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A Partially Articulated Cynodont Encased in a Putative Burrow Structure from the *Cynognathus* Subzone C.



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Abstract

A sedimentary structure containing a fossilized therapsid, and bioglyphs on the surface morphology, was found during a field expedition to *Cynognathus* subzone-C in the Eastern Cape, South Africa. A combination of surface scanning, petrographic thin sections, bone mapping and anatomical comparison were used to determine the deposit type and taxonomic identity of the encased therapsid, and examine the implications for biostratigraphy and faunal assemblage of the *Cynognathus* Assemblage Zone. The deposit is hypothesized to be a portion of a cynodont burrow (burrow margin) that was constructed in fluvial sediment near a river bank. This is the first account of a burrow in subzone-C. Pattern and directionality analysis of the bioglyphs suggest that the bioglyphs are scratch marks made by the burrower during excavation. The scratch marks are mediolaterally narrow, with some exhibiting indentation marks, indicating that the tracemaker had mediolaterally narrow unguals at the distal phalanx (claws). Anomodonts and cynodonts were common burrowers during the Triassic, however comparisons of *Thrinaxodon* and *Lystrosaurus* scratch marks to the bioglyphs on this deposit suggests that the bioglyphs were likely constructed by a cynodont as anomodont unguals are laterally wider, and are unable to create mediolaterally narrow markings. The tracemaker is hypothesized to be closely related to *Thrinaxodon* based on scratch mark comparison. However, bioglyph published literature is limited, and therefore the tracemaker cannot be identified. The therapsid was identified as *Diademodon* based on cranial and dental morphology. There is limited published literature on *Diademodon* constructing and/or exploiting burrows, however the taphonomy suggests that the *Diademodon* was near the entrance or in the tunnel of burrow nearing/during death. This is the first account of *Diademodon* encased in a burrow.

Keywords: Burrow margin, bioglyph, gomphodont, diademodontid

Introduction:

Burrows are a common sedimentary structure of the Triassic, and has allowed many species to survive catastrophic events. Many Triassic therapsids constructed/exploited burrows to survive the hot and dry conditions of the era. Burrowing behaviour enabled the therapsid lineage to continue past the Permo-Triassic extinction as cynodonts. Middle – Late Triassic cynodonts are found in the *Cynognathus* Assemblage Zone, Karoo Basin, South Africa, and many cynodont burrows (including *Thrinaxodon* and *Langberia*) have been found at this assemblage zone. Burrows are important as few examples exhibit the internal preservation of small-sized therapsids, hypothesized to be the remains of the burrow maker (Colombi *et al.*, 2012).

During a recent field expedition to the *Cynognathus* subzone C in the Eastern Cape, researchers Jonah Choiniere (Wits ESI) and Richard Butler (Birmingham, UK) discovered a sedimentary structure containing a fossilized therapsid inside. This research project aims to determine the deposit type, the taxonomic identity of the encased fossil, and examine the implications for biostratigraphy and faunal composition of the *Cynognathus* subzone-C. This research will contribute to the understanding of burrow morphology and burrow makers during the Triassic era, and within subzone-C, ultimately contributing to the biostratigraphy of subzone-C.

Geological Setting

The Karoo Basin preserves sediments from the Late Carboniferous to the Early Jurassic periods, a timespan of nearly 120 million years (Catuneanu *et al.*, 2005; Sun 2002).

The assembled stratigraphy in the basin is known as the Karoo Supergroup (Catuneanu *et al.,* 2005; Sun 2002). The basin experienced a variety of climatic conditions from glacial to arid during the deposition of the Karoo Supergroup, differences in timing and climatic stresses are reflected in the lithology and biostratigraphy (Catuneanu *et al.,* 2005; S.A.C.S 1980; Schluter 2008; Sun 2002).

The *Cynognathus* Assemblage Zone (AZ) forms part of the Karoo Basin that is hypothesized to represent fauna from the Early - Middle Triassic (Catuneanu *et al.,* 2005). Due to clear differences in spatial and temporal distribution of fauna, the AZ has been subdivided into three subzones, namely A, B and C – with subzone C being the stratigraphically uppermost and temporally youngest (Abdala *et al.,* 2005; Catuneanu *et al.,* 2005; Damiani and Hancox 2003; Hancox *et al.,* 1995; Hancox and Rubidge 2001; Neveling 2004).

Subzone C is an essential research assemblage as it preserves fossiliferous terrestrial sedimentary rocks from Early-Middle Triassic, a time period poorly represented in global terrestrial stratigraphy (Abdala *et al.,* 2006b; Abdala *et al.,* 2006c; Bordy *et al.,* 2010; Catuneanu *et al.,* 2005; Damiani *et al.,* 2003; Neveling 2004). This subzone is only present in the southeastern of the Karoo Basin, and compared to the other subzones (A and B), has a smaller geographic distribution and poor fossil record (Abdala *et al.,* 2005; Catuneanu *et al.,* 2005).The presence of key indicator fossils in subzone C has provided tentative associations with other parts of southern Gondwana, including; Argentina, Brazil, Canada, China, Russia, Namibia and Tanzania (Abdala *et al.,* 2005; Abdala *et al.,* 2006c; Groeneweld *et al.,* 2001; Wopfner *et al.,* 1991).

History of burrows in South Africa

Tetrapod burrows are a common phenomenon in the Karoo Basin, South Africa that have been found throughout Pangea, dating back to the early Mesozoic (Colombi *et al.,*

2012). Burrowing is hypothesized to be a widespread adaptation for predator avoidance, protection from extreme conditions, brooding and, in some cases, seasonal dormancy (Bordy *et al.,* 2010; Colombi *et al.,* 2012; Damiani *et al.,* 2003; deBraga 2003; Fernandez *et al.,* 2013; Groeneweld *et al.,* 1991; Groeneweld *et al.,* 2001; Smith and Botha 2005; Smith and Botha-Brink 2009). These structures are commonly associated with early therapsids found above and below Permo-Triassic boundary of the Karoo Basin, South Africa (Abdala *et al.,* 2006b; Bordy *et al.,* 2010; Damiani *et al.,* 2003; Fernandez *et al.,* 2013; Groeneweld *et al.,* 2001; Sumbera *et al.,* 2011). Burrow specimens have been discovered in abundance in the upper-units of the Beautfort group including the Katberg Formation (*Lystrosaurus* Assemblage Zone) and Burgersdorp Formation (*Cynognathus* Subzone C) (Abdala et al., 2006b; Abdala et al., 2006c; Bordy et al., 2010; Modesto and Botha-Brink 2010).

The large number of specimen in these formations suggests that burrowing was a survival strategy adopted because of harsh climatic conditions of the Permo-Triassic (Damiani *et al.,* 2003; Fernandez *et al*., 2013; Groeneweld *et al.,* 2001; Sahney *et al.,* 2010; Smith and Botha 2005; Smith and Botha-Brink 2009). Burrows improve the preservation of skeletal elements (preserving whole skeletons in some cases) and indicate that different therapsids used/constructed burrows within their lifetime (Abdala *et al.,* 2006a; Smith 1987; Smith and Swart 2002; Voorhies 1975). Several fossilised therapsids have been found curled up in burrows suggesting that these animals rested in burrows (Bordy *et al.,* 2010; Brink 1958; Damiani *et al.,* 2003; Fernandez *et al.,* 2013).

Fossilised burrow specimen are crucial trace fossils as they are widespread in space and time, are found in place and largely record animal behaviour and response, making them ideal indicators of environmental conditions (Abdala *et al.,* 2006a; Damiani *et al.,* 2003; Fernandez *et al.,* 2013; Modesto and Botha-Brink 2010; Rhoads 1975). The morphology and orientation of burrow specimen, along with their encased fossilized specimen, are used

contribute to the reconstruction of faunal assemblage for a formation (Rhoads 1975). The greatest contribution of burrows, or any other trace fossil, is when evidence is combine with other sources of palaeoecological data to interpret their environment, feeding modes and other various behavioural and social aspects (Rhoads 1975).

The earliest-known terrestrial vertebrate burrow specimen is attributed to the dicynodont *Diictodon* (Damiani *et al.,* 2003; Smith 1987). The articulated skeleton of *Diictodon* was found coiled inside the burrow cast from the Upper Permian in the Karoo Basin (Damiani *et al.,* 2003; Smith 1987). Similar burrow structures were found in the Lower Triassic of the basin (Damiani *et al.,* 2003; Damiani *et al.,* 2011; Groeneweld *et al.,* 2001). These early burrows of the Triassic were constructed by cynodonts, specifically *Thrinaxodon* and *Langbergia* (Abdala *et al.,* 2006b; Damiani *et al.,* 2003; Fernandez *et al.,* 2013; Groeneweld *et al.,* 2001). *Thrinaxodon* exhibited the earliest evidence of cynodont burrowing (Brink 1958; Damiani *et al.,* 2003; Fernandez *et al.,* 2013). These animals were considered burrowers as they died, and were fossilized, in a burrow cast (Damiani *et al.,* 2003; Fernandez *et al.,* 2013; Smith 1987).

Early ancestors of the group Mammalia were burrowers, this plesiomorphic state allowed the continuation of Mammalia to modern day (Bordy *et al.,* 2010; Damiani *et al.,* 2001; Groeneweld *et al.,* 2003). Fossilized burrow specimen have been found after the Permo-Triassic mass extinction boundary layer (Katberg Formation), providing evidence that burrowing continued through the extinction, thus allowing the continuation of burrowing taxa into the Jurassic (e.g. *Lystrosaurus*) (Bordy *et al.,* 2010; Groeneweld *et al.,* 1991). (Bordy *et al.,* 2010: Groeneweld *et al.,* 1991).

Burrow Morphology

There are two types of burrows: communal and solitary burrows (Dean and Milton 1999). Communal burrows have multiple entrances and tunnels, leading to a communal terminal compartment, and has been adopted by taxa with high social activity (Dean and Milton 1999). Solitary burrows have a simple layout; one opening with a single tunnel leading to a single terminal compartment (Dean and Milton 1999). Many solitary burrowers construct more than one burrow during the course of their activity, as they small and construct burrows wherever they may be rather than returning to same burrow (Dean and Milton 1999). This provides immediate protection from predators and/or extreme conditions (Dean and Milton 1999).

Tunnels either exhibit a helical structure or a straight narrowing orientation (Damiani *et al.,* 2003; Groeneweld *et al.,* 2001; Smith 1987). Smith (1987) discovered several large helical *Diictodon* (dicynodont) burrows in the Teekloof Formation. The burrow has a single opening with a single coiled/helical tunnel leading to a single terminus. Whereas the *Trirachodon* (later revised as *Langberia* by Abdala *et al.,* (200b)) burrow complex found by Groeneweld *et al.,* (2001) has numerous tunnels and terminal compartments; the tunnels are straight, with a constant inclination which leads into the terminus (Groeneweld *et al.,* 2001). This burrow forms part of a large network which indicates that *Trirachodon* lived in large communities (Groeneweld *et al.,* 2001).

Cynodont burrow morphology varies amongst species. Generally, the burrows have a single opening with an inclined tunnel(s) that leads to a rounded terminus/termini (Bordy *et al.,* 2010). Burrow morphology changes depending on the shape and orientation of the tunnel and whether the burrow was occupied by single or multiple occupant(s) (Damiani *et al.,* 2003; Groeneweld 1991; Groeneweld *et al.,* 2001; Smith 1987).

Preservation of burrows occurs best in mud and sand interbeds of medium thickness, filling with deposits of fine-grained siltstones and mudstones (Groenewald *et al.* 2001; Krummeck and Bordy 2014; Laporte and Behrensmeyer 1980). Burrowers prefer loose sand/soil as it is easier to excavate and allows minimal energy expenditure when constructing the burrow during harsh conditions (Dean and Milton 1999).Fine grained siltstones and mudstones represent floodplain or riverbank sediment deposits, i.e. burrows preserve well when filled with sediment or debris originating from a water source (Krummeck and Bordy 2014; Laporte and Behrensmeyer 1980).

Bioglyphs commonly associated with burrows

Bioglyphs are features produced by vertebrates when digging into the ground, including such actions as scratching, drilling, plucking, poking and etching (Ekdale and De Gibert 2010). Bioglyphs allow scientists to make palaeoethologic interpretations of the trace maker because they provide an understanding of the mechanism of excavation, the identity of the trace maker and the purpose for excavation (Ekdale and De Gibert 2010; Rhoads 1975).

