Taphonomy of tortoises at Blombos Cave

Tortoise taphonomy and tortoise butchery patterns at Blombos Cave, South Africa

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Abstract

Tortoises are one of the most common faunal components at many Palaeolithic archaeological sites across the Old World. They provide protein, fat, and other 'animal' resources in a 'collectable' package. However, for most sites their interpretation as human food debris is based only on association, rather than demonstrated through taphonomic analysis. Because of their very different anatomical configuration compared to mammals, it is difficult to conduct such analyses by directly applying the taphonomic methods used to interpret large mammal assemblages. Tortoise-specific taphonomic analysis is presented here for the Still Bay layers at the important Middle Stone Age (MSA) site of Blombos Cave (BBC), Western Cape, South Africa. Research on MSA subsistence systems at sites such as BBC has almost exclusively relied on analysis of large ungulate remains, in spite of the fact that many of these key sites contain equal or greater numbers of tortoise fragments. In this analysis we show that human modification is common on the BBC tortoises, and that there are consistent patterns of fragmentation and burning that indicate set processing sequences including cooking while in the shell, hammerstone percussion, and human chewing of limbs. The almost exclusive dominance of the angulate tortoise, *Chersina angulata*, is confirmed by full skeletal element analyses rather than only counts of single elements such as humeri. The sex distribution can be reconstructed for this species, and is female-biased. For all tortoise assemblages, taxonomic and skeletal element abundance data should be calculated from a sample of complete elements, or at minimum the entoplastron and humerus. A sample of shell and limb/girdle elements should also be subjected to microscopic bone surface modification analysis, as modifications are often rare or subtle but highly informative. Using this approach, analysis of breakage patterns, bone surface modification, and burning patterns can be understood together to specifically reconstruct tortoise collection, processing, and human dietary significance across a range of archaeological sites.

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1. Introduction

1.1 Overview

Tortoise remains are common at Palaeolithic sites across the Old World. Where they are assumed to represent human food refuse they have formed the basis of studies examining diet breadth, palaeodemography, and subsistence (Blasco and Fernández Peris, 2012a; b; Stiner et al., 2000; Stiner et al., 1999). However, only a few studies have directly addressed the issue of tortoise taphonomy (Blasco, 2008; Sampson, 2000; Speth and Tchernov, 2002). Much work has been done on understanding how larger mammals are captured and processed, but there are no established ways of presenting taphonomic data from tortoises. Although basic zooarchaeological methods of data collection and analysis will be applicable, the unique anatomy of tortoises suggests that processing patterns – and their archaeological traces – should be very different to that of mammals.

1.2 Tortoises in the South African record

In South Africa, tortoise remains are found in archaeological deposits ranging from Middle Pleistocene to historic sites (Cruz-Uribe and Schrire, 1991; Klein et al., 1999). They are common in both Middle Stone Age (MSA) and Later Stone Age (LSA) sites in the Western Cape, for example reaching densities of 49-304 individuals/m^3 at the LSA site of Byneskranskop (BNK) and 3–18 individuals/m^3 at the LSA/MSA site of Die Kelders Cave 1 (DK1) (Cruz-Uribe and Schrire, 1991). Several MSA sites in the Western Cape of South Africa, such as Ysterfontein 1 (YFT1), DK1, Boomplaas Cave (BPA), Diepkloof Rock Shelter (DRS) and BBC have produced large tortoise assemblages but these have only been studied in terms of basic counts of individuals and body size comparisons, with emphasis on their palaeodemographic and palaeoenvironmental implications (Faith, 2011; Henshilwood et al., 2001b; Klein et al., 2004b; Klein and Cruz-Uribe, 2000; Steele and Klein, 2013).

Most of these studies have assumed that humans preyed on tortoises and that the remains were accumulated at living sites (Henshilwood et al., 2001b; Klein and Cruz-Uribe, 1983; 1987; 2000). At DK1 Klein and Cruz-Uribe (2000:190) conclude that because

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tortoise numbers in both the LSA and MSA layers are inversely correlated with the (presumably non-anthropogenic) abundances of Cape dune molerats (*Bathyergus suillus*), "…people almost certainly introduced most of the tortoises in both units". At BBC tortoises were assumed to be the result of human predation because of the overall association of the faunal assemblage with artefacts, the degree of charring on faunal specimens, and the lack of macroscopically-visible carnivore damage (Henshilwood et al., 2001b).

