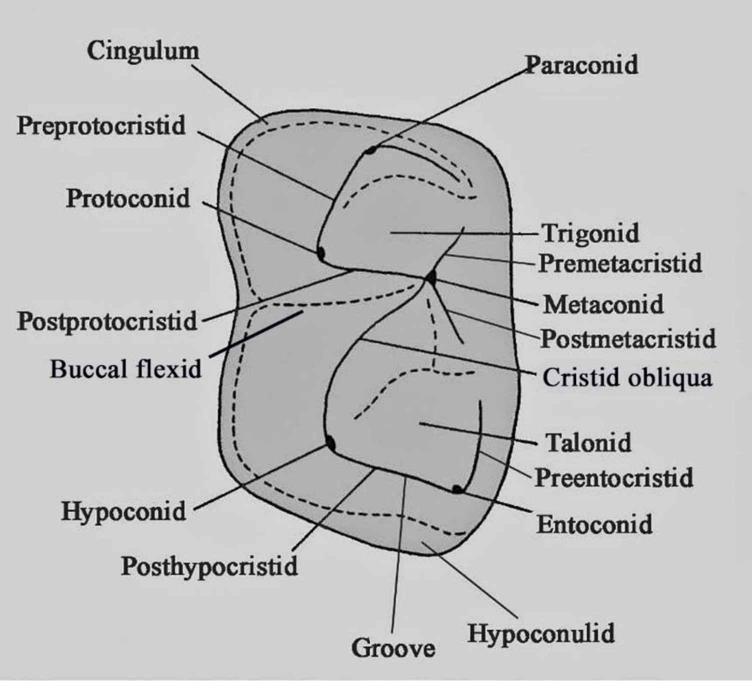

Figure 1. Nomenclature of hyracoid left lower molar modified from Rasmussen & Simons (1988).

Systematic Palaeontology

Order Hyracoidea Huxley, 1869

Genus *Namahyrax* Pickford *et al*, 2008b

Species *Namahyrax corvus* Pickford *et al*, 2008b

Description

GSN BC 1'19 is the symphysis and left mandible of a hyracoid slightly larger than that of extant *Procavia capensis* (the Rock Hyrax) (Figs 2-6). It contains the left p/1-m/3.

The specimen was broken in the matrix but has been successfully reconstructed and preserves the complete symphysis and the left body as far back as the base of the ascending ramus. The jaw beneath the posterior molars is missing but from the m/1 anteriorly it is complete.

In lateral view four mental foramina are observed forming a linear group. The posterior one is beneath the junction between p/3 and p/4 at about mid-height of the ramus. The next one is beneath the p/1, the third is beneath the diastema between the p/1 and the alveolus of i/3, whilst the fourth foramen lies in an elongated gutter beneath the i/3 alveolus. On the right side, the two anterior foramina are preserved, but there is no alveolus for the i/3.

Behind the m/3 the coronoid foramen is conspicuous and it passes backwards and downwards into the mandibular canal. The ascending ramus does not hide the rear of the m/3 in lateral view.

The symphysis is elongated and bends slightly downwards anteriorly such that the incisors would have emerged almost horizontally. The symphysis is compressed in the dorso-volar direction (only 4 mm thick) but deepens beneath the p/1 (ramus 16 mm deep). The ramus is 20.5 mm deep at the rear of m/1, indicating that the jaw as a whole deepens posteriorly.

In superior and ventral views the symphysis is observed to be solidly fused in its anterior three quarters, but the posterior quarter is weakly fused or unfused. On the left side of the symphysis the alveolar margin between the alveoli for the i/2 and i/3 forms a long diastema, and there is a second diastema between the i/3 alveolus and the p/1. On the right side, in contrast, there is no sign of an alveolus for the i/3, so the diastema is continuous from i/2 to p/1 (the latter tooth is missing on this side). The gap measures 22.5 mm in length on the right and left sides.

There is no sign of mandibular swelling in this specimen, but it is noted that the mandibular canal is well-developed and there is cancellous bone above it between the roots of the lower molars.

The alveoli of the i/1s are smaller (l x b : 2.2 x 3.5 mm) and not as deep as those for the i/2s (l x b : 3.0 x 3.8 mm). The single alveolus for the left i/3 is steeply inclined and measures 2.5 x 1.7 mm.

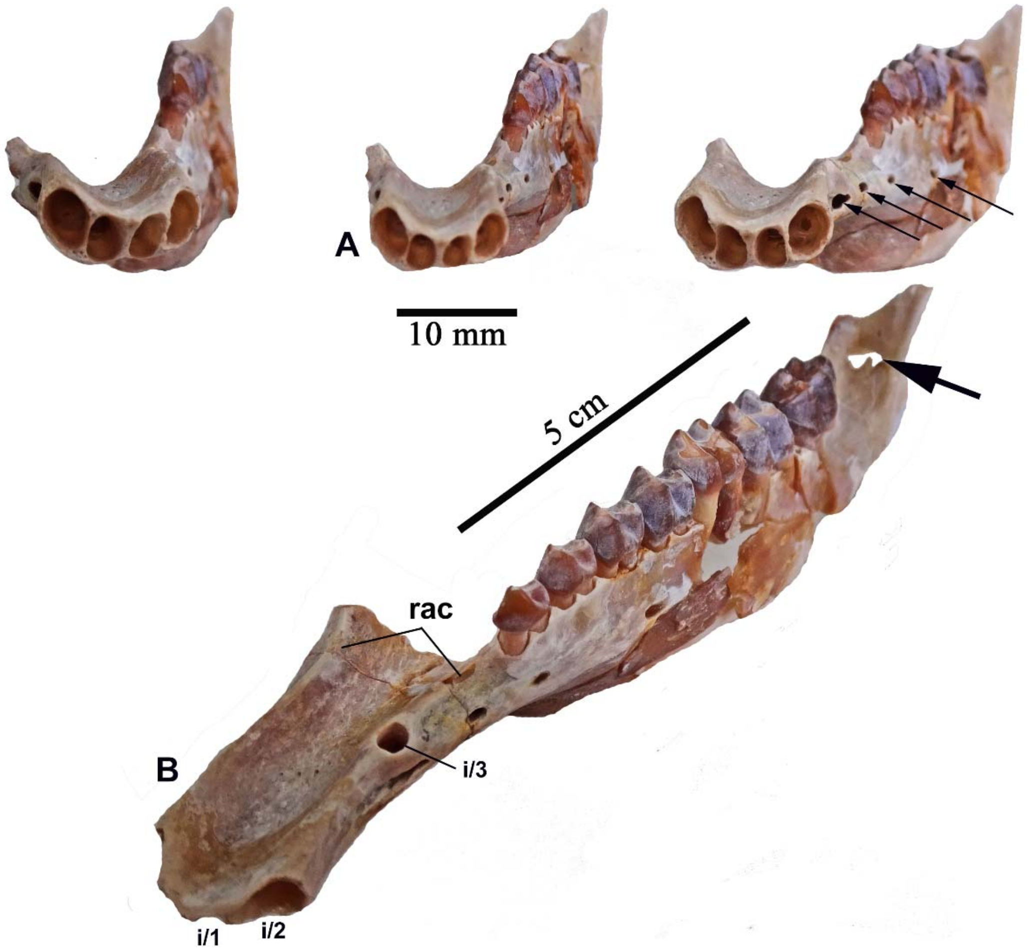

Figure 2. GSN BC 1’19, adult mandible of *Namahyrax corvus* from Black Crow, Namibia. A) stereo anterior views and B) an oblique lateral-occlusal view. Note in particular the alignment of four enlarged mental foramina (thin arrows in ‘A’), the large coronoid foramen (thick arrow in ‘B’) and the absence of i/3 on the right side and the complete suppression of the lower canines (rac : resorbed alveoli of the lower canines).

Figure 3. Stereo occlusal views of adult mandible, GSN BC 1'19, of *Namahyrax corvus* from Black Crow, Namibia.

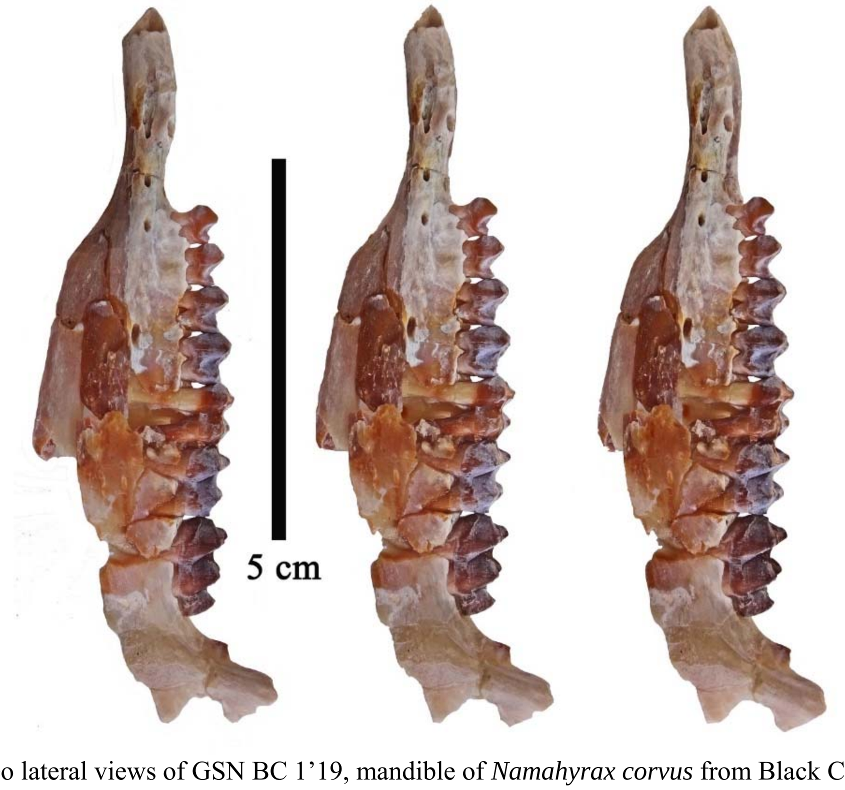

Figure 4. Stereo lateral views of GSN BC 1'19, mandible of *Namahyrax corvus* from Black Crow, Namibia.

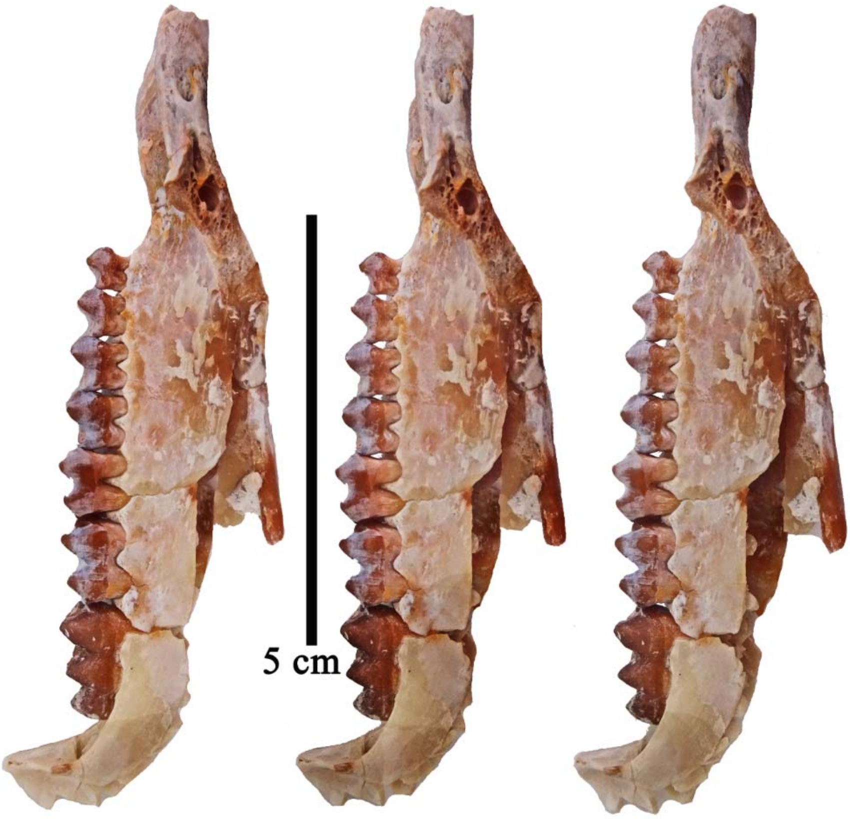

Figure 5. Stereo lingual views of left mandible, GSN BC 1’19, *Namahyrax corvus* from Black Crow, Namibia.

Figure 6. Stereo ventral view of GSN BC 1’19, mandible of *Namahyrax corvus*, from Black Crow, Namibia.

Table 1. Measurements (in mm) of the cheek teeth of GSN BC 1’19, *Namahyrax corvus*, from Black Crow, Namibia. In brackets are measurements of the corresponding teeth in GSN BC 10’08 (m/1 and m/2, paratype of *Namahyrax corvus*) and GSN NC 2’17 (p/2).

Tooth	Mesio-distal length	Bucco-lingual breadth
p/1 lt	5.0	3.1
p/2 lt	5.6 (5.6)	3.7 (3.4)
p/3 lt	6.1	4.5
p/4 lt	6.7	5.3
m/1 lt	8.2 (8.9)	6.1 (6.2)
m/2 lt	9.6 (9.8)	7.2
m/3 lt	13.0	7.3

The four premolars in the mandible each have two roots, the anterior molars have four and the m/3 has five. The p/1 is weakly molariform, the trigonid being reduced anteriorly and the talonid is low and narrow. The main cusp is comprised of coalescent protoconid and metaconid, with low relief postprotocristid and postmetacristid, a stronger preprotocristid and an almost obsolete premetacristid. The hypoconid is nearly in the centre-line of the crown, and shows a low cristid obliqua (prehypocristid) and a short, transverse posthypocristid. There is no hypoconulid and no sign of a buccal cingulum.

The p/2 is similar in morphology to the p/1 but is larger, and the cristids are more in evidence. There is no hypoconulid.

The p/3 is larger than the p/2 and is more molariform, having a better developed preprotocristid leading to the paraconid, the protoconid and metaconid are distinct from each other (even if still closely applied to each other) and the hypoconid, cristid obliqua and posthypocristid form a crescentic cusp.

The p/4 is even more molariform and is larger than the p/3 and the hypoconid is relatively taller, being about ¾ the height of the protoconid. The protoconid and metaconid are well-separated from each other apically, but are fused to each other over most of their height. The cristid obliqua rises anteriorly ending close to the apex of the metaconid. There is a low entoconid adjacent to the termination of the posthypocristid.

The m/1 is heavily worn, but shows classic hyracoid cusp layout, with distinct protoconid, metaconid, hypoconid and entoconid and a small hypoconulid. There is a tiny remnant of a buccal cingulum in the buccal flexid.

The m/2 is less worn than the m/1 and serves as a model for interpreting the first lower molar. The protoconid has a preprotocristid that runs towards the midline of the crown anteriorly, where it ends in a low, weak paraconid. The postprotocristid is transversely oriented and joins the metaconid near its apex. The metaconid is smaller than the protoconid but is slightly taller than it. The premetacristid is subtle, the postmetacristid stronger. The hypoconid is the largest cusp, and has a well-formed cristid obliqua leading upwards towards the metaconid, and a low-relief posthypocristid leading backwards towards the hypoconulid. There is a weak buccal cingulum, and a distal cingulum either side of the hypoconulid.

The m/3 is like the m/2 but the hypoconulid and distal cingular complex are enlarged to form a distinct cusp at the rear of the tooth slightly to the lingual side of the midline. This extra cusp is supported by a fifth root which is coalescent with the root beneath the entoconid.

The entire lower cheek tooth row in GSN BC 1’19 is 54 mm long (premolars : 23 mm, molars : 31 mm), which compares with ca 60 mm for the length of the upper tooth row in the holotype of the species (P2/-M3/ ca 53.6 plus the length of the P1/ which is missing in the holotype). The difference in lengths of the upper and lower cheek tooth rows is probably not taxonomically significant, but it is noted that the upper tooth row in hyracoids is usually slightly shorter than the lower one.

Discussion

In 2008, the only mandible of *Namahyrax* available for study corresponded to a juvenile individual with the deciduous anterior cheek teeth and two permanent molars. The peculiar shape of the symphysis, its lack of fusion and the presence of four mental foramina were pointed out as being unusual in a hyracoid context (Pickford *et al*. 2008b).

The new adult mandible underlines those observations and it shows the presence of other peculiar features such as the suppression of the canines and the absence of the right i/3 whereas the tooth was present on the left as shown by the deep single-rooted alveolus. The diastemata are elongated, as was already visible in the previously available specimen, and this feature reveals that there was probably a clear separation between food acquisition and food mastication. The presence of four well-developed mental foramina arranged in linear fashion along the side of the jaw from the p/3 forwards indicates the possibility of enhanced vascularisation and innervation of the lips and other soft tissues surrounding the symphysis.

An isolated hyracoid tooth from Black Crow was interpreted to be a p/1 by Pickford (2018c) but the newly available jaw indicates that the tooth in question is in fact a p/2. The height of the paraconid and the dimensions are revelatory.

The combined evidence suggests that *Namahyrax corvus* should indeed be included in Geniohyidae as thought by Pickford (2018c) even though there are some differences in mandibular morphology and dimensions between *Namahyrax* and *Geniohyus*. Both taxa show a slender mandibular symphysis which slopes anteriorly, and the presence of long diastemata between the incisors and the cheek teeth. Unlike *Namahyrax*, *Geniohyus* retains the i/3 and canines (Matsumoto, 1926) and it has a large lateral swelling of the lower jaw and a capacious mandibular chamber which is lacking in *Namahyrax*. But overall the similarities in the dentitions of the two genera indicate reasonably close phylogenetic affinities.

The lower permanent dental formula of *Namahyrax corvus* is now known to comprise 2-3 incisors (i/3 sometimes present sometimes absent) 0 canines, 4 premolars, 3 molars.

It is pointed out that some of the modifications in the symphyseal area and the tardy fusion of the symphysis observed in *Namahyrax* occur in sirenians such as *Metaxytherium*, a genus which also has rather buno-selenodont lower cheek teeth. *Metaxytherium* has taken recurving of the symphysis to extremes, whereas in *Namahyrax* the tendency is present but relatively weak when compared to *Metaxytherium*. Both genera also appear to have possessed well vascularised labial and surrounding soft tissues.

Whether these similarities denote phylogenetic proximity, or whether they point towards functional convergence remains to be examined.

Comparisons with the mandible of the brachyodont early Priabonian hyracoid *Dimaitherium patnaiki* Barrow *et al*. (2010) from the Fayum, Egypt, are limited due the fact that the symphysis of that species is not preserved. The molars of *Dimaitherium* are more elongated than those of *Namahyrax*, the hypoconulid of the m/3 is more buccally aligned than in the Namibian genus and the buccal cingulids are more strongly developed, confirming that they are distinct genera, despite being similar in overall dimensions (m/3 in *Dimaitherium patnaiki* ranges in length from 12.3 to 14.8 mm and in breadth from 6.6 to 7.8 mm, whereas the same tooth in *Namahyrax corvus* measures 13.0 x 7.3 mm).

Conclusions

An adult mandible of *Namahyrax corvus* from Black Crow underlines the peculiar morphology of the symphysis and peri-symphyseal osteology of this buno-selenodont hyracoid. The presence of four prominent mental foramina and the great separation of the incisor battery from the cheek teeth suggest that facial elongation has occurred, with enhanced vascularisation and innervation of the lips and neighbouring soft tissues. All this suggests that food acquisition and mastication were separated from each other, and that mobile lips probably played an important role in food acquisition.

The symphysis of *Namahyrax* is peculiar in that it shows tardy fusion in this fully adult individual : the rear quarter of the symphysis is still not fully fused. It is noted that some of these features, such as ventrally recurved symphysis with late fusion and well-vascularised lips and peri-labial tissues occur in the Sirenia, but in this group they have been taken to extreme. Whether there is phylogenetic proximity between *Namahyrax* and sirenians seems doubtful, but the possibility of some degree of convergent evolution seems to be present.

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New Chrysochloridae (Mammalia) from the middle Eocene of Black Crow, Namibia

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Abstract: Among the fossils extracted from middle Eocene freshwater limestone at Black Crow, Namibia, are a lower molar and a maxilla with three teeth that are interpreted to belong to a primitive Chrysochloridea (Golden Moles). The specimens are too small to belong to *Diamantochloris inconcessus* but are similar in dimensions to a previously listed but un-named chrysochlorid tooth from the site. The material is here attributed to a new genus and species and its significance for understanding the homogeneity of Afrotheria is discussed.

Key words: Golden mole, New genus, New species, Ypresian/Lutetian, Sperrgebiet

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Introduction

In previous papers on Chrysochloridea from Black Crow, Namibia, allusion was made to a second Golden Mole species in the deposits which is smaller than *Diamantochloris inconcessus* Pickford (2015b, 2018a). The small form was left in open nomenclature in the hope of recovering additional material.

The 2019 campaign of acid treatment of limestone from Black Crow resulted in the recovery of several mandibles and maxillae of small mammals, among which there is a maxillary specimen containing three cheek teeth which is here interpreted to belong to this un-named species of fossil golden mole. There is also a small m/3 which is compatible in dimensions and occlusal morphology with the maxillary teeth.

The new material is described and its relationships to other golden moles is interpreted.

Geological context

The geological setting of the Black Crow freshwater limestone has been described on several occasions (Pickford *et al*. 2008a, 2008b, 2014; Pickford, 2015a). Fossils are dispersed rather randomly in the limestone without forming concentrations or fossil-rich layers. The fossils comprise both aquatic and terrestrial taxa, crocodiles dominating in terms of numbers of specimens (mostly isolated teeth) but mammal specimens tend to be more complete. Among the molluscs, only land snails have been found, suggesting a palustral setting which was for some reason (alkalinity?) unsuitable for freshwater snails. There are abundant rhizoliths preserved in the limestone and there are occasional layers of silicified algal mats.

Material and methods

Blocks of limestone from Black Crow were bathed in 7% formic acid without buffer. Once the fossils had been extracted from the limestone they were rinsed in fresh water for 24 hours, dried and consolidated with a solution of plexigum dissolved in acetone. Images were obtained using a Sony Cybershot camera by placing the lense over the eyepieces of a stereo microscope and treating the images with Photoshop Elements15 to increase contrast and remove unwanted background. Scales were added manually.

Abbreviations

BC - Black Crow (Sperrgebiet, Namibia)
GSN - Geological Survey of Namibia, Windhoek

Systematic Palaeontology

Order Chrysochloridea Broom 1915

Family Chrysochloridae Gray 1825

Genus *Damarachloris* nov.

Diagnosis: Protocone of P4/ and upper molars mesio-distally compressed and supported on a large ovoid root, metacone and paracone close to each other, but separated at their apices, metacone much smaller than paracone, metaconule and paraconule suppressed, parastylar hook short, depressions in palate between the protocones of the upper cheek teeth. Anterior margin of orbit above the M1/. Infra-orbital foramen opens above the mesial root of P4/. Post-palatine torus present. Smaller than *Diamantochloris inconcessus*. Trigonids of lower molars strongly mesio-distally compressed. Precingulid of lower molars well-developed and steeply inclined. Talonids of lower molars large comprising three cusplets (hypoconid, hypoconulid and entoconid). Lower molars with two conical roots tilted at different angles. Distal roots of lower molars more robust than mesial roots.

Etymology: The genus name refers to '*Damara'* a region and ethnic group in Namibia and '*Chloris'* Greek Goddess of flowers (hence the greenish connotations of the name, equivalent to the Latin '*Floris'*).

Species *Damarachloris primaevus* nov.

Holotype: GSN BC 2'19, right maxilla containing P4/-M2/, part of the distal alveolus of P3/ and three alveoli of M3/.

Paratypes: GSN BC Di 2'17, left m/2 (Pickford, 2018a); GSN BC 5'19, right m/3.

Diagnosis: As for genus. Length M1/-M3/ measured at protocones : 3 mm, measured at buccal sides of teeth : 3.3 mm.

Etymology: '*Primaevus'* : Latin for «*primitive*», «*original*», «*first born*» in allusion to the proposition that this the earliest known chrysochlorid in the fossil record.

Description

GSN BC 2'19 is a right maxilla containing P4/-M2/, the alveoli of M3/ and a partial alveolus for the P3/ (Fig. 1). The infra-orbital foramen is large and is located above the anterior root of the P4/. The orbital rim is partly preserved above the molar row, but the anteriormost part of the margin is missing. The distance between the orbit and the infra-orbital foramen is short (ca 2.5 - 3 mm). The root of the zygomatic arch is low down, departing distally from the body of the maxilla just to the rear of the paraconal root of the M3/. Part of the post-palatine torus is preserved disto-lingually to the protoconal root of the M3/. There is a depression in the palatine on its anterior side. A narrow ridge of bone extends anteriorly from the lateralmost part of the post-palatine torus, extending as far as the gap between the P4/ and M1/, where it terminates againt a palatal foramen. There are expansive depressions in the palatal surface of the maxilla between the protocones of the P3/, P4/, M1/, M2/ and M3/ (Fig. 2). The bone surrounding the molar alveoli is dense.

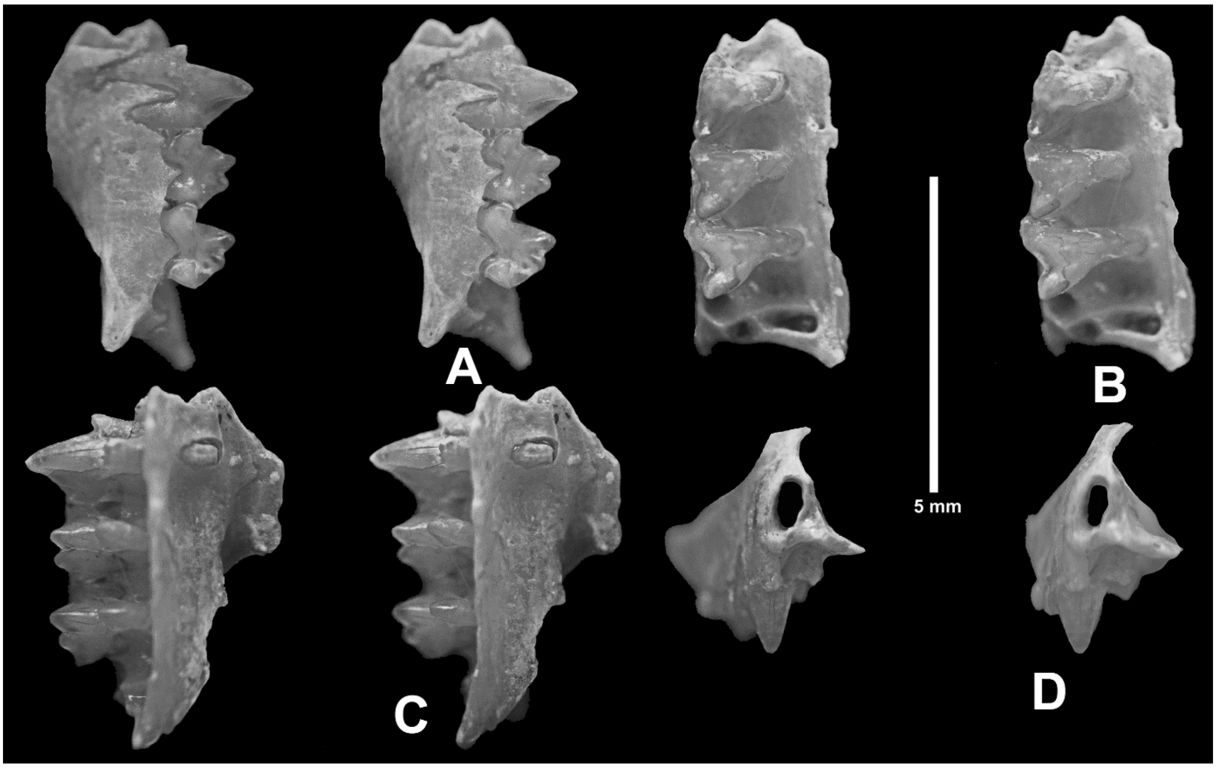

Figure 1. Stereo images of GSN BC 2'19, holotype right maxilla of *Damarachloris primaevus*, nov. gen. nov. sp. from Black Crow, Namibia. A) buccal view, B) occlusal view, C) lingual view, D) anterior view (scale : 5 mm).