Bioglyphs are often not well preserve as they need a specific set of circumstances to fossilize but the examples in the fossil record are commonly associated with fossilized burrows (Ekdale and De Gibert 2010; Krummeck and Bordy 2014; Laporte and Behrensmeyer 1980). Bioglyphs preserve best in fluvial deposited and fine-medium grained sediment (Krummeck and Bordy 2014; Laporte and Behrensmeyer 1980). Although bioglyphs have been commonly associated with fossilized burrows, neither burrows nor bioglyphs have ever been recorded in Subzone C.

Bioglyphs are commonly associated with burrows and generally manifest as scratch marks as the burrowers used their limbs to excavate soil, leaving markings on the burrow

floors and walls (Ekdale and De Gibert 2010; Groenewald *et al.* 2001). Uniform and well-developed scratch marks are often present nearer the entrance and tunnel of the burrow due to the cynodont digging into the ground (Dean and Milton 1999; Ekdale and De Gibert 2010; Groeneweld *et al.,* 2001). The *Thrinaxodon, Diictodon* and *Langberia* burrows (mentioned above) all exhibited scratch marks on the burrow deposit (Abdala *et al.,* 2006b; Groeneweld *et al.,* 2001; Smith 1987). Actualistic studies of bioglyphs found in modern hare (*Pedetes capensis*) and a variety of rodent burrows in the Karoo (*Aethomys namaquensis, Desmodillus auricularis, Gerbillurus paeba, Mastomys natalensis, Micaelamys granti, Xerus inauris*) attribute bioglyphs to scratch marks or lining the tunnels and terminal compartments with grass or straw for thermoregulation (Dean and Milton 1999). Although fossilised burrows lack evidence of lining, this could be an alternative explanation to unidentified bioglyphs.

Cynodont Anatomy and Evolutionary History in South Africa

Cynodonts are an essential part of the faunal assemblage from the Late Permian through the Early Jurassic in South Africa due to their abundance and the evolutionary evidence they provide for the development of mammalian traits - they have been hypothesized as a key transitional group that bridges the final gap from reptiles to mammals (Abdala *et al*., 2005; Hopson and Kitching 1972). They are characterised by their 'mammal-like' features; narrow snout and post-canines that extend antroposteriorly (Abdala *et al.,* 2005; Brink 1963; Broom 1903; Broom 1904). The most distinctive feature of cynodonts are their post-canines. Different species of cynodonts are identified by the shape, orientation and cusps of their post-canines (Abdala *et al.,* 2006c; Martinell *et al.,* 2009). Cynodonts are well-represented in the Beaufort Group, and more well-known genera include *Diademodon*, *Cynognathus*, *Trirachodon* and *Thrinaxodon* (Abdala *et al*., 2005; Abdala *et al*., 2006c; Damiani *et al*., 2003). They have been collected within the Karoo Basin in the Eastern Cape

and southern and northern Free State (Abdala *et al*., 2006c; Welman *et al*., 1991). They have also been found outside of southern Africa, including; Tanzania, Argentina, Brazil, Canada, China, and Russia (Abdala *et al.,* 2005; Groeneweld *et al.,* 2003; Haugton 1924; Hopson and Kitching 1972).

Langberia and *Thrinaxodon* were the first cynodonts to have been recorded showing fossil evidence for burrowing behaviour (Abdala *et al.,* 2006c; Damiani *et al.,* 2003; Groeneweld *et al.,* 2001). Many cynodonts were found fossilized in burrow compartments (Damiani *et al.,* 2003; Fernandez *et al.,* 2013; Groeneweld *et al.,* 2001). Burrowing is hypothesized to have allowed some species to survive the Permo-Triassic mass extinction, allowing some species to continue into the Jurassic (Abdala *et al.,* 2005; Abdala *et al.,* 2006b; Abdala *et al.,* 2006c; Bordy *et al.,* 2010; Retallack *et al.,* 2003; Modesto and Botha-Brink 2010).

One particularly diverse clade, Gomphodontia, are distinguished by wide and closely spaced molar-like teeth, which are convergent to modern mammals (Sues and Hopson 2010). Gomphodontia are a clade of cynognathian cynodonts that includes Diademodontidae, Trirachodontidae and Traversodontidae (Broom 1903; Broom 1904; Hopson and Kitching 1975; Sues and Hopson 2010). They are characterized by buccolingually wide, molariform (gomphodont) post-caniniform teeth that met in complex crown-to-crown occlusion similar to that in mammals, upper post-caniniform with three or more cusps spanning their widths and lower post-caniniform with two cusps spanning their widths (Abdala and Ribeiro 2003; Abdala *et al.,* 2006b; Crompton 1972; Hopson 1991; Kemp 2005; Sues and Hopson 2010). Gomphodonts first appeared in the Early Triassic and went extinct in the Jurassic, with fossils being spread without Pangea, including; southern Africa, Argentina, Brazil, eastern North America, Europe, China and Antarctica (Sues and Hopson 2010).

Diademodontids are commonly found throughout Pangea, although there is no evidence suggesting that they were burrowers (Hammer 1995; Martinelli *et al.,* 2009; Sun 1991). This project describes diademodontidae specimen that was found encased in putative burrow found in the Cynognathus subzone-C, this is also the first account of burrow specimen in subzone-C.

Materials and Methods

The research problem will be approached using a variety of methods ranging from microscopic investigation of the sedimentology of the specimen, digital isolation and pattern analysis for ichnology, to manual preparation and comparative anatomical analysis for taxonomic identification.

Microscopic investigation of the sedimentology of the specimen

To assess the micro-sedimentation and mineralogy of the deposit, a sample of the encasing matrix was extracted from the putative burrow (~2 cm width and ~20 cm length) and a petrographic thin sections were prepared from this sample (Figures 2 and 3).

The petrographic thin sections were also viewed under a petrographic microscope with crossed and uncrossed polarizing filters to assess the mineral composition difference between the burrow margin and host. Chemical composition as well as the mineral types were identified.

The area of the grains and matrix per petrographic thin section taken at 4X-maginification were measured using FIJI. These images were uploaded to FIJI where 10 randomly placed rectangles (1mm by 1mm) were cropped out of each slide. The area (mm^2)

of 10 randomly selected grains and 5 randomly selected continuous matrix sections were measured and recorded for the putative burrow and host rock.

Grains were selected on the basis of fragmentations, i.e. if the grain appeared to be fragmented (not have a definite border), it was excluded from the measuring process. The matrix was defined as the space between the grains, which includes porosity and any minerals. An area of matrix was measured until grains were placed closely together so that the matrix appeared to terminate at these closely packed grains

The raw data of the grain and matrix area measurements were tested for normality first by plotting them on a histogram to visualize data distribution, and then by applying Kolmogorov-Smirnov and Sharpio-Walk normality tests to test whether they departed from a normal distribution. Data which were found to be normally distributed were subjected to student's T-test to assess whether significant differences between means were present. Data which were found to deviate significantly from the normal distribution were subjected to non-parametric tests for significant differences between means, including Mann-Whitney U-test.

Before the normality tests were conducted, outliers represented in the histograms (Figures 5,6, 7 and 8) were removed from the sample, and were attributed to sampling error, fragmented grains and/or abnormally large grains within the sample (possibly shale fragments). This was done to correct for sampling error and to attain optimum results.

The raw data of the grains and matrix were compiled and ordered (ascending) in Excel. The sample sizes of the raw matrix and grain area measurements of the burrow margin and host rock were unequal, thus the measurements were compiled to a sample size of 30. The sample size was unequal as the thin sections exhibit greater burrow margin data than host rock data, this enabled better statistical test results as samples of equal size reflect a better result than unequal sample sizes.

A visual comparison was conducted using burrows that had already been extracted and identified as a basis for a detailed point-by-point consideration of the morphology of the specimen under study.

Ichnology

The bioglyphs were scanned using Arch-Tech white light scanner, and a three-dimensional surface model was generated. Each scratch mark series will be digitally isolated, and the individual depths of each scratch will be quantified using distance to reference plan in the software (using Avizo or similar software for analysis of three dimensional data).

High resolution digital pictures of the specimen were traced using vector editing software to highlight the directions and paths followed by the scratch marks as a means of assessing pattern and directionality.

Taxonomic identification

The skull of the cynodont specimen was detached from the burrow using standard preparation techniques and underwent manual preparation on its lateral surface. The incisors were also specifically manually prepared to yield taxonomic information

Size estimation

To estimate the body size of the specimen and assess whether the specimen could have fit into the burrow dimensions, the orbital, temporal and bicanine lengths were calculated via a multiple regression analysis done in the statistical program SPSS. These measurements were compared to the previously measured cranial elements of gomphodonts found in the ESI Karoo collections.

Comparisons

The National Museum in Bloemfontein contains fossil records of cynodonts, burrows and scratch mark specimen extracted from Karoo Basin. Burrow and scratch mark examples were photographed and compared to the specimen of this study.

Results:

Microscopic investigation of the sedimentology of the specimen

Abbreviations: Bg – Burrow margin grain area measurements (mm^2); Hg – Host rock grain area measurements (mm^2); Bm – Burrow margin matrix area measurements (mm^2); Hm – Host rock matrix area measurements (mm^2)

Grain Measurements and Analysis

I subjected the raw grain area data of Bg and Hg to a Kolmogorov-Smirnov (K-S) and Sharpiro-Walk (S-W) normality test (Table 2). I also placed these data onto a histogram to visualize whether they were distributed normally (the data would fit into the bell curve) (Figures 5 and 6). I only considered the test results from the S-W as the compiled sample size is < 50. This analysis indicated that the data was non-normally distributed ($p < 0.05$) (Table 2).

The bell curve for Bg and Hg indicates the values of the outliers – all values > 0.02 mm^2 for Bg and Hg (Figures 5 and 6). 5 outliers were removed from the raw data of Bg and 3

outliers were removed from the raw data of Hg before compiling the data. The outliers are attributed to sampling error, abnormal large grains or shale fragments.

The mean area grains of Bg (0.0076795) and Hg (0.0071262) were statistically indistinguishable using the Mann-Whitney U-test, therefore these data failed to reject the null hypothesis that Bg=Hg, meaning there is no difference in mean grain size between the burrow margin and the host rock ($p > 0.05$) (Table 3). The p-value of the 1-tailed test was only considered as I only considered the difference between Bg and Hg in one direction.

Matrix Measurements and Analysis

I subjected the raw matrix area data of Bm and Hm to a K-S and S-W normality test to test whether the area data were normally distributed (Table 5). I also placed a histogram to visualize whether they were distributed normally (Figures 7 and 8). I only considered the test results from the S-W as the compiled sample size is < 50. This analysis indicated that the data was non-normally distributed ($p < 0.05$) (Table 5).

The mean matrix area of Bm (0.0096284) and Hm (0.126575) were statistically distinguishable using the Mann-Whitney U-test, therefore these data rejected the null hypothesis that there is no difference in mean matrix area between the burrow margin and host rock ($p < 0.05$) (Table 6). There is greater mean matrix area at the burrow margin. The p-value of the 1-tailed test was used as I only considered the difference between Bm and Hm in one direction.

The mean matrix area at the burrow margin centre and the burrow margin outer boundary (Figure 2) were statistically distinguishable using the Mann-Whitney U-test, therefore these data rejected the null hypothesis that there is no difference in mean matrix area between the burrow margin centre and the burrow margin outer boundary (Table 7).

There is greater mean matrix area at burrow margin outer boundary. The p-value of the 2-tailed test was used as I considered the difference between burrow margin outer boundary and burrow margin centre in any direction.

Chemical Composition of Sediment

The chemical composition of the burrow margin and host rock were not significantly different. The grains present in both the burrow margin and host rock were mainly quartz crystals, some mica and iron oxide, which were surrounded by matrix. The burrow margin has large, irregular shale fragments (alluvial sediment) that are hypothesized to have fallen into the putative burrow during excavation or collapse. The greatest difference that is visible between the burrow margin and host rock is the amount of matrix present. The host rock has larger spaces between the grains, therefore more matrix was present in the host rock.

Ichnology

The bioglyphs present on the surface morphology of the putative burrow demonstrate a pattern of directionality and consistency in the number of digits/objects involved in making the bioglyphs.