The smaller tortoise assemblage from Pinnacle Point Cave 13B (PP13B) is the only MSA assemblage that has been studied using microscopic taphonomic methods, and for which full NISP and MNI counts are available for both limb and shell elements (Thompson, 2010). This study found that hominin modification such as cut marks for defleshing, percussion marks for opening the shell, and preferential burning patterns from cooking were all rare but present on the assemblage, and in different proportions than similar damage on large mammal bones. This raised the possibility that tortoises underwent specific modes of processing quite different from mammals, and so should have different fragmentation and bone surface modification patterns. One way to test this hypothesis is to conduct the same analysis on a larger tortoise assemblage from BBC, which is a site that has comparably-collected taphonomic data from the large mammals (Thompson and Henshilwood, 2011).

1.3 Background to Blombos Cave

BBC is located on the southern coast of South Africa, approximately 300km east of Cape Town (Figure 1). Excavations between 1992 and 2009 uncovered a stratified sequence of LSA and MSA deposits (Henshilwood, 2008; Henshilwood et al., 2009; Henshilwood et al., 2001b). The MSA levels at Blombos Cave are divided into four phases, M1, upper M2, lower M2 and M3. These have been dated using thermoluminescence (TL), optically stimulated luminescence (OSL), electron spin resonance (ESR) and thorium/uranium to between ca. 75 to > 130 ka (Henshilwood et al., 2002; Henshilwood et al., 2011; Jacobs et al., 2003a; Jacobs et al., 2006; Jacobs et al., 2013; Jacobs et al., 2003b; Jones, 2001; Tribolo, 2003; Tribolo et al., 2006). Summaries of the chronology of the BBC deposits, their associated ages, and material culture are provided in Table 1 and Figure 2.

BBC has played an important role in establishing that complex material culture and the expression of symbolic behaviour was present in Africa by at least 100 ka (Henshilwood, 2009; Henshilwood et al., 2009; Henshilwood et al., 2011). The upper two phases at BBC contain Still Bay points (Mourre et al., 2010; Villa et al., 2009), bone tools (d'Errico and Henshilwood, 2007; Henshilwood et al., 2001a; Henshilwood and Sealy, 1997), engraved ochres (Henshilwood et al., 2009; Henshilwood et al., 2002), and perforated *Nassarius kraussianus* shell beads (d'Errico et al., 2005; Henshilwood et al., 2004). The ochres and beads have been regarded as primary evidence for modern cognitive and symbolic behaviour (Henshilwood, 2009; Vanhaeren et al., 2013). The lowest phase (M3) coincides with the high sea-level stand during Marine Isotope Stage (MIS) 5c, and contains basin shaped hearths, abundant ochre (some engraved), some fish remains, high frequencies of shellfish, and an ochre-processing workshop (Henshilwood, 2012; Henshilwood, 2009; Henshilwood et al., 2011; Henshilwood et al., 2001b).

The taxonomic composition of the BBC MSA faunal remains has been previously reported by Henshilwood et al. (2001b) and taphonomic work has been reported by Thompson and Henshilwood (2011). Bovids dominate the large mammal sample, with small size 1 ungulates such as grysbok/steenbok (*Raphicerus* spp.) very common in the M3 and Upper/Lower M2 phases but with more representation of larger ungulates in the M1 phase. Carnivores are rare, which suggests that prolonged carnivore denning did not take place (Cruz-Uribe, 1991; Pickering, 2002). Across ungulate body size classes, MSA people are implicated as the primary accumulators, with perhaps slightly less human input of small ungulates in the lowermost M3 phase (Thompson and Henshilwood, 2011).

A central line of enquiry concerning the emergence of modern human behaviour is how changes in human behaviour may have been reflected in or perhaps even facilitated by changes in diet, subsistence, and foraging efficacy (Dusseldorp, 2010; Faith, 2008; Klein and Cruz-Uribe, 1996; Marean et al., 2007). The BBC finds support the early use of marine resources recorded at other MSA sites along the southern Cape coastline (Klein et al., 2004a; Marean et al., 2007; Wurz, 2012). However, many unaddressed issues remain; for example the actual dietary contribution of the tortoises represented by the large quantities of their fossils found at sites such as BBC.

1.4 Ecology of the angulate tortoise

Southern Africa has the world's richest diversity of terrestrial chelonians (Branch, 1984; Ramsay et al., 2002). At least one palaeontological lair site in the Western Cape documents the presence of several chelonian species during the Late Pleistocene (Peterhans and Singer, 2006), whereas at other non-anthropogenic sites chelonians are extremely rare or not reported in taxonomic detail (Klein, 1975; Rector and Reed, 2010). Despite this, almost all tortoises that have been reported from MSA sites are *Chersina angulata*, the angulate tortoise (Faith, 2011; Henshilwood et al., 2001b; Kandel and Conard, 2012; Klein et al., 2004b; Klein and Cruz-Uribe, 2000; Steele and Klein, 2013; Thompson, 2010). This is a small to medium tortoise not exceeding 250-300mm in maximum length (Branch, 1984; Hofmeyr, 2009; van Heezik et al., 1994). It is currently distributed throughout southwestern South Africa and southwestern Namibia (Figure 1). They tolerate a broad range of habitats and are found in all major floral biomes of South Africa (Boycott and Bourquin, 1988; Joshua et al., 2010).