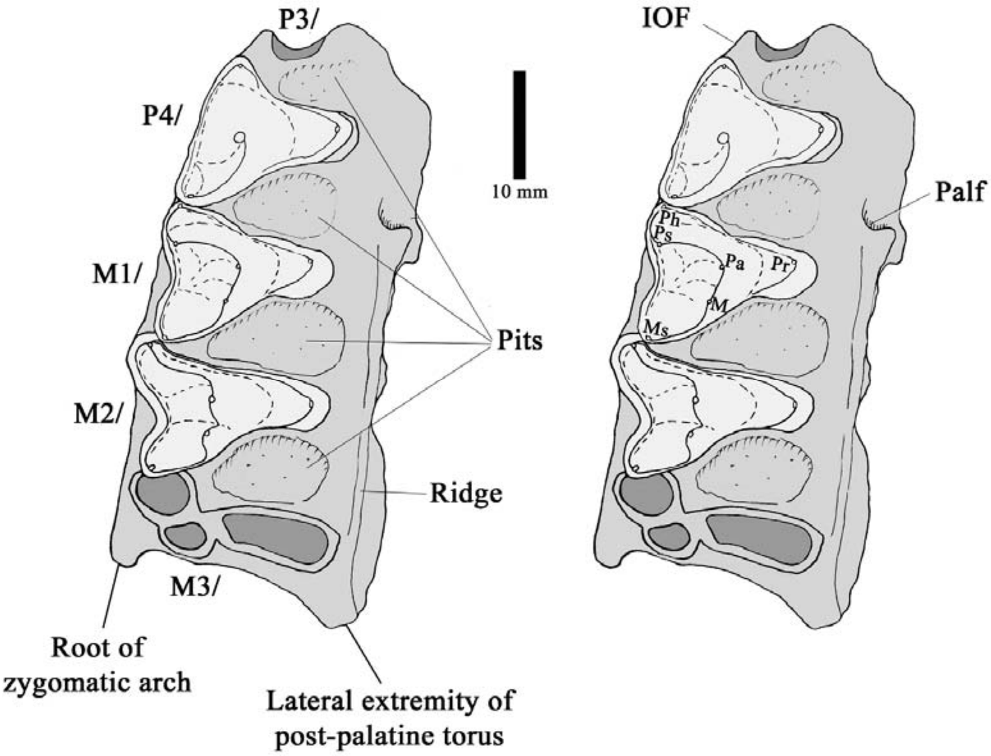

Figure 2. Interpretive sketch of the holotype maxilla of *Damarachloris primaevus*, gen. et sp. nov. from Black Crow, Namibia. IOF - Infraorbital Foramen (on side of maxilla), M - Metacone, Ms - Metastyle, Pa - Paracone, Palf - Palatal foramen, Ph - Parastylar hook, Ps - Parastyle, Pr - Protocone, Light grey - bone, dark grey - dental alveoli, white - teeth (scale : 10 mm).

The P4/ has a low protocone supported by a surprisingly robust root. The protocone is mesio-distally compressed being considerably shorter than the buccal side of the tooth. The postprotocrista and preprotocrista are well-developed and course towards the buccal side of the tooth, but there is no sign of metaconule or paraconule. The paracone is tall and pointed with a well-developed postcrista curving distally and buccally to terminate in a small, low metatsylar tubercle, there being no distinct metacone. The preprotocrista is weak to absent, the mesial surface of the paracone being conical. There is a low parastyle with crista descending disto-lingually and disto-buccally from its apex. The buccal shelf is narrow and the buccal cingulum subtle.

The M1/ and M2/ have comparable crown elements, but the M2/ is slightly bucco-lingually broader than the M1/ and mesio-distally longer. In contrast, judging from the alveoli, the M3/ was extremely compressed mesio-distally, such that the metaconal root is only a short distance behind the line joining the protoconal and paraconal roots. In all three molars the protoconal root is mesio-distally compressed but bucco-lingually enlarged, being by far the largest of the three roots of each tooth, despite the reduced dimensions of the cusp that it supports.

The M1/ has a low protocone which is mesio-distally compressed, with pre- and postcrista extending buccally towards the base of the paracone and metacone respectively. There is no sign of paraconule or metaconule in this tooth. The preprotocrista ends in the midline of the tooth, but buccally there is a cingular extension reaching towards the parastylar hook. The paracone is the largest and tallest cusp and close to it, on its disto-buccal side, is the metacone, between which run the postparacrista and the premetacrista. The preparacrista curves mesio-buccally terminating at the parastyle, which has a precrista reaching anteriorly towards the parastylar hook. The metacone has a distally directed postcrista which curves buccally to terminate at the metastyle. Between the parastyle and the metastyle there is a cingular rim forming a margin to an expansive buccal depression between the paracone-metacone pair and the buccal cingulum.

The M2/ is constructed along similar lines to the M1/, but the crown is slightly broader bucco-lingually and appreciably longer mesio-distally.

Table 1. Measurements (in mm) of the teeth of *Damarachloris primaevus* from Black Crow, Namibia.

Tooth	**Mesio-distal length**	**Bucco-lingual breadth**
GSN BC 2’19, right P4/	1.5	1.36
GSN BC 2’19, right M1/	1.4	1.30
GSN BC 2’19, right M2/	1.9	1.31
GSN BC 2’19, right M3/ alveolus	0.7	1.8
GSN BC Di 2’17, left m/2	0.93	0.67
GSN BC 5’19, right m/3	1.3	0.77

The left lower molar (GSN BC Di 2’17) was described previously (Pickford, 2018a) (Fig. 3). The root are tilted slightly lingually and the distal one is more robust than the mesial one while the mesial one is tilted slightly more than the distal one.

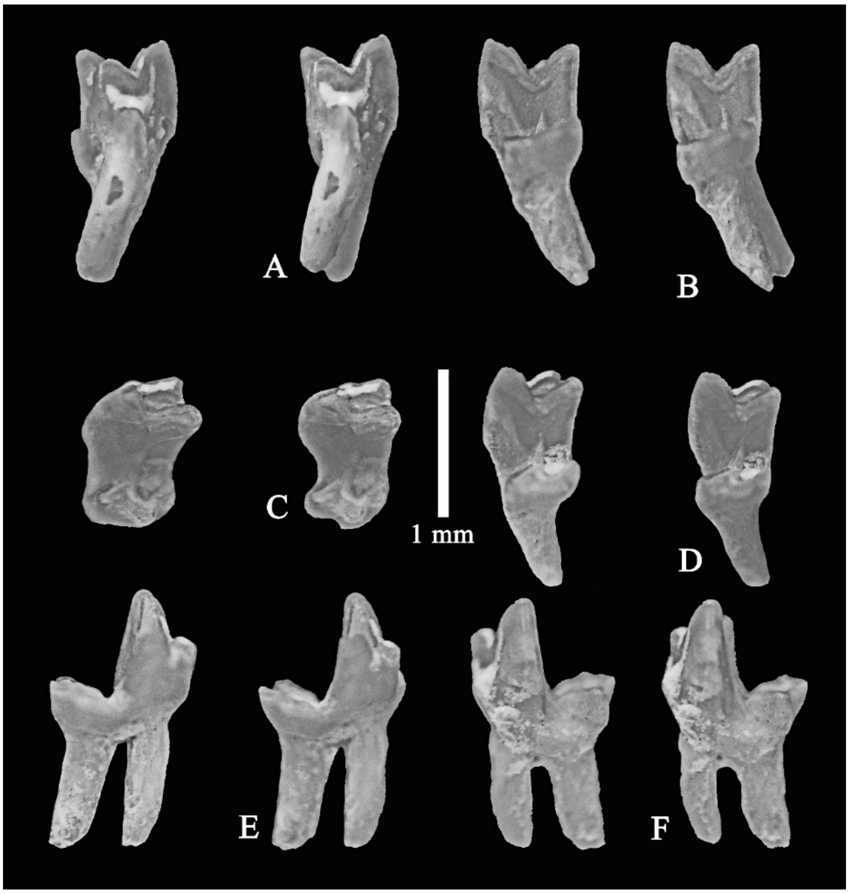

Figure 3. Stereo images of GSN BC Di 2'17, paratype left lower molar of *Damarachloris primaevus* from Black Crow, Namibia. A) mesial view, B) distal view, C) occlusal view, D) oblique disto-occlusal view, E) lingual view, F) buccal view (scale : 1 mm).

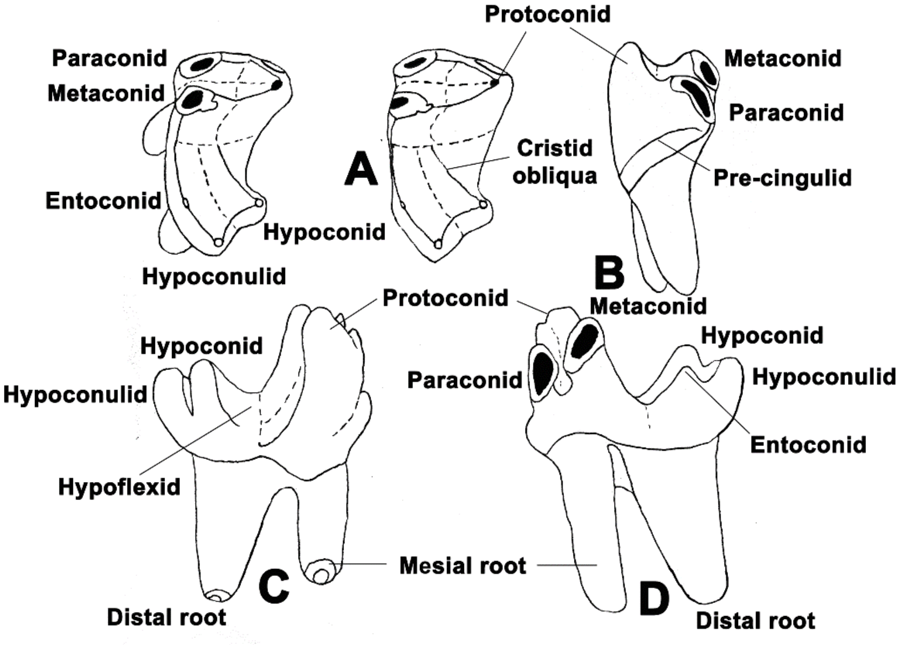

Figure 4. Interpretive sketches of right m/3 of *Damarachloris primaevus*, gen. et sp. nov. from Black Crow, Namibia (Middle Eocene). A) stereo occlusal view, B) anterior view, C) buccal view, D) lingual view. Length of tooth : 1.3 mm.

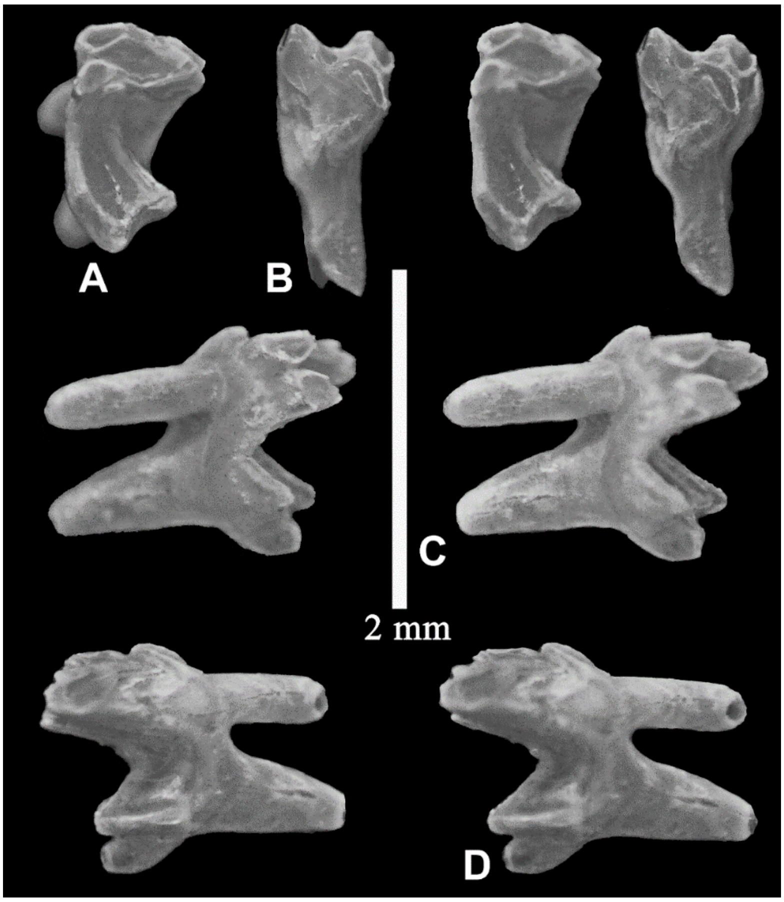

Figure 5. Stereo images of GSN BC 5'19, paratype right m/3 of *Damarachloris primaevus* from Black Crow, Namibia. A) occlusal view, B) mesial view, C) lingual view, D) buccal view (scale : 2 mm).

GSN BC 5'19, a right lower molar has a mesio-distally compressed trigonid, with the paraconid close to the protoconid with a slit between them (Fig. 4, 5). The protoconid is slightly taller than the metaconid and the paraconid is slightly lower than the metaconid. There is a slanting mesial cingulid. The talonid is tricuspid, with a large hypoconulid distally, a tall hypoconid on the buccal side and a small entoconid, all joined to each other by crests. The cristid obliqua descends anteriorly from the hypoconid, terminating at the base of the trigonid in the midline of the tooth. The talonid is lower than the trigonid, the hypoconid being about half the height of the protoconid.

The roots of this tooth are interesting in that the anterior one is smaller than the distal one and it is tilted slightly lingually compared to the more vertically oriented distal root.

Discussion

The maxilla of *Damarachloris primaevus* has several features that align it with the chrysochlorid from Eocliff (*Namachloris arenatans*) (Pickford, 2015c, 2018a). The root of the zygomatic arch takes off in line with the parastyle of the M3/ and is directed distally, there is a post-palatine torus with a depression in the palatine anterior to it, the infraorbital foramen is large and is close to the anterior rim of the orbit and there are depressions in the palate in between the protocones of the P3/, P4/, M1/, M2/ and M3/. In addition there is a subtle ridge of bone extending anteriorly from the lateral end of the post-palatine torus, reaching the level of P4/ where it terminates in a small palatal foramen.

The roots supporting the protocones of the upper molars are bucco-lingually expanded but mesio-distally compressed as in other chrysochlorids, despite the fact that the protocones that they support are reduced in dimensions. The metacone and paracone are close together, more so than in *Diamantochloris*, imparting a more developed zalambdodont morphology to the crowns.

The lower molars have mesio-distally compressed trigonids and relatively large talonids and the roots are tilted with respect to each other and to the crown, much as in *Namachloris* and *Diamantochloris*. The distal root of the molars is larger than the mesial one, despite the fact that the talonids are lower and less voluminous than the trigonids.

All these peculiarities of the maxilla and teeth of *Damarachloris primaevus* appear to be linked to enhanced seismic transmission and reception, with the teeth and maxilla playing a role in the transmission of sound energy from the individual's vocal chords (and possibly dental chatter?) to the surrounding ground and for the reception of seismic vibrations from the ground, transmitting the energy received by the head via the dense parts of the maxillary bone and tooth roots towards the inner ear. In summary, *Damarachloris* appears to have been using its head as a sounding board for transmitting and receiving seismic and sound energy to and from the surrounding ground.

It remains to be determined whether the distal part of the mandible in *Damarachloris* was lingually bent as in *Diamantochloris* and *Namachloris*, but the tilted roots and the differential development of the distal roots of the molars suggest that when found its mandible will show a bent distal half.

As an assemblage, the Middle Eocene Black Crow mammals, both large and small, reveal a degree of endemism in the southern extremities of the African continent (Afrotheres, *Namalestes*) but with signs of faunal interchanges with the rest of Africa and with the northern continents, including North America (rodents, primates). The chrysochlorids strengthen this impression of endemism.

A great deal more is to be learnt from the Black Crow deposits about the evolution and composition of Middle Eocene mammalian faunas of Africa. To some extent, study of the Black Crow biota is rectifying a bias in the African fossil record of the period which has, until recently, been focussed largely on faunas from the northern margins of the continent. By the Late Eocene, the Eocliff tufas of the Sperrgebiet, Namibia, indicate faunal interchanges (rodents in particular) with South America (Pickford, 2018b).

Conclusions

A small insectivoran from the Middle Eocene limestones at Black Crow, Namibia, is interpreted to be a primitive member of the Chrysochloridea (Golden Moles). The trigonids of the lower molars are mesio-distally compressed as in extant Golden Moles and are tall, slotting into depressions in the palate situated betwen the protocones of the upper cheek teeth. The protocones of the upper molars are mesio-distally compressed and are supported by robust roots, again as in extant Golden Moles. There are other signs of affinities to this order of mammals, including the presence of a post-palatine torus, and the roots of the lower molars are tilted at different angles.

However, the talonids of the lower molars are tricuspid, comprising a large hypoconid, a hypoconulid and a moderately developed entoconid. The cristid obliqua is elongated and descends from the hypoconid to the midline of the crown at the base of the trigonid. In the upper molars the paracone and metacone are distinct but closely joined to each other, and the parastylar hook is small.

The dental and maxillary morphology of *Damarachloris primaevus* appear to indicate that the superfamily Chrysochloridea is remote from other Afrotheres and indeed from other Afroinsectiphilians such as tenrecoids and Tubulidentata. It would appear to be closer in lower molar talonid morphology to some Eurasian and North American «insectivorans» than to any of the Afrotheres and tenrecoids. If *Damarachloris* is indeed a Chrysochloridea, then it calls into question the homogeneity of the Afrotheria as currently understood. If not then one would be in the presence of an interesting case of convergent evolution. Further discoveries, especially of the cranial and postcranial skeleton should throw light on these questions.

Acknowledgements

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Preliminary overview of the fossil record of bats (Chiroptera, Mammalia) from the Miocene sites of Otavi Mountainland (Northern Namibia)

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Abstract: The preliminary results of the research on the bat fossils from the Miocene breccias of the Berg Aukas I site are presented. In total 4866 fossil bat fragments comprising mostly dentary fragments and isolated teeth from the 116 breccias blocks were analyzed. The fossil bat material comprises the representatives of Megachiroptera (cf. Pteropodidae) and at least seven different bat families of Microchiroptera belonging to Hipposideridae, Rhinolophidae, Vespertilionidae, Emballonuridae, Molossidae, Nycterdae and Megadermatidae. The rhinolophids and hipposiderids combined are the most common species in the Miocene assemblages. The emballonurids and vespertilionids occupy second place in occurrence, while the megadermatids and molossids occur in fewer than one third of all breccia blocks. Records of Megachiroptera were the rarest. More tropical conditions of the Otavi Mountainland region during Miocene time is confirmed by the rather high occurrence of emballonurids and megadermatids in the Miocene assemblages from the Berg Aukas I site. Full study of the fossil material from the site could provide additional information on the origin, evolution and dispersion of bat fauna of Africa.

Keywords: Mammalia, Chiroptera, Miocene, Africa, Namibia, Berg Aukas

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Introduction

Bats (Order Chiroptera), the only mammals capable of powered flight and sophisticated laryngeal echolocation, represent one of the most ubiquitous orders of mammals (Simmons *et al.* 2008). With more than 1,100 extant species (Simmons, 2005) and about 200 fossil taxa (Eiting & Gunnell, 2009), bats comprise an extraordinary taxonomic diversity that is second only to rodents among living mammals. Molecular studies suggest that the diversification of extant bats occurred at the Cretaceous-Tertiary boundary approximately 65 million years ago when the crown group bats last shared a common ancestor (Eick *et al.* 2005; Teeling *et al.* 2005). Gunnell *et al.* (2017) mention that modern families of bats began to appear in the late early or middle Eocene of Europe and North Africa. Most researchers seem to agree that bats originated in Laurasia in the early Eocene (52 to 50 million years ago), coincident with a significant global rise in temperature, increase in plant diversity and abundance and the zenith of Tertiary insect diversity (Teeling *et al.* 2005).

Palaeogene and Neogene sites with fossil bats are well known from Africa. The earliest bat records come from the Early Eocene site Chambi (50 Ma) of Tunisia: philisid *Dizzya exultans* Sigé, 1991 and rhinolophid sp. (Sigé, 1991) and from the Middle Eocene site Mehenge (46 Ma) of Tanzania: *Tanzanycteris mannardi* Gunnell *et al.* 2003, a member of the rare bat family Tanzanycteridae (Gunnell *et al.* 2003). Recently the earliest records of Megachiroptera (a distal humerus and a lightly worn left lower molar) were discovered in the Ypresian/Lutetian limestone at Black Crow, Namibia (Pickford, 2018). From the Late Eocene formations of Fayum Quarry of Egypt the Megadermatidae (*Saharaderma pseudovampyrus* Gunnell *et al.* 2008), Rhinopomatidae (*Qarunycteris moerisae* Gunnell *et al.* 2008), Philisidae (*Witwatia schlosseri* Gunnell *et al.* 2008 and *W. eremicus* Gunnell *et al.* 2008), Emballonuridae (*Dhofarella sigei* Gunnell *et al.* 2008), Vespertilionidae (*Khonsunycteris aegypticus* Gunnell *et al.* 2008) and *Phasmatonycteris butleri* Gunnell *et al.* 2014 were described. Early Oligocene bats are also known from the Fayum: *Vampyravus (=Provampyrus) orientalis* (Fam. Indet. Schlosser, 1910, 1911), philisid *Philisis sphingis* Sigé, 1985 and *Phasmatonycteris phiomensis* Gunnell *et al.* 2014.

The Neogene is an important period in bat evolution during which major taxonomic radiations occurred in most of the bat families. The Miocene bat communities comprise a high taxonomic diversity and include many extinct genera and species (e.g., *Miostrellus* Rachl, 1983, *Submyotodon* Ziegler, 2003 and *Eptenonnus* Rosina & Semenov, 2012) which are well-known from Eurasia, in particular from Europe (Rachl, 1983; Ziegler, 2003; Rosina & Semenov, 2012).

Early Miocene bat assemblages are known from Kenya (Rusinga Island, Koru, Songhor, Chamtwara) (Butler, 1969, 1984) and Uganda (Napak and Moroto II sites) Pickford (& Mein, 2006). The assemblages include emballonurids (*Taphozous incognita* Butler & Hopwood, 1957), molossids (*Tadarida rusingae* Arroyo-Cabrales *et al.* 2002), hipposiderids and megadermatids (Butler, 1969, 1984; Butler & Hopwood, 1957; Arroyo-Cabrales *et al.* 2002; Pickford & Mein, 2006).

Propotto Simpson, 1967, was originally published as a primate, but was transferred to Megachiroptera by Walker (1969) but has recently been re-interpreted as a primate (Gunnell *et al.* 2018). However, the ordinal status of this genus requires further study (T. Harrison, pers. comm.).

Early late Miocene bats are known from Beni Mellal of Morocco including two species of megadermatids (*Megaderma gaillardi* Trouessart, 1898, and *M. jaegeri* Sigé, 1976), *Hipposideros (Syndesmotis) vetus* Lavocat, 1961, *Rhinolophus ferrumequinum mellali* Lavocat, 1961, and some unidentified specimens of molossids and vespertilionids (Lavocat 1961; Sigé, 1976). The Middle Miocene bats of Africa, however, are sparse. Mein & Pickford (2003) described *Rhinolophus contrarius* from the basal Middle Miocene of Arrisdrift, Namibia (ca 17.5 Ma), the only other African bat record from this period being from the Early Middle Miocene site of Jebel Zelten, Libya (14-16 Ma) where a member of the family Philisidae (*Scotophilisis libycus* Horáček *et al.* 2006) is documented, which in certain respects recalls the Recent *Scotophilus* and the Late Paleogene Afro-Arabian genus *Philisis* (Horáček *et al.* 2006). Some Late Miocene bats are mentioned from the cave breccia sediments of Sheikh Abdallah in Egypt, which include *Rhinolophus* sp., *Megaderma* sp. and *Hipposideros (Syndesmotis)* sp. (Wanas *et al.* 2009). A preliminary list of bats from the Late Miocene fossiliferous cave breccias of Harasib 3a and Berg Aukas in the Otavi Mountainland of northern Namibia was presented (Pickford, 1992) including *Myotis* sp., *Rhinolophus* sp., *Megaderma* sp., some forms of *Hipposideros* and Molossidae indet. A fossil fruit bat (cf *Rousettus*) was described from the Lukeino Formation (6 Ma), Kenya, where it was associated with four species of Microchiroptera (Emballonuridae (?) *Taphozous*, Vespertilionidae *Chamtwaria* sp. *Myotis* sp. and an indeterminate genus) (Mein & Pickford, 2006).

In this paper we present preliminary results of research on the bat fossils from the Otavi Mountainland of northern Namibia, most material of which is represented by Middle Miocene fossils from the Berg Aukas I site. The presence of bat remains at the Berg Aukas I site was earlier established by P. Mein, to whom we are grateful for the preliminary sorting of the fossil material.

Geological setting and biostratigraphic considerations

The Namibian karst are typical near-surface manifestations of the dissolution of the dolomite and limestone by vadose and surface waters. The Namibian karst fillings are ideal for biostratigraphy in that some of the sites, such as Berg Aukas, contain faunas that accumulated at different times within the same cave system. Thus, Berg Aukas palaeocave has yielded a comprehensive series of micromammal faunas that range in age from late Middle Miocene to Holocene (Senut *et al.* 1992; Pickford & Senut, 2010).

Preliminary studies of the Berg Aukas I site revealed that it consists of spelean sediments. Most of the spelean deposits found in Namibia occur near extant caves, but not inside them. The Berg Aukas I locality occurs in the open-cast pit at Berg Aukas (Pickford & Senut, 2010: Fig. 16, p. 24, Fig. 17, p. 26) and consists of red sandy to silty breccia collected from the mine dump. A detailed description of the geological conditions of the locality was already given in Pickford & Senut (2010: pp. 22-23). Most of the breccia blocks yielded middle Miocene faunas and tended to be shades of purple and rose with abundant masses of different minerals. These blocks were cemented by calcium carbonate and were easy to treat in 10% solution of acetic acid. Fossils of Plio-Pleistocene age are often dark brown to black in colour and the breccia blocks are also rich in calcium carbonate. The Upper Miocene breccia tends to be brick-red and massive. These breccia blocks were rich in clay minerals, thus to treat these hydrogen peroxide or hot acid was used.

The bulk of the mammals from the Berg Aukas site consists of microfauna, in particular rodents. It would appear that most of the micromammal fossils were carried into the cave by owls and other predators. Some vertebrates such as the frogs, lizards and bats may well have inhabited the cave or lived near the cave entrance. However, a few medium-sized mammals were also found including one of the earliest known Miocene hominoids south of the Equator – *Otavipithecus namibiensis* (Conroy *et al.* 1992). Taken together, the Berg Aukas Miocene mammal fauna consists of diverse and abundant squirrels, rodents and bats and it includes rarer viverrids, hyracoids, macroscelidids and insectivorans that indicate that the deposits span the late Middle Miocene (12-13 Ma) to Recent periods (for faunal lists of each breccia block see Pickford & Senut, 2010: Table 5, pp. 29-31).

Material and methods

The stratigraphy of the Otavi Mountain karst is complex and in addition to the usual stratigraphic complications found in many palaeocave systems, the fossiliferous breccias at Berg Aukas have been mined and are no longer in their original geological context. Because of this, the basic unit of research is the breccia block, a tactic employed to minimise the chances of mixing samples of faunas from different time periods. Thus, each block of the Berg Aukas breccias was numbered with a locality prefix and a number and the year of collection. The faunal remains from each block of breccia are kept together as an assemblage sample (Pickford & Senut, 2010).

Fossil bat materials from the Berg Aukas I site are abundant and comprise mostly dentary fragments and isolated teeth. Occasionally there are almost undamaged lower jaws, rostral parts of skulls in varying degrees of integrity and humeral fragments (Fig. 1, 2).

In total 4866 fossil bat fragments from 116 breccia blocks (Table 1), collected from 1991-1996, 2001 and 2005, were analyzed. The chiropteran tribe taxonomy follows Simmons (2005).

The osteological collections of recent Chiroptera curated by the Zoological Museum of Moscow University (Moscow, Russia) and in the Senckenberg Research Institute (Frankfurt-am-Main, Germany) have been used for the comparisons. The photographs have been taken by a SEM (scanning electron microscope) of the AMU (Applied Materials Laboratory, University of Augsburg, Germany) and that of the Borissiak Paleontological Institute of the Russian Academy of Science (Moscow, Russia).

Abbreviations

BA - Berg Aukas
Ch - Chiroptera
LM - late Miocene
MM - middle Miocene

Results and discussion

The oldest of the present day bat families start to appear in the lower Eocene of Africa, whereas on the other continents they only appeared in the middle Eocene. This points to the great importance of Africa during the earliest phases of evolution of modern bats (Ravel *et al.* 2016).

The extant fauna of African bats is very rich and abundant with a high diversity, comprising 13 extant families, 58 genera and 328 species (ACR, 2018, Appendix 1). Moreover, the Afrotropics has the highest percentage of endemics (with 211 out of 237 bat species) in comparison with the Neotropics that shows, however, higher bat diversity (Maas *et al.* 2015). In Africa today the Vespertilionidae contain the largest quantity of taxa, followed by the Molossidae and Pteropodidae (ACR, 2018: Fig. 1, p. 2). The Megadermatidae is the rarest group of bats in Africa (ACR, 2018: p. 1).

Our preliminary observations on Neogene and Quaternary bat assemblages from Berg Aukas I site reveals that it includes members of a minimum of seven microbat families: Hipposideridae, Rhinolophidae, Vespertilionidae, Emballonuridae, Molossidae, Megadermatidae, Nycteridae and also some records of cf. Pteropodidae (Table 1). All these bat families are extant. Furthermore, together with Phyllostomatidae the five extant families (Rhinolophidae, Hipposideridae, Molossidae Vespertilionidae and cf. Pteropodidae) contain about 75% of all species worldwide (Shi & Rabosky, 2015: p. 1529).