The bioglyphs are made up of a minimum of 3 lines and a maximum of 5 lines involved in each, separate mark, lines 2, 3 and 4 tend to be deeper and longer than lines 1 and 5 (Figures 10 and 12) (Figure 11 – red, blue and dark green). The markings cluster at a more deeply excavated portion on the burrow (Figures 9), and tend to curve to the right (Figure 12).

The origin of the some bioglyphs have indentation markings that appear to be the initial claw marks of the organism when inserting its limb into the ground (Figure 4; Figure 10 – dark blue, light blue, pink and grey). The indentation marks are most common on lines 2, 3 and 4, although there are some markings that have indentation marks at all 5 lines (Figures 10 – dark blue, light blue, pink and grey). Indentation marks appear to be deeper than the line created by the bioglyphs, and exhibit a conical shape (Figures 4 and 10 – dark blue, light blue, pink and grey).

Most bioglyphs are found at the centre of the block on the surface where the burrow margin is (Figure 9). The rock dips at the where majority of the bioglyphs are present (Figure 9). The indentation marks at the origin of the bioglyphs at the centre are deeper, suggesting more force applied at this specific area (Figure 10 – dark blue, light blue, pink and grey).

The bioglyphs found on deposit WK-34-14 are mediolaterally narrow, curving markings compared to the laterally wide *Lystrosaurus* scratch marks found on deposit NMQR 4001 at the National Museum, Bloemfontein. The bioglyphs similar to that of the *Thrinaxodon* scratch mark specimen, QR309/C392 – National Museum, Bloemfontein, although the bioglyphs on WK-34-14 are longer in length (applies for all lines of bioglyphs) and are slightly laterally expanded (not to the extent of *Lystrosaurus*). The tracemaker is therefore hypothesized to be closely related, but larger than, *Thrinaxodon.*

Taxonomic Identification

Anteriorly exposed lower incisors were present in the fossil at the time of collection, indicating that the specimen was a cynodont (Figure 14). Initial preparation exposed enough of the molariforms dentition for identification of the specimen as a diademodontid (Figure 15 – yellow.). More preparation was completed on the skull exposing the upper incisors,

caniniforms, diastema, post-caniniforms on the mandible and dentary, nasal, temporal,; along with some post crania found overlying the skull - the scapula and dorsal vertebra (Figures 15 and 16). The scapula is overlying the right side of the lower jaw and the neural spine is overlying to the anterior end of the snout (Figures 16).

Examination under the microscope shows three visible incisors on each side, but it is possible that one incisor is obscured by the dorsal vertebra. CT scanning is needed to further investigate the true number of upper incisors. The number of upper incisors are crucial to identify which diademodontid species the specimen is, diademodontid species with three incisors are *Titanogomphodon* whereas four incisors are *Diademodon*.

The three upper and four lower incisors are mediolaterally narrow, with rounded mesial and distal surfaces (Figure 16 – purple). The crowns of the incisors are worn and slightly fragmented, and curve posteriorly. The incisors and caniniforms are separated by small diastema. The two fragmented caniniforms are rounded mesially and distally, and laterally wider than the incisors, molariforms and sectoral teeth (Figure 16 – green). Immediately abutting the caniniforms are large diastema – a bony plate created by plugged conicals – which is indicative of gomphodonts who have ceased tooth replacement, indicating that the organism has reached adulthood (Osborn 1975) (Figure 16). Immediately posterior to the large diastema are three transversely expanding occluding molariforms (upper and lower), the occlusal surface is flattened, and mesial and distal surfaces are rounded in lateral view (Figure 16 – red). The molariforms are laterally wider and shorter than the incisors (Figure 16). The three upper occluding molariforms are worn, fragmented and smaller than the lower occluding molariforms (Figure 16). One sectorial tooth (upper and lower) immediately abuts the occluding molariforms (Figure 16 – blue). The sectorial teeth are labellolingually narrow, shorter than the incisors and bear three cusps, with the medial cusp extending ventrally

(lower jaw)/dorsally (upper jaw) (Figure 16 – blue). The upper sectorial tooth is worn down, with a fragmented medial cusp (Figure 16 – blue).

The measurements of the skull were calculated using linear regressions. The temporal length (R = 0.9822) (Figure 18) and bicanine length (R = 0.9087) (Figure 19) are good predictors of basal skull length, whereas orbital length (R = 0.7878) (Figure 17) is not. The *Diademodon* (WK-36-14) skull measurements are the smallest compared to other *Diademodon* specimen in the ESI Karoo vertebrate collection (Table 8).

Discussion

Microscopic Investigation of the Sedimentology

The burrow margin and host rock is composed of fluvially deposited sediment. Several lines of evidence support this hypothesis. Firstly, we know that burrows are most commonly preserved when they were dug in fluvial sediments (Groeneweld *et al.*, 2001; Krummeck and Bordy 2014; Laporte and Behrensmeyer 1999). Burrowers in past environments seem to have preferred to excavate in loose, fine-grained sediment as it is easier to excavate (Dean and Milton 1999). Burrows during the Triassic were typically constructed near river banks as burrowers preferred wet sediment as it was easier to excavate as the sediment was fine-grained (Dean and Milton 1999; Krummeck and Bordy 2014; Laporte and Behrensmeyer 1980).

Second, the decrease in matrix at the margin of the burrow suggests that the sediment contained water at the time of excavation (Table 6). Sediment containing water allows individual grains to move without compromising the integrity of the burrow walls. This makes it possible to compact the sediments, moving the porosity and matrix from the burrow

margin into the host rock, resulting in greater porosity, and therefore greater matrix, at the host rock (Table 6).

The mean grain areas of the burrow margin and host rock show no significant statistical difference (Table 3). This conclusion is attributed to the poor stratification of sediment at the site the burrow was constructed. In general, fluvial sediment is identified by upward-fining cycles (Godin 1991), but the results show homogeneous grain sizes in both the burrow margin and the host rock (Table 3). This allows me to infer that there was rapid homogeneous deposit of the host sediment possibly caused by a flash flood (Smith *et al.,* 1993; Ortega and Heydt 2009). The lack of upward fining could also be attributed to the unknown mechanism of deposition. It is unclear how the host sediment was deposited into the burrow as the sediment shows no evidence of which mechanism was used to fill the burrow (e.g. wind, gravity etc.). This is unlikely as fluvial sediment generally originates from a fluvial system (Smith *et al.,* 1993; Ortega and Heydt 2009).

The lesser amount of matrix in the burrow margin suggests that the sediment was compacted (pressed down) during excavation (Table 6). While compacting the soil, the porosity, along with other minerals making up the matrix, are displaced from the burrow margin sediment to the host rock, packing the homogeneous burrow sediment closer together, consequently resulting in greater porosity and matrix into the host rock.

It was hypothesized that the burrow margin would undergo greater compression as the burrower is constructing the walls to be sturdy. The sturdy burrow margin outer boundary (Figure 2- slide 3) would allow little to no exchange of matrix with the host rock as the burrow margin sediments are packed tightly. However, the results held a different result, the burrow margin outer boundary in fact had statistically more matrix than the centre of the burrow margin (Figure 2- slide 1), therefore the initial hypothesis was rejected (Table 7).

Greater compaction of burrow margin centre is attributed to rapid compaction during fossilization.

There is limited published literature for geological and statistical analysis on burrows and their margin, and it is difficult to compare my conclusion to these drawn from the burrow systems. However, my study shows that when describing burrows, the analysis of thin sections and microsedimentology yields informative data.

Ichnology

Bioglyphs are hypothesized to be scratch marks as scratch mark specimen are commonly associated with burrows (Ekdale and De Gibert 2010; Groenewald *et al.* 2001). There is limited literature on the classification of bioglyphs presumably because they are rare in the fossil record as they fossilize under specific conditions (Ekdale and De Gibert 2010; Krummeck and Bordy 2014; Laporte and Behrensmeyer 1980). Despite the limited research background, there are some conclusions formulated from the bioglyphs present in my project fossil.

I hypothesize that the bioglyphs on the burrow are scratch marks, and several lines of evidence support identification. First, the clustering of markings suggests that they were made by a therapsid (Figures 9). The bioglyphs have a minimum of 3 lines and a maximum of 5 lines involved in each, separate mark (Figures 10, 11 and 12). These 'lines' almost certainly have one-to-one correspondence with the digits of the forelimb. Triassic cynodonts generally have 5 digits (Figure 13), with some species having digits 2, 3 and 4 greater in length than digits 1 and 5 (Figure 13). This provides an explanation to why some markings only have 3 'lines'/digits, the longer, stronger digits have deeper depths than the shorter digits

(Figure 11- red, blue and dark green). It is hypothesized that deeper marking are most likely to preserve better as there is more space for sediment to settle

Second, directionality and indentation marks (Figure 12) supports the marks as having been made by the hands and feet of a vertebrate that was intentionally excavating. The bioglyphs tend to curve to the right (Figure 12) and are more abundant in more deeply excavated portions of the preserved burrow (Figure 10 and 12). Most of the makings have circular indentation (Figure 4; Figure 10 – dark blue, light blue, pink and grey) marks which suggests that the burrow had claws on the distal phalanx. This suggests that the tracemaker was moving the soil to a predetermined destination, and working/digging at particular area to make way for themselves, or other individuals, to enter and exit the burrow. The directionality suggests that the tracemaker was an organism that commonly dug and perhaps inhabited burrow systems.

The tracemaker cannot be identified as there is not enough evidence imply such. Although, comparisons of scratch marks of *Lystrosaurus* (NMQR 4001/JB041306 – National Museum, Bloemfontein) and *Thrinaxodon* (QR309/C392 – National Museum, Bloemfontein) scratch marks suggest the tracemaker was not *Lystrosaurus* (or any cynodont with similar hand morphology) as the scratch markings of *Lystrosaurus* are wide suggesting that it had laterally wide unguals at the distal phalanx.

The scratch marks observed in specimen WK-36-14 are quite similar to those observed in burrows of *Thrinaxodon*. Both *Thrinaxodon* and WK-36-14 bioglyphs are mediolaterally narrow, curving, and have 3-5 lines. The tracemaker is therefore hypothesized to have mediolateral narrow unguals at the distal phalanx similar to those of *Thrinaxodon*. These similarities suggest that the bioglyphs maker in *Cynognathus* subzone-C had narrow

claws (unlike those of anomodonts), and three main digits with two other, less prominent digits.

Taking into account that the specimen was found in Middle-Late Triassic stratigraphy, it is assumed that the burrow is a cynodont burrow as cynodont burrows are common in the *Cynognathus* Assemblage Zone (Abdala *et al.,* 2006b; Bordy *et al,* 2010; Damiani *et al.,* 2003; Fernandez *et al.,* 2013; Groeneweld *et al.,* 2001; Sumbera *et al.,* 2011). However, this is the first burrow ever recorded from *Cynognathus* subzone-C.

Assuming the specimen is a cynodont burrow, the scratch marks are hypothesized to have been created by a cynodont closely related phylogenetically to *Thrinaxodon*. The tracemaker is hypothesized to have a larger body size than *Thrinaxodon* as *Thrinaxondon* scratch marks are narrower and shorter (distance) than the scratch marks present on WK-36-14.

Taxonomic Identification

The encased skull (WK-36-14) is hypothesized to be a small diademodontidae species based on the cranial and dental morphology (Figure 16; Table 8). The diademodontid exhibits incisors, caniniforms, diastema, occluding molariforms and sectorial teeth, this is typical gomphodont dentition that is attributed to *Diademodon* (Osborn 1974) (Figure 16). However, the number of upper incisors are obstructed by the overlying of the neural process of a dorsal vertebra at the anterior end of the snout (Figure 15). The number of incisors are crucial as it differentiates diademodontid species.

Diademodontidae species with 3 incisors are identified as *Diademodon* – a species commonly found in the *Cynognathus* Assemblage Zone, and specimen with 4 incisors are identified as *Titangomphodon* – a species commonly found in the Omnigonde Formation,

Namibia, both of which are cynodonts that date to the Middle-Late Triassic (Abdala and Smith 2009; Martinellii *et al.,* 2009). The Omnigonde Formation and *Cynognathus* subzone-C are linked stratigraphically as they exhibit similar cynodont specimen, with some species even overlapping, and date to the Middle-Late Triassic (Abdala *et al.*, 2014).