The species is monotypic and sexually dimorphic, with males slightly larger than females (Berry and Shine, 1980; Branch, 1984) and little morphological variation across its geographic distribution (Van Den Berg and Baard, 1994). The sex ratio in wild populations from two study areas has been near 1:1, with a preponderance of adults in the population (Branch, 1984; van Heezik et al., 1994). Most growth occurs within the first ten years of an individual's lifespan, which likely lasts about 25 years (Branch, 1984). Males are significantly more active than females during the summer and spring (Keswick et al., 2006; Ramsay et al., 2002), when most fighting and courtship occurs. By the time the tortoise has achieved an age of about 7-8 years and a weight of approximately 300g, or 125 mm in total length males exhibit significant morphological differences from females (Branch, 1984). The most prominent sexually dimorphic feature likely to preserve archaeologically is the projecting unpaired gular scute (Mann et al., 2006), manifested skeletally as paired elongated epiplastra bones.

Potential predators for the angulate tortoise are each expected to accumulate and modify remains in a way that can be separated from human processing and consumption.

Black eagles (*Aquila verreauxii)* have been known to drop tortoises from a height (Boshoff et al., 1991; Steyn, 1884), and accumulations of tortoise bone occur under raptor roosts (Sampson, 2000). The kelp gull (*Larus dominicanus*) does the same, accumulating smaller tortoises up to approximately 130g (Branch and Els, 1990). Snakes such as the Cape cobra (*Naja nivea*) may prey on juvenile angulate tortoises (Haacke et al., 1993). Chacma baboons (*Papio cynocephalus ursinus*) observed at De Hoop Nature Reserve are unable to open larger tortoises, but do prey on smaller individuals (Hill, 1999). All of these agents would be expected to accumulate mainly small tortoises or strictly limb and head elements from larger tortoises, with evidence of ingestion in the form of gastric etching and punctures from beaks, talons, and teeth on the bones (Lloveras et al., 2009). Bushfires also pose substantial risk to tortoise populations (Avery et al., 2004; Stuart and Meakin, 1983), and this may have been taken advantage of by MSA collectors.

Although no longer common within the geographic distribution of angulate tortoises today, larger African mammalian predators were also potential tortoise accumulators in the Western Cape in the past. Analogies can be made to the hingeback tortoise (*Kinixys spekii*) in Zimbabwe, which has a large number of mammalian and avian predators. Predation rates have been shown to be very high on this tortoise, which is a smaller tortoise that reaches maximum lengths of between 130 – 140mm (Coulson and Hailey, 2001). In the Western Cape, brown hyenas were likely important accumulators and modifiers of angulate tortoises (Avery et al., 2004; Peterhans and Singer, 2006; Rector and Reed, 2010).

2. Material and Methods

2.1 Data collection and entry

Taphonomic (including microscopy), taxonomic, and skeletal element abundance (SEA) data were collected from a sample of the top level (CA/NA) of the M1 (Still Bay) phase, which is present across the site. Because all elements were examined in detail, the sample was by necessity smaller than that reported from the 1992, 1997, 1998, and 1999 excavation seasons, and which included only humeri (Henshilwood et al., 2001b). Specimens received individual records in the database even if the specific bone in the

sequence could not be identified. Specimens that could only be identified generically as "carapace or plastron" and that were < 1cm in maximum length were bulk recorded and bagged together, without individual records or microscopic study in either phase. Epiplastra were sexed morphologically and more complete specimens were measured to obtain a basic area estimate of the triangle formed by the epiplastron tip. This area was hypothesised to be larger in males because of their larger body size and the additional projection of their gulars. The M3 phase was sub-sampled to provide SEA data from its top portion (levels CH/CI) for comparative purposes, but a full study of the M3 sample (including microscopy and bulk analysis) fell outside the scope of the present work, which focuses on the Still Bay deposits.