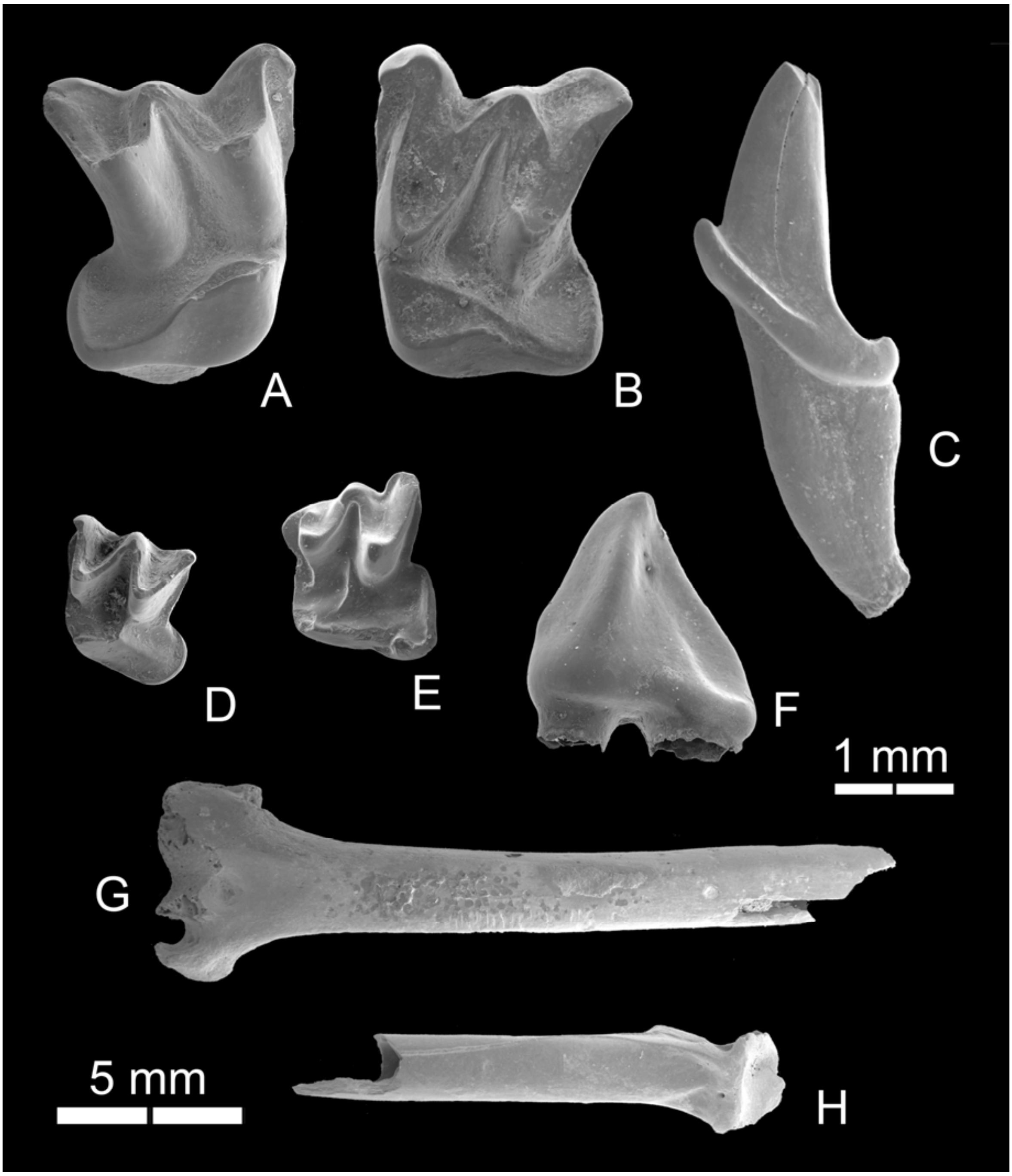


Figure 1. Fossil bats from Berg Aukas I : Emballonuridae, Taphozoinae **(A-C, G)**, Emballonuridae, Emballonurini (**E**), Hipposideridae (**D**) cf. Pteropodidae (**F**) and Chiroptera indet. (**H**). **A**) BA92-45Ch2-2, right M2/, occlusal view; **B**) BA95-1Ch2-3, left M2/, occlusal view; **C)** BA95-2Ch1-2, right C sup., lingual view; **D**) BA95-2Ch3-2, left M1/, occlusal view; **E**) BA94-52Ch51-8, left M1/, occlusal view; **F**) BA92-66Ch1-3, right P4/, lingual view; **G**) BA95-45Ch2-1, distal epiphysis and part of diaphysis of the left humerus, posterior view; **H)** BA95-1Ch1-5, proximal epiphysis and part of diaphysis of the left radius, ventral view (A-F scale : 1 mm; G-H scale : 5 mm).

Such high diversity and richness of bat fossils in the breccias of Berg Aukas I are due to their karstic origin and taphonomic conditions. All the fossil bat assemblages studied herein originated from karst fissure filling deposits. As a rule, fossil bat faunas from karst sites demonstrate great taxonomic diversity (Rosina & Sinitsa, 2014; Rosina & Rummel, 2017). The environment of karst landscapes in the past, as well as at present, provided opportunities for the accumulation of bat remains in the karst deposits as the result of both natural death of animals occurring in large colonies inhabiting karst cavities and from avian regurgitation pellets. This is well-known in the numerous Neogene karst sites of Europe (Ziegler, 2003; Rosina & Rummel, 2012, 2017).

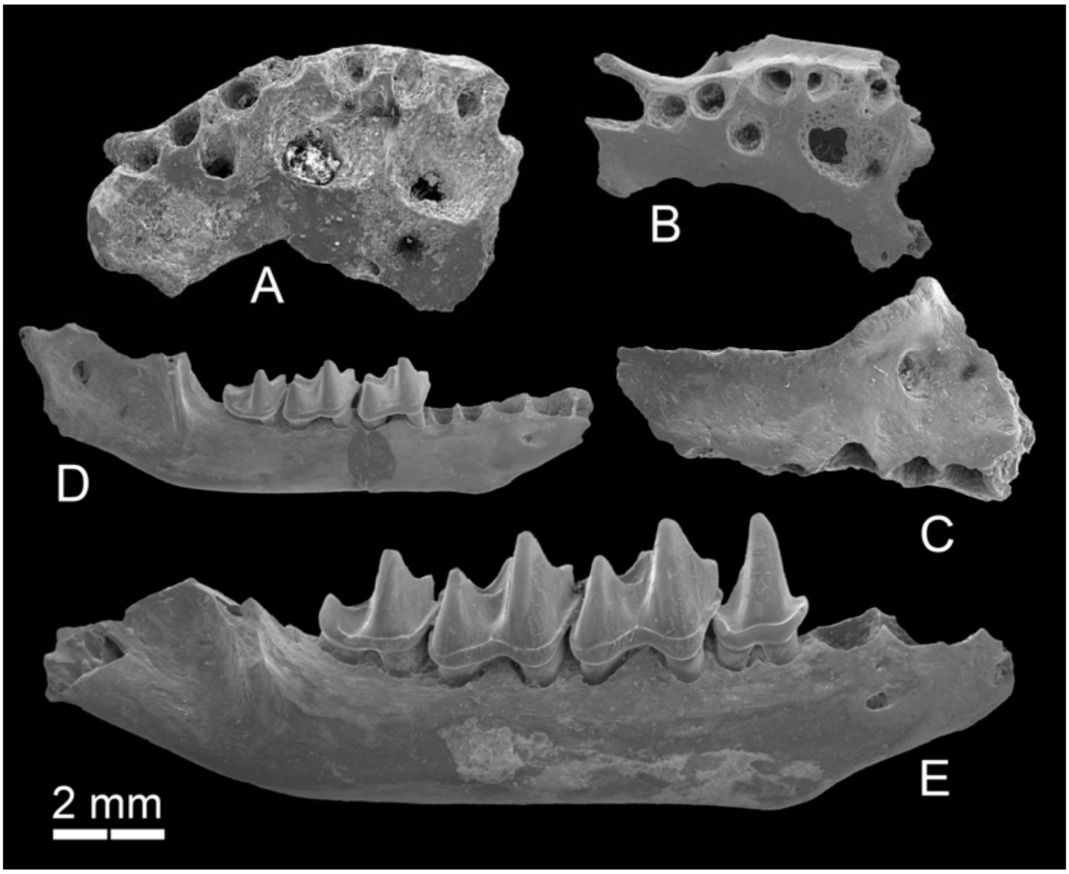
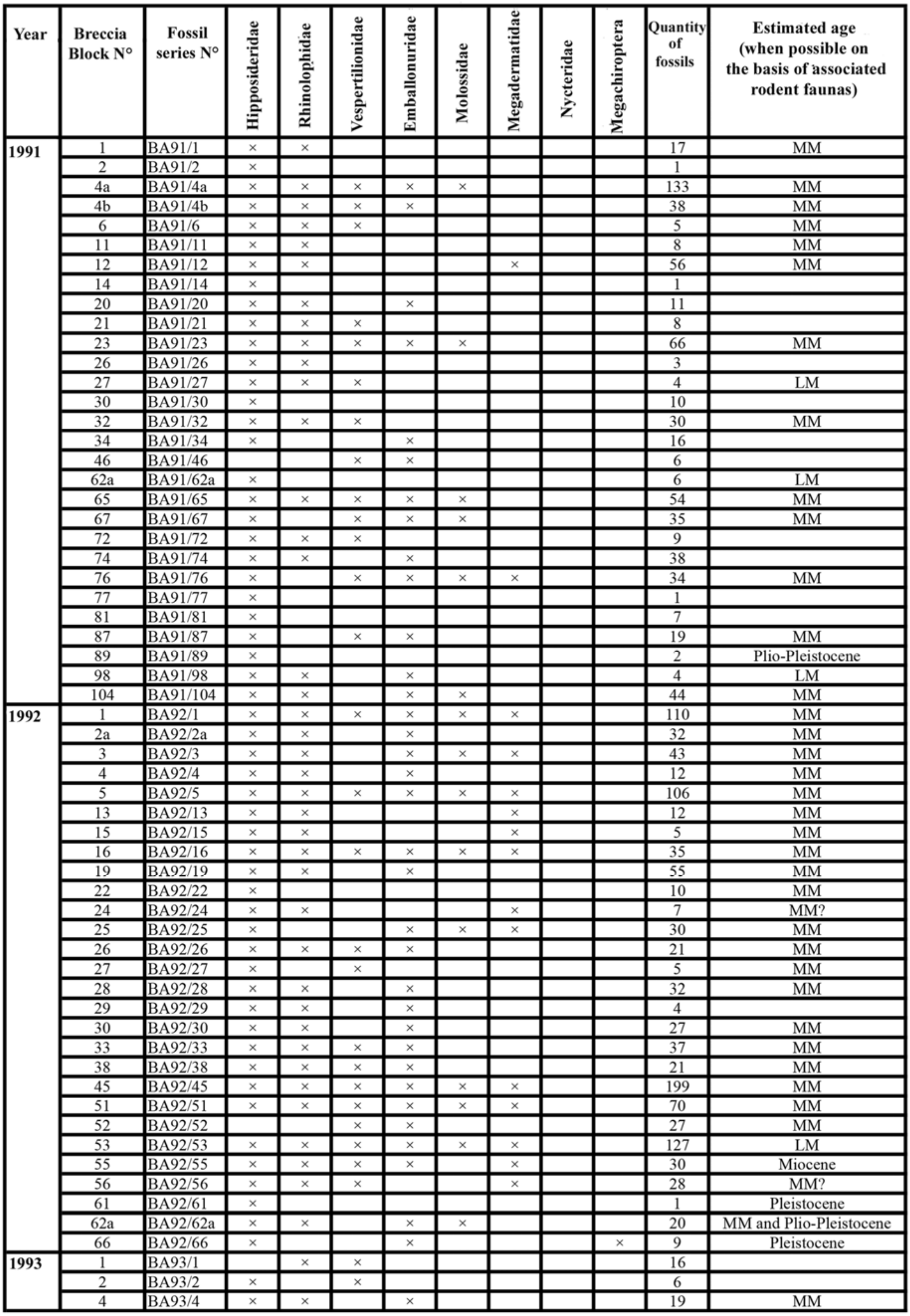


Figure 2. Emballonurid bats from Berg Aukas I : Taphozoinae **(A-C, E)** and Emballonurini (**D**). **A)** BA92-1Ch3-1, fragment of left maxilla, ventral view; **B)** BA92-28Ch2-1, fragment of left maxilla, ventral view; **C)** BA91-87Ch2-1, fragment of right maxilla, buccal view; **D)** BA91-76Ch1-2, right mandible, lateral view; **E)** BA92-5Ch3-1, right mandible, lateral view (scale : 2 mm).

Reconstructions of the Berg Aukas Palaeocave for ca 12 Ma show the subterranean cavity breaking through to the surface upon which it became accessible to various animals such as owls, bats, lizards and hyraxes etc. (Pickford & Senut, 2010: Fig. 19, p. 28). Soil and other surface materials were washed into the palaeocave and contributed to sedimentation within it and consequently to fossilization of the bone remains.

The fossil material of the Middle and Late Miocene assemblages of Berg Aukas I site comprises representatives of at least seven different families of microbats belonging to Hipposideridae, Rhinolophidae, Vespertilionidae, Emballonuridae, Molossidae, Megadermatidae and Nycteridae, as well as one or more species of megabat, cf. Pteropodidae (Fig. 3). Rhinolophids and hipposiderids are the most common species in the assemblages in the Miocene breccia blocks of Berg Aukas I site. They occur in at least 90% of all blocks which yielded bat remains. The emballonurids and vespertilionids occupy second place in occurrence (not less than 50%), while the megadermatids and molossids occurred in fewer than 30% of the breccia blocks that yielded bat remains. Records of Megachiroptera were the rarest (no more than 6%).

Table 1. Preliminary list of fossil bat assemblages from Neogene and Quaternary Breccia Blocks of the Berg Aukas I site (MM - Middle Miocene, LM - Late Miocene, M – Miocene)



Year	Breccia Block N°	Fossil series N°	Hipposideridae	Rhinolophidae	Vespertilionidae	Emballonuridae	Molossidae	Megadermatidae	Nycteridae	Megachiroptera	Quantity of fossils	Estimated age (when possible on the basis of associated rodent faunas)
1991	1	BA91/1	×	×							17	MM
	2	BA91/2	×								1	
	4a	BA91/4a	×	×	×	×	×				133	MM
	4b	BA91/4b	×	×	×	×					38	MM
	6	BA91/6	×	×	×						5	MM
	11	BA91/11	×	×							8	MM
	12	BA91/12	×	×				×			56	MM
	14	BA91/14	×								1	
	20	BA91/20	×	×		×					11	
	21	BA91/21	×	×	×						8	
	23	BA91/23	×	×	×	×	×				66	MM
	26	BA91/26	×	×							3	
	27	BA91/27	×	×	×						4	LM
	30	BA91/30	×								10	
	32	BA91/32	×	×	×						30	MM
	34	BA91/34	×			×					16	
	46	BA91/46			×	×					6	
	62a	BA91/62a	×								6	LM
	65	BA91/65	×	×	×	×	×				54	MM
	67	BA91/67	×		×	×	×				35	MM
	72	BA91/72	×	×	×						9	
	74	BA91/74	×	×		×					38	
	76	BA91/76	×		×	×	×	×			34	MM
	77	BA91/77	×								1	
	81	BA91/81	×								7	
	87	BA91/87	×		×	×					19	MM
	89	BA91/89	×								2	Plio-Pleistocene
	98	BA91/98	×	×		×					4	LM
	104	BA91/104	×	×		×	×				44	MM
1992	1	BA92/1	×	×	×	×	×	×			110	MM
	2a	BA92/2a	×	×		×					32	MM
	3	BA92/3	×	×		×	×	×			43	MM
	4	BA92/4	×	×		×					12	MM
	5	BA92/5	×	×	×	×	×	×			106	MM
	13	BA92/13	×	×				×			12	MM
	15	BA92/15	×	×				×			5	MM
	16	BA92/16	×	×	×	×	×	×			35	MM
	19	BA92/19	×	×		×					55	MM
	22	BA92/22	×								10	MM
	24	BA92/24	×	×				×			7	MM?
	25	BA92/25	×			×	×	×			30	MM
	26	BA92/26	×	×	×	×					21	MM
	27	BA92/27	×		×						5	MM
	28	BA92/28	×	×		×					32	MM
	29	BA92/29	×	×		×					4	
	30	BA92/30	×	×		×					27	MM
	33	BA92/33	×	×	×	×					37	MM
	38	BA92/38	×	×	×	×					21	MM
	45	BA92/45	×	×	×	×	×	×			199	MM
	51	BA92/51	×	×	×	×	×	×			70	MM
	52	BA92/52			×	×					27	MM
	53	BA92/53	×	×	×	×	×	×			127	LM
	55	BA92/55	×	×	×	×		×			30	Miocene
	56	BA92/56	×	×	×			×			28	MM?
	61	BA92/61	×								1	Pleistocene
	62a	BA92/62a	×	×		×	×				20	MM and Plio-Pleistocene
	66	BA92/66	×			×				×	9	Pleistocene
1993	1	BA93/1		×	×						16	
	2	BA93/2	×		×						6	
	4	BA93/4	×	×		×					19	MM

Table 1 continued 1994-2005

Year	Breccia Block N°	Fossil series N°	Hipposideridae	Rhinolophidae	Vespertilionidae	Emballonuridae	Molossidae	Megadermatidae	Nycteridae	Megachiroptera	Quantity of fossils	Estimated age (when possible on the basis of associated rodent faunas)
1994	2	BA94/2	×	×	×	×					29	MM
	3	BA94/3	×	×							3	MM
	5	BA94/5	×	×	×						38	LM
	6	BA94/6	×	×	×	×	×				56	MM
	9	BA94/9	×	×	×						10	LM?
	11	BA94/11	×	×	×						3	LM
	14	BA94/14	×	×	×					×	22	MM
	15	BA94/15	×								2	LM
	16	BA94/16	×	×		×					3	MM?
	18	BA94/18	×		×						22	MM?
	19	BA94/19	×	×							7	MM?
	20	BA94/20	×	×			×	×			16	
	21	BA94/21						×			1	LM
	29	BA94/29	×	×							5	
	32	BA94/32	×	×	×	×	×	×			20	LM
	33	BA94/33	×			×					8	LM
	34	BA94/34	×	×	×						22	
	35	BA94/35	×	×							9	LM
	37	BA94/37							×		1	
	39	BA94/39	×	×	×						7	LM
	41	BA94/41		×	×						11	LM
	42	BA94/42				×					4	LM
	43	BA94/43				×					1	MM
	44	BA94/44	×	×							12	
	46	BA94/46	×	×	×	×					80	LM
	47	BA94/47				×					1	LM
	49	BA94/49	×	×	×		×				4	
	51	BA94/51	×	×							2	
	52	BA94/52	×	×	×	×	×	×			1880	MM
	53	BA94/53	×	×							3	MM
	54	BA94/54	×	×	×	×					13	MM or LM
	58	BA94/58	×	×	×						11	
	59	BA94/59	×	×		×					20	LM
	60	BA94/60	×	×	×	×	×	×			102	MM
1995	1	BA95/1	×	×	×	×	×	×			129	MM
	2	BA95/2	×	×	×	×	×				82	MM
	3	BA95/3	×	×	×	×					9	MM
	4	BA95/4	×	×	×	×					45	MM
	5	BA95/5	×	×	×	×					60	MM
	6	BA95/6	×			×					5	LM
	8	BA95/8						×			1	LM
	9	BA95/9	×	×						×	6	MM
	14	BA95/14				×					3	MM
	15	BA95/15	×								1	LM
	17	BA95/17	×	×		×	×				50	MM
	23	BA95/23	×	×							3	LM
	27	BA95/27	×	×	×						5	LM
	28	BA95/28	×	×	×					×	84	MM
	31	BA95/31	×	×		×		×		×	27	MM
	32	BA95/32	×	×				×			15	MM
	34	BA95/34	×	×		×				×	13	MM
1996	86	BA96/86	×	×	×					×	9	
2001	11	BA01/11	×	×	×	×	×	×			39	MM
	12	BA01/12	×	×	×	×		×			13	MM
2005	1	BA05/1	×	×	×						15	LM
	2	BA05/2				×					2	
Total Blocks	**116**									**Grand Total**	**4866**	

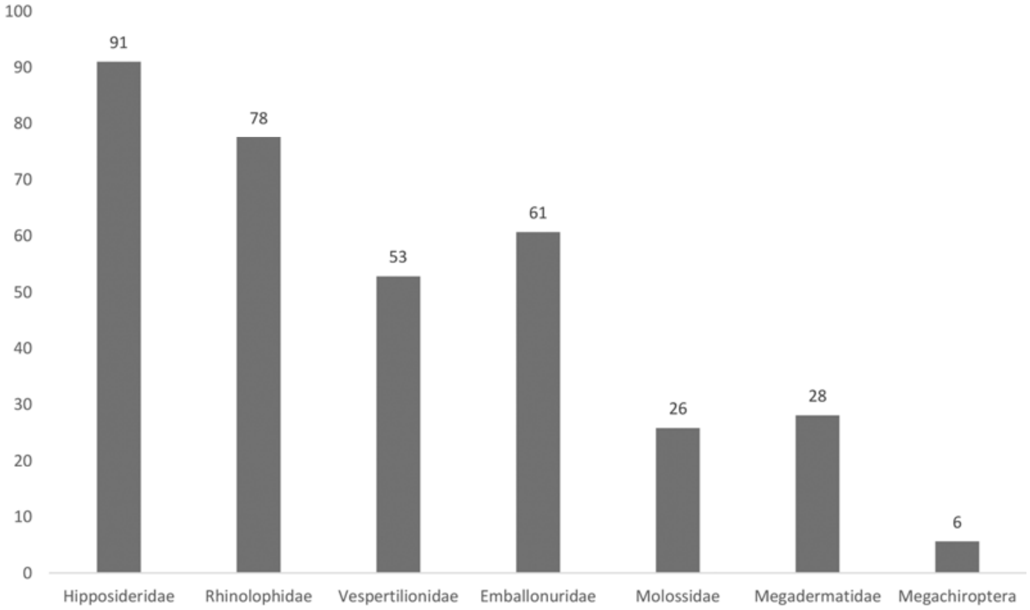


Figure 3. The occurrence of bat remains in the Miocene breccia blocks of the Berg Aukas I site (in %). For the list of the Miocene breccia blocks of Berg Aukas I see Table 1.

Remains of emballonurids are very common in the Miocene assemblages of the Berg Aukas I site in which they occur more often than even vespertilionid bats (Fig. 3). The family Emballonuridae comprises small to moderately large microchiropteran bats recently occurring in the Old and New Worlds. Two subfamilies are recognized within Emballonuridae: Taphozoinae, the representatives of which are large and the smaller Emballonurinae, which is represented by tribe Diclidurini in the New World and tribe Emballonurini in the Old World (McKenna & Bell, 1997). The Taphozoinae are most abundant among the emballonurid records from Berg Aukas I site. In modern times the Taphozoinae is widely distributed across Africa, the islands of the western Indian Ocean, Australia, Asia and the southwest Pacific (Ruedi *et al*. 2012).

Four extant genera (*Coleura, Emballonura, Mosia* and the Malagasy genus *Paremballonura*) comprise the other tribe Emballonurini. *Coleura* inhabits mainland Africa, the Arabian Peninsula and Madagascar. *Emballonura* has a broad distribution across islands in the Indo-Pacific and southern Asia. The monospecific genus *Mosia* is known from New Guinea and surrounding islands (Flannery, 1995). *Paremballonura* is endemic to Madagascar (Goodman *et al*. 2012). Some Middle Miocene assemblages from the Berg Aukas I site e.g. from the blocks of BA92/1 and BA94/52, comprise some new representatives of small-sized bats of the tribe Emballonurini, which may throw some light on the questions of faunal exchanges and diversification of the group during the past 14 Ma.

The Miocene is a key period in the evolution of the Vespertilionidae, the richest family among extant bats with an almost cosmopolitan distribution (Horáček, 2001). At this time a significant species radiation took place within this family (Sigé & Legendre, 1983). In Europe climatic deterioration and pronounced seasonality occurred during the late Neogene and disadvantaged most specialized representatives of the emballonurids and the molossids. In contrast, the vespertilionids apparently profited from the disappearance of these other bats by occupying a wider range of habitats (Horáček, 2001). Thus, at the beginning of the Miocene emballonurids had already disappeared from Europe, whereas they previously held leading positions among the Palaeogene bat communities. Obviously in Africa the situation developed differently.

In the Middle Miocene assemblages from the Berg Aukas I site emballonurid remains are more common than vespertilionids and molossids combined (Fig. 3). Evidence now available suggests an appreciably more humid and more tropical palaeoclimate in the Otavi Mountainland during the latter part of the Middle Miocene than occurs today (sub-humid woodland and savanna). It may well have been forested with fruiting trees. By the Plio-Pleistocene in contrast, the climate appears to have become semi-arid. At present, the Otavi Mountains lie within the southern sub-tropical or warm-temperate zone of Africa and the region is semi-arid with woodland vegetation (Pickford & Senut, 2010). More humid palaeoclimatic conditions during the Miocene contributed to a high diversity of bats including emballonurids. Given that nowadays the Megadermatidae is the rarest group of bats in Africa (ACR, 2018: p. 1), it is notable that in the Miocene bat assemblages from the Berg Aukas I site, the remains of megadermatids are even more common than those of molossids (Fig. 3). Thus, the rather high proportion of megadermatids in the Miocene assemblages from the Berg Aukas I site confirm the existence of more tropical conditions in the Otavi Mountainland region until the beginning of the Pleistocene (Fig. 3).

Conclusions

The fact that many of the bat groups found in the Miocene assemblages of the Berg Aukas I site are geographically widespread means that biostratigraphic correlations between Namibian, South European and South Asian bat faunas would be possible. Correlation of the Namibian bat fauna with those from the other sites of Africa, Europe and South Asia may throw some light on the questions of faunal exchanges and diversification of the group during the Neogene. In addition, new data about Miocene bats of Africa can be applied for the reconstructions of palaeoecology of fossil bats and their communities in general.

Among the Berg Aukas fossils there are many taxa new to science, including some extant taxa which were previously unknown in the fossil state. All this points to the enormous potential of the materials from the fossiliferous breccia of the Otavi Mountainland for the study of the evolution not only of some bat families, but also the Neogene biota of Africa as a whole.

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Southern African Tetraconodontinae : Recent discoveries

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Abstract: Tetraconodont suids are in general rather poorly represented in Southern Africa, except at Langebaanweg, Cape Province and the Chiwondo Beds, Malawi. We here describe material from two localities in Namibia and one in South Africa in order to fill out the fossil record of this subfamily of artiodactyls in the subcontinent. The oldest specimens (*Nyanzachoerus* sp. cf *jaegeri*) are from Kaukausib Fontein, Namibia (ca 4-6 Ma), the next oldest (*Gerontochoerus koobiforaensis*) are from Brad Pit 'A', Bolt's Farm, South Africa (ca 3.7 Ma) and the youngest (*Gerontochoerus scotti*) are from Ekuma Rhino Site, northern Namibia (ca 3.2 Ma).

Key words: Suidae, Pliocene, Pleistocene, Southern Africa, Biochronology

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Introduction

Ongoing palaeontological field surveys in Southern Africa have resulted in the discovery of abundant fossil plants and animals of Late Miocene to Pleistocene age. This report deals with fossil suids (pigs) found in Namibia and South Africa, which belong to the subfamily Tetraconodontinae. The fossils belong to three different species and they throw light on the ages of the strata from which they were extracted as well as yielding information about their diet. The species were collected from three localities : 1) Kaukausib Fontein, Sperrgebiet, Namibia, 2) Brad Pit 'A', Gauteng, South Africa and 3) Ekuma Rhino Site, Etosha Basin, Namibia.

The aim of this paper is to describe and interpret the new suid fossils from Southern Africa within the framework of what is known about Tetraconodontinae in the equatorial and septentrional latitudes of the continent. The fossils belong to well-established taxa, the ages of which are reasonably well-constrained in other parts of Africa and on this basis, the ages of the localities from which the fossils were collected are estimated.

An additional value in the fossils is that they throw light on the long-standing debate about the affinities of the genus *Notochoerus*, supporting the hypothesis that this genus is a Suinae rather than a Tetracondontinae.

Background and discovery context

Kaukausib Fontein

Two suid specimens from indurated grits at Kaukausib Fontein, Sperrgebiet, Namibia, belong to the *Nyanzachoerus kanamensis/ jaegeri/ australis* group, all three species of which are relatively brachyodont Tetraconodontinae. The fossils indicate that deposition of the Kaukausib Fontein travertines and grits likely took place sometime between 6 and 4 Ma. This period is more or less coeval with the deposition of the so-called 50 metre littoral marine package along the western coast of South Africa and Namibia (Pether, 1986).

The biochronology provides constraints on the timing of deposition of the grits in the Tsirub and Kaukausib drainages and of the tectonic activity which affected these sediments. The fossils attest to a somewhat more humid and possibly cooler palaeoclimate than occurs in the region today. Travertine activity could be related to higher rainfall in the interior of Namibia than occurs today, or it could be linked to the fact that sea-level was 50 metres higher during the period of deposition than it is today, leading to a concomitant rise in the altitude of the water table, which thereby increased flow at the Kaukausib spring and in the Tsirub and Kaukausib drainage networks in general.