It is unlikely that the diademodontidae species of this project is in fact *Titanogomphodon*. Several lines of evidence support this hypothesis. Firstly, *Titanogomphodon* has never been recorded in the Karoo Basin, South Africa, all species are exclusively found in the Omnigonde formation, Namibia (Abdala and Smith 2009; Martinelli *et al.,* 2009). *Titanogomphodon* documented to have a larger skull and body size than *Diademodon,* with the average *Titanogomphodon* skull length being 40 cm and the average *Diademodon* skull length is 29 cm (Martinelli *et al.*, 2009). WK-36-14 is considered small bodied as its skull measurements are below average (Table 8) – the diastema immediately abutting the caniniforms indicates that tooth replacement has ceased, indicating that the organism has reached adulthood – therefore it is considered a small bodies *Diademodon* rather juvenile (Osborn 1974) (Figure 16).

Secondly, *Diademodon* is not commonly associated with burrows. Most *Diademodon* species are larger bodied than the common burrowing cynodonts of the Triassic, like *Thrinaxodon* (QR309/C392). However, there is no published literature against *Diademodon* exploiting burrows that were constructed by other burrowers. WK-36-14 is considered to be *Diademodon* that is hypothesized to have used the burrow for provide shelter and protection. The *Diademodon* cannot be identified to species level as the as the skull has been crashed medially (Figure 18), the number of upper incisors are unclear (Figure 18) and post-crania has not been prepared from the deposit. CT scanning of the skull and the unprepared post-crania is needed to provide species level.

The skull was found to have post-crania overlying the lower jaw and snout (Figure 15). The scapula is overlying the right-lower jaw and the neural spine of dorsal vertebra is overlying to the anterior of the snout (Figure 15). The disarticulation of the scapula and dorsal vertebra that the animal was near the entrance or in the tunnel of the burrow (Coard and Dennell 1995). Dorsal vertebra and the scapula are loosely articulated and light-weight bones, and are commonly disarticulated first when an organism has experienced death (Coard and Dennell 1995). The disarticulation and overlying of the scapula and dorsal vertebra to the anterior of the *Diademodon* skull suggests that the *Diademodon* experienced movement (possibly tumbling) during/after death (Coard and Dennell 1995). However, the movement was not excessive as only loosely articulated and weight-bones were disarticulated from the skeleton, suggesting that the *Diademodon* was either near the entrance or in the tunnel of the burrow (Coard and Dennell 1995).

Improvements for future research

1. A greater number of petrographic thin sections should be extracted from WK-36-14, along with other burrows, need to be done and analysed to strengthen hypothesises stated above.
2. Depth analysis of the scratch marks and initial indentation (claw marks), as well as more quantitative analysis, needs to be conducted to establish guidelines when classifying bioglyphs and identifying the tracemaker.
3. CT scanning is needed to investigate the full articulation of the post-crania still encased in deposit. The exact taphonomy of the *Diademodon* can only be determined once CT scans have been done and examined.

Conclusions

My inspection of the putative burrow from subzone-C is that the deposit is a burrow with the bioglyphs identified as scratch marks. This is the first account of a burrow extracted from subzone-C. The scratch marks were made by a cynodont closely related to *Thrinaxodon* as both the tracemaker and *Thrinaxodon* exhibit mediolateraly narrow scratch marks, although the tracemaker is hypothesized to be larger bodied than *Thrinaxodon*. It is hypothesized that the burrow specimen is part of the entrance or tunnel margin based the actualistic literature of hare and rodent burrows. The encased therapsid is identified as *Diademodon,* however it is unlikely that *Diademodon* died at the burrow terminal as it was fossilized at the burrow margin. The disarticulation of the *Diademodon* suggests that it was near the entrance or in the tunnel of the burrow. This is the first account of *Diadedomodon* encased in a burrow.

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Appendix:

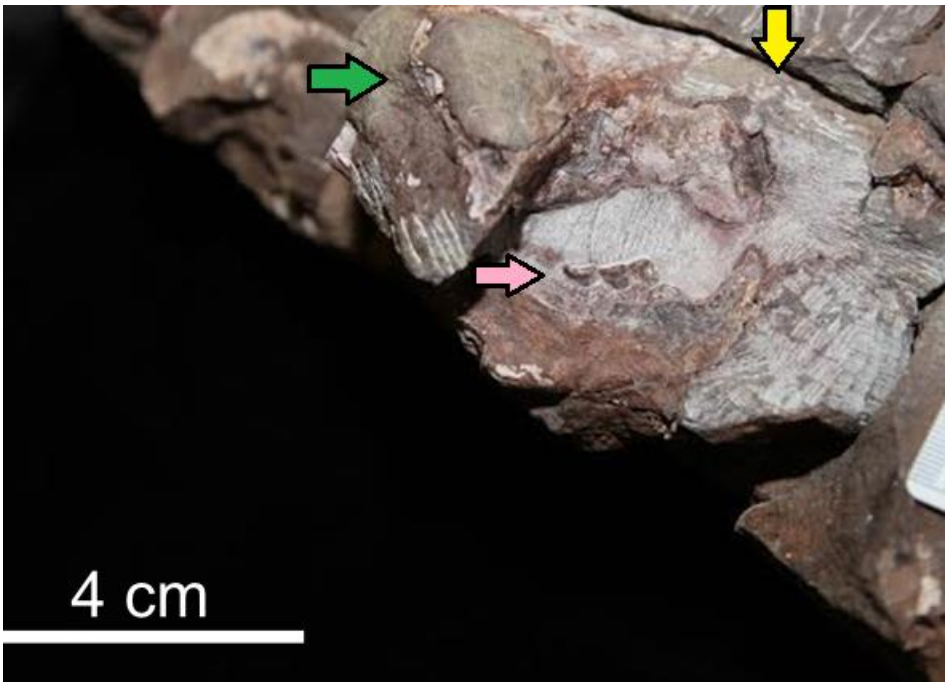


Figure 1: The encased WK-36-14 skull showing molariforms (**pink**), snout (**yellow**) and temporal fenestra (**green**) that aided in the initial identification. Photo credit: Jonah Choiniere; Editing: Nadia Afonso.

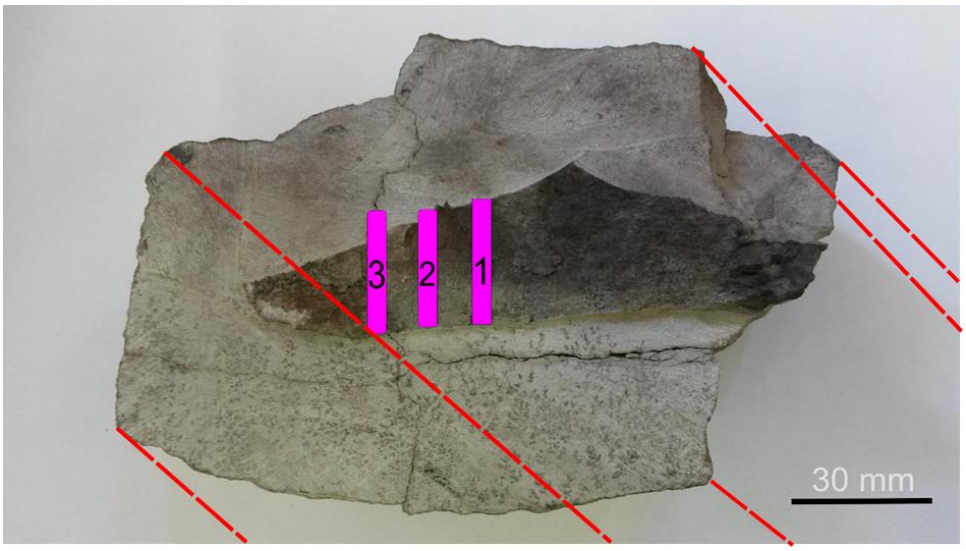


Figure 2: A cross section of the deposit (putative burrow) that was used to prepared petrographic thin sections. There were three thin sections prepared. The rectangles (**pink**) and numbers indicate where the thin sections (slides) were prepared from; slide 1 being the furthest from the burrow margin outer boundary (burrow margin centre) and slide 3 being the closet to burrow margin outer boundary. The **red** dotted lines indicate position of the cross section in relation to the deposit. The cross section was taken from taken from rock that was protruding of the right of the deposit. Photo credit and editing: Nadia Afonso.

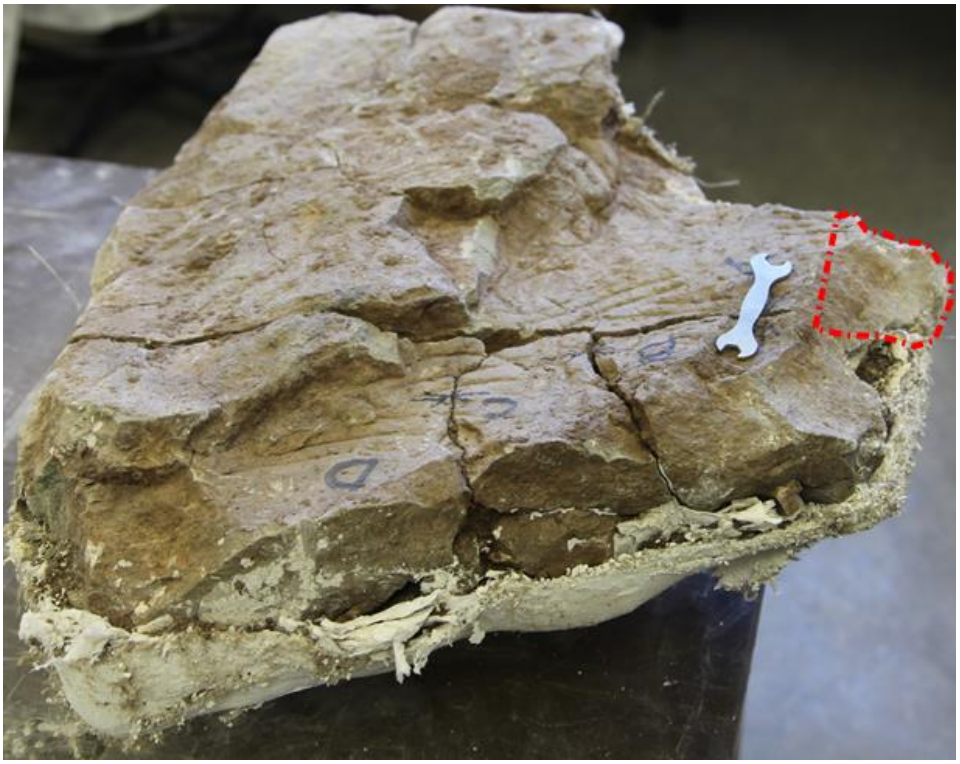


Figure 3: Unprepared deposit (WK-36-14) indicating the area (red) where the cross section was extracted from. Photo credit: Jonah Choiniere; Editing: Nadia Afonso.

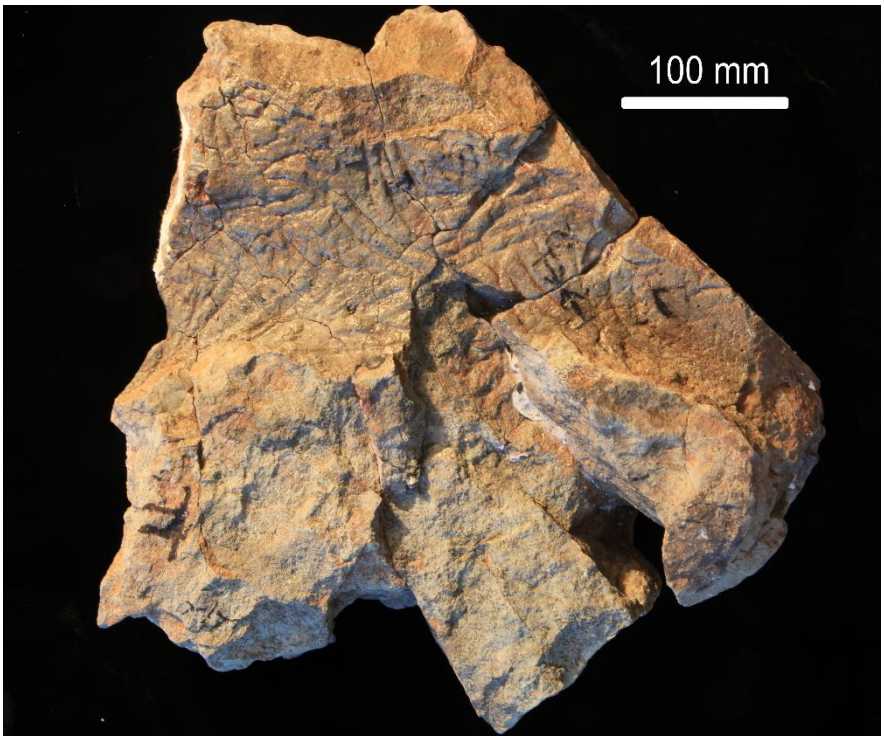


Figure 4: A mould of the bioglyphs (putative scratch marks) (WK-36-14) present on the surface morphology of the deposit. Photo credit: Nadia Afonso.