2.2 Taxonomic and skeletal element abundances

A modern skeletal collection was used to identify each specimen to taxonomic affinity, element, and side. The normal configuration is provided in Figure 3. Apart from the neurals, it is typically possible to tell from where in the shell (which bone and which bone number) any given complete bone derives. Skeletal element abundances were evaluated using the Number of Identified Specimens (NISP) and the Minimum Number of Elements (MNE); the highest count on the latter provided the Minimum Number of Individuals (MNI). The fraction-summation approach was a time-effective and accurate means of estimating the MNE and MNI for most elements (Marean et al., 2001). This approach entails recording the fraction of a given element that a specimen represents, for example if 50% is present than 0.5 is noted in the record. Then all element fractions are summed to obtain the MNE. This approach is highly effective for tortoises because their elements fragment in consistent portions and at consistent landmarks compared to mammals, and are frequently nearly complete. Thus, it was not necessary to determine the MNE using the visual overlap method or its digital derivative (Marean et al., 2001) for each individual element, which can be time-consuming (Lyman, 2008).

Conjoining was performed on the M1 sample, which also assisted with sexing, as it allowed greater confidence in estimations of plastron concavity and allowed bones conjoined to the diagnostic epiplastra to be sexed. Tortoises are relatively simple to

conjoin, particularly in the plastron where bones are thick, preserve in a relatively complete state, and there are only 9 elements. Conjoining sets of tortoise bone were digitally photographed from at least two different aspects, and unlike individual elements these conjoins were drawn as shape files into ArcGIS following protocols adapted from Marean *et al.* (2001) and Abe *et al.* (2002). This provided a visual rather than simply a tabular record of the conjoins, and allowed the spatial distribution of burning across multiple elements to be recorded more objectively.

2.3 Fragmentation and burning

Specimens were determined as being either complete or broken. Broken specimens had the fracture type specified as either a fresh (excavation) or postdepositional (old) break. The percentage present of the complete specimen was also recorded, as this was the basis for the fraction-summation for MNE analysis. The MNE presented here is the highest count on that element *type*, not that specific individual element within its row and side. For example, there are 22 marginals – 11 on each side – and MNE data were calculated for each, then the highest number taken as the MNE for all marginals.

A maximum burning stage was recorded from each specimen, on a scale of $0 - 6$, with 0 representing an unburned specimen and 6 representing a fully calcined specimen. Different methods of tortoise preparation, including cooking in the shell, should result in differential burning patterns. It was therefore recorded if burning was located on the interior of the shell, the exterior, or both. It was noted during conjoining that burning patterns often continued from one element to the next, clearly indicating that heating had taken place while the specimens were connected to one another. To better understand these burning patterns they were also drawn into ArcGIS.

The excellent preservation of the BBC fossils (typically pale brown or light tan) made colour a ready attribute for recording burning patterns. The intensity of burning was recorded for each polygon drawn onto the template as either 0 (not present), 1 (present but unburned), 2 (slightly discoloured or with other evidence of burning such as light peeling or charcoal flecking), 3 (discoloured and with a slight texture change from being heated), 4 (carbonised), and 5 (calcined). The polygons were then summed to provide an overall map

of burning intensity across the shell. The burning intensity map represented where elements of the shell had been most commonly and intensely burned, but the map would be affected by differential skeletal part representation. For example, if a place on the carapace was burned, but that location was only represented once in the assemblage, then the burning intensity would appear to be very low. An MNE map of the conjoins was therefore also generated following Marean et al. (2001), and divided into the burning intensity map using the raster math function in ArcGIS. This changed the value of each pixel so that the map represented burning intensity at each location on the shell divided by the number of times that specific location was present in the assemblage.

2.4 Bone surface modification

Each fragment in the M1 sample was examined under a 10 – 40x binocular zoom light microscope with a fibre-optic halogen light shining obliquely across the bone surface following Blumenschine *et al.* (1996). Although microscopic taphonomic methods of bone surface modification analysis have been well-developed for large mammal assemblages, the only similar-aged sites with comparable treatment are PP13B in South Africa (Thompson, 2010) and Bolomor Cave in Spain (Blasco, 2008) – both of which have much smaller assemblages than BBC. In addition to examining each surface for hominin modification, the microscopic work allowed detailed recording of taphonomic data such as surface weathering, trampling, and geochemical alteration (Behrensmeyer, 1978; Domínguez-Rodrigo, 2009; Thompson, 2005), rodent gnawing, and gastric etching (Lyman, 1994). Marks were identified based on descriptions and photographs in this body of literature but also on the senior author's experience with fossil assemblages and with experimental cut-, percussion-, tooth-, and trample-marked assemblages. The majority of this research has been done on mammalian bone, so identification of modifications were conservative and only high-confidence marks are presented here.