Fossils were first recorded in the grits exposed in the Kaukausib Valley in 1996. An extract from the field report of the Namibia Palaeontology Expedition compiled by Pickford & Senut (1996) reads « *Kaukausib Fountain lies well inland from Grillental in the upper reaches of the same valley. Fossils were found by R. SPAGGIARI and D. WARD during geological mapping, and a follow-up study was carried out by the authors. The site consists of several steeply dipping travertine layers intercalated with grits. The strata appear to have originally formed a tufa dome which has since been incised, revealing the various strata dipping away from a central "eye" area which probably represents the site of a former hard-water spring. Abundant vertebrate fossils were observed in several of the grit layers, but only plant fossils were seen in the travertine, which is onyx-like. The mammal assemblage, although restricted, appears to be of Late Pliocene to Pleistocene affinities, but collection and preparation of fossils is needed to confirm this estimate. The grit is extremely indurated, which is why the bulk of fossils was left in situ for careful extraction in the future. Some of the fossils occur as partly articulated skeletons, and it was decided to leave this material in place as a possible tourist attraction. Indeed, several of the bone patches would be of great interest to the public, as the bones are easily visible, and the occurrence is spectacular, as is the surrounding countryside* ».

In 2019, the suid fossils were extracted from the outcrop using rock cutters and drills (Pickford & Senut, 2019) and a new specimen was collected in a loose block of grit lying on the surface (Fig. 3, 4). In the laboratory, the fossils were extracted from the grit by a combination of formic acid attack and airscribe techniques and then consolidated with plexigum dissolved in acetone.

Brad Pit 'A'

Excavations at Brad Pit 'A', a karst infilling in the Bolt's Farm Karst System (Pickford & Gommery, 2016, in press) have yielded several teeth of a large suid, including premolars of typical tetraconodont morphology and a moderately hypsodont, elongated m/3. The specimens differ markedly from suid remains from the nearby site of Aves Cave I attributed to *Notochoerus capensis* by Pickford & Gommery (2016). The presence of these two taxa in neighbouring sites (of roughly similar ages) is of interest, and adds fuel to the long-lasting debate about the subfamilial status of *Notochoerus capensis* (is it a suine or is it a tetraconodont?). The Brad Pit 'A' fossils are described and compared with East African members of the Tetraconodontinae and it is concluded that they represent the species *Gerontochoerus koobiforaensis*, a mid-Pliocene species. From this we deduce that the Brad Pit 'A' deposits are about 3.7 Ma, but could be as old as 4 Ma or as young as 3.2 Ma.

Ekuma River Rhino Site

At the main Ekuma Site 1 in the Etosha Basin, the fossils which are in the Ekuma Delta Member in the upper part of the Andoni Formation are estimated by Miller *et al*. (2010) to be about 4 Ma, but the strata at the Ekuma Rhino Site are somewhat younger (ca 3.2 Ma) (Pickford *et al*. 2016). The Ekuma Main Site 1 (ca 4.5 Ma) yielded a large suid talus and a calcaneum, but so far no cheek teeth (only a fragment of tusk) and the underlying Etosha Pan Clay Member which is ca 6 Ma yielded a large suid patella. Pending the discovery of suid teeth in these older levels, we refrain from naming the taxa to which these postcranial bones belong, merely observing that they belong to huge suids calculated to have weighed between 360 and 960 kg (Pickford *et al*. 2013).

The fossil suid m/3 from Ekuma Rhino Site was mentioned briefly by Pickford *et al*. (2016) who attributed it to *Gerontochoerus koobiforaensis*. However, the specimen has five pairs of cusps, and thus accords better with the more derived species *Gerontochoerus scotti*.

Locations and geological context of fossiliferous sites

The tetraconodont fossils described herein came from three localities - in chronological order Kaukausib Fontein (Namibia), Brad Pit 'A' (South Africa) and Ekuma Rhino Site (Namibia). The locations of these sites is given in Figs 1 and 2, along with the positions of other African localities discussed in the text.

Kaukausib Fontein, Sperrgebiet, Namibia

The superficial geology of the Kaukausib Fontein and surrounding areas was described by Pickford (2018) who built on pioneer mapping by Bennett & Kalbskopf (1978). The suid fossils described herein were enclosed in coarse, poorly sorted grit cemented by calcium carbonate. The grit layers are intercalated between pure onyx-like travertine deposits (Fig. 3).

Figure 1. Location of African sites discussed in the text which have yielded remains of tetraconodont suids (*Nyanzachoerus* and *Gerontochoerus*) and suines *Notochoerus* (BF - Bolt's Farm (with Brad Pit 'A'), KF - Kaukausib Fontein).

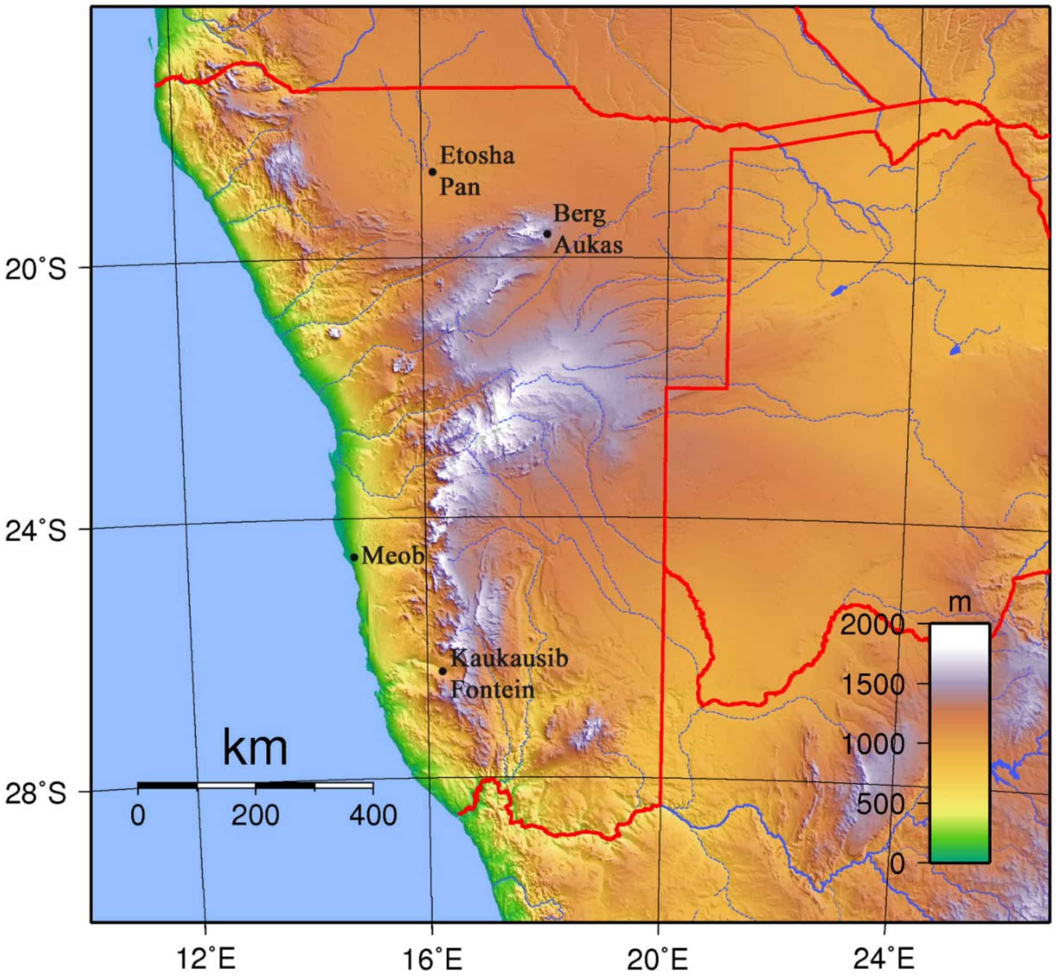

Figure 2. Digital Elevation Map of Namibia showing the distribution of Late Miocene to Basal Pliocene sedimentary deposits that have yielded fossil mammals (not shown are aeolianites spanning the same period that have yielded eggshells of struthious birds).

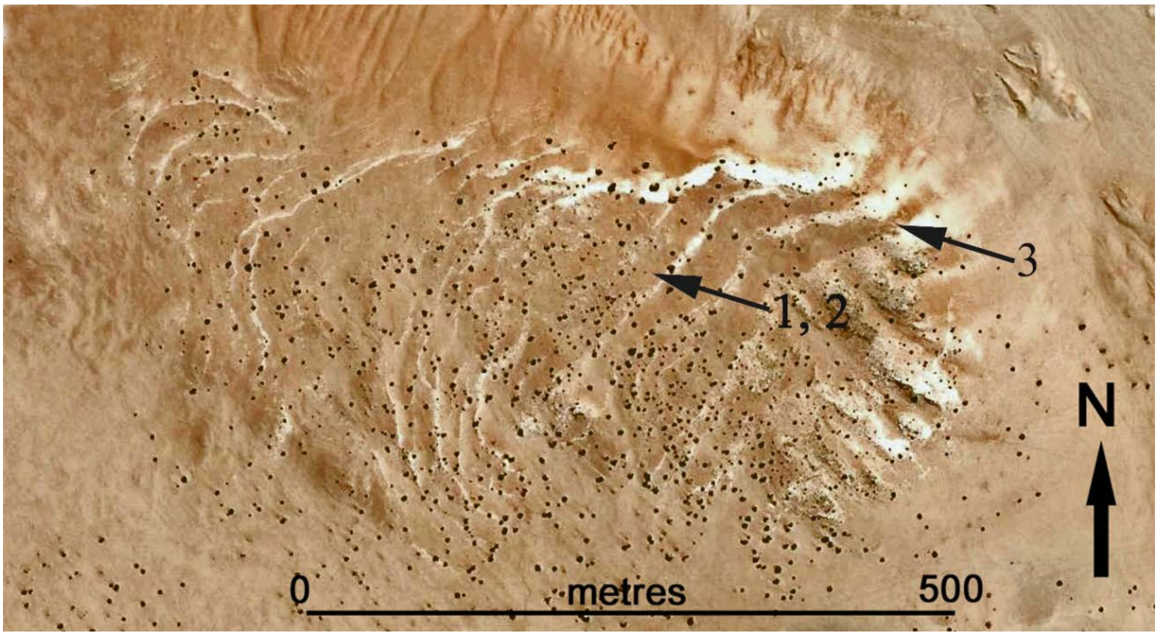

Figure 3. The Kaukausib Fontein Travertine - Grit complex. The precise positions of specimens GSN KF 1'19 to GSN KF 3'19 are shown (1, 2, 3) (Base map is from Google Earth).

Brad Pit ‘A’, Bolt’s Farm Karst System

The geological context and age of the Bolt’s Farm Karst System (Figs 1, 4) has been discussed on several occasions (Sénégas, 2000, 2004; Sénégas & Avery, 1998; Sénégas *et al.* 2002; Thackeray *et al.* 2008; Gommery *et al.* 2012; Pickford & Gommery, 2016). On the basis of the presence of a late form of *Euryotomys* older than the Aves Cave I form, but younger than the species from Waypoint 160, the episode of karst infilling at Brad Pit ‘A’ is estimated to have occurred about 3.7 Ma (Fig. 4) (range 4-3.2 Ma).

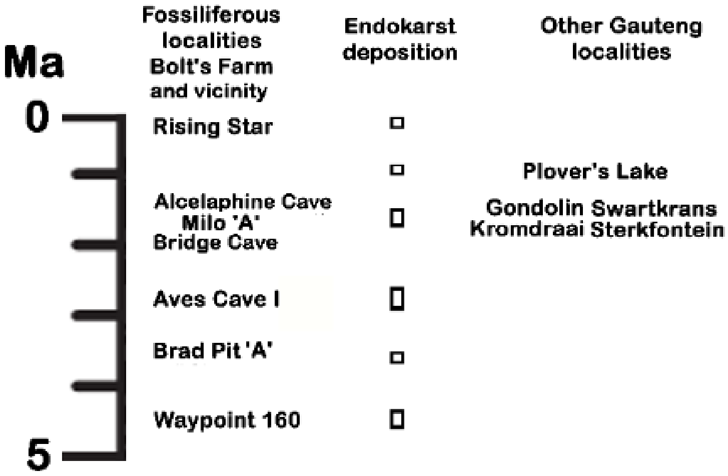

Figure 4. Estimated ages of karst infillings in the Cradle of Humankind, Gauteng, South Africa. The suid teeth described herein were collected from the Brad Pit ‘A’ infilling (from Pickford & Gommery, in press).

Ekuma Rhino Site, Etosha, Namibia

The geological context of the Ekuma Rhino Site was published by Miller *et al.* (2010) and Pickford *et al.* (2013, 2016). The specimens are from the Ekuma Delta Clay Member, which spans the period ca 4.5 to 3.2 Ma, the Rhino Site being in the younger levels of the unit for which we estimate an age of ca 3.2 Ma.

Material and methods

The fossils described herein comprise suid specimens from Kaukausib Fontein (GSN KF) and Ekuma Rhino Site (GSN EKR), curated at the National Earth Science Museum, Geological Survey of Namibia, Windhoek, and three teeth curated at the Ditsong National Museum of Natural History, Pretoria (DNMNHP where fossils from Brad Pit ‘A’ are catalogued under the abbreviation BPA). Other fossils are curated at the Natural History Museum, London (abbreviations NHMUK and NHML) and the Kenya National Museum (KNM including its previous name CM (Coryndon Museum)). Images were taken with a Sony Cybershot camera and treated with Photoshop Elements15 to improve contrast and to remove unwanted background. Scales were added manually. Measurements were taken with sliding calipers to the nearest tenth of a mm.

Dental nomenclature

Figure 5 shows the nomenclature utilised in this paper. There are many terms used for hypsodont suid teeth which do not conform to classic dental nomenclature, and this has given rise to a certain degree of confusion as was pointed out by Pickford (2013). For example, many authors (Cooke, 1976, 2007; Kullmer, 1999, 2008) have used the term ‘laterals’ (or ‘lateral pillars’) for the transversely arranged cusp pairs in such teeth, but only the buccal cusp of each pair can legitimately be called lateral, the lingual one by definition being medial.

Cooke (1976) for example, described the third molars of *Notochoerus euilus* as having « only four or five pairs of lateral pillars » by which he meant four or five pairs of pillars, each 'pair' of cusps being called a 'lateral' despite the fact that each such 'pair' comprises a buccal (lateral) and a lingual (medial) cusp. Other informal names such as skirts, pillars and columns have been used to describe hypsodont cingular structures, tall basal pillars, and tall anterior, median and posterior accessory cusplets. These non-conformant terms have in a way distanced hypsodont suids from their brachyodont and bunodont ancestors to such an extent that most authors failed to realise that all the structures in hypsodont suid teeth have corresponding structures in their bunodont ancestors and this has obscured the evolutionary relationships between the brachyodont (and bunodont) ancestral lineages and their highly derived hypsodont descendants (Pickford, 2013).

Hypsodonty in suids has been achieved independently by at least five different lineages, each of which emphasised different parts of the tooth crowns at different ontogenetic stages, and in different ways along the tooth row (White, 1959). Whereas some lineages such as *Gerontochoerus* (Tetraconodontinae), *Kolpochoerus* and *Hylochoerus* (Suinae) added cusp pairs to the third molars, thereby increasing the length of the teeth, others emphasised the distal cingular complex (*Potamochoeroides*, *Metridiochoerus*, *Stylochoerus*, *Phacochoerus*) to produce a complicated multicusped complex of pillars at the rear of the tooth.

Some suid lineages emphasised the hypsodonty of the apical parts of the crown, others the mid-crown parts of the tooth, and yet others the crown base. The results are quite different in detail, yet all can be described as hypsodont. Furthermore, the upper and lower molars may achieve hypsodonty in slightly different ways, so it is not always obvious to identify isolated upper molars on the basis of what the lowers look like and vice versa.

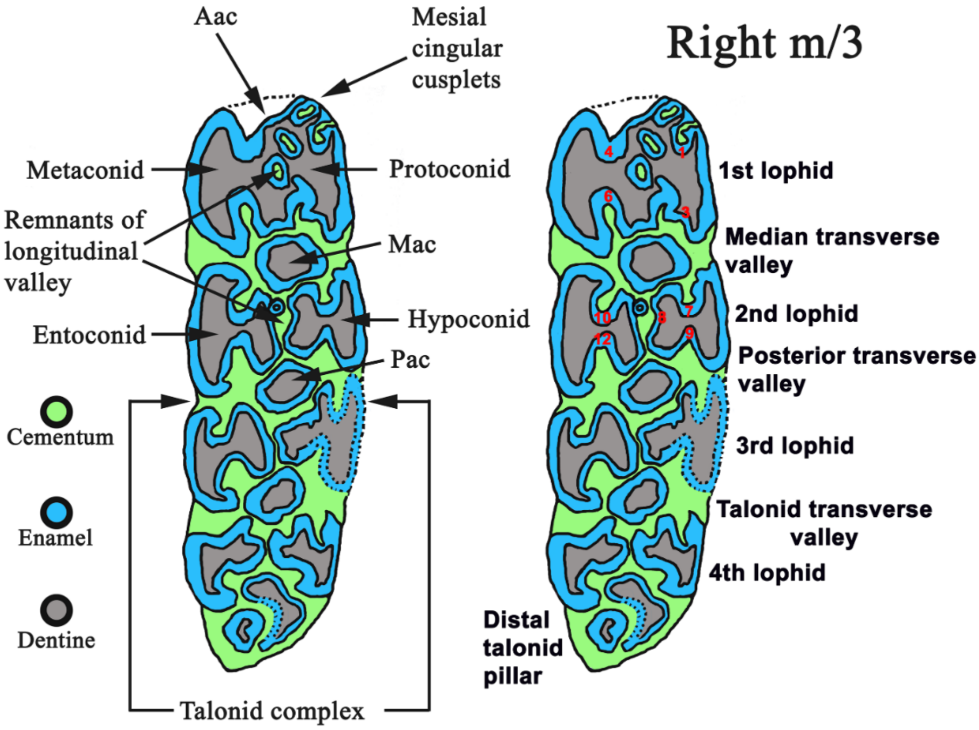

Figure 5. Nomenclature of the lower third molar of *Gerontochoerus koobiforaensis* from Brad Pit 'A', South Africa (Aac - anterior accessory cusplet, Mac - median accessory cusplet, Pac - posterior acessory cusplet). 1-12 (in red figures) are Furchen (some have been obliterated by wear) which impart the characteristic 'H'-shape to the occlusal outline of each cusp.

Systematic Palaeontology

Family Suidae Gray, 1821

Genus *Nyanzachoerus* Leakey, 1958

Diagnosis: A genus of the family Suidae that possesses large posterior (third and fourth) premolars in relation to the anterior premolars and in general, simple bunodont molars similar to those of *Potamochoerus* Gray, 1854, but taller and with thicker enamel; molars have cusps that, when worn, show dentine islands forming a star shape; more derived specimens show a trend towards increased elaboration of the third molars and reduced premolars; incisors wide and large; upper canines oval to flattened oval in transverse section; lower canines verrucose with thin, weakly grooved enamel on two lateral faces; strong sexual dimorphism characterized by larger size, robustness, massiveness of skull, and the presence of large zygomatic knobs in males; robust mandibles, with thick corpus that contrast with the unusually thin bone forming the angle (after Cooke & Ewer, 1972; Harris & White, 1979; Bishop, 2010; Reda *et al*. 2017).

Species *Nyanzachoerus* cf *jaegeri* Coppens, 1971

Diagnosis: A progressive species of the genus *Nyanzachoerus* with dental attributes that are intermediate in morphology and size between a more typical *Nyanzachoerus* condition and a more derived tetraconodont condition (genus *Notochoerus*) skull morphology, number of premolars, number, morphology and size of incisors and enamel thickness as in *Nyanzachoerus*. Derived dental characteristics include longer third molars, molars with more enamel folding and smaller premolars; otherwise general teeth architecture as in *Nyanzachoerus kanamensis* (from Reda *et al*. 2017).

Material :

GSN KF 1’19, left maxilla fragment containing base of M3/ (length x breadth : -- x 33 mm).

GSN KF 2’19, upper molar base (length x breadth : 37 x -- mm).

GSN KF 3’19, juvenile right mandible fragment with broken m/1 and m/2 germs (length x breadth x lingual height - m/1 : 29.5 x 18 x 14.0 mm; m/2 : 32 x -- x 17.5 mm).

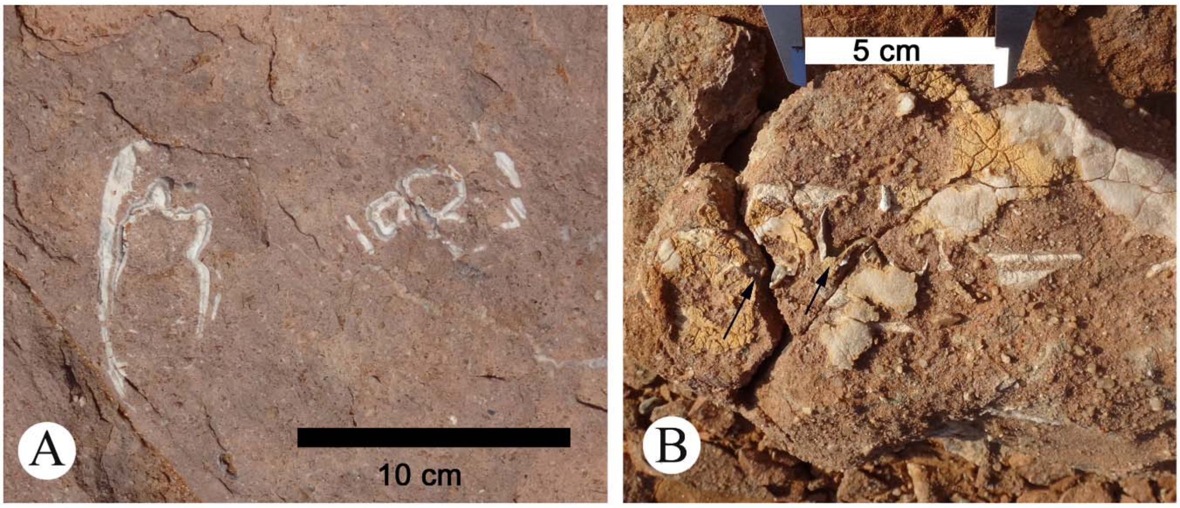

Figure 6. The suid fossils from Kaukausib Fontein prior to extraction from their enclosing grit. A) GSN KF 1’19 and GSN KF 2’19, B) GSN KF 3’19 (Black arrows in B show the teeth).

Description

The best preserved suid tooth from Kaukausib Fontein is the right m/1 germ, GSN KF 3’19 (Fig. 6b, 7). Part of the buccal side was eroded away prior to collection, but extraction using an airscribe has revealed much of the distal lophid and the rear half of the anterior lophid with well-preserved median and posterior accessory cusplets. The lingual notch is antero-posteriorly broad with a U-shaped base and no basal cusplets. The Furchen are shallow and the postmetacristid, preentocristid and postentocristid are well-defined, as are the prehypocristid and posthypocristid. The endocristids of the entoconid and hypoconid are directed towards the median transverse valley and slightly anteriorly. The median and posterior accessory cusplets are about 2/3 the height of the main cusps. The distal cingulum is low and distinct from the posterior accessory cusplet. The poorly preserved lingual side of the m/2 is preserved in its crypt. The enamel surface reveals that the crown was incompletely formed at the time of death, but crown height can be estimated. In general what remains of the morphology of this tooth is like that of the m/1.

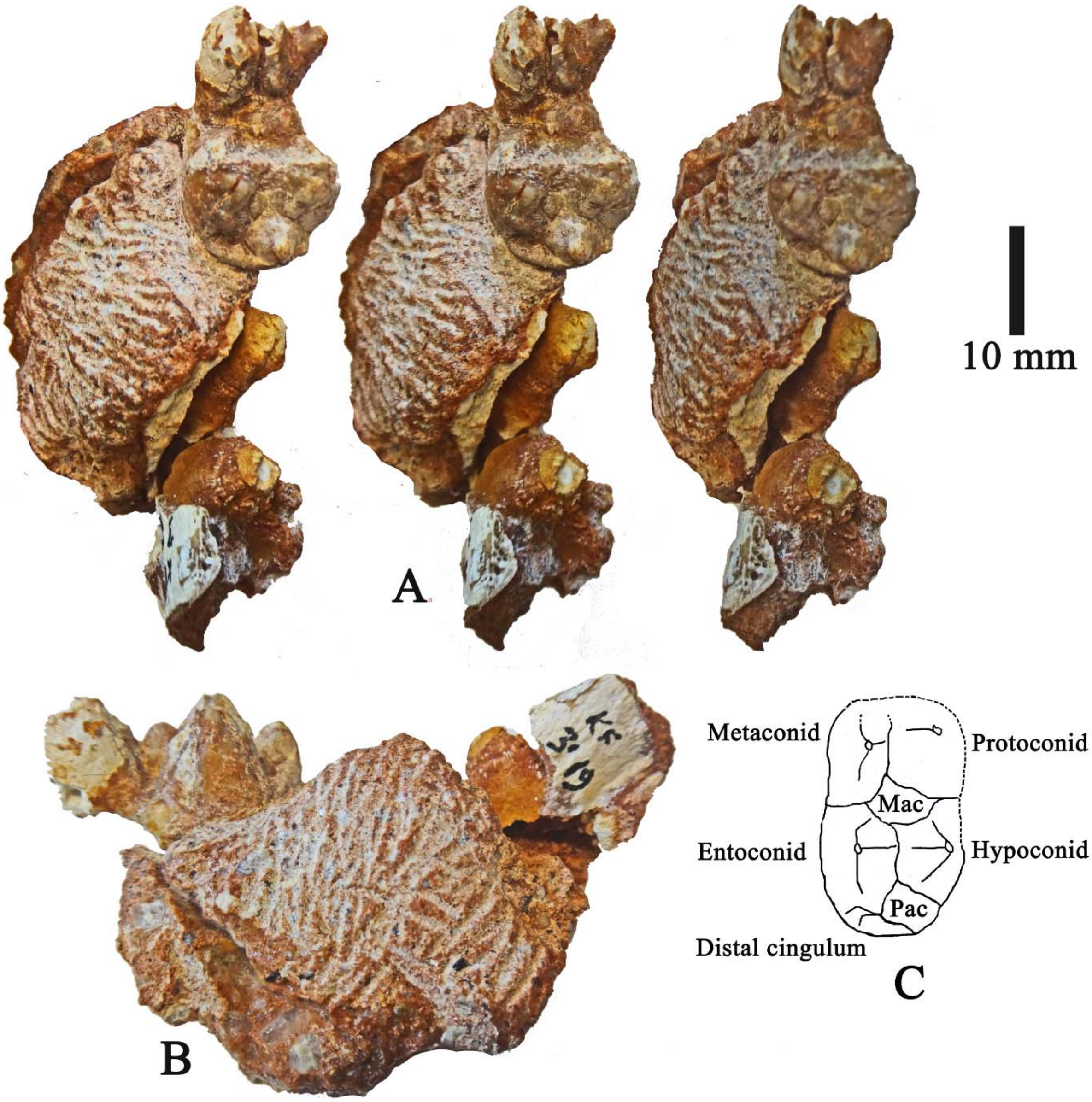

Figure 7. GSN KF 3’19, right m/1 and m/2 germs in a fragmentary mandible. A) stereo occlusal views, B) buccal view, C) interpretive drawing of m/1 (Mac - median accessory cuspet, Pac - posterior accessory cusplet) (scale : 10 mm).

The left M3/, GSN KF 1’19, is missing most of the crown which was eroded off prior to collection (Fig. 6a). Parts of the maxilla and palatine bone are preserved, but are in poor condition. What remains of the tooth has been exposed using an airscribe. The anterior cingular complex is reasonably well-preserved on the buccal half, and reveals that it is low in comparison with the dimensions of the tooth. The base of the anterior accessory cusplet is preserved and it is distinct from the mesial cingulum. The cervix is well-defined, and overhangs the roots to a small extent. The base of the median transverse valley is preserved, and it appears to have been mesio-distally broad with a U-shaped profile and there are no signs of cusplets in its base.

The other specimen from Kaukausib Fontein (GSN KF 2’19) is so deeply eroded that no useful details can be obtained, other than an estimate of its dimensions and proportions which reveal that it is likely to be an upper molar, possibly an M2/. The base of the crown is comprised of coarsely wrinkled enamel as in some specimens of *Nyanzachoerus*.

Discussion

The two molar germs in GSN KF 3’19 are brachyodont (crown height is less than the breadth : 14/18 mm), whereas lower molars of species of *Potamochoeroides*, *Metridiochoerus*, *Notochoerus*, *Phacochoerus* and *Hylochoerus* are hypsodont (crown height is greater than the breadth). Some species of *Kolpochoerus* are relatively weakly hypsodont, but unlike the Kaukausib specimens, they generally have tall mesial cingular complexes and tall anterior, median and posterior accessory cusplets (Pickford, 1994). The anterior cingular complex in the M3/ (GSN KF 1’19) is low, and the cervix is clearly defined between the crown and the roots. The brachyodonty of the Kaukausib Fontein suid teeth indicate that the specimens are unlikely to belong to large species of *Libycochoerus* or *Kubwachoerus* (Pickford & Tsujikawa, 2019) which have bunodont molars with marked lingual and buccal flare. The same observations apply to species of *Sivachoerus*.

The dimensions of the Kaukausib Fontein suid teeth excludes the possibility that they might pertain to *Potamochoerus* which is a much smaller genus.