Table 1: Descriptive statistics of the compiled sample sizes of the burrow margin (Bg) and host rock (Hg) grain area measurements (mm^2).

			Statistic	Std. Error
Bg	Mean		.0076795	.00126318
	95% Confidence Interval for Mean	Lower Bound	.0050960	
		Upper Bound	.0102630	
	5% Trimmed Mean		.0066830	
	Median		.0064637	
	Variance		.000	
	Std. Deviation		.00691872	
	Minimum		.00146	
	Maximum		.04094	
	Range		.03948	
	Interquartile Range		.00347	
	Skewness		4.030	.427
	Kurtosis		19.457	.833
Hg	Mean		.0071262	.00065772
	95% Confidence Interval for Mean	Lower Bound	.0057810	
		Upper Bound	.0084714	
	5% Trimmed Mean		.0068284	
	Median		.0067706	
	Variance		.000	
	Std. Deviation		.00360251	
	Minimum		.00270	
	Maximum		.01918	
	Range		.01648	
	Interquartile Range		.00576	
	Skewness		1.265	.427
	Kurtosis		2.835	.833

Table 2: The normality tests of grain areas of the burrow margin (Bg) and host rock (Hg) performed in SPSS.

Tests of Normality

	Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	Statistic	df	Sig.	Statistic	df	Sig.
Bg	.263	30	.000	.571	30	.000
Hg	.110	30	.200*	.900	30	.008

Table 3: Mann-Whitney U-test performed on the burrow margin (Bg) and host rock (Hg) grain area measurements (mm^2).

Ranks

	Group	N	Mean Rank	Sum of Ranks
Area	Bg	30	30.07	902.00
	Hg	30	30.93	928.00
	Total	60		

Test Statistics[a]

	Area
Mann-Whitney U	437.000
Wilcoxon W	902.000
Z	-.192
Asymp. Sig. (2-tailed)	.848
Exact Sig. (2-tailed)	.854
Exact Sig. (1-tailed)	.427
Point Probability	.006

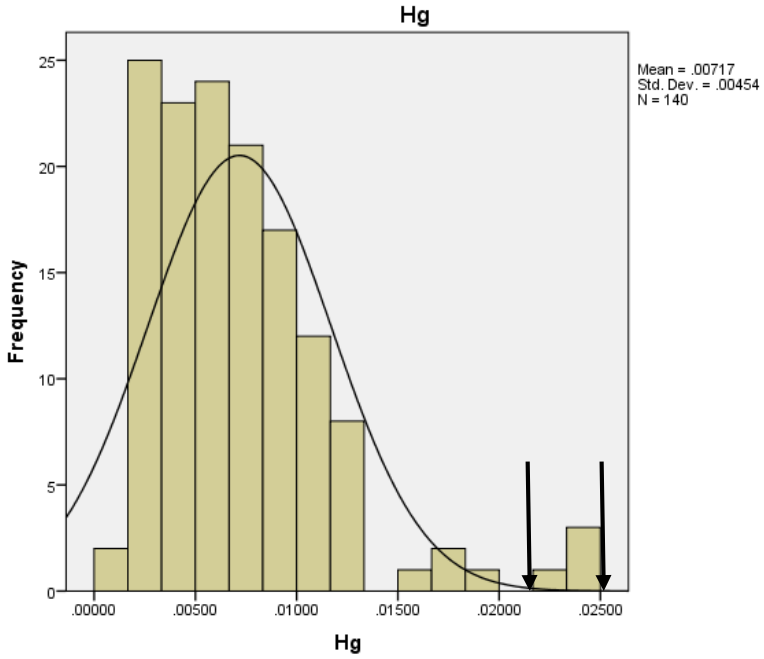


Figure 5: A histogram representing the normal distribution (slight left skewness) of the grain areas (mm^2) of the host rock. The data (uncompiled) is normally distributed as the sample fits the bell curve. The graph also represents the outliers (> 0.02 mm^2) that were removed when compiling the sample. The outliers are the values included in between the arrows.

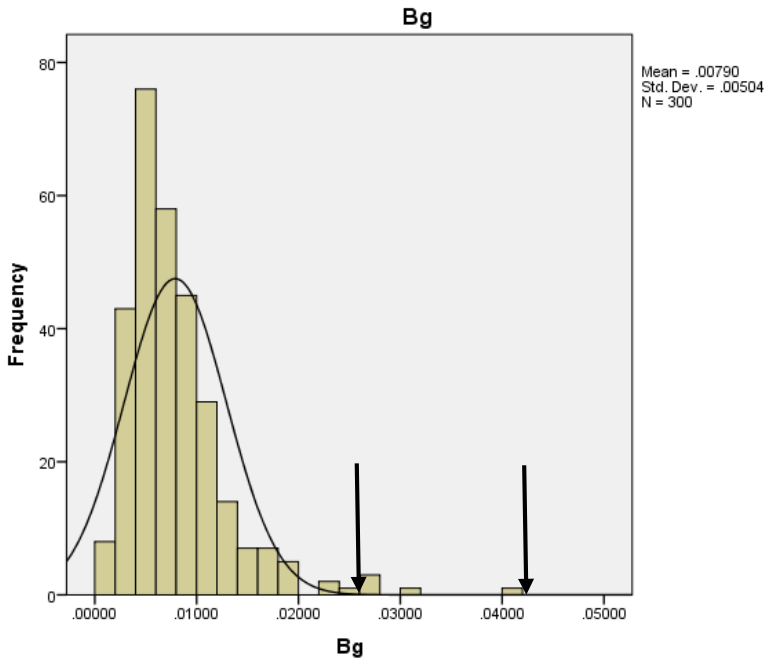


Figure 6: A histogram representing the normal distribution (slight left skewness) of the grain areas (mm^2) of the burrow margin. The data (uncompiled) is normally distributed as the sample fits the bell curve. The graph also represents the outliers (> 0.02 mm^2) that were removed when compiling the sample. The outliers are the values included in between the arrows.

Table 4: Descriptive statistics of the compiled sample of the burrow margin (Bm) and host rock (Hm) matrix area measurements (mm^2)

			Statistic	Std. Error
Bm	Mean		.0096284	.00168066
	95% Confidence Interval for Mean	Lower Bound	.0061911	
		Upper Bound	.0130658	
	5% Trimmed Mean		.0084055	
	Median		.0067988	
	Variance		.000	
	Std. Deviation		.00920535	
	Minimum		.00157	
	Maximum		.03987	
	Range		.03830	
	Interquartile Range		.00844	
	Skewness		2.413	.427
	Kurtosis		6.268	.833
Hm	Mean		.0126575	.00175763
	95% Confidence Interval for Mean	Lower Bound	.0090627	
		Upper Bound	.0162522	
	5% Trimmed Mean		.0116082	
	Median		.0106010	
	Variance		.000	
	Std. Deviation		.00962692	
	Minimum		.00285	
	Maximum		.04337	
	Range		.04052	
	Interquartile Range		.01026	
	Skewness		1.799	.427
	Kurtosis		3.508	.833

Table 5: The normality tests of matrix area measurements of the burrow margin (Bm) and host rock (Hm) performed in SPSS.

Tests of Normality

	Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	Statistic	Df	Sig.	Statistic	df	Sig.
Bm	.191	30	.007	.710	30	.000
Hm	.183	30	.012	.813	30	.000

Table 6: Mann-Whitney U-test performed on the burrow margin (Bm) and host rock (Hm) matrix area measurements (mm^2).

Ranks

	Group	N	Mean Rank	Sum of Ranks
Area	Bm	30	26.47	794.00
	Hm	30	34.53	1036.00
	Total	60		

Test Statistics

	Area
Mann-Whitney U	329.000
Wilcoxon W	794.000
Z	-1.789
Asymp. Sig. (2-tailed)	.074
Exact Sig. (2-tailed)	.075
Exact Sig. (1-tailed)	.037
Point Probability	.001

Table 7: Mann-Whitney U-test performed on the matrix at the burrow margin outer boundary (slide 3) and burrow margin centre (slide 1) (Figure 2).

Ranks

	Grouping	N	Mean Rank	Sum of Ranks
2.6667199999999999E-2	Slide 1	50	40.78	1998.00
	Slide 3	50	59.04	2952.00
	Total	100		

Test Statistics[a]

Mann-Whitney U	773.000
Wilcoxon W	1998.000
Z	-3.163
Asymp. Sig. (2-tailed)	.002

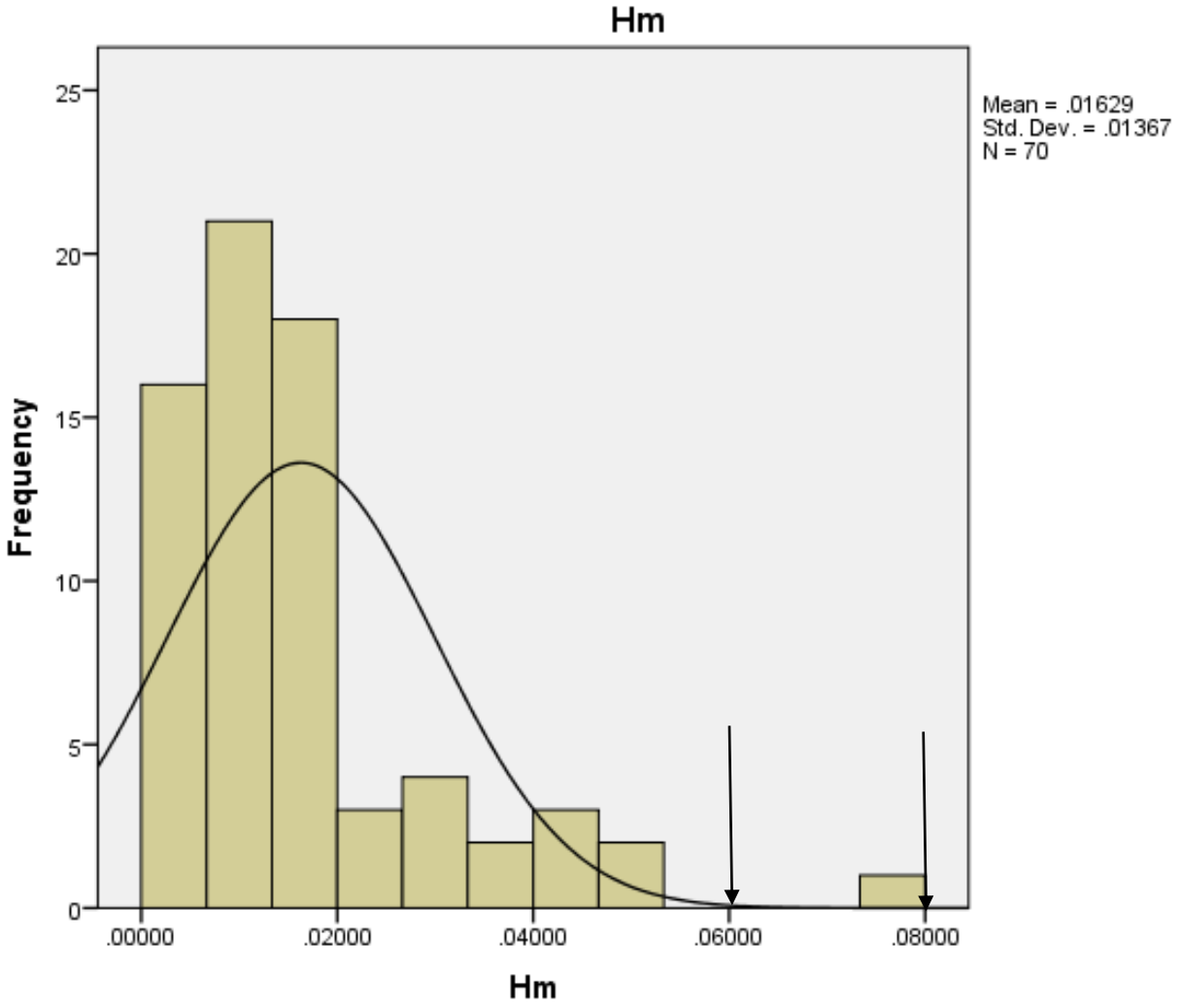


Figure 7: A histogram representing the non-normal distribution of the matrix areas (mm^2) of the host rock. The data (uncompiled) has an non-normal distribution as the sample does not fit the bell curve. The graph also represents the outliers (> 0.06 mm^2) that were remove when compiling the sample. The outliers are the values included in between the arrows.