2.5 Details of the Sample

The total sample (M1 and M3) comprised 9686 specimens, with 5846 larger than 1 cm and thus receiving an individual record. Of these, 4817 were from M1 and 1029 were

from M3. A total of 1197 specimens were conjoined from M1, comprising 311 conjoining units. Of the conjoining units, 296 included at least one element conjoined to another along a suture rather than a break. 213 conjoins were from the carapace, three from limb and head elements, and the remainder were plastral elements. The largest number of components to any conjoining unit was 26.

3. Results

3.1 Taxonomic and skeletal element abundances

Within the sample, 3191 specimens could be confidently identified to taxon. Of the identifiable specimens, 3190 were *Chersina angulata* and one was from the leopard tortoise *Geochelone pardalis*. It is reasonable then to assume that the vast majority of non-identified specimens may also be assigned to *Chersina.* This assignment also gains confidence by the substantial size difference between the two species, the fact that tortoises and aquatic turtles have different shell textures, and the ready differentiation of most elements between *Homopus* (the pancake tortoise) and *Chersina*. This result fits well with previous reports of taxonomic representation performed only using humeri (Henshilwood et al., 2001b).

From the M1 phase a total NISP of 70 could be assigned to females and 50 to males. Counts on epiplastra in this phase provide MNE data that show the same pattern: an MNE of 17 females versus 10 males. Fisher's Exact Test shows that there is no significant difference in the sex ratio obtained using the NISP or the MNE (p = 0.83). Of the 164 epiplastra preserved in the M1 sample, 103 were sufficiently complete for measurement. As a total sample there is only a single mode in the data, which are right-skewed, suggesting a female-biased sex distribution and the inclusion of a few very large males. When the morphologically sexed epiplastra are separated the males are clearly larger, and the majority of specimens classed as "ambiguous" fall towards the female end of the distribution (Figure 4). A Kruskall-Wallis test confirms that there are significant differences in the median sizes between the male and female datasets, and between the male and ambiguous datasets (Hc = 10.31; p = 0.006), further suggesting that many of the ambiguous specimens are females.

The NISP and MNE data (Table 2) show that elements within the carapace and plastron are differentially preserved. Limb and girdle elements are poorly represented compared to shell elements, and cranial and pedal elements are barely present. The entoplastron provides the highest MNE count overall and an MNI of 80 tortoises for both the M1 and M3 samples combined. Within individual phases, BBC M1 yielded a total MNI of 74 (on the entoplastron) and BBC M3 yielded a total MNI of 14 (on the humerus). The layers from which the M1 and M3 samples derived were widely separated, and there is minimal evidence for stratigraphic mixing between phases at BBC (Henshilwood, 2005). Therefore, the total sample studied here represents at least 88 individual tortoises.

3.2 Fragmentation

The plastron, which is thicker, was much less fragmented than the carapace and most often broken along the 'arms' that extend from the hypo- and hyoplastra and connect to the 4th – 7th marginals. This join is likely one of the weakest places on the tortoise carapace and plastron. Limb and girdle elements were frequently complete or simply broken into halves or thirds, unlike mammal long bones (Table 3). A comparison of all summed carapace and plastron elements to all summed girdle and limb elements shows that significantly more complete specimens from the shell are found in the M1 phase than the M3 phase (p < 0.0001).

Another measure of fragmentation is the relationship between the NISP and the MNE (Lyman, 2008). The ratio of NISP: MNE is provided in Table 4. For paired or numbered elements, the NISP was first divided by the number of times that element occurs in the skeleton to compensate for the way the MNE was presented. The almost 1:1 relationship between NISP and MNE in the M1 sample suggests very low levels of fragmentation. This is in contrast to both the mammal data and the assertion by Henshilwood *et al.* (2001b:435) that, "The tortoise sample comprises mainly small fragments of carapace and plastron". In fact, these elements are frequently complete or nearly-complete and have simply become disassociated from one another. However, there is relatively more fragmentation in all elements (including limbs) in the M3 phase. The

relationship is not nearly as strong between NISP and MNE, and the datapoints are more widely scattered (Figure 5).

3.3 Burning

Detailed burning data are available for the M1 sample only (N = 4343). Sampson (2000) indicates that human-accumulated tortoise assemblages should have an incidence of burning between 30 – 40%. Charring in the M1 phase is even higher than this, at 66.1%. Speth and Tchernov (2002), Thompson (2010), and Blasco (2008) all suggest that if tortoises were cooked whole on the fire, they should exhibit more charring on the exterior portion of their shell than the interior. If most burning was post-depositional rather than related to cooking, then it should be randomly distributed. 59.3% of all burned specimens were burned on the outside only, 38.9% were burned on both the outside and the inside, and only 1.8% were burned on the inside only. The carapace was more commonly burned than the plastron, and the limbs more commonly burned than girdle elements (Table 5). In addition, several of the carapace and plastron specimens were burned only in specific and consistent locations (Figure 6), which map onto what would be predicted for tortoises subjected to burning carapace side down in the complete shell.