The only known African taxon which accords with the morphology and dimensions of the Kaukausib Fontein teeth is *Nyanzachoerus*. Several species of this genus have been defined (Fig. 8). Some, such as *Nyanzachoerus waylandi*, are small whereas there are several which are large including species with rather bunodont molars (*cookei, syrticus, khinzir*) which are sometimes classified in the genus *Sivachoerus*. The dimensions and brachyodont morphology of the Kaukausib Fontein suid teeth accord with three species of the genus *Nyanzachoerus* (*N. kanamensis*, *N. jaegeri*, *N. australis*).

Even though a definitive species identification of the Kaukausib suid teeth is not possible, given the limited nature of the sample, the best morphometric fit is with the small subgroup of *Nyanzachoerus jaegeri* described from the Western Rift, Uganda (Pickford, 1994) and with the fossils from Kanam, Kenya (the type locality of *Nyanzachoerus kanamensis* Leakey, 1958).

If this identification is valid, then it suggests that the fossils correlate to the latest Miocene or basalmost Pliocene (between 6 and 4.5 Ma) but given the uncertainty they could be as young as 4 Ma. There is a possibility that the specimens could pertain to the well-known Langebaanweg, South Africa, taxon *Nyanzachoerus australis* Cooke & Hendey, 1992, which has also been recovered from the 50 metre littoral marine package at Hondeklip Bay in Namaqualand (Pickford & Senut, 1997). This littoral marine package is considered to date from ca 6 Ma (Pether, 1986; Pickford, 1998).

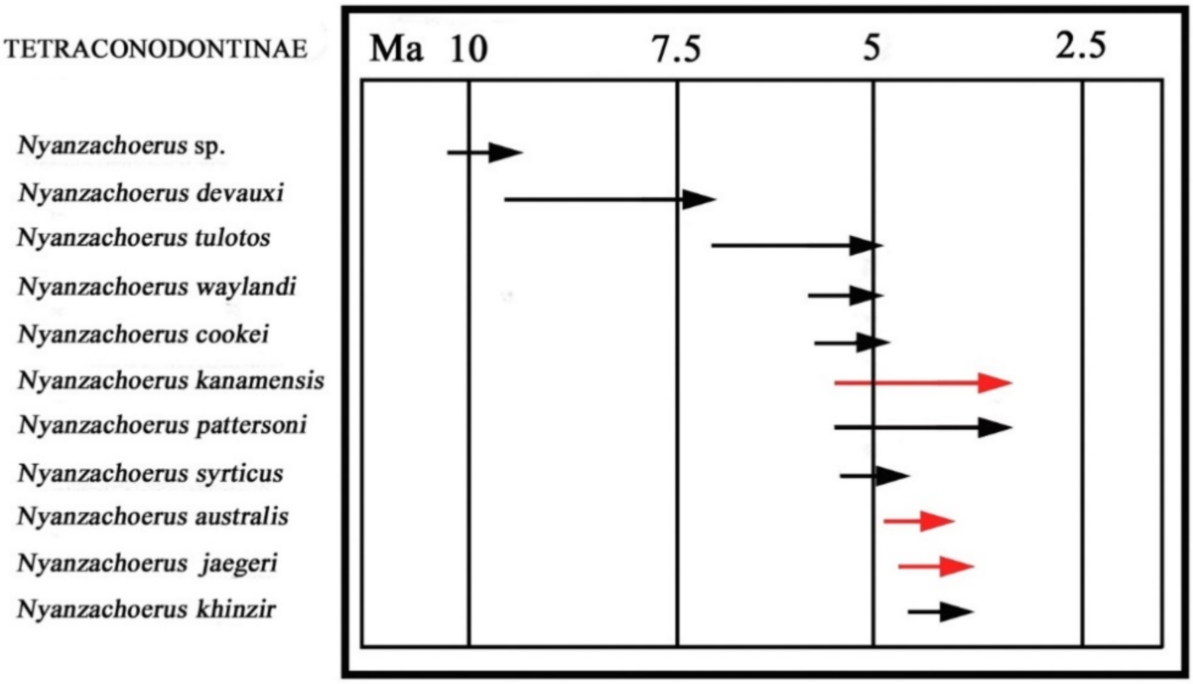

Figure 8. Biochronology of African brachyodont and bunodont tetraconodonts. Some authors classify the more bunodont species such as *devauxi*, *tulotos*, *cookei*, *syrticus* and *khinzir* in the genus *Sivachoerus*, and the brachyodont forms in *Nyanzachoerus*. The Kaukausib Fontein suid teeth are closest in dimensions and crown morphology to the taxa represented by red arrows (*Nyanzachoerus jaegeri*, *N. australis* and early forms of *N. kanamensis*) (Figure modified and extended from Pickford, 2006).

Conclusion

Three suid teeth from coarse grits interbedded with onyx-like travertine at Kaukausib Fontein in the Sperrgebiet, Namibia, are closest in morphometric details to large, brachyodont species of *Nyanzachoerus*. Given the limitations of the material, it is not possible to provide a secure species identification, but comparisons with 1639 fossil and extant African suid molars (779 M3/s, 343 m/1s and 517 m/2s) of all ages (20 Ma to Present day) reveals that the specimens accord best with basal Pliocene specimens of *Nyanzachoerus jaegeri*, late Miocene specimens of *Nyanzachoerus kanamensis* and basal Pliocene specimens of *Nyanzachoerus australis*.

If the identification is valid, then travertine deposition at Kaukausib Fontein likely occurred at the Miocene-Pliocene transition, at the same time as deposition of the 50 metre littoral marine package defined by Pether (1986) a possibility that invites scenarios of cause and effect. In brief, an eustatic rise in sea level would likely cause a concomitant rise in groundwater levels in the vicinity of the coast, meaning that the water table would rise, likely leading to increased flow at springs such as Kaukausib Fontein, which today flow at reduced rates or at other springs in the region that have dried up altogether as a result of subsequent lowering of the water table.

Mapping of the travertines exposed in the Kaukausib and Tsirub drainages has not been completed (Pickford, 2018) but it is clear that spring flow was orders of magnitude greater during the late Miocene and basal Pliocene than it is today. An alternative scenario is that regional climate may have been cooler and somewhat more humid than it is today resulting in greater volumes of groundwater.

If the biochronology proposed on the basis of the suid teeth from Kaukausib Fontein is valid, then this record extends the geographic representation of the late Miocene to basal Pliocene fossil register of Namibia into the Sperrgebiet. Previously, the only known deposits of this period of time in the country were reported from the Otavi Mountains (Pickford, 2002) from Etosha Pan (Miller *et al*. 2010; Pickford *et al*. 2016) and from Meob (Morales *et al*. 2011) (Fig. 2).

Genus *Gerontochoerus* Leakey, 1943

Type species: *Gerontochoerus scotti* Leakey, 1943

Original genus diagnosis: Suidae with high-crowned and long-rooted third molars composed of four or more pairs of pillars and a small talon. The line of demarcation between crowns and roots very clearly differentiated. Upper third molars more complex than lowers (from Leakey, 1943).

Emendation to diagnosis: Tetraconodont Suidae in which the upper and lower third molars possess additional cusp pairs resembling the first two pairs, plus more or less complex talon(id)s. Anterior, median and posterior accessory cusplets distinct and tall and not intervening between the main cusps. Third and fourth premolars significantly larger than the second premolars (which are often absent) but with a tendency for them to be smaller than those of other tetraconodonts such as *Nyanzachoerus*, *Sivachoerus* and *Tetraconodon* in which the second premolars are always present. Cementum present on molars, molar enamel finely and intensely wrinkled. Tendency for the main cusps to produce 'H'-shaped (or mushroom shaped) enamel outlines at the occlusal surface due to the presence of deeply indented Furchen and tall basal cusplets which, with wear coalesce with the anterior and posterior ends of the pre- and postcristids of the main cusps.

Species *Gerontochoerus koobiforaensis* Pickford, 2013

Holotype: KNM ER 3541, a skull and mandible (Harris & White, 1979, Plates 1-3).

Type locality and age: Unit 2 of the Koobi Fora Formation, East Turkana, Kenya (ca 4 Ma).

Diagnosis: A species of *Gerontochoerus* intermediate in dimensions between *Gerontochoerus euilus*, which is smaller, and *Gerontochoerus scotti*, which is larger (from Pickford, 2013). The species has four pairs of cusps in the third molars, as opposed to five or more in the other species.

Descriptions of the fossils from Brad Pit 'A'

<u>DNMNHP BPA 852, right m/3</u> (Fig. 9).

This tooth is deeply worn; even the terminal pillars at the distal end of the crown are in light wear, signifying a fully adult individual but not a senile one. The crown as preserved is ca 19 mm tall at the entoconid and 21.5 mm tall at the distal end on the lingual side (unworn the distal cusps would have been ca 23 mm tall). This tooth, even though hypsodont, is not nearly as hypsodont as teeth of *Potamochoeroides*, *Metridiochoerus*, *Stylochoerus*, *Phacochoerus* and *Notochoerus*, in all of which the talonid cusps are considerably taller than in *Gerontochoerus*.

The cervix is clearly expressed and is almost rectilinear, and there are remnants of root beneath all the cusps as well as the talonid. Distal to the third lophid, the cervix rises at a gentle angle beneath the talonid indicating that this is a lower molar. This is confirmed by the fact that the occlusal surface and the cervix are sub-parallel to each other (Pickford, 2013). The slope of the root beneath the talonid indicates that this is a right lower third molar, as do the positions of the median and posterior accessory cusplets, the mesial cingular cusplets and the slightly greater buccal flare of the crown on the right aspect of the talonid, the left side being almost vertical. The crown is slightly distorted by damage such that in occlusal view it bends gently to the left rather than being straight or gently curved to the right.

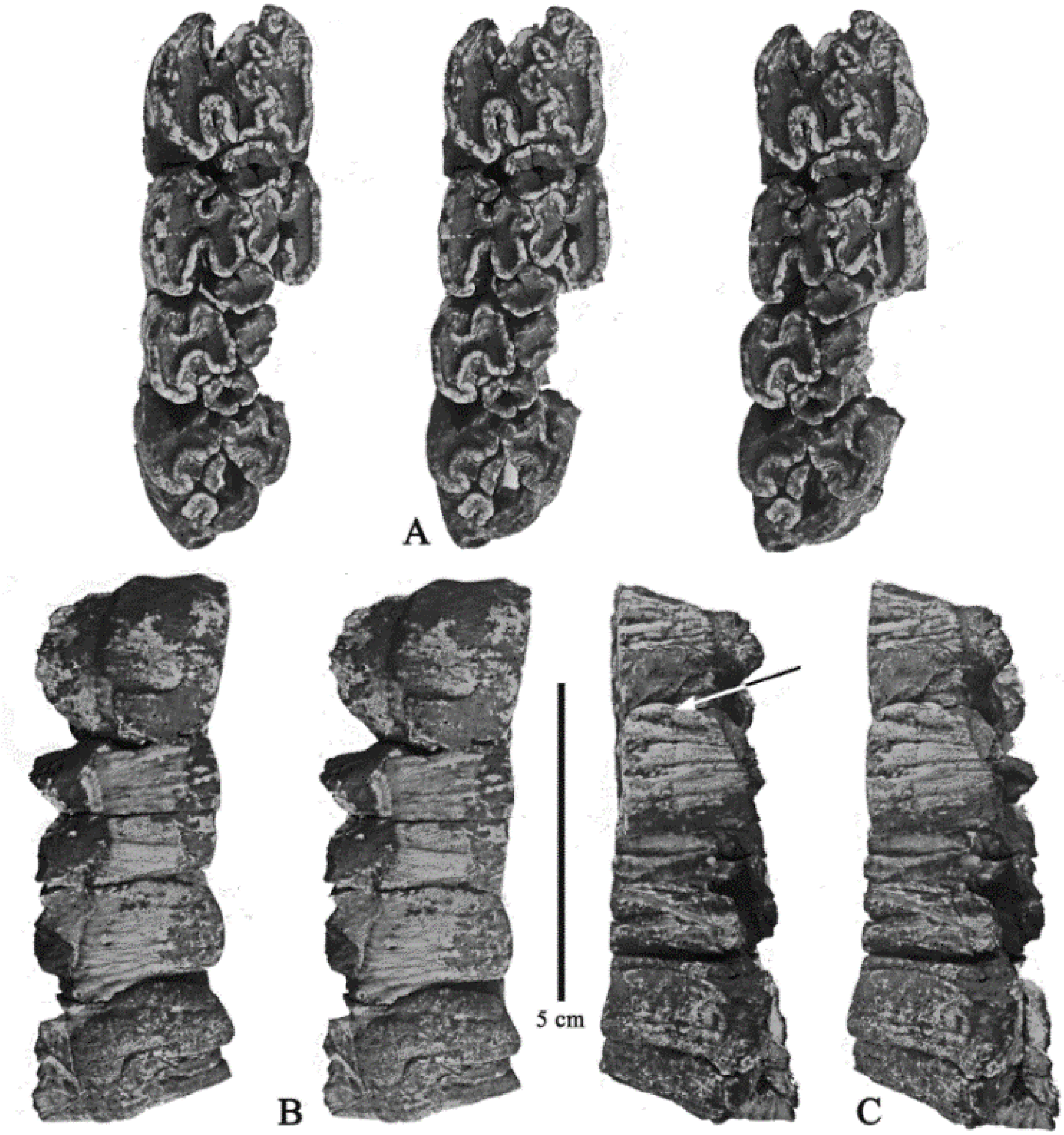

Figure 9. DNMNHP BPA 852, right m/3 of *Gerontochoerus koobiforaensis* from Brad Pit 'A', Bolt's Farm Karst System, South Africa. A) stereo occlusal views, B) stereo lingual view, C) stereo buccal view. Arrow shows a tall basal pillar coalescent with the prehypocristid which contributes to the 'H'-shaped outline of the occlusal surface. Note the remnant of cementum filling the median transverse valley between the metaconid and entoconid on the lingual side and on the buccal side of the protoconid (scale : 5 cm).

The crown is composed of four bicuspid lophids ('pairs of pillars' in the terminology of Leakey, 1943; 'laterals' in the terminology of Cooke, 1976, 2007) and a short distal cingular complex. Each lophid is comprised of two main cusps with deep indentations anteriorly and posteriorly, which impart an 'H' shaped occlusal outline to each cusp (sometimes called a mushroom shape). These indentations correspond to Furchen (Fig. 5 right image) (N°s 1, 3, 4, 6, 7, 9, 10, 12) (see Hünermann, 1968; Pickford, 2013, for definitions of the groove system or Furchenmuster of suid molars). There are accessory pillars close to the mesial and distal ends of the buccal sides of the protoconid and hypoconid and the lingual sides of the metaconid and entoconid, which with wear coalesce with the main cusps, thereby lengthening the mesio-distal length of the 'H' outline on the outer edges of the tooth and thereby narrowing the exits of the transverse valleys. These accessory pillars impart shallow, narrow vertical grooves to the buccal surface of the crown. They represent hypsodont basal pillars that often occur in bunodont and brachyodont suid teeth at the buccal end of the median transverse valley.

The four anterior cusps are the protoconid, metaconid, hypoconid and entoconid, as in suids in general. The anterior accessory cusplet has broken off but part of the anterior cingular complex and the deep foveae (cement-filled pits) are preserved. The median accessory cusplet and the posterior accessory cusplet are present near the midline of the crown blocking the median transverse valley and the posterior transverse valley respectively. Behind the posterior accessory cusplet lies the talonid complex which is comprised of two pairs of large cusps, with a central pillar between them (much like the posterior accessory cusplet). The morphology of the cusps in each talonid cusp pair resembles those in the anterior lophids but the cusps are shorter mesio-distally with less indented Furchen. Behind the 4th lophid there is another central pillar, and a lingual cingular pillar on the disto-lingual end of the crown.

The surface of the enamel is partly hidden by a cover of cementum, but where this has spalled away it is possible to observe that the surface of the enamel is lightly but intensively wrinkled, like shagreen.

DNMNHP BPA 1356, right P3/ (Fig. 10).

This tooth is typical of Tetraconodontinae, comprising a large, inflated paracone closely fused to the smaller protocone. In occlusal view, the crown is an equilateral triangle, with one apex pointing mesially. The preparacrista extends in the midline of the tooth towards a tall prominent mesial cingular cusplet, the accompanying cingulum extending slightly buccally and lingually as it descends towards cervix. The postparacrista extends disto-buccally to join the distal cingulum which is tall, forming a depression on the buccal side of the lateral surface of the tooth. The hypocone is coalescent with the distal cingulum, forming a low cusp on the disto-lingual corner of the tooth. There are three robust roots, one anteriorly and two posteriorly which are partly fused together beneath cervix but separated from each other apically.

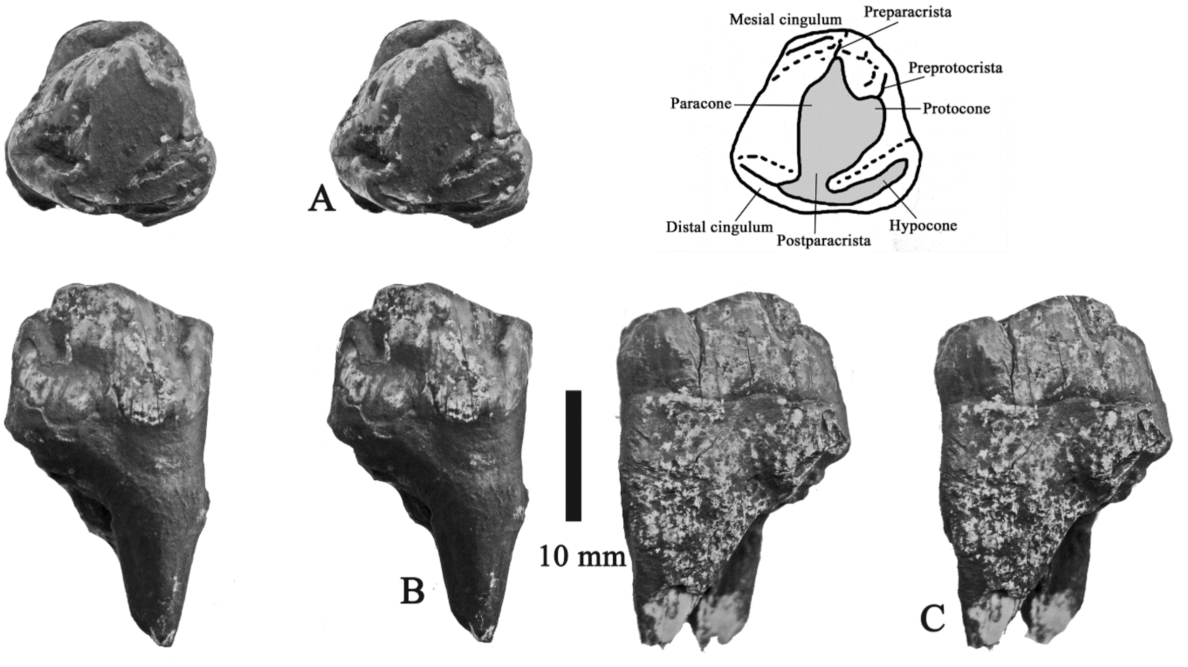

Figure 10. DNMNHP BPA 1356, right P3/ of *Gerontochoerus koobiforaensis* from Brad Pit 'A', Bolt's Farm Karst System, South Africa. A) stereo occlusal view and interpretive drawing (grey is dentine), B) stereo buccal view, C) stereo lingual view (scale : 10 mm).

DNMNHP BPA 1481, right p/3 (Fig. 11).

Only the distal half of this moderately worn tooth is preserved. It shows the inflated morphology of the main cusp that is typical of Tetraconodontinae, accompanied distally by a tall distal cusplet and weak distal cingulum forming a small but distinct cingular cusplet close behind and to the buccal side of the distal cusplet. There is a strong interstitial wear facet caused by contact with the p/4 behind, which has worn a hollow into the disto-lingual side of the tooth near cervix. The root is transversely broad and mesio-distally compressed with a deep mesial re-entrant groove, as is usual in tetracondont teeth (and suid teeth in general).

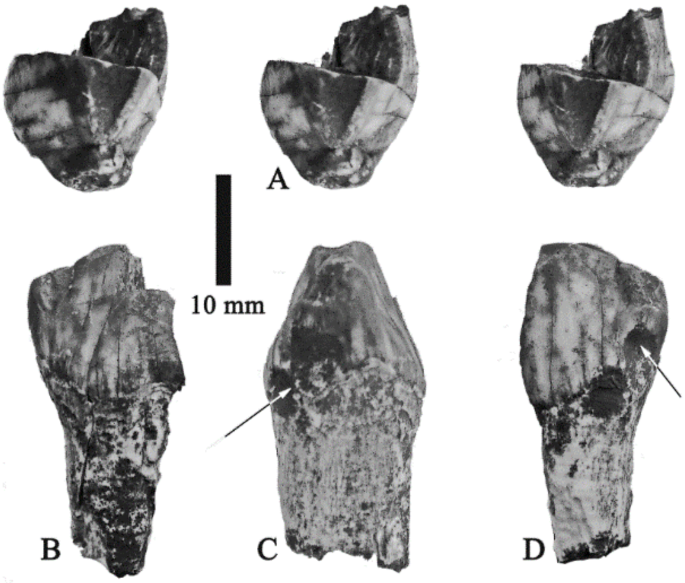

Figure 11. DNMNHP BPA 1481, distal half of right p/3 of *Gerontochoerus koobiforaensis* from Brad Pit 'A', Bolt's Farm Karst System, South Africa. A) stereo occlusal views, B) buccal view, C) distal view, D) lingual view. Arrows show the interstitial wear facet caused by contact with the p/4 (scale : 10 mm).

<u>DNMNHP BPA 152, upper canine fragment</u> (Fig. 12).

Brad Pit 'A' yielded a fragment of suid upper canine which is remarkable for its large dimensions and for the presence of a broad but shallow dorsal gutter. Although such a fragment would generally be considered unidentifiable at the genus level, it accords with upper canines of *Gerontochoerus koobiforaensis* which possess large upper canines with broad, shallow dorsal gutters. The holotype of the species shows this feature well (Harris & White, 1979).

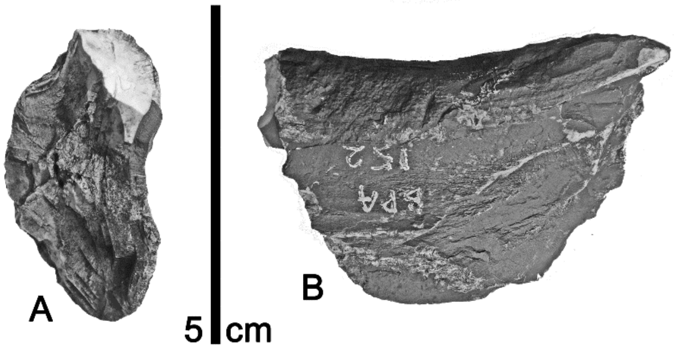

Figure 12. DNMNHP BPA 152, fragment of upper canine of a large suid attributed to *Gerontochoerus koobiforaensis*. A) cross section, B) dorsal surface. Note the broad but shallow dorsal gutter (scale : 5 cm).

Table 1. Measurements (in mm) of the teeth of *Gerontochoerus koobiforaensis* from Brad Pit A, Bolt's Farm Karst System, South Africa.

Tooth	**Mesio-distal Length**	**Breadth 1st lophid**	**Breadth 2nd lophid**	**Breadth 3rd lophid**	**Breadth 4th lophid**
BPA 852 right m/3	91.0	28.8	30.7	--	28.8
BPA 1356 right P3/	18.0	16.0			
BPA 1481 right p/3	--	14.7+			
BPA 152 upper canine	40.7	--			

Discussion

The large suid teeth from Brad Pit 'A' are clearly tetraconodont, the enlarged and inflated P3/ and p/3 being characteristic of this subfamily of suids. The m/3 is moderately hypsodont and mesio-distally elongated by the addition of two extra pairs of cusps which are basically similar in morphology to the two anterior pairs of cusps and there is a small but tall distal cingular pillar. The tooth has a clearly defined cervix below which there are remnants of roots. The fragment of upper canine from Brad Pit 'A', even though undiagnostic, reveals that the suid it came from was of huge dimensions, the section being over 4 cm across. The dimensions of the BPA teeth, plus the length/breadth proportions of the m/3 and the ratio of the dimensions of the P3/ to the m/3 (Fig. 13) all coincide with the species *Gerontochoerus koobiforaensis*, a taxon which is well-known in East Africa, generally under the name *Notochoerus euilus* (Cooke, 1976; Harris & White, 1979 and references therein; Harris, 1983). The m/3 of this species typically has a total of four pairs of cusps accompanied by a simple posterior talonid pillar, but some authors include specimens with three or five pairs of cusps.

The canine of East African specimens possess a broad, shallow dorsal gutter (Harris & White, 1979) like that observed in BPA 152.

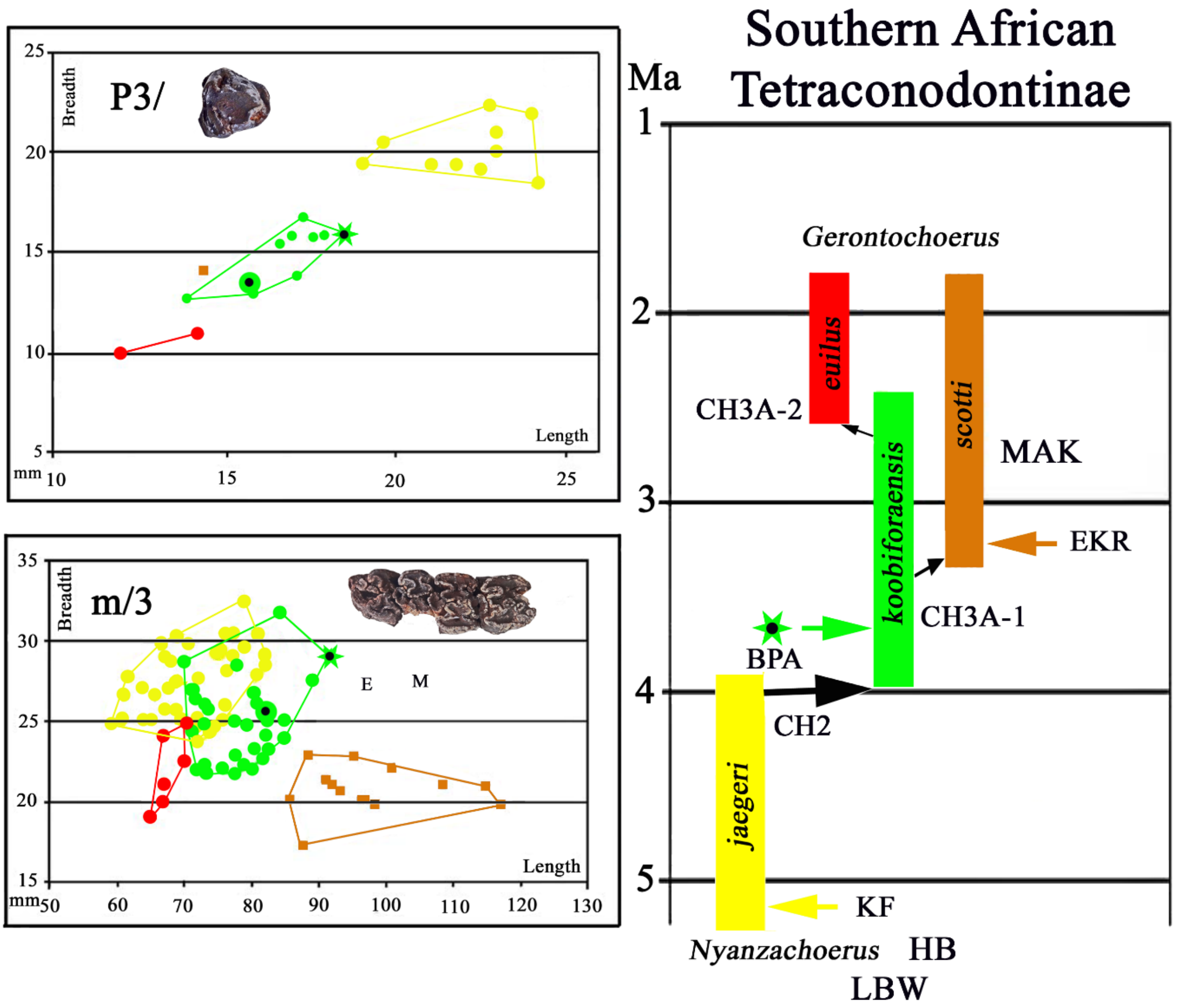

Figure 13. Bivariate length : breadth plots of the P3/ and m/3 of *Nyanzachoerus jaegeri* (yellow) and three species of *Gerontochoerus* (green, brown, red) and a phylogeny and biostratigraphy of these African tetraconodonts. BPA (green star with black centre) represents the fossils from Brad Pit 'A'. Figure modified from Pickford (2013) with additions (CH : Chiwondo (with different stratigraphic levels 2, 3A-1, 3A-2, Kullmer, 2008), E (EKR) : Ekuma Rhino Site (Pickford *et al*. 2016), HB : Hondeklip Bay (Pickford & Senut, 1997), KF : Kaukausib Fontein, LBW : Langebaanweg, M (MAK) : Makapansgat). Large green dots with black centres represent the holotype of *Gerontochoerus koobiforaensis*.