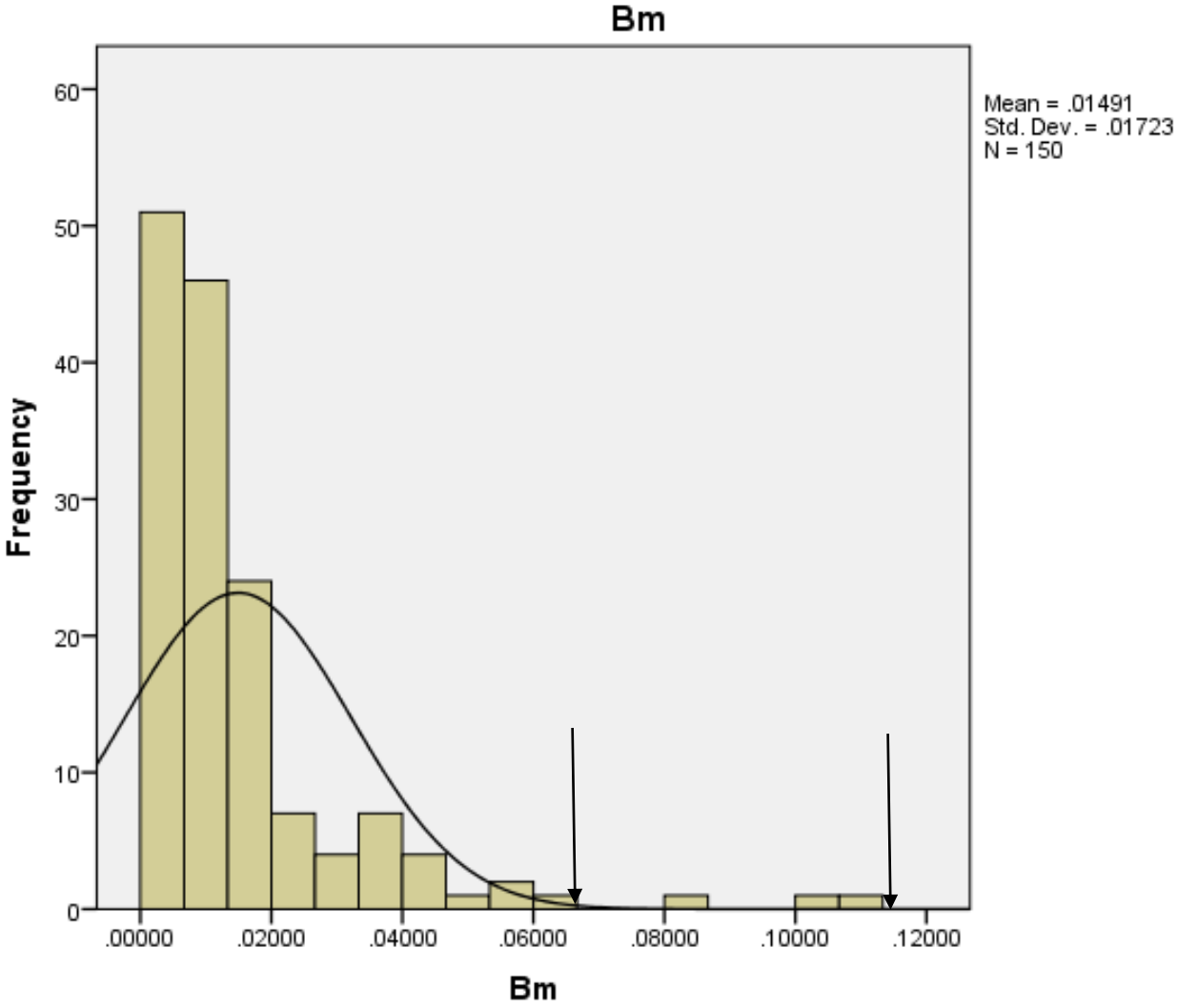


Figure 8: A histogram representing the non-normal distribution of the matrix areas (mm^2) of the burrow margin. The data (uncompiled) has an unknown distribution as the sample does not fit the bell curve. The graph also represents the outliers (> 0.07 mm^2) that were removed when compiling the sample. The outliers are the values included in between the arrows.

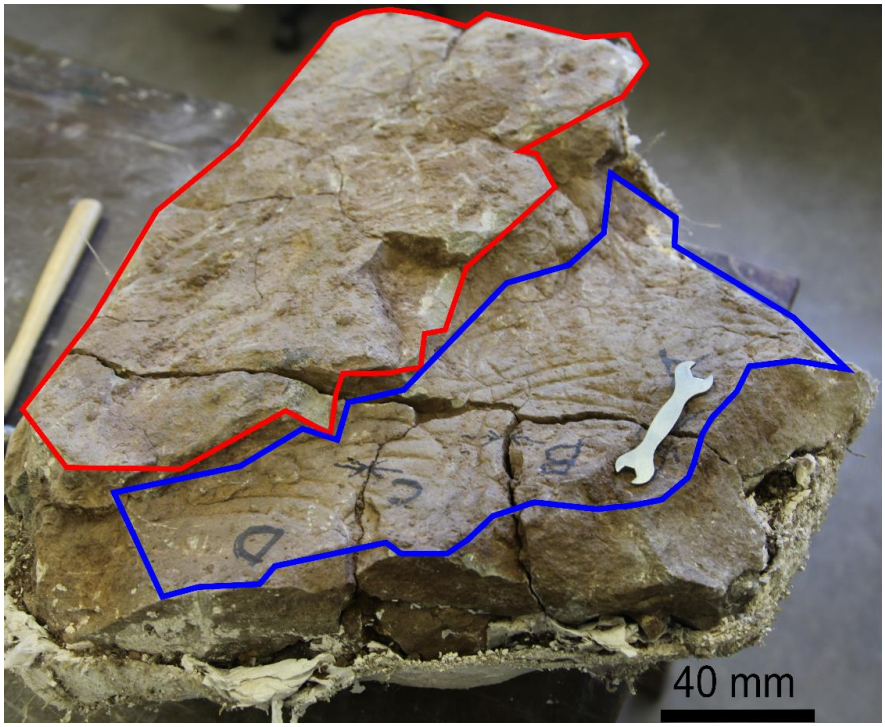


Figure 9: Unprepared deposit (WK-36-14) showing the location of the putative burrow (red) and bioglyphs (blue) on the deposit. Photo credit: Jonah Choiniere; Editing: Nadia Afonso.

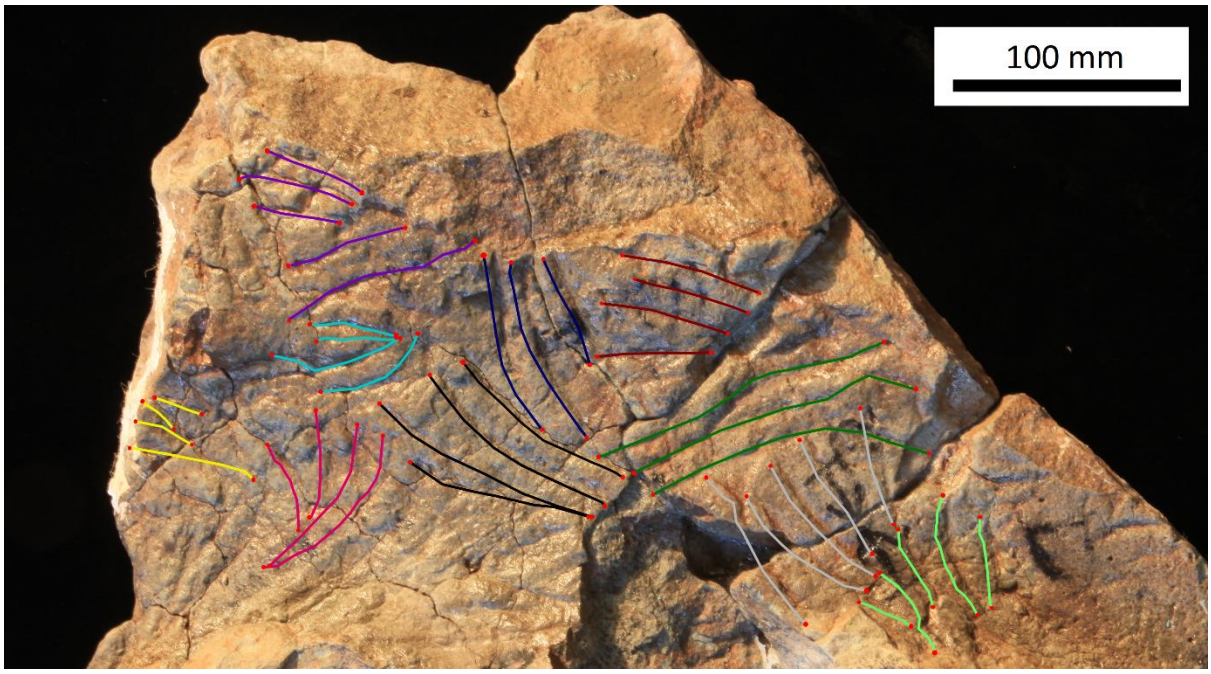


Figure 10: Bioglyphs that were traced using Inkscape of the putative scratch marks (WK-36-14) found on the surface morphology of the putative burrow. The different colours represent individual markings. Photo credit: Jonah Choiniere; Editing: Nadia Afonso.

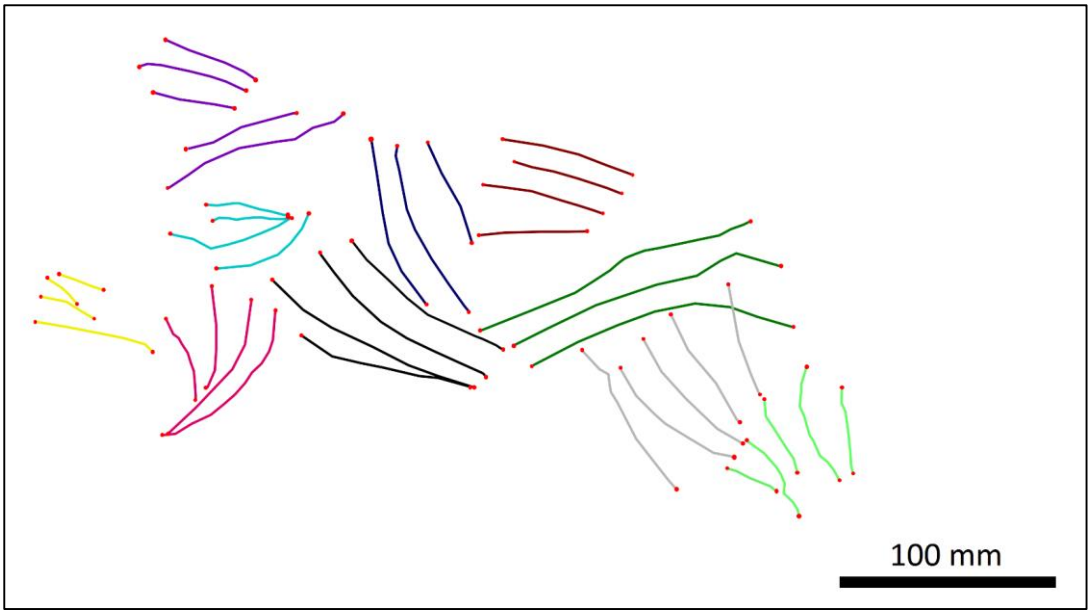


Figure 11: A schematic of the individual markings found on the surface morphology of the putative burrow. The red dots represent that starting and end points of the markings. The markings seem to follow right-downward directional pattern and to have at least 3 digits/objects involved in the making of the markings. Editing: Nadia Afonso.