3.4 Bone Surface Modification

Surface modification was readily visible on the BBC tortoises. 95.4% of all specimens had at least half of their surfaces visible, and 85.7% of all specimens had their complete surface visible. 99.3% of all specimens had surfaces that were not badly exfoliated, unlike some of the larger mammal specimens from BBC (Thompson and Henshilwood, 2011). 99.8% did not have any dendritic etching that might be indicative of roots, fungus, or other bioerosion. Manganese 'flowers' were observed on some surfaces, diagnosed under the microscope as structurally different from burned patches.

98.4% of the specimens had no evidence of being smoothed or polished. For those that did, the damage may be from carnivores or people licking or sucking the bone and in these cases should be associated with other damage such as tooth marks, crushing, or gastric etching. In a few rare cases some abrasion occurred well after the nutrient extraction

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phase, after the scutes had worn away and exposed the underlying bone (Supplementary Materials 1).

The incidence of diagnostic bone surface modifications that occur during the nutritive phase is provided in Table 6. Gastric etching overall occurred on 2.6% of the assemblage. As a proportion of overall skeletal representation in the same sample there were many more gastrically-etched limb and girdle elements (6.6%) than carapace/plastron elements (2.2%). This difference is highly significant ($p < 0.0001$) using Fisher's Exact Test. Tooth marks occur on all elements, but proportions were higher for limb elements than other skeletal part categories. They were second highest on girdle elements and also occur on the carapace and plastron (often along fracture edges). Tooth marks came in a variety of different forms, such that it was not possible to establish a direct relationship between tooth mark abundances and carnivore activity, as is often assumed for larger mammal assemblages.

Figure 7a, b, c, and d show damage to tortoise fossils at BBC that suggest human consumption. The tooth marks were associated with crushing and peeling of the bone, with small, overlapping, bunodont (not punctured) depressions. This damage typically occurred along the margins of smaller carapace or plastron fragments, and on the ends of limb or girdle elements. Many of the incomplete limb or girdle elements had ends that were chewed away, rather than simply snapped or broken off. This type of damage was oftem associated with polishing or smoothing of the fracture edge. Several authors have described such marks left by human mastication on mammalian bone (Landt, 2007; Lupo and Schmitt, 2005; Pickering and Wallis, 1997; White, 1992), and Blasco (2008) has also identified human chewing on tortoise fragments from Bolomor Cave. Only sixteen marked specimens listed in Table 6 could be confidently assigned as carnivore damage. The remainder more closely resembled human damage because the damage comprised generalised crushing rather than individual marks and drags, but it should be cautioned that such damage can be ambiguous.

Tooth marks ascribed to non-human activity (Figure 7 e, f, g, and h) came in the form of small parallel scratches, deeper subparallel grooves with a sharp margin for tooth entry, and large punctures, usually along the margins of bones. Two fragments exhibited

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small, triangular marks indicative of raptor beak marks (Sanders et al., 2003), and these are not included in Table 6. This is possible even at sites where no obvious raptor roosts are apparent, as some raptors (particularly the spotted eagle owl, *Bubo africanus*) will roost on the ground as well as in roof cavities (Fry et al., 1988; Reed, 2005).

All stone tool cut marks occurred either on the inside of the shell or on limb elements (Figure 8), with most on the interior of the carapace. Hammerstone percussion marks occurred on the exterior of the shell only, usually in association with a crack or fracture edge (Figure 9). It was not expected that they would be common, given that while the tortoise still retains some nutritive value the shell is covered in tough scute material. Bevelled fracture edges on the interior of the shell also occurred, and this has been taken as an indication of percussion that may preserve even without corresponding percussion marks (Blasco, 2008).

71.8% of all percussion marks occurred on carapace elements, 19.7% on the plastron, and the remainder on non-identifiable fragments. Most of the percussion marks on the carapace occurred on the marginals and costals, although this could be partially because these elements are more common the skeleton overall. It is noteworthy that approximately half (47%) of all percussion marks on marginals were on bone numbers 4 – 7, which are those identified as being at a weak point where the carapace joins the plastron.