Harris & White (1979) and Cooke (2007) provided summary statistics of dental metrics of teeth attributed to *Nyanzachoerus kanamensis*, *Notochoerus capensis*, *Notochoerus euilus* (equivalent to *koobiforaensis* in this paper), *Notochoerus scotti* and *Notochoerus clarki* (declared to be a synonym of *euilus* by Pickford, 2013), the sorting of the third molars being based on the number of 'laterals' or pairs of pillars in them and the degree of hypsodonty. The ranges of variation calculated by the authors are somewhat different, especially at the lower end of the range, with minimum lengths significantly shorter in Harris & White (1979) than in Cooke (2007).

On the basis of the number of cusp pairs in the talonid (two plus a cingular pillar behind the two anterior cusps, making a total of four cusp pairs for the whole tooth), the m/3 from Brad Pit 'A' belongs to *Gerontochoerus koobiforaensis*, an identification which agrees with the relatively low distal pillar which, even though slightly worn, would have been only ca 30 mm tall. Appurtenance to *Gerontochoerus scotti* can be discounted, because this taxon has more cusp pairs in the talonid, and it is considerably more hypsodont. The Brad Pit 'A' tooth plots well outside the range of metric variation of *Gerontochoerus euilus*.

The BPA 852 third molar is large within the context of *Gerontochoerus koobiforaensis*, agreeing best with specimens from Hadar (Sidi Hakoma) and Koobi Fora (Tulu Bor) but it is appreciably shorter than specimens from Ekuma River (Pickford *et al.* 2016) and Makapansgat (Pickford & Gommery, 2016) (Fig. 13). On this basis, it is considered to be likely that the BPA specimen correlates best to the time period spanned by the Sidi Hakoma and Tulu Bor successions, which would imply an age of ca 3.7 +/- 0.4 Ma, but an age as old as 4 Ma or as young as 3.2 Ma cannot be ruled out.

The quantity of upper and lower premolars of these suids is restricted, but Harris & White (1979) noticed a tendency towards reduction in the dimensions of the third and fourth premolars through time. Thus *Nyanzachoerus kanamensis* possessed larger premolars than those of *Gerontochoerus koobiforaensis* which are larger than those of *Gerontochoerus scotti* and *Gerontochoerus euilus* (Fig. 13). The BPA 1356 and BPA 1481 specimens plot close to the range of variation of *Gerontochoerus koobiforaensis*, thereby supporting the identification based on the m/3.

Two suid lower third molars, one (GSN EKR 63'13, see below) from Ekuma Rhino Site, Namibia (Pickford *et al.* 2016) the other (M 2077) from Makapansgat are here attributed to *Gerontochoerus scotti*, but are appreciably broader than the other specimens attributed to the species, perhaps because the cementum cover is thick (thereby increasing the breadth measurement compared with teeth that have lost the cementum).

General Discussion

Several teeth from Brad Pit 'A', Bolt's Farm Karst System, South Africa, belong to the tetraconodont suid *Gerontochoerus koobiforaensis*, implying an age of ca 3.7 Ma (span 4 to 3.2 Ma) for the deposits in which it occurs. The genus was previously represented in the subcontinent by the more derived taxon *Gerontochoerus scotti*, some specimens of which were for a long time misattributed to the suine *Notochoerus capensis*.

Pickford (2013) showed that the lectotype of *Hylochoerus euilus* from Kaiso, Uganda, was an upper molar and not a lower one, as had been thought since its erection by Hopwood (1926) and that, as such, the specimen plots within the range of morphometric variation of *Notochoerus clarki* White & Suwa (2004) meaning that the latter species falls into synonymy with the former. This decision was accepted by Geraads & Bobe (2017). Furthermore, Pickford (2013) showed that the holotype of *Notochoerus capensis* Broom, 1925 (the type species of the genus considered by its creator to be a lower left tooth but which is in fact an upper right one) differs fundamentally in its morphology from the lectotype of *Hylochoerus euilus* (both teeth are upper third molars, so can be compared directly with each other) so much so that the two teeth can no longer be considered to represent the same genus. Pickford (2013) therefore resurrected the name *Gerontochoerus* Leakey, 1943 (type species *Gerontochoerus scotti*). This recommendation was not accepted by Geraads & Bobe (2017) who continued to attribute the species *euilus* to the genus *Notochoerus*. Nevertheless, the holotype of *Notochoerus capensis* does not resemble any of the East

African specimens which have traditionally been admitted within the genus (Pickford & Gommery, 2016).

Pickford (2013) noted that « *an upper left third molar attributed to* Notochoerus hopwoodi *Leakey, 1958 (NHML M 17115) from Olduvai Bed IV, Tanzania, is similar in many respects to the holotype of* Notochoerus capensis*, but it is less deeply worn. The tooth is slightly narrower than the South African tooth (25 mm versus 30 mm) but* in toto *the two specimens are very similar to each other and probably belong to the same specie*s ». Harris & White (1979) attributed M 17115 to *Mesochoerus limnetes*, but there are no particular similarities between it and the holotype of the species from Kaiso, Uganda, which is a relatively brachyodont tooth (Hopwood, 1926; Cooke & Coryndon, 1970) which probably belongs to the genus *Nyanzachoerus* (Pickford, 1994) (but see Cooke, 1997, who considered it to be closer to the small primitive suine *Kolpochoerus afarensis*, which he transferred to *Potamochoerus*).

Images of the Olduvai tooth are provided (Fig. 14) which reveal the similarities between this tooth and the holotype of *Notochoerus capensis* from Longlands (South Africa) and highlight how divergent it and the Longlands specimen are from the Kaiso lectotype of *Hylochoerus euilus*. A particular morphological similarity which is rare in suids concerns the positions of the median and posterior accessory cusplets intervening between the hypocone and metacone. In other suids, the inner margins of the hypocone and metacone are close to each other and the accessory cusplets far apart.

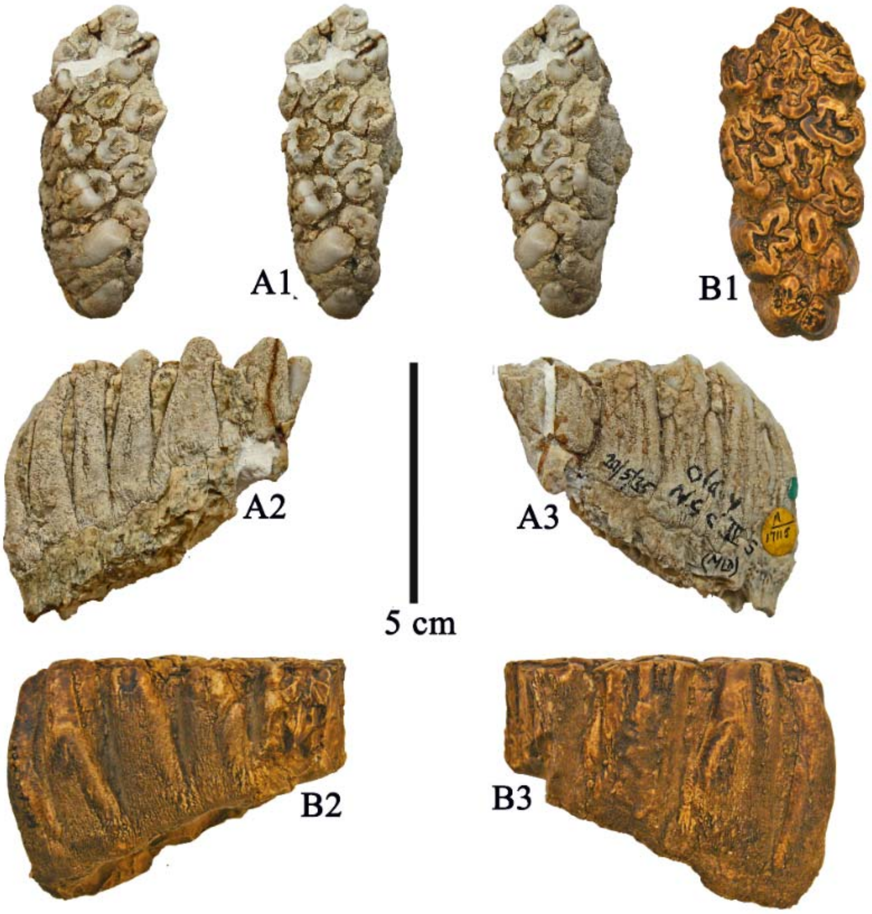

Figure 14. A) NHMUK M 17115, left M3/ from Olduvai Bed IV, Tanzania, attributed by Leakey, 1958, to *Notochoerus dietrichi* Hopwood, 1934. A1) stereo occlusal views, A2) lingual view, A3) buccal view. B) cast of holotype right M3/ of *Notochoerus capensis* from Longlands, Vaal River, South Africa (images reversed for ease of comparison). B1) occlusal, B2) lingual, B3) buccal views. Teeth are oriented with the occlusal plane horizontal (scale : 5 cm).

Assuming that the provenience of the Olduvai tooth (M 17115) is correctly reported (Leakey, 1958) then it follows that *Notochoerus capensis* may have survived later than species of the genus *Gerontochoerus* which died out about 1.8 Ma (Cooke, 2007). Olduvai Bed IV is Pleistocene (0.6-0.8 Ma) (Ashley *et al*. 2010).

Our estimates of the dimensions of the holotype of *Notochoerus capensis* are 72 x 30 mm (Van der Made, 1998, gave two estimates for the length : 72 and 81 mm, depending on how its mesial end is reconstructed). Harris & White (1979) identified skull KNM ER 448 as *Notochoerus capensis*, giving the measurements of its M3/ as 91.8 x 31.6 mm, but the fossil was later removed from this species and identified as *Notochoerus scotti* by Harris (1983) who gave its M3/ measurements as 89 x 33.7 mm. With the removal of this skull from *Notochoerus capensis*, the species is no longer recognised by that author in the East African fossil record.

Pickford & Gommery (2016) described some large suid remains from Aves Cave 1, South Africa, not far from Brad Pit 'A'. Among the specimens is a partial M3/ with marked resemblances to the holotype of *Notochoerus capensis*. From the same strata there are upper and lower premolars of large dimensions which are of typical suine morphology and are radically different from the corresponding teeth in Tetraconodontinae. This evidence supports the hypothesis that *Notochoerus* is a suine rather than a tetraconodont. The deposits at Aves Cave I are estimated to be ca 3.0-2.7 Ma (Pickford & Gommery, 2016).

Recently, Lazagabaster *et al*. (2018) reported the presence of *Notochoerus capensis* at Lee Adoyta in the Ledi-Geraru area, Ethiopia (ca 2.7 - 2.5 Ma). The specimens accord with this species not only in dimensions, but also in some aspects of crown morphology, notably by the fact that the median and posterior accessory cusplets intervene between the hypocone and metacone and the 'H'-shape of the lingual cusps is not as fully developed as it is in the buccal cusps. However, their definition of the species was based on the work of Harris & White (1979) in which the upper third molars of *Notochoerus capensis* (i.e. in reality *Gerontochoerus scotti*) are illustrated as possessing six lophs and the lower third molars seven lophids. However, the holotype M3/ of the *Notochoerus capensis* possesses only four lophs (Shaw, 1938; Pickford, 2013) or five if one accepts Broom's (1925) reconstruction of the missing parts (Cooke, 1949; Cooke & Coryndon, 1970). The definition of the taxon used by Lazagabaster *et al*. (2018) was therefore based on two fossils, neither of which matches the holotype of *Notochoerus capensis* in dimensions or in morphology : a) skull KNM ER 448, with an M3/ 89 mm long, which has subsequently been transferred to *Notochoerus scotti* by Harris (1983) (*Gerontochoerus scotti* in this paper (Pickford & Gommery, 2016)) and B) a lower third molar from Makapansgat (M 2077) which is far too large to belong to the same species as the holotype (length of the holotype M3/ of *Notochoerus capensis* is ca 72 mm : and the length of the m/3 from Makapansgat is 116.7 mm). Thus, even though the Lee Adoyta specimens have a distinct possibility of belonging to *Notochoerus capensis*, they do not represent the same species as the fossils from East Turkana and Makapansgat attributed to this species by Harris & White (1979). The latter specimens are more properly attributed to *Gerontochoerus scotti*. It is noted that the Lee Adoyta stratigraphic sequence spans the period 2.8 to 2.5 Ma (Lazagabaster *et al*. 2018).

Conclusions

Three suid teeth from Brad Pit 'A' in the Bolt's Farm Karst System are identified as *Gerontochoerus koobiforaensis* Pickford, 2013. The inflated morphology of an upper third premolar and half a lower third premolar indicate affinities with the subfamily Tetraconodontinae and the teeth plot within the range of metric variation of *G. koobiforaensis*. A lower third molar has four lophids (each comprised of two cusps) accessory cusplets in the transverse valleys between the lophids and there is a cingular pillar at the distal extremity of the crown. The crown is moderately hypsodont, is covered in cementum and possessed roots, and its dimensions accord with *Gerontochoerus koobiforaensis*.

The recognition of this species at Brad Pit 'A' accords with previous age estimates of the deposits based on other faunal elements found there (Pickford & Gommery, in press). The most likely age based on the suids is ca 3.7 +/- 0.4 Ma, but the deposits could be as old as 4 Ma or as young as 3.2 Ma. The hypsodont nature of its m/3 together with the presence of cementum suggests that *Gerontochoerus koobiforaensis* included grass in its diet.

Species *Gerontochoerus scotti* Leakey, 1943

Holotype: KNM OS 5 (old number CM Omo I), (cast in NHMUK M26590), right maxilla fragment containing M2/ and M3/.

Type locality and age: Shungura, Omo, Ethiopia.

Original diagnosis: A *Gerontochoerus* of very large size in which the enamel pattern of the third molars exhibits an extreme degree of folding in the upper third molars, the lateral pillars of each pair are separated from each other by median pillars except in the case of the anterior pair of pillars, but in the lower third molars the enamel of the lateral pillars comprising each pair touches along the median line and the median pillars merely separate each pair from the next succeeding pair (from Leakey, 1943).

Emendation to diagnosis: A species of *Gerontochoerus* larger than *Gerontochoerus koobiforaensis* and *Gerontochoerus euilus*, in which the talonid complex behind the fourth pair of cusps is itself multicusped often forming a fifth pair of cusps or more.

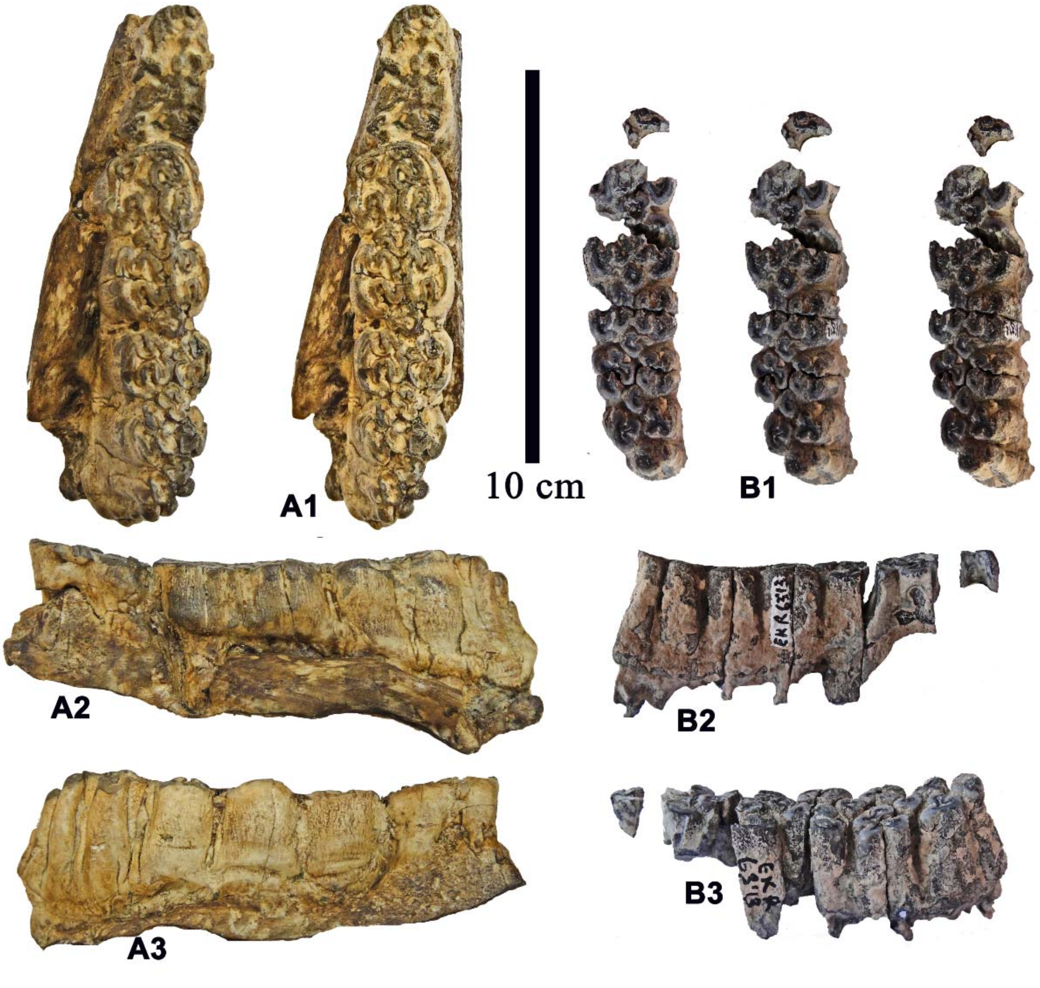

Figure 15. Comparison between m/3s of *Gerontochoerus scotti*. A) CM Omo 2, the paratype left mandible containing m/2 and m/3 from Ethiopia (Leakey, 1943) (cast in NHMUK) and B) GSN EKR 63'13, right m/3 from Ekuma Rhino Site, Etosha, Namibia. 1 - stereo occlusal views, 2 - buccal views, 3 - lingual views (scale : 10 cm).

Description of the m/3 from Ekuma Rhino Site

As preserved the right m/3 from Ekuma Rhino Site comprises a moderately worn crown missing fragments of the first pair of cusps (protoconid, metaconid) and some of the anterior cingular complex, which is detached from the rest of the tooth (Fig. 15b). In total there are five pairs of cusps (lophids) and a posterior cingular pillar. The median and posterior accessory cusplets are tall, and block the median and posterior transverse valleys in their middle. The talonid consists of three pairs of cusps constructed along the same lines as the anterior lophids, but the enamel outlines are less clearly defined. The Furchen are deeply indented, there is a thick cover of cementum and the cervix is well-defined and almost rectilinear. There are remnants of roots preserved beneath the hypoconid-entoconid pair and beneath the distal end of the talonid.

Because of the damage to the mesial end of the tooth it is not possible to provide an accurate measurement of its length, but it was in the neighbourhood of 10 cm long and the second lophid is 27 mm broad.

Discussion

The suid from Ekuma Rhino Site was previously attributed to *Gerontochoerus koobiforaensis* by Pickford *et al*. (2016) but it has five lophids in the m/3, so in this respect it agrees better in morphology with *Gerontochoerus scotti*. However, the tooth appears to be rather broad for the latter taxon (range of breadths 17-23 mm) (Fig. 13) and thus closer to *G. koobiforaensis*, but this is likely due in part to the fact that there is a thick cover of cementum on the lingual and buccal sides of the crown, which is lacking in many of the specimens from East Africa. The estimated crown length of ca 100 mm agrees with the larger subset of specimens attributed to *Gerontochoerus scotti* (sometimes classified as a separate species *Gerontochoerus harrisi* Van der Made, 1998).

Conclusions

The tetraconodont fossil record of Southern Africa is generally rather poor except at selected sites such as Langebaanweg, Cape Province (*Nyanzachoerus kanamensis australis* Cooke & Hendey 1992) and the Chiwondo Beds, Malawi (Kullmer, 2008). A few specimens of *Gerontochoerus scotti* from Makapansgat were for a long time misattributed to *Notochoerus capensis*, but the specimens are far too large to belong to this species, which is, in any case, a suine and not a tetraconodont. A mandible from Hondeklip Bay was attributed to *Nyanzachoerus australis* by Pickford & Senut (1997).

The discovery of additional tetraconodont specimens from sites in South Africa and Namibia extends the known geographic range of the subfamily in the subcontinent to the west coast of Namibia and to the Etosha Basin in northern Namibia. Of particular value is a small sample from Brad Pit ‘A’ in the Cradle of Humankind, Gauteng, South Africa, part of the Bolt’s Farm Karst System. At this site an m/3 was found associated with a P3/ and a p/3 which provide sound evidence of the tetraconodont affinities of the species, the premolars of this subfamily being highly diagnostic and radically different from those of suines. It is worth pointing out that a karst infilling at Aves Cave I, not far from Brad Pit ‘A’, yielded large premolars that are typical of suines associated with a broken upper molar that closely resembles the holotype of *Notochoerus capensis*. For this reason, among others, *Notochoerus capensis* is considered to belong to Suinae rather than to Tetraconodontinae. It is stressed, however, that most of the East African and Malawi specimens previously attributed to *Notochoerus capensis* do not belong to this species, but are tetraconodonts more properly classified in *Gerontochoerus*.

It is concluded that the grits at Kaukausib Fontein which are interbedded with onyx-like travertine accumulated about 5 Ma (range 6-4 Ma), the karst infilling at Brad Pit ‘A’ was deposited about 3.7 Ma (range 4-3.2 Ma), and the Ekuma Delta clays at the Rhino Site, about 3.2 Ma.

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Kaokoland Cascade Tufa Survey : Interim Report

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Abstract: Kaokoland is a semi-arid to desert region in northwestern Namibia. The presence of numerous cascade tufa deposits in the area attests to a more humid, cooler climate during the past. A preliminary palaeontological survey of the tufas in 2017 resulted in the discovery of rich and diverse fossil faunas which indicate that the tufas accumulated during the late Pliocene and early Pleistocene. Some of the tufa deposits contain stone tools and burnt bones yielding evidence concerning ancient human activities. This paper provides a preliminary report on the Kaokoland Tufa Survey.

Key words: Cascade Tufas, Fossil fauna, Palaeoclimate, Pliocene, Pleistocene, Namibia

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Introduction

A brief survey of Cascade Tufas in Kaokoland was undertaken in 2017 in order to assess the palaeontological and archaeological potential of the deposits (Pickford *et al*. 2016) and to refine the age of tufa deposition. This paper provides a preliminary assessment of some of the faunal and archaeological remains encountered.

This preliminary report does not pretend to present an exhaustive description of the fossils or stone tools, but is intended to give a reliable impression of the potential of the region for further studies in palaeontology and archaeology, as well as of the timing and mode of development of cascade tufas in this arid environment. The palaeontological potential of the Kaokoland tufas is vast, and it will take several years of concerted effort to describe the fossils already obtained from the breccias associated with the tufas.

Geological context

The geological setting of the Kaokoland tufas was described by Pickford *et al*. (2016). In brief, the tufa deposits form barrages in valleys incised into the edges of dolomite plateaux (Fig. 1). Most of them are still the sites of freshwater springs but active tufa deposition is much reduced compared with the rates of precipitation that prevailed during the late Pliocene and early Pleistocene.

During tufa deposition, tufa curtains formed, behind which there were cavities, some large enough to be called caves. Some of these cavities subsequently filled with carbonates but because they were not accessible to surface water flow, the breccias contain almost no clastic deposits, being almost pure calcium carbonate with fine dust residues. Many of the cavities acted as refuges for animals such as lizards, birds such as owls, and small mammals. Animal remains that accumulated on the floors of the cavities represent regurgitated owl pellets and skeletons of animals that died in the cavities or were brought into them by small predators. There are few large mammal remains in the deposits.

Figure 1. Okongwe tufa lobes near the village of Okozonduno, Kaokoland, Namibia. These lobes formed during the Pliocene and Pleistocene, blocking the valley eroded into the dolomite plateau behind.

Table 1. Location and age estimates of Kaokoland fossiliferous breccia samples.

Locality	Latitude	Longitude	Altitude	Age
Okongwe 2015 Site	18°53’54.6’’S	14°04’10.9’’E	1191 m	Pleistocene
Okongwe 2017 Site	18°53’53.9’’S	14°04’12.4’’E	1202 m	Pliocene
Okongwe Lower Site	18°53’54.6’’S	14°04’11.3’’E	1234 m	Pliocene
Okongwe Up Site	18°53’42.9’’S	14°04’20.3’’E	1272 m	Pliocene
Omatapati	18°53’38.5’’S	14°08’50.7’’E	1199 m	Pleistocene
Otjitaime	18°51’54.9’’S	13°44’55.0’’E	1312 m	Pleistocene

Material and Methods

200 kg of fossiliferous breccia was delivered to Paris for laboratory treatment in order to extract the fossils from the rock. Breccias were treated in a 7% solution of formic acid buffered by calcium triphosphate.

The laboratory process is relatively slow, each batch of 25 kg taking about two weeks to digest, after which the insoluble residue was dried, sorted and then examined under a microscope to pick out the fossils.

Once sorted, the fossils have to be consolidated one by one with a dilute solution of glyptol dissolved in acetone. The Kaokoland tufas need to be consolidated, otherwise the specimens crumble to powder after a few weeks. In blocks that have more complete specimens such as skulls, the fossil specimens are consolidated before extraction from the block, which means that the blocks have to be dried and the specimens consolidated as they are exposed by the acid attack. This procedure is slow, as it requires repeated episodes of drying, consolidating and reimmersion in acid, but it is essential to preserve the more complete specimens intact. Such complete specimens are relatively rare in the fossil record, which is why they deserve special attention and treatment, even if it results in delays in extracting other fossils from the breccia.

The cleaned and consolidated fossils were then sorted into taxonomic groups and labelled with the locality data and other information, after which selected specimens were photographed and measured. Scientific study of the specimens will be carried out as and when experts agree to do the research.

Results

Rich and diverse faunas have been recovered from breccia at all tufa localities in Kaokoland examined so far (Okongwe, Omatapati and Otjitaime). Most of the faunal remains comprise Pleistocene taxa, but Okongwe is somewhat different from the others in that it has yielded breccias of two different ages, one of which is Pliocene (with extinct rodent taxa) the other Pleistocene (with extant genera) (Fig. 2-20).

The faunas from the breccias comprise a rich assemblage of frogs, snakes, lizards, chamaeleons, birds and small mammals (bats, rodents, soricids, macroscelidids) medium-sized mammals (lagomorphs, hyracoids, small carnivores, small bovids) and a few large mammals (medium-to-large equids, suids, bovids and giraffids). When combined with the gastropods and fossil plant remains, these tufa-related biological remains will permit reliable reconstructions of the palaeoenvironments.

Several of the Pleistocene breccias have yielded stone tools (Omatapati, Okongwe 2015 Site). The Pliocene sites at Okongwe (Okongwe 2017 Site, Okongwe Up Site) also yield stone tools, possibly the oldest known from sub-equatorial Africa.

The stone tools at Omatapati are associated with burnt bones and teeth, indicating that hominids were probably cooking food at the site. In contrast, the Pliocene breccias from Okongwe which yield stone tools, show no signs of burnt bones.

The majority of fossils in the Kaokoland breccias comprise microfauna. It is likely that these remains represent owl pellets which accumulated in cavities in the tufa lobes as they grew. It is also likely that some of the remains, especially those of the lizards, small birds and bats, represent the remains of animals that lived in, or sheltered in the cavities, and that some of them died therein. A few of the cavities were large enough to admit larger animals, including hominids, and this accounts for the occasional presence of large mammal remains (equids, bovids, giraffids) in the breccias. The bones and teeth of large mammals were likely introduced into the cavities by hominids or predators, rather than from the animals themselves climbing into the caves and dying inside. The hyracoids, lagomorphs and small bovids (Klipspringer) in contrast could themselves access some of the cavities, as they still do today.

Some of the breccias comprise immense concentrations of post-cranial bones and jaws, often showing preferred alignment of the specimens. These concentrations are likely to be locally reworked remains of disaggregated owl pellets, gently transported a few cm by water flowing inside the cavities and concentrated at the point where the water percolated out of the cavity. The bones are not rolled or abraded, meaning that transport was minimal and gentle.

In a few cases, it is clear that there were two phases of accumulation of fossils, shown by the presence of fossils of two different colours, an older assemblage comprising rare bones and teeth with brownish/blackish coloration (often isolated teeth or broken bones and jaws) intermixed with abundant pale yellow/cream fossils in excellent condition.

Apart from their fossil content the Kaokoland breccias are composed of almost pure limestone. All the breccias yield rare sand grains, but only a few contain the occasional stone larger than 1 cm. The Okongwe Pliocene breccia at the 2017 Site yielded two large stones (larger than a fist) which show signs of percussion damage at one pole. These stones are interpreted to have been introduced into the cavity by early hominids and employed as hammer stones. The presence of small waste flakes in the breccia from the same site (and at Okongwe Up Site) suggest that hominids were making stone tools inside the cavities, but were carrying the completed tools out when they left, leaving behind the waste flakes and hammer stones.

In contrast, the Pleistocene breccia at Omatapati is rich in stone tools, waste flakes, cores and hammer stones, along with burnt bones of large mammals (equids, bovids). The assemblage indicates more frequent occupation of the cavity by early hominids.

Pictorial Palaeontology and Archaeology

Okongwe 2017 Site

Figure 2. Stereo lateral view of the spur from the leg of a spurfowl from Okongwe 2017 Site.