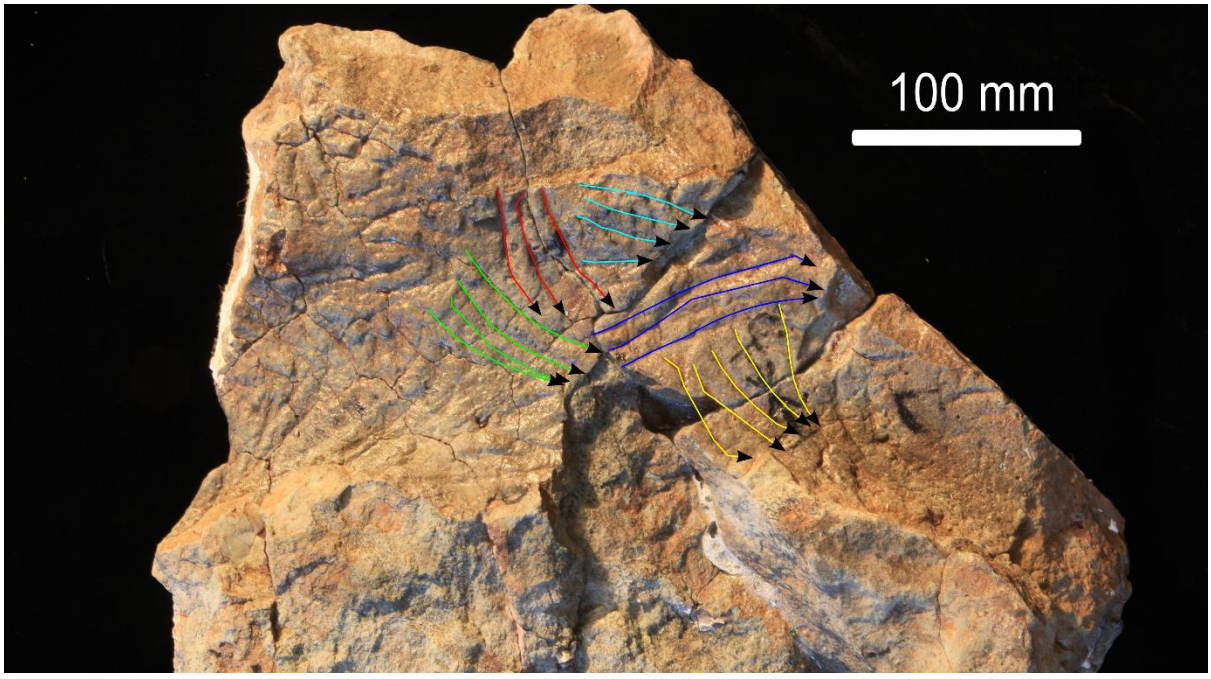


Figure 12: Tracings of a few of the putative scratch marks showing the directionality. The putative scratch marks (WK-36-14) tend to curve to the right and are accumulated within the 'dip' rock. Photo credit: Jonah Choiniere; Editing: Nadia Afonso

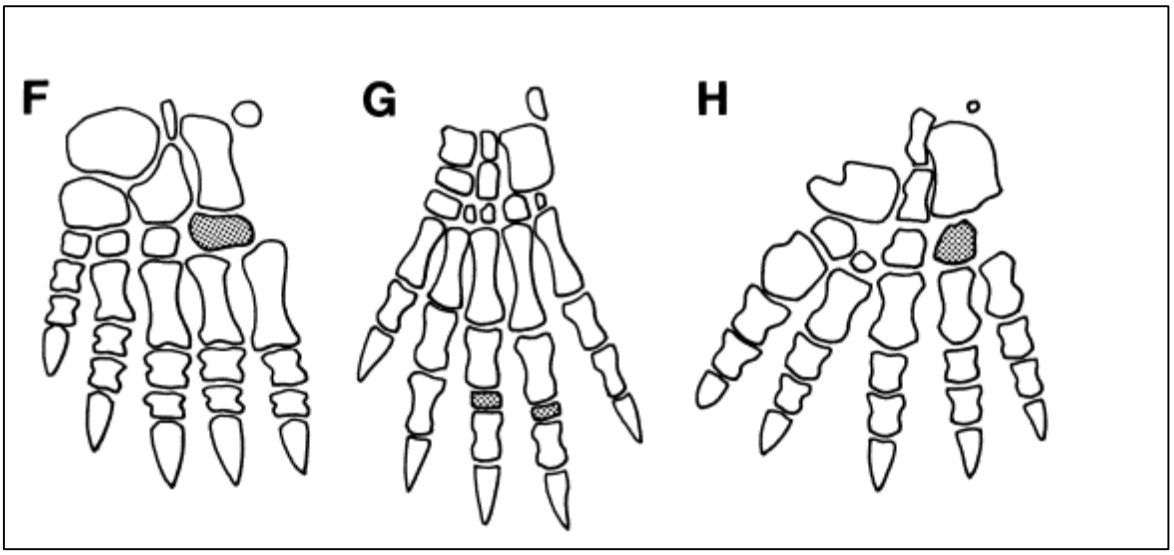


Figure 13: Variation in the structure of the manus in therocephalians. **F**, a scylacosaurid therocephalian (modified from Boonstra, 1964); **G**, the Early Triassic cynodont *Thrinaxodon* (from Parrington, 1939); **H**, the late Triassic cynodont *Exaeretodon* (modified from Bonaparte, 1963). Source: Hopson 1995.

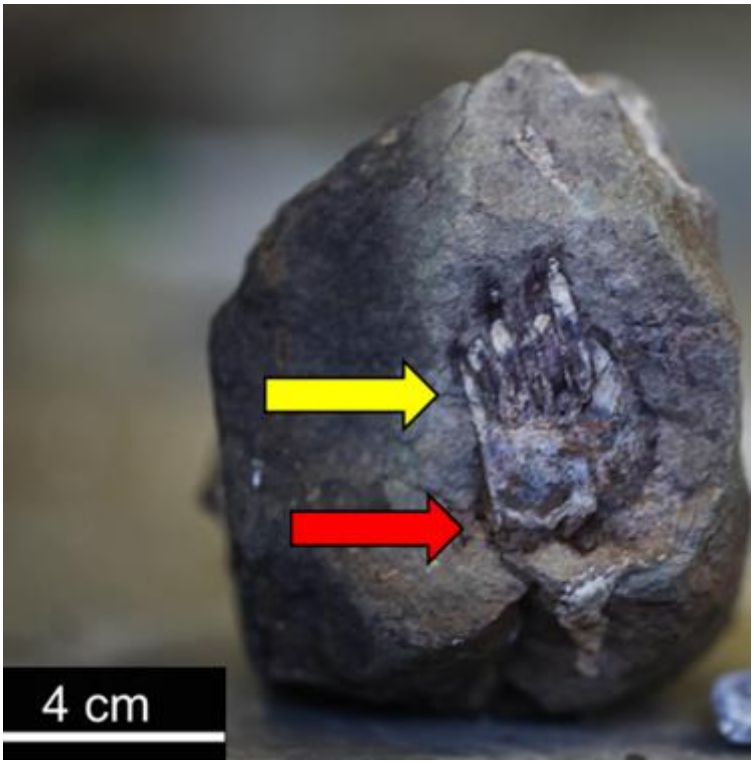


Figure 14: Skull of WK-36-14 before preparation. The skull was initially as a diademodontidae identified by the anteriorly exposed lower incisors (**yellow)** and anterior portion of lower jaw (**red**). Photo credit: Jonah Choiniere.

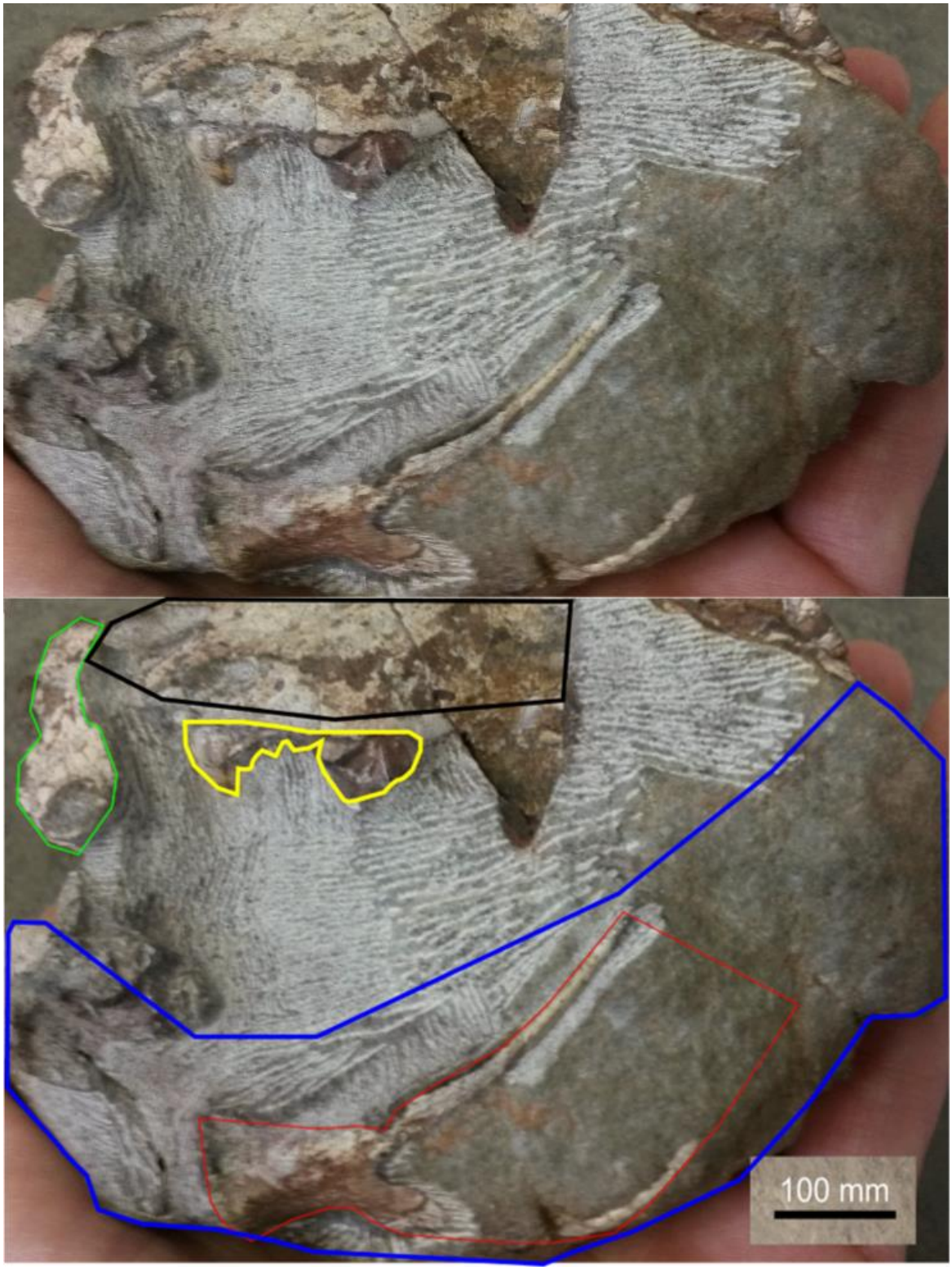


Figure 15: Right side of the skull of WK-36-14 showing unidentified upper teeth (**yellow),** the scapula (**red**) overlying the lower jaw (**blue**) and the neural spine of dorsal vertebra (**green**) overlying the anterior of the snout (**black)**. Much of the matrix is still fused to the upper and lower jaw. Photo credit and editing: Nadia Afonso.