4. Discussion

4.1 Agent(s) of collection and modification

The majority of complete skeletal elements derived from adult tortoises, based on both their size and bone surface texture. It is difficult to quantify the population age structure of tortoises at BBC based on available published data, which only measure humerus size (Henshilwood et al., 2001b). Ecologists have noted several tight allometric relationships between various parts of living tortoises (Branch, 1984), but unfortunately those that can be measured skeletally (for example complete carapace length) require complete tortoises. The BBC tortoise elements were disarticulated to such a degree as to make this unfeasible, but future work with modern tortoises will allow humerus size data to

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be translated into absolute estimates of tortoise size. This will establish cut-offs that would eliminate all tortoise predators except humans and larger mammalian carnivores.

In the absence of these data, this discussion will focus on taxonomic representation, skeletal element abundance, and bone surface modification. The assemblage is effectively monotaxic, with fewer male than female *Chersina* at a ratio of 1:1.4 (by NISP) or 1:1.7 (by MNI). In extant populations the sex ratio has been 1:1.17 and 1:1.18 in favour of males over an 11-year study period for one area (van Heezik et al., 1994), and 1:1.2 in favour of females in another (Branch, 1984). The bias in favour of females in M1 may account for the smaller overall tortoise size in this phase observed by Henshilwood *et al.* (2001b).

Sampson (2000) has shown that raptors preferentially drop limb, girdle, and skull elements relative to shell elements. However, Figure 10 shows that the BBC data are instead dominated by carapace and plastron elements. A closer look shows that each of the distributions is significantly different from the other (M1 versus M3: $Ch^2 = 3468.7$, DF = 2, $P < 0.0001$; M3 versus VFT: $Ch^2 = 846.69$, DF = 2; M1 versus VFT: $Ch^2 = 60419$, DF = 2, $P < 0.0001$), implying significant variability between shell and limb/girdle representation. There are relatively more limb and girdle elements present in the M3 phase than the Still Bay M1 phase. This could imply more raptor input into the assemblage during M3 times.

However, *differential* fragmentation between shell and limb/girdle elements in each of the phases may lead to over-representation of one element class relative to another. The intensity of fragmentation has a large part in determining how identifiable a given specimen is to a particular element, which then controls the threshold at which MNE data can be reliably calculated and understood relative to NISP (Lyman, 2008). In the context of BBC it is also important because mammal bones were found to be less fragmented in the M3 phase (Thompson and Henshilwood, 2011), suggesting that there was an increased intensity of human occupation, trampling, and burning in the more recent phases at the site. In this case, it was found that during the M3 phase tortoise limb and girdle elements were more fragmented relative to carapace and plastron elements than during the M1 phase. These factors account for the relatively high proportions of limbs/girdles during the M3 phase using the NISP, but the MNE data still suggest that further microscopic study is needed to

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fully assess whether it was differences in human processing strategies and site use or slight differences in the accumulator that best explain variability between phases.

Comparisons of skeletal element abundances between the two phases also have some important lessons about which tortoise elements to use to calculate MNE and MNI data. The entoplastron provided an MNI of 74 for M1, whereas the humerus only provided a count of 24. In contrast, the humerus provided the highest MNE count in the M3 phase (14), while the entoplastron only provided a count of 5. A very tight correlation between NISP and MNE was found for M1, but the M3 data were not as closely correlated and girdle elements in particular deviated from the trend because they were more highly fragmented. This suggests that different taphonomic processes may render samples from different contexts incomparable if only a single element or element class is used in MNE and MNI calculations. The abundance of the entoplastron in the M1 phase highlights the value of this element as a robust bone that is likely to preserve in a whole state, be easily identified and counted, and not require siding. These factors make it a good candidate for quickly evaluating plastron representation at a site relative to limb representation, which can be done using the humerus or femur.

There is a large body of literature on how diagnostic marks such as cut, percussion, and tooth marks are manifested and preserved under a variety of experimental conditions (Blumenschine et al., 1996). However, there are no comparative experimental models for how tortoise bone retains surface modifications compared to mammal bone. Most of the nutrients in a tortoise are on the inside of a hard skeleton, whereas most of the nutrients on mammals are on the outside. It is therefore quite likely that the unique anatomy and bone structure of tortoises also means that chelonian consumption will have a very different signature from large mammal consumption.

In spite of this, there is abundant evidence from the surface modification analysis that the tortoises at BBC were predominantly, if not exclusively, collected and processed by MSA people. Particularly in the case of the Still Bay sample, all major forms of hominin modification are present, and in some cases abundant: preferential burning throughout the skeleton, percussion marks, bevelled internal fracture edges, human tooth marks, cut marks on limb elements, and scrape marks on the internal portions of the carapace and plastron.