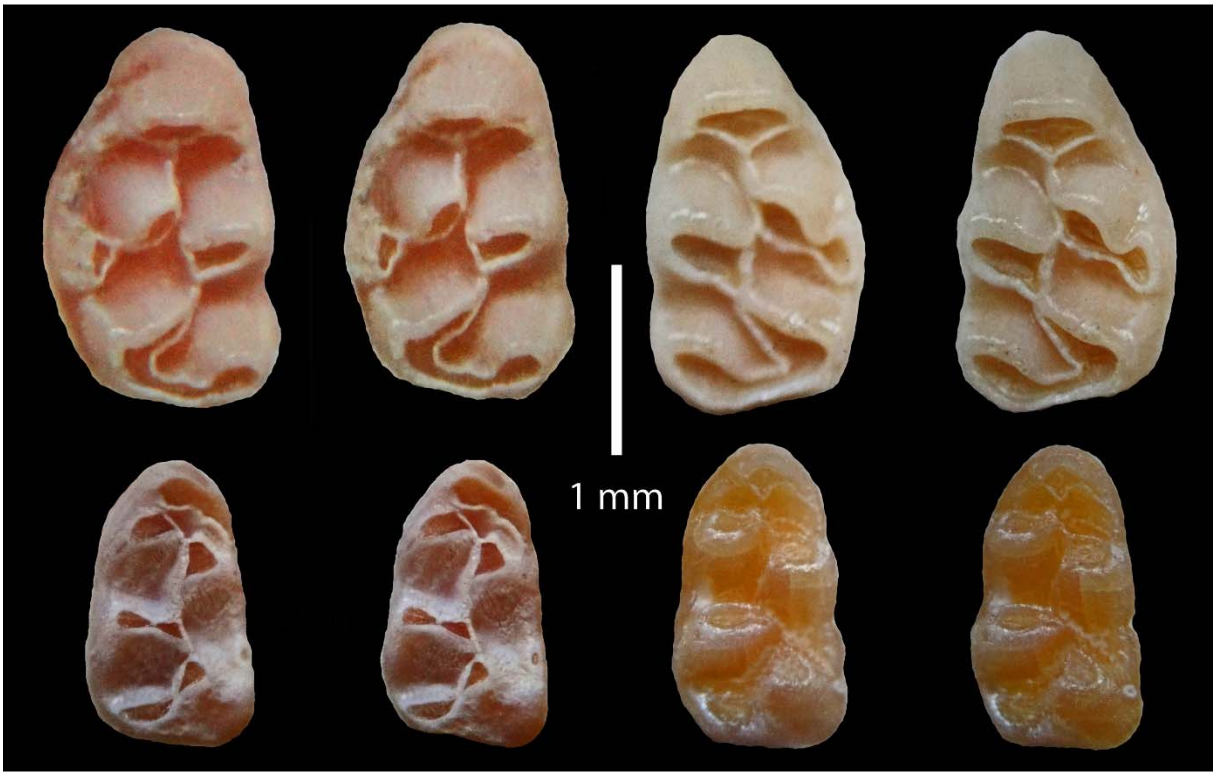

Figure 3. Stereo occlusal views of upper (top row) and lower (bottom row) first molars of the rodent *Petromyscus collinus* from Okongwe, 2017 Site.

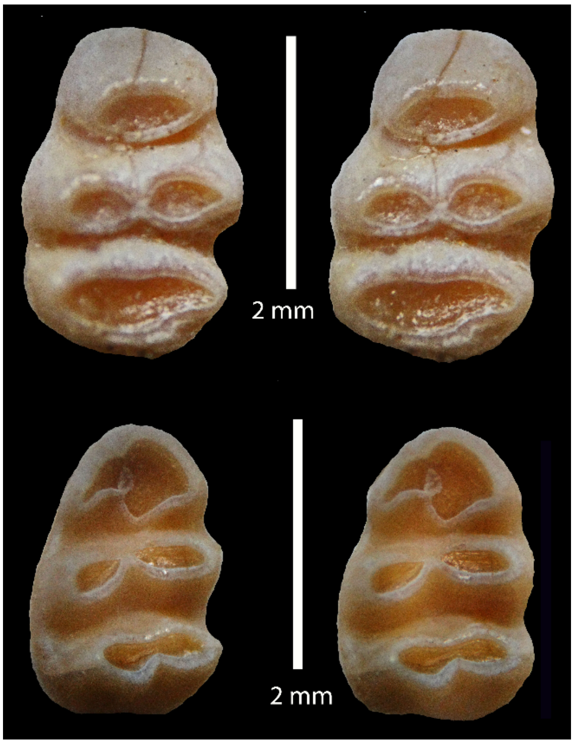

Figure 4. Stereo occlusal views of first upper and lower molars of *Desmodillus* sp. from Okongwe, 2017 Site, Kaokoland, Namibia.

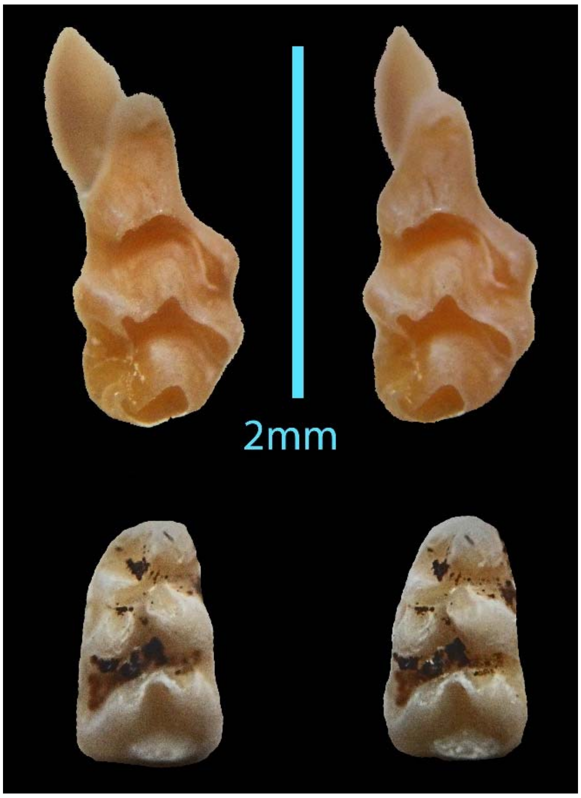

Figure 5. Stereo occlusal views of upper and lower first molars of *Acomys* / *Mus* sp. from Okongwe 2017 Site.

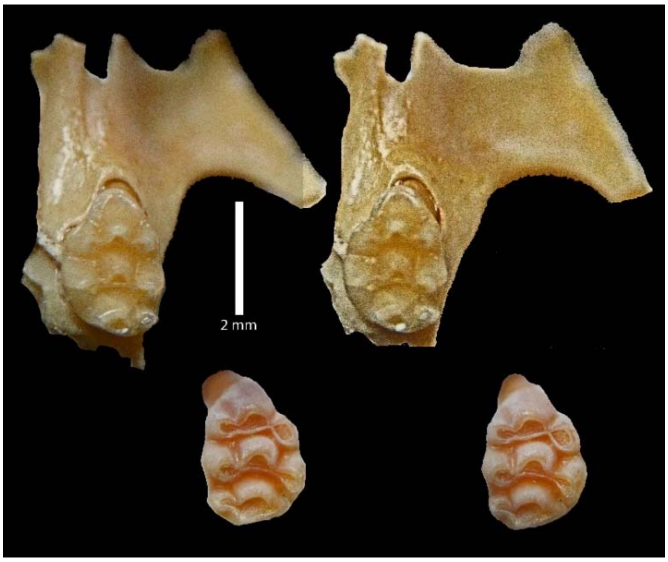

Figure 6. Stereo occlusal views of upper first molars of *Aethomys* sp. from Okongwe, 2017 Site.

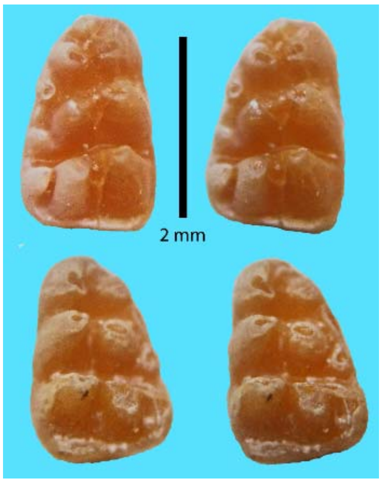

Figure 7. Stereo occlusal views of lower first molars of *Aethomys* sp. from Okongwe 2017 Site.

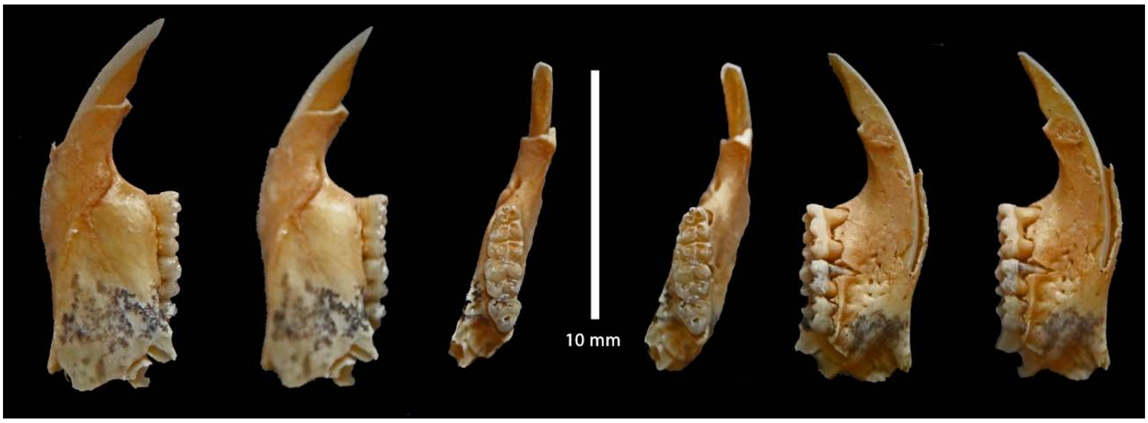

Figure 8. Stereo views of left mandible of *Aethomys* sp. from Okongwe 2017 Site, buccal, occlusal, lingual views.

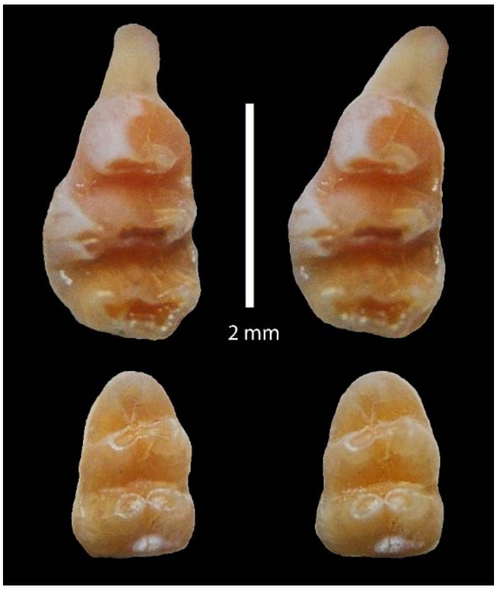

Figure 9. Stereo occlusal views of upper and lower first molars of *Steatomys* sp. from Okongwe 2017 Site.

Figure 10. Stereo views of teeth and a mandible of a small bat (Chiroptera) from Okongwe 2017 Site.

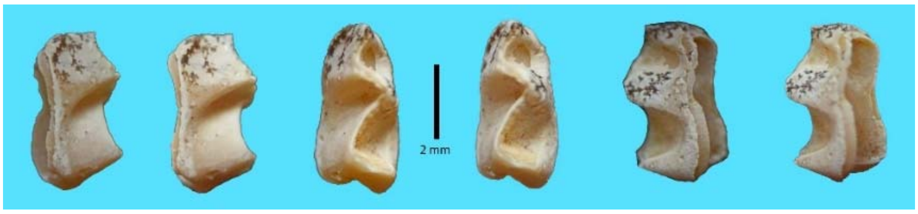

Figure 11. Stereo views of a left lower premolar of a dassie (*Procavia* sp.) from Okongwe, 2017 Site.

Figure 12. Ventral view of a right maxilla of *Procavia* sp. from Okongwe, 2017 Site. The length of the specimen as preserved is 3.5 cm.

Figure 13. Leporidae from Okongwe 2017 Site. Upper molar stereo occlusal view and lower premolar stereo occlusal and lateral views.

Figure 14. Stone (black quartzite) in fossiliferous breccia from Okongwe 2017 site, Kaokoland, Namibia. This stone was likely introduced into the cavity by early hominids and employed as a hammer stone. Note the percussion damage at the pole (pale patches at the top of the black stone).

Figure 15. Stereo views of quartz waste flakes recovered from late Pliocene fossiliferous breccia at Okongwe 2017 Site.

Otjitaime

Figure 16. Fossiliferous breccia from Otjitaime, Kaokoland, Namibia. The long bones in this immensely rich concentration of fossils show a preferential alignment indicating transport and deposition by flowing water. These remains are probably locally reworked from disaggregated owl pellets. The fauna indicates a Pleistocene age.

Figure 17. Stereo views of a molar of *Otomys* sp. from Otjitaime, Kaokoland, Namibia. The associated fauna suggests a Pleistocene correlation.

Omatapati

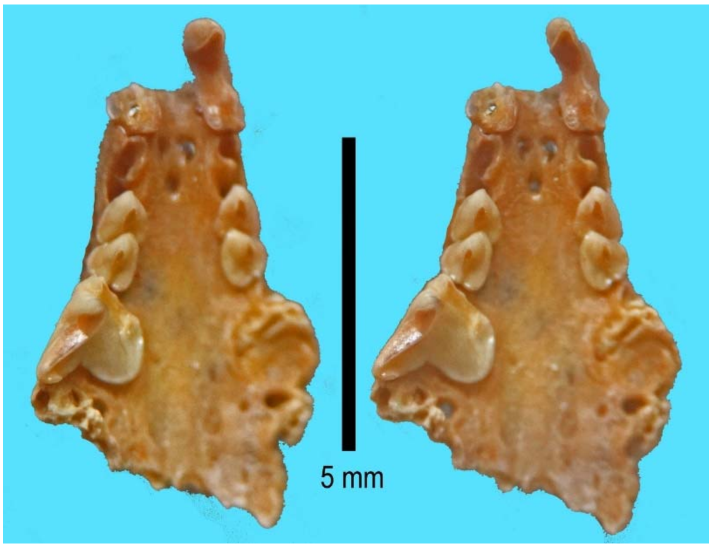

Figure 18. Stereo palatal view of a well-preserved snout of *Crocidura* from Omatapati, Kaokoland, Namibia. The associated fauna is Pleistocene.

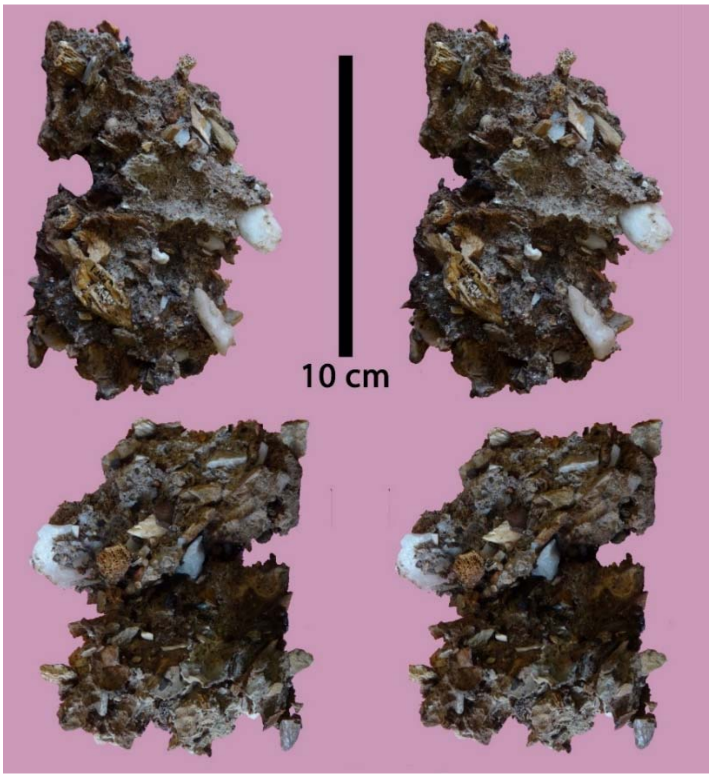

Figure 19. Stereo images of stone tools and bones (some burnt) in breccia from Omatapati, Kaokoland, Namibia – upper and lower views of the same block.

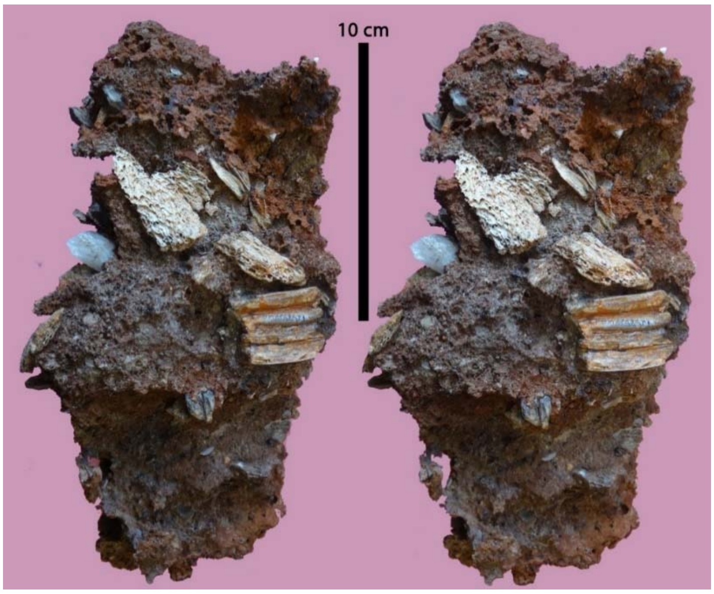

Figure 20. Stereo images a block of breccia from Omatapati, Kaokoland, Namibia, containing an equid tooth, several bones (some burnt) and stone tools.

Discussion and conclusion

The cascade tufas of Kaokoland represent a rich source of information about the faunas that lived in the region during the Plio-Pleistocene. Some of the deposits contain evidence of ancient human activities in the form of lithic implements and burnt animal remains.

The faunal remains indicate that the tufas are latest Pliocene to early Pleistocene, but there is evidence of older tufas beneath or to one side or other of the surveyed examples. Future surveys should examine these potentially older deposits in detail because they may yield evidence of interest to palaeoclimatology.

The discovery of tiny quartz waste flakes in some of the breccias such as Okongwe 2017 Site while picking through the residues for microfauna was a surprise because the deposits contain no obvious signs of human activities such as stone tools or burnt bones. It is hypothesised that early humans used the cavities in which the breccia accumulated as temporary shelters and while therein manufactured stone tools, leaving behind the waste flakes, but taking the finished tools with them when they left. On occasion, they would also leave behind the hammer stones.

One implication of the serendipitous discovery of waste flakes in the Okongwe breccias, is that researchers working on other Plio-Pleistocene breccias in Africa should be encouraged to keep an eye open for similar occurrences in the samples on which they are working. This may help fill out the map of early hominid occurrences in the continent.

Other Kaokoland Tufas such as the one at Omatapati contain abundant evidence of stone tools and the use of fire, and these sites were likely places of more frequent habitation by early hominids.

It is stressed that many of the faunal remains found in the Kaokoland breccias remain to be identified, this report being in the nature of an interim report rather than a definitive statement about them. Skeletal remains of bats, macroscelidids, birds, frogs and small reptiles abound in the breccias, and there are a few large mammals such as bovids, suids, giraffids and equids.

The Kaokoland tufas are also richly endowed with plant remains (Mocke, 2014) but these were not studied in detail during the 2017 survey.

Finally, the huge volumes of tufa in these Kaokoland deposits suggest that the rates of tufa deposition were greater during the Plio-Pleistocene than they are today (minor deposition at some sites such as Okovanatje Tufa - front cover of this issue of the Communications of the Geological Survey of Namibia - none at all at others). This in turn implies the existence of a different climatic regime in the region during the Plio-Pleistocene, possibly more humid, cooler, or a combination of both.

Acknowledgements

The field research carried out in Kaokoland and the laboratory work done in Paris was possible because of the efficient aid, support and encouragement provided by the Nambian National Heritage Council (Erica Ndalikokule, Helvi Elago and Alma Nankela), the Geological Survey of Namibia (Dr Vicky Do Cabo, Dr Gloria Simubali, Dr Anna Nguno, Helke Mocke, Ute Schreiber) the French Embassy in Namibia (Mme Claire Bodonyi) the Muséum National d'Histoire Naturelle, Paris (Prof. B. Senut) and UMR 7207 of the CNRS (Dr S. Crasquin). Thanks to the field assistants in Kaokoland (Herunga Nkahima, Smokey Muhaea, Division Tsijeua and Nancy Tsijeua).

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Stratigraphy, Palaeontology and Archaeology of Klinghardtfelder, Sperrgebiet, Namibia

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Abstract: The Southeast-Northwest oriented ridge between Buntfeldschuh and the coast of Namibia was called Klinghardtfelder by early 20th Century diamond prospectors. It is the site of extensive travertine deposition and there are still active saline springs along the northern and southern margins of the ridge. Surveys of the area by the Namibia Palaeontology Expedition in 2019 led to the discovery of fossils and stone tools at several localities. These occurrences throw some light on the timing of geological and geomorphological events in the sector, and are thus of interest for understanding the Neogene to Recent evolution of the region.

Key words: Travertine, Oysters, Phragmites, Oligo-Miocene, Pleistocene, Biochronology, Stone tools

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Introduction

At the beginning of the 20th Century, diamond prospectors were active in the coastal region of Namibia, known since 1908 as the Sperrgebiet (Forbidden Zone) (Kaiser & Beetz, 1926) (Fig. 1, 2). On account of the abundant presence of agates in the broad area between the Buntfeldschuh Cliffs and the coast the region was intensively prospected and there are still visible signs of trenches and several claim markers along the Klighardtfelder Ridge (Fig. 3). The aim of this contribution is to provide succinct descriptions and interpretations of the post-Cretaceous deposits at Klinghardtfelder and to point out their interest for understanding local geomorphological history. The fact that there are ancient human artefacts and middens in the rock sequence adds interest to the region and provides constraints on the ages of the travertines.

Materials and Methods

The field surveys consisted of tramping over the outcrops looking for evidence of fossils, stone tools and noting the rock types in which they occurred. Co-ordinates of localities were obtained using a Garmin GPS unit set to WGS 84 (Table 1).

Abbreviations

GPS - Geographic Positioning System
msl - mean sea level
KF - Klinghardtfelder
NPE - Namibia Palaeontology Expedition
WGS - World Grid System

Geological context and Stratigraphy

Much of the region known as Klinghardtfelder, west of Buntfeldschuh and Kakaoberg, is covered in travertine, but, as was recognised by Kaiser & Beetz (1926) there are diverse layers of other rock types in the area, most of which were mapped by them as Pomona Schichten (Fig. 1). Three brief visits to the region by the NPE resulted in the discovery of abundant fossils and stone tools at diverse sites and in various layers of sediment (Tables 1, 2). Commonest are plant remains (*Phragmites*, *Cyperus*) in red sand/silt and grey sand, and algae in limestone.

Table 1. Fossiliferous and implementiferous localities at Klinghardtfelder, Sperrgebiet, Namibia.

Locality	Latitude	Longitude	Altitude	Content
KF 1	27°35'32.2''S	15°32'56.3''E	112 m	Filamentous algae in limestone
KF 2	27°35'10.4''S	15°32'54.4''E	111 m	Stone tools
KF 3	27°35'52.1''S	15°32'49.3''E	100 m	Oysters *in situ*
KF 4	27°35'53.2''S	15°32'34.7''E	108 m	Silcrete boulders on wave-cut platform
KF 5	27°35'55.5''S	15°33'23.3''E	118 m	*Phragmites* in red sandstone
KF 6	27°35'54.9''S	15°33'23.4''E	121 m	*Phragmites* in grey sandstone
KF 7	27°35'52.6''S	15°33'33.2''E	125 m	Agates *in situ*
KF 8	27°35'59.2''S	15°33'17.8''E	108 m	Stone tools *in situ* with *Patella*, oysters, mussels, ostrich eggshells

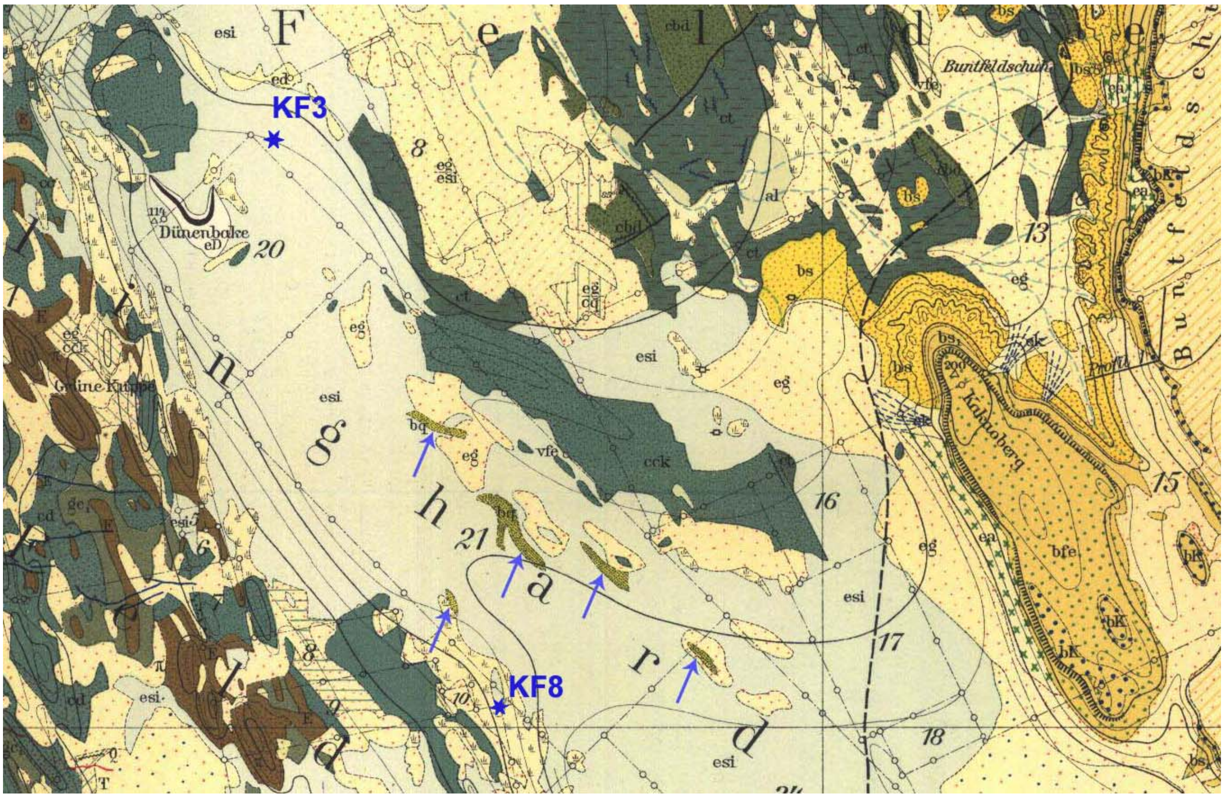

Figure 1. Geological map of the Klinghardtfelder area showing the positions of the Oyster site (KF 3) and the richest of the stone tool sites (KF 8). Blue arrows depict outcrops correlated by Kaiser & Beetz (1926) to the Pomona Schichten (light green tones, esi - travertine).

Table 2. Stratigraphic succession at Klinghardtfelder, Sperrgebiet, Namibia.

Rock unit	Age
Loose sand (Aeolian) and deflation lag (agates, quartz)	Recent
Indurated grey sand (Aeolian, cemented by limestone) with stone tools, fauna	Pleistocene
Travertine terraces and veins	Plio-Pleistocene
Limestone with plant remains (yellowish to white)	Oligo-Miocene
Marls and sand with agates, rounded quartz clasts, oysters, and locally derived silcrete boulders	Oligo-Miocene
Ferruginised marl, sand	Oligo-Miocene
Kätchen Plateau Silcrete (all reworked)	Ypresian/Lutetian
Bo Alterite	Ypresian-Lutetian
Basement rocks (Dolomite)	Proterozoic

Figure 2. Saline spring at Klinghardtfelder Travertine Plateau close to an *in situ* occurrence of fossil oysters and marine gravel at 100 m altitude (view eastwards towards Kakaoberg and Buntfeldschuh in the background).

Figure 3. Diamond claim markers at Klinghardtfelder constructed on top of a travertine terrace which itself reposes on ferruginised Basement complex rocks (Gariep Group).

The post-Cretaceous stratigraphic record of the Klinghardtfelder area is incomplete and patchy, as was recognised by Kaiser & Beetz (1926). The oldest such rocks recognised by the NPE comprise alterite (weathered basement rocks, generally of deep red and brown tones) attributed to the Bo Alterite which is most likely of pre-Lutetian age (Pickford, 2016). There are a few loose blocks of silicified conglomerate along the top of the ridge which are interpreted to be locally derived blocks of Kätchen Plateau Silcrete, also of Palaeogene age (Pickford, 2015). There are discontinuous patches of ferruginous crusts which are correlated to the Oligo-Miocene. Similar ferricretes occur at Buntfeldschuh a few km to the east and northeast, as well as more widely in the Sperrgebiet (Pickford, 2016). There are discontinuous patches of agate-rich silts and gravels overlying the ferricrete and older rocks and underlying widespread travertine terraces. At one outcrop, these agate-bearing deposits contain *in situ* oysters at an altitude of ca 100 metres above msl.