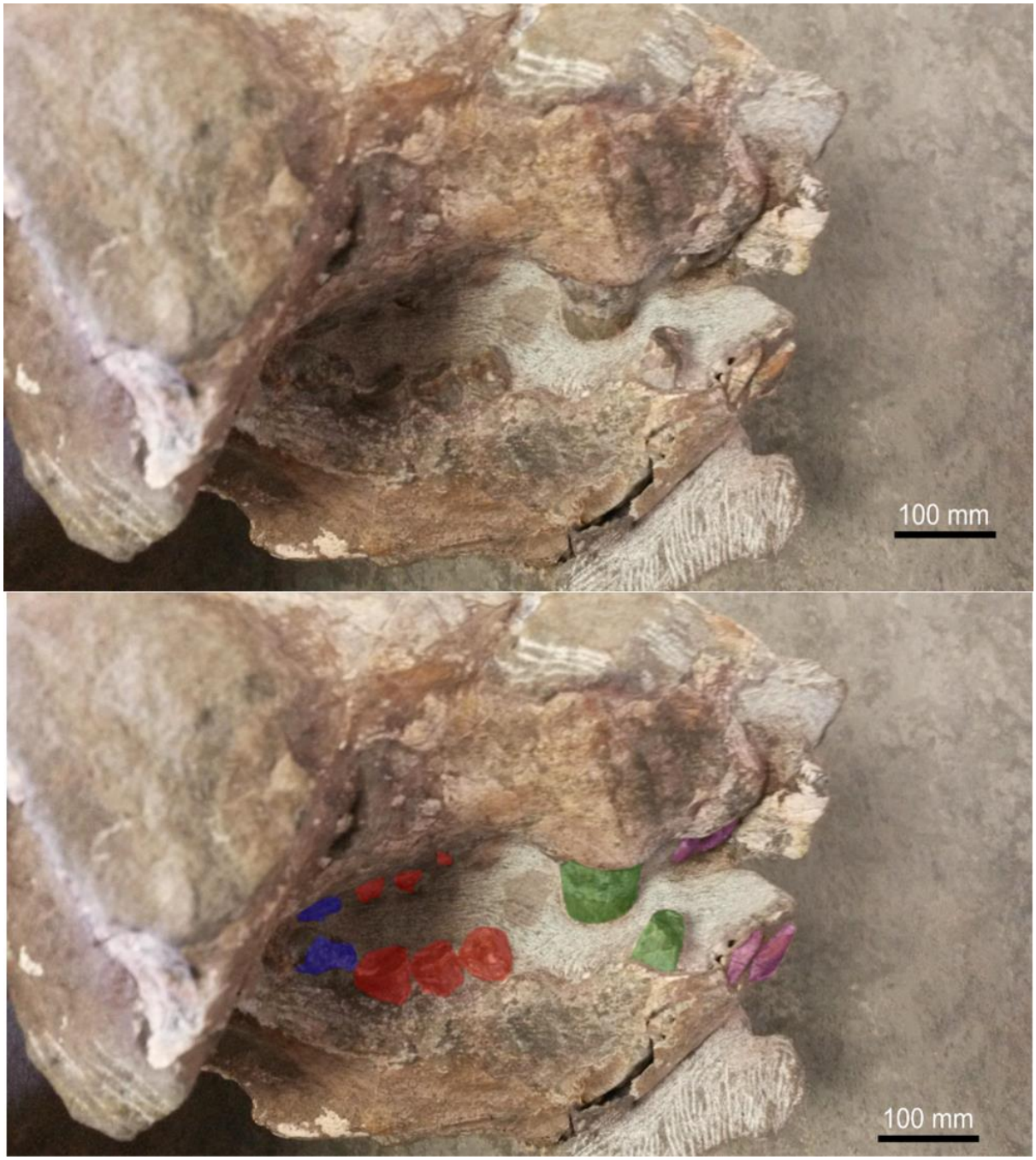


Figure 16: Left side of the prepared diademodontidae skull (WK-36-14) of the lower and upper jaw. The incisors, caniniforms and post-caniniforms are exposed. **Purple**: upper and lower incisors; **Green**: upper and lower caniniforms; **Red**: occluding molariforms of the post-caniniforms (typically seen in *Diademodon*); **Blue**: sectoral teeth of the post-caniniforms. The post-caniniforms exhibit a gomphodont dentition (top). Photo credit and editing: Nadia Afonso.

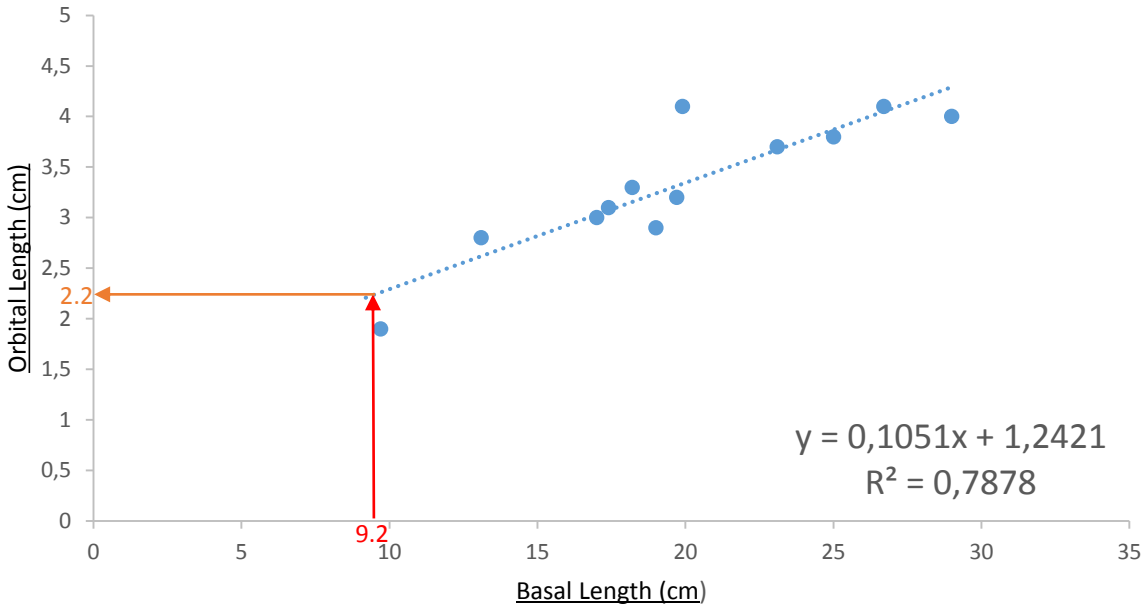


Figure 17: Linear regression of the basal skull length vs. the orbital length of specimens measured in the ESI Karoo vertebrate collections. The regression equation and y-intercept (**orange**) were- used to calculate the orbital length for the diademodontidae specimen (WK-36-14).

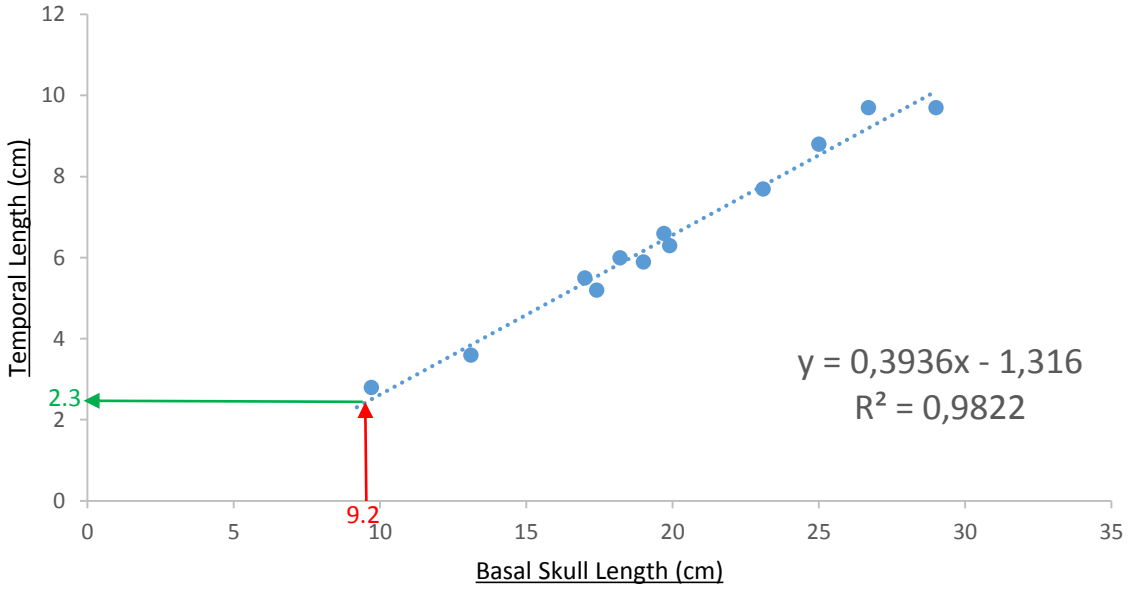


Figure 18: Linear regression of the basal skull length vs. the temporal length of specimens measured in the ESI Karoo vertebrate collections. The regression equation and y-intercept (**green**) were used to calculate the temporal length for the diademodontidae specimen (WK-36-14).

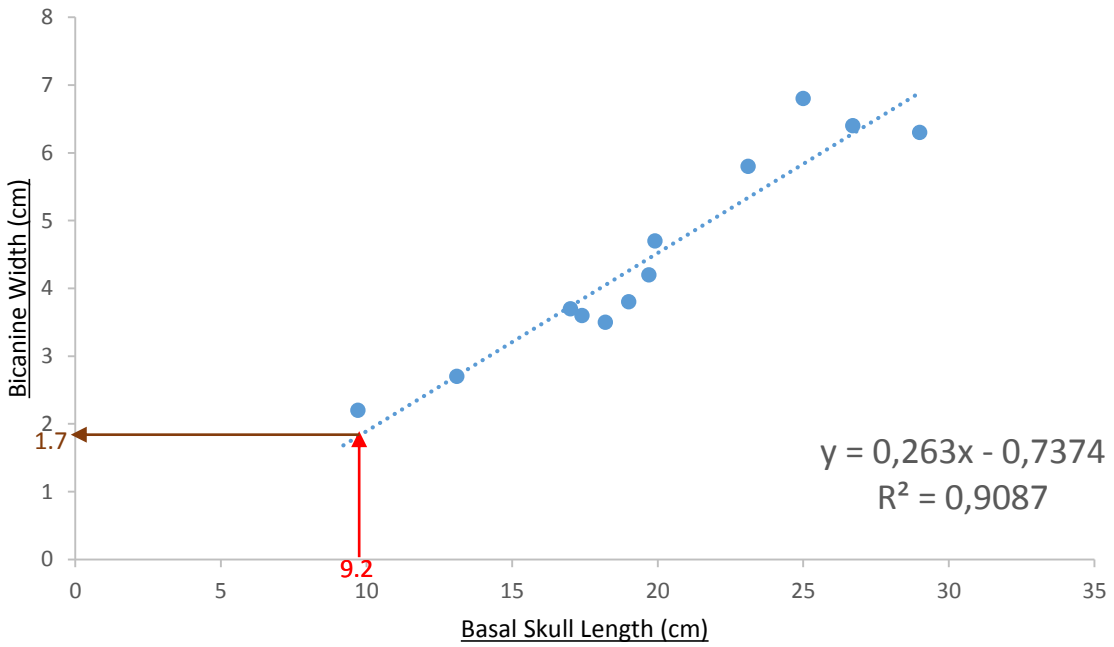


Figure 19: Linear regression of the basal skull length vs. the bicanine width of the specimens measured in the ESI Karoo vertebrate collections. The regression equation and y-intercept (**brown**) were used to calculate the bicanine length for the diademodontidae specimen (WK-36-14).

Table 8: The skull measurements (cm) of the diademodontidae skull (WK-36-14). The basal skull and snout lengths were measured directly from the specimen. The orbital, temporal and bicanine lengths were calculated using the linear regression and y-intercepts.

	Basal skull length (cm)	Snout length (cm)	Orbital length (cm)	Temporal length (cm)	Bicanine width (cm)
BP/1/3769	9,7	4,9	1,9	2,8	2,2
BSP 1934 VIII 14	13,1	5,9	2,8	3,6	2,7
BSP 1934 VIII 15	17	7,5	3	5,5	3,7
BPI 4669	17,4	8,2	3,1	5,2	3,6
BSP 1934 VIII 16	18,2	7,1	3,3	6	3,5
SAM PK-K5223	19	8,7	2,9	5,9	3,8
SAM PK-K-5716	19,7	9,4	3,2	6,6	4,2
MB R1004	19,9	8,5	4,1	6,3	4,7
BSP 1934 VIII 17	23,1	9,7	3,7	7,7	5,8
BSP 1934 VIII 19	25	12,1	3,8	8,8	6,8
BPI/1/3754	26,7	11,8	4,1	9,7	6,4
MCP 42446	29	13,6	4	9,7	6,3
WK-36-14	9,2	3,7	2.2	2.3	1.7