The differential placement of these modifications is as informative as their simple presence, and this also allows for a reconstruction of how the tortoises were processed.

4.2 Tortoise processing strategies

Of the 80 entoplastra represented in the sample, 32 were parts of conjoining units – in most cases as part of a substantial conjoining unit of three or more individual bones. This speaks to a considerable level of integrity within the plastron. This, together with the placement of the entoplastron in the centre of the plastron indicates that the tortoises were brought to the site complete.

Differential burning throughout the skeleton indicates tortoises were burned while they were still complete. Burning was significantly more common on the exterior than the interior of the shell, more common on the carapace than the plastron, and it followed a distinctive pattern around the shell that suggested the most heat was delivered to the top, margins, and where the limbs of the tortoise emerge. Limbs were burned more commonly than girdle elements. This pattern is consistent with what would be expected if the tortoise was placed upside down in the fire, as has been documented ethnographically and archaeologically around the world (Blasco, 2008; Sampson, 2000; Schneider and Everson, 1989; Speth and Tchernov, 2002).

Avery *et al.* (Avery et al., 2004) report that tortoises killed in sweeping bushfires do not exhibit much charring on the bone. In contrast, tortoises burned in a campfire should be exposed to prolonged and direct heating. Furthermore, the shell was often broken in areas with the most intense burning. This may have been a post-depositional result of increased bone brittleness or MSA people may have purposefully heated tortoises to the point that their shells became brittle and easier to access (Stiner et al., 1995).

The presence of cut marks on the limbs and scrape marks on the interior of the carapace and plastron indicate that stone tools were used to facilitate butchery in different ways. Tools were used occasionally to disarticulate limbs and scrape meat from inside the shell – though actualistic work is still required to determine how frequently such marks are left. Human chewing and tooth marks on the limbs and around the margins of the shell indicate direct consumption with limited used of stone tools in comparison with large

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mammal remains, where stone tools left large quantities of butchery marks (Thompson and Henshilwood, 2011). Finally, the presence of percussion marks restricted to the exterior of the shell indicates that hammerstone percussion was used to open the shell – likely at the weakest point along the side of the carapace.

A likely sequence of processing is that the tortoise was first placed upside down in the fire. After removal any limbs that had become charred were either twisted or cut off and chewed. The tortoise was placed on its side on an anvil and struck with a hammerstone. The meat was then consumed, with stone tools used as needed to scrape remaining meat from inside. After the girdle elements were consumed, they and the entire tortoise were discarded. In many cases they were likely thrown back onto the fire, to account for the burning observed on both the interior and exterior of the shell.

Indigenous people at the Cape have been recorded using tortoise shells as drinking receptacles and storage containers. This extract is from the journal, dated 1673, of Wilhelm ten Rhyne (Schapera 1933:121): "They do sometimes use cups.....or the shells of tortoises which they have eaten". In the ca. 2 ka LSA levels at Blombos Cave a carapace of the turtle *Pelomedusa subrufa* showed evidence of scrape marks on the interior and grinding on the edges suggest its use as a bowl, possibly to store or mix ochre, as both the edges and inner surface were ochre stained (Henshilwood, 2008). Worked tortoise carapaces are reported from LSA levels at Uniondale in the Eastern Cape (Brooker, 1989) and Nelson Bay Cave in the southern Cape (Inskeep, 1987), but there is no evidence of the tortoise shells examined macro- or microscopically from the MSA levels at BBC being worked or used as containers. Similarly, no such evidence has been reported for other MSA sites. It is possible that at BBC the potential value of the shells as containers in the MSA was lessened by extensive burning. This, combined with the butchery mark data, show that during Still Bay times tortoise processing for food was both consistent and common. It is therefore important to consider how significant tortoises may have actually been as food sources.

4.3 Tortoises as Nutritional Packages

Tortoises are effectively a protein and fat package available in collectable form. Studies of different species of tortoise show that fat content ranges between about 2% and

up to 13% (Kienzle et al., 2006; Lapid et al., 2005; Pearse et al., 1925), but most chelonians do not have masses of dissectible fat (Pond, 1978). These data suggest that tortoises have similar percentages of fat relative to lean meat as wild ungulates (Crawford et al., 1970; Crawford et al., 2010; Skinner and Louw, 1996; van Zyl and Ferreira, 2004). An average-sized adult *Chersina* weighs about 860g (van Heezik et al., 1994). The shells of tortoises comprise approximately one-third of total body weight (Kienzle et al., 2006), and the estimated gross caloric yield for