There then follows a widespread but thin and discontinuous deposit of travertine, often cementing reddish and greyish sand of aeolian origin. In detail, these travertine deposits reveal a complex pattern of cross-cutting relationships, indicative of shifting centres of spring activity and local superficial neo-tectonic activity, producing veins and terraces of more-or-less pure travertine as well as cementing surface deposits such as wind-blown sand and silt. The presence of stone tools and fossils in the grey cemented sands indicate a Late Pleistocene age for some of the travertine activity, which is still continuing today at active saline water seepages (albeit at reduced discharge rates) (Fig. 2). Some of the travertine, however, could be older than the Pleistocene, but no indicative fossils have been found in them, although a few outcrops contain abundant plant remains (sedges, filamentous algae).

Finally the area is covered in a discontinuous but thin layer of loose aeolian sand and locally deflated concentrations of agate clasts and well-rounded quartz pebbles.

Bo Alterite, Kätchen Plateau Silcrete and agate-rich beds

The oldest post-Proterozoic sediments in the Klinghardtfelder area comprise weathered basement rocks (Bo Alterite, Fig. 4, 5) ferruginised alterite and sand (Fig. 7) and locally derived blocks of silcrete (Fig. 8) similar in composition, colour and clast content to outcrops of Kätchen Plateau Silcrete in the Pomona area (Pickford, 2015). Comparable outcrops of Bo Alterite and silcrete occur *in situ* in the northern part of the Buntfeldschuh, 3.8 km to the northeast, where they underlie the marine silts, sands and gravels of the Buntfeldschuh Formation (Corbett, 1989). Agate-rich layers overlying ferruginised alterite are probably correlative with the basal marine layers at Buntfeldschuh (Fig. 9, 10).

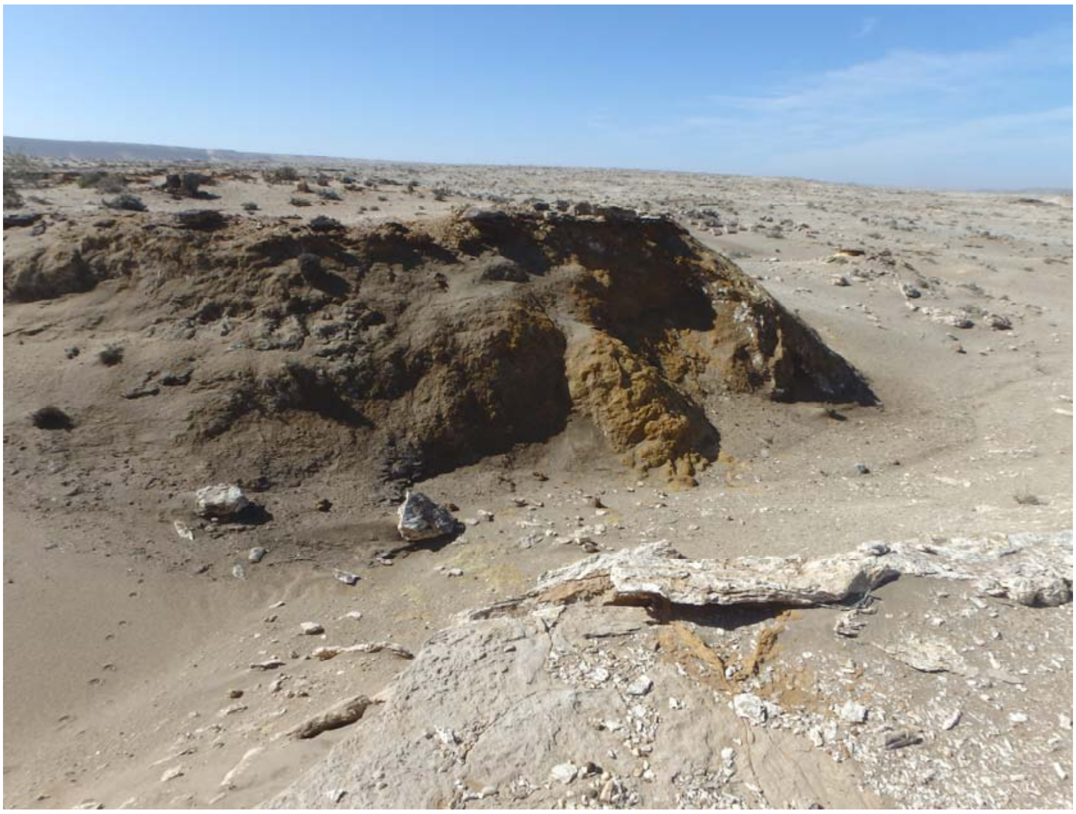

Figure 4. A 3+ metre thick layer of Bo Alterite exposed in the Klinghardtfelder Ridge, capped by a terrace of white travertine (view eastwards towards Kakaoberg).

Figure 5. *Phragmites* root systems and stalks *in situ* in orange Bo Alterite in the Klinghardtfelder. There are many places in the region with remains of this plant preserved, attesting to the former presence of open water at the surface.

Figure 6. Well-preserved *in situ* stems and roots of *Phragmites* in grey calcified sand at Klinghardtfelder, Namibia.

Figure 7. Ferruginised sand and silt layer at Klinghardtfelder overlain by limestone and travertine. The ironstone level probably correlates to the Oligo-Miocene.

Figure 8. Locally derived boulders of silcrete atop the Klinghardtfelder Ridge, correlated to the Kätchen Plateau Silcrete, overlying Gariep Group dolomite, with the bases of some of the boulders cemented by travertine. A) Boulders lying on a wave-cut platform at ca 108 m above msl; B) Intensely silicified conglomerate boulders overlying Basement rocks.

Figure 9. Well-rounded fist-sized quartz pebbles and other clasts in partly ferruginised marls derived from Bo Alterite at Klinghardtfelder, Namibia, at an altitude of ca 125 metres above msl. These pebbles attest to a marine transgression considered to pre-date the 90 metre marine package of Pether (1986). The ferruginisation likely occurred during the Oligo-Miocene transition.

Figure 10. Thin layers of well-rounded agate and quartz pebbles intercalated with marly silt layers overlain by limestone beds and travertine and loose sand at Klinghardtfelder, Sperrgebiet, Namibia. These deposits are at an altitude of ca 125 metres above msl.

The Klinghardtfelder Oyster Site

A layer of silt and conglomerate containing fossil oysters mixed with marine pebbles was recognised in a bed of red sand overlying Bo Alterite and underlying travertine (Fig. 11, 12). The precise stratigraphic position and age of this occurrence of oysters needs to be examined further, but our preliminary assessment is that it postdates the Oligo-Miocene ferricrete which is widespread but sporadic in the Buntfeldschuh depression, as at Klinghardtfelder itself, and it pre-dates the travertine deposits. As such it is probably early Miocene, but older than the 90 metre marine package. These fossil oysters crop out at an altitude of 100 metres above msl. Most of the shells are oriented vertically in the sediment, probably in their life positions.

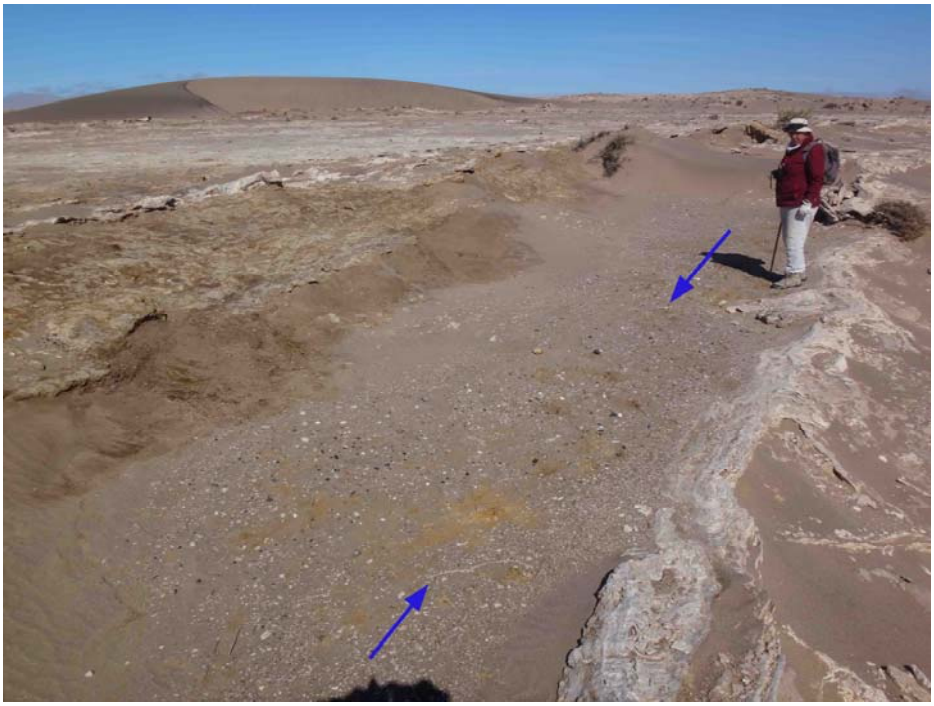

Figure 11. Fossil oyster site (KF 3) at Klinghardtfelder at an altitude of 100 metres above msl. The oysters are in the orange pebbly marl (blue arrows) interbedded between Bo Alterite to the left (brown marly deposit) and white travertine sloping to the right (northwards). Note the recently deflated lag of agates, quartz and other well-rounded pebbles.

Figure 12. Close-up view of *in situ* oyster shells locality KF 3, Klinghardtfelder, west of Buntfeldschuh, Sperrgebiet, Namibia (inset - stereo view of oyster shells associated with well-rounded quartz pebbles).

The Klinghardtfelder travertine deposits

The Klinghardtfelder Ridge is largely blanketed by a thin layer of travertine, mostly white, but often mixed with sand of various hues, grey and brown predominating (Fig. 13-17).

At present the ridge is the site of several seepages of highly saline water (Fig. 2, 18) and it is likely that during the past the springs were more abundant, more active and possibly somewhat fresher.

The ridge possibly owes its presence to the fact that it was a focus for long-term groundwater leakage to the surface, which dampened the surface and retarded the deflation processes that removed rock mass from the drier areas north and south of the ridge to a depth of more than 50 metres. The summit of the ridge is ca 125 metres above msl, whereas the depressions north and south of it lie at an altitude of ca 65 - 70 metres above msl.

There are vast numbers of travertine-filled veins in the region, which attest to the presence of minor neo-tectonic activity localised to the ridge and possibly related to water pressure fracturing semi-consolidated superficial sediments through which the water was flowing towards the surface.

As such an extremely complex series of veins and terrace deposits cross-cut each other in an amazing fashion. The terraces are seldom more than a metre thick, often only a dozen or so centimetres, but can cover areas of tens to hundreds of square metres.

The abundant presence of root systems of *Phragmites* (Fig. 5) and of stem fossils of *Cyperus* (Fig. 17) indicate that the water seeping to the surface probably formed pools and swampy areas. However, no gastropods or fish remains were found, suggesting that the waters may have been saline, as they are today.

Figure 13. General view of the travertine sheets and veins blanketing the Klinghardtfelder Ridge, with Kakaoberg in the distance. Note the sand dune, and the thin layer of loose sand cover in local depressions and forming sand shadows in the lee of plants.

Figure 14. Vertical veins and inclined layers of travertine in the northern margin of the Klinghardtfelder. The inclined travertine layers were deposited along the north-facing slope of the ridge as water flowed downhill from the seepage. The veins of travertine infill fissures in the sand and underlying rocks.

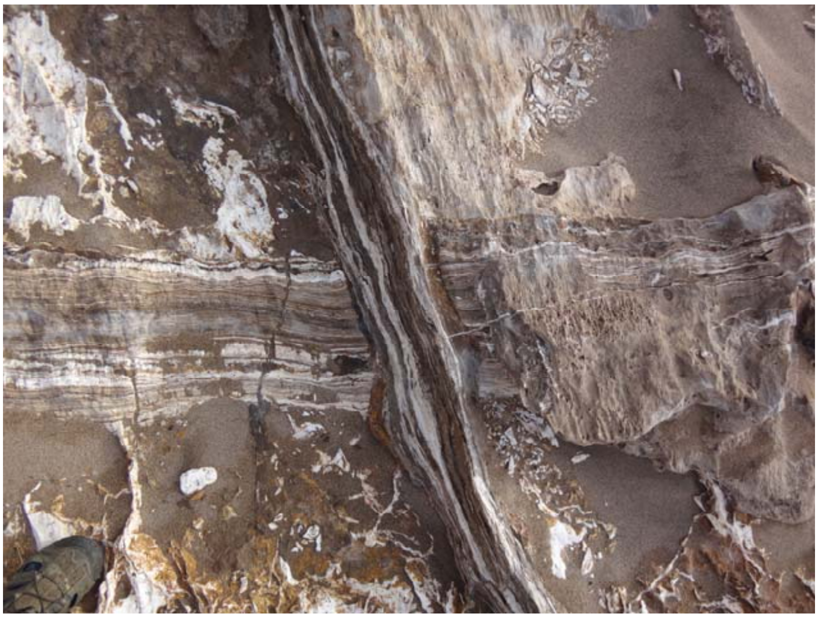

Figure 15. Cross-cutting veins of travertine and grey/brown sand deposited in fissures in Bo Alterite at Klinghardtfelder, Namibia.

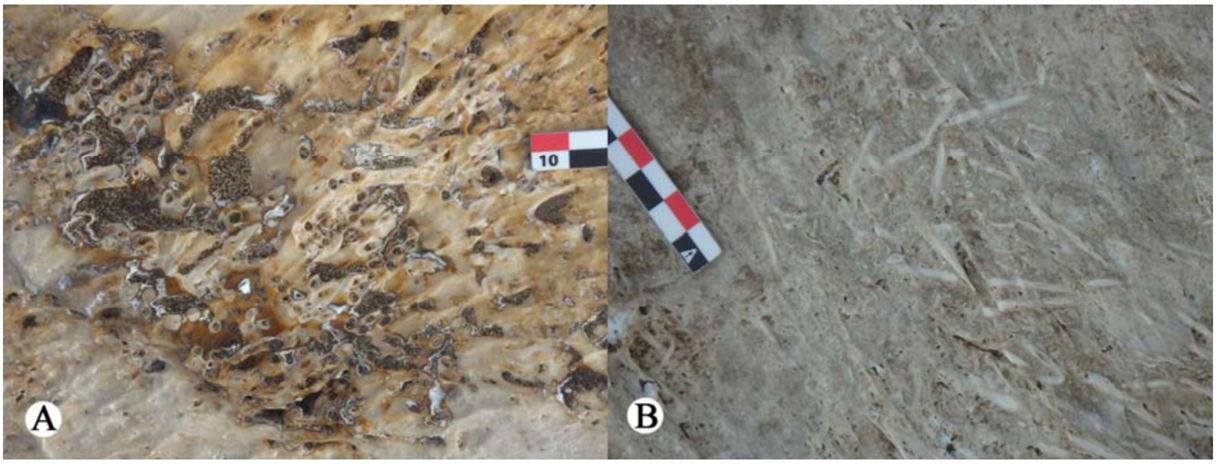

Figure 16. Yellow (A) and grey (B) limestone containing plant remains (algae, *Cyperus*) overlying agate-bearing marls at locality KF 1, Klinghardtfelder, Namibia.

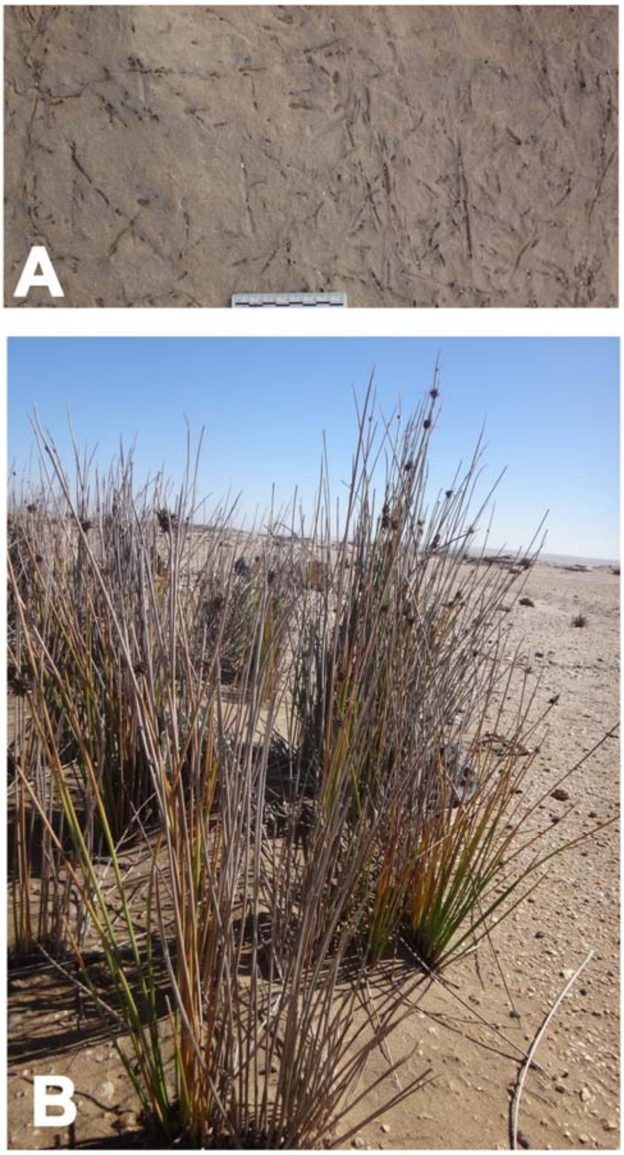

Figure 17. *Cyperus* in the Klinghardtfelder. A) Fossil stem imprints in calcareous grey sand. B) Living plants growing in damp grey sand.

Archaeological remains

In the Klinghardtfelder area there are lithic implements scattered over the surface, often close to water seepages (Fig. 18). At locality KF 8, a rich assemblage of stone tools, oysters, *Patella* shells and ostrich eggshell fragments is present, many of which are *in situ* in indurated grey sandstone (lime-cemented aeolian sand) (Fig. 19-23). There is a diverse fauna scattered on the surface, including a variety of marine gastropods and bivalves, as well as poorly preserved mammalian bones. This site is 5.1 km inland from the nearest point of the coastline.

The occurrence shows resemblances to that at Hexen Kessel described in previous reports (Pickford & Senut, 2016; Pickford *et al.* 2018). No signs of fire (charcoal or burnt bones) were observed and no pottery sherds were seen.

Figure 18. Locality KF 8, Klinghardtfelder, the site of a water seepage (dark tones in the middle of the image with saline water seeping downwards into the foreground). The surrounding area contains a rich assemblage of stone tools, marine mollusc shells and ostrich eggshells.

Figure 19. Surface scatter of lithic implements and faunal remains at locality KF 8, Klinghardtfelder, Namibia.

Figure 20. « Oldowan-style » stone chopper tool from surface context at Site KF 8, Klinghardtfelder, Namibia.

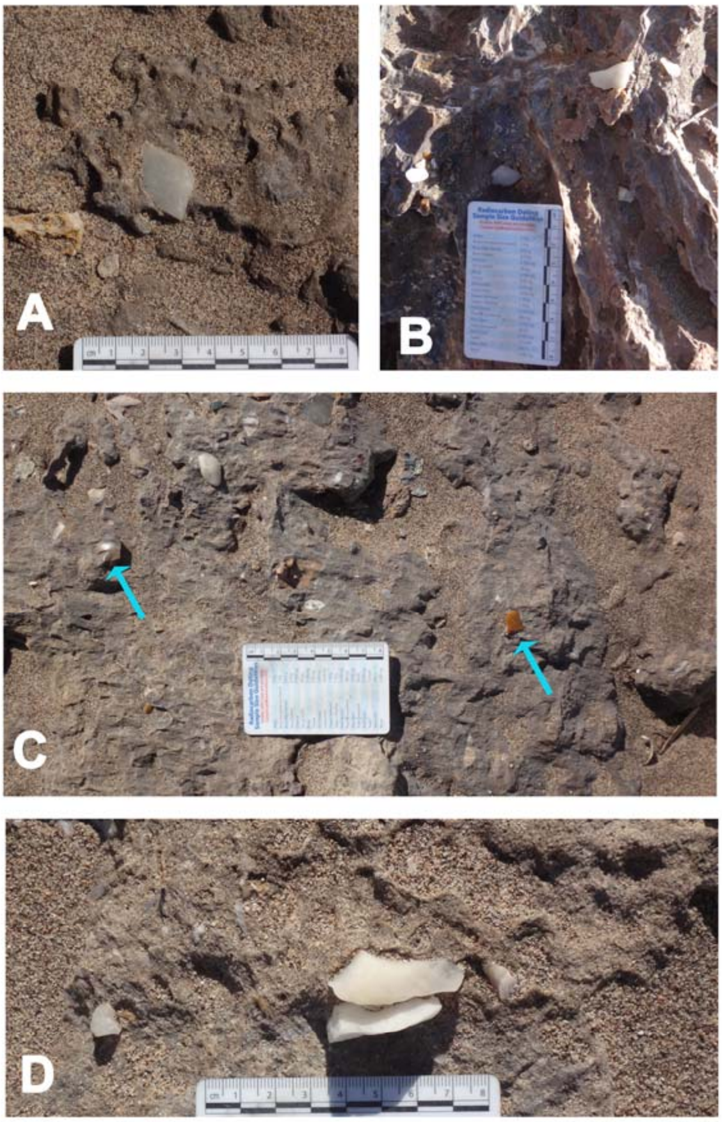

Figure 21. Stone flakes (chert, quartz, quartzite) *in situ* in lime-cemented grey sand at Site KF 8, Klinghardtfelder, Namibia. The blue arrows in (C) show two *in situ* flakes (scale : 8 cm).

Figure 22. A mass of marine shell fragments including oysters and *Patella* as well as lithics *in situ* in indurated grey sandstone at locality KF 8, Klinghardtfelder, Namibia.

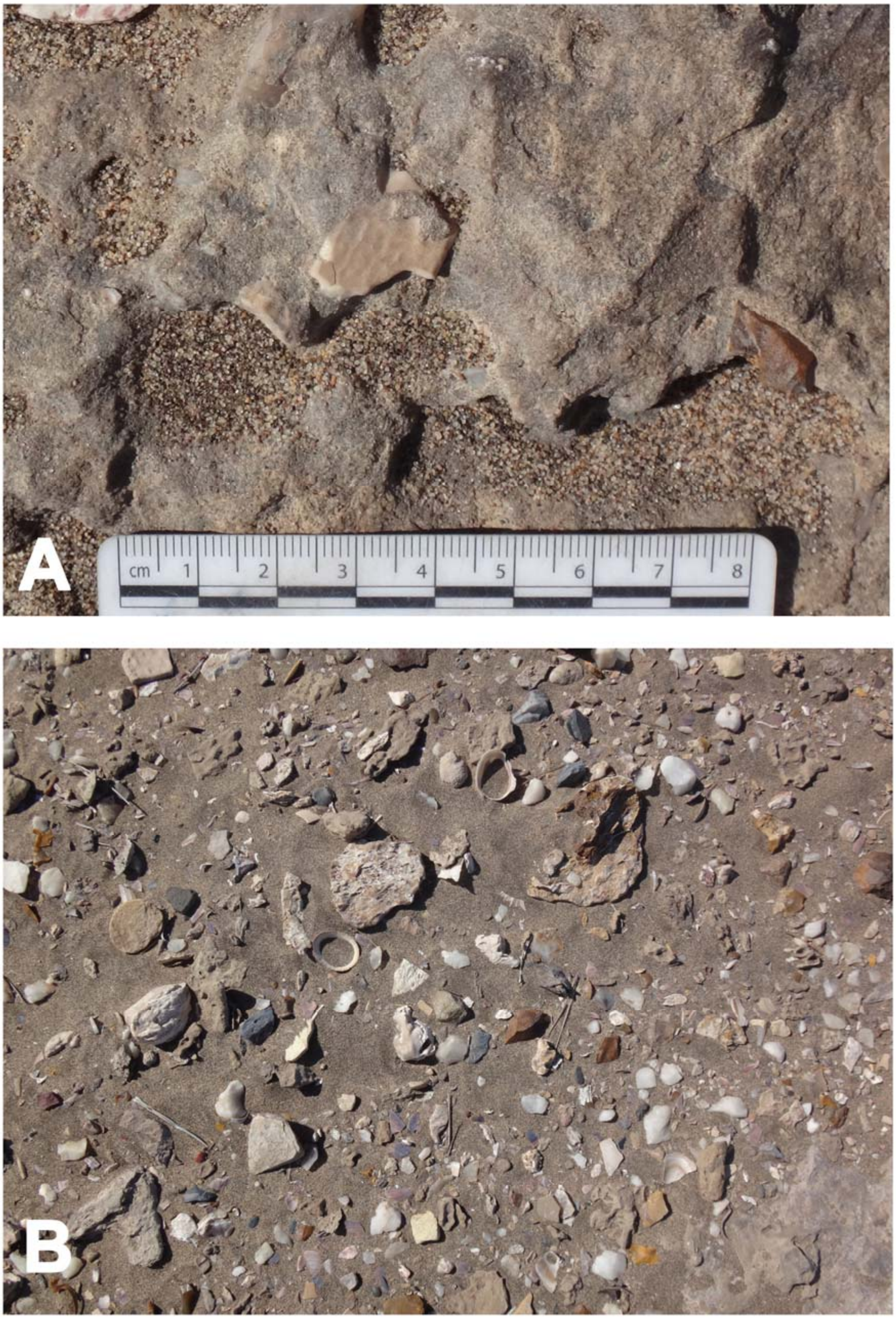

Figure 23. A) Ostrich eggshell fragment (left) and chert flake (right) *in situ* in grey sandstone at Klinghardtfelder, Site KF 8. B) Rich surface scatter of lithic implements and marine mollusc shells, Klinghardtfelder, KF 8, Namibia. Note reworked fragments of travertine.

At present the water seeping to the surface at Klinghardtfelder is too saline for human consumption, being even more saline than sea-water. However, wild animals such as *Oryx*, ostrich and jackals regularly imbibe the water, so it is possible that ancient humans were attracted to the area because of the presence of game animals around the springs. However, with greater rates of flow during the past the springs may have been fresher than they are at present. There may also have been seasonal fluctuations in salinity related to local rain showers. Whatever the case, judging from the quantity of seashells preserved in the deposits, it seems that the ancient humans were largely dependant upon marine food resources for survival, with addition of ostrich eggs and occasional mammals to the diet.

Discussion and Conclusion

Survey of the Klinghardtfelder Ridge in the Sperrgebiet, Namibia, has revealed the presence of a patchy, discontinuous succession of post-Cretaceous deposits, capped by widespread travertine deposits and recent aeolian sands. There are outcrops of weathered Basement rock (dolomite) which are attributed to the Bo Alterite of pre-Lutetian age, although it is likely that weathering continued for a long time after the Lutetian, depending on the topographic position of the weathered rocks. In several places at Klinghardtfelder, there are *in situ* fossilised root systems of *Phragmites* which grew in near-surface occurrences of these alterites as well as in grey sands overlying the alterite. Younger than the Bo Alterite is a scatter of locally derived large to huge silcrete boulders which attests to the former presence of a layer of silcrete in the area, now broken up into boulders which are strewn over the top of a wave cut platform ca 100 - 125 metres above msl.

Before the silcrete bed was broken up, however, there was a phase of ferruginisation, during which ferricrete of Oligo-Miocene age was deposited, cementing silt, sand and gravels.

There then followed a period of marine activity which brought in a great deal of agates and quartz pebbles which occur in silts and gravels underlying the travertine terraces. This is likely the period during which the silcrete bed was eroded and broken up by wave activity. In one place, agates and quartz pebbles are associated with *in situ* oyster remains (locality KF 3) at an altitude of 100 metres above msl. It is estimated that these oysters are of Oligo-Miocene age and that they appear to predate the 90 metre marine package of Pether (1986) (Pickford, 1998). However, further study is advised.

During Plio-Pleistocene times the Klinghardtfelder was the site of intensive travertine deposition. Veins and sheets of travertine are widespread, and are often mixed with grey or reddish sand, much of which is of aeolian origin.

Because of the presence of water seepages, even though the water is highly saline, the area was apparently attractive to early humans, as suggested by the abundant presence of stone tools and faunal remains in several discrete locales along the top and margins of the ridge. At locality KF 8, grey sand which has been cemented by travertine is rich in lithic remains and fossils, in particular marine gastropods and ostrich eggshell fragments. The lithic assemblage suggests a Late Stone Age or, less likely, a Neolithic correlation.

As such, even though the stratigraphic record at Klinghardtfelder is incomplete, it provides evidence concerning the geomorphological evolution of the immediate area, and indicates that during the Oligo-Miocene, sea-level was at least 125 metres above its present day level. Either that, or there has been localised uplift of geomorphological features related to the well-known early Miocene 90 metre package. Further studies are indicated.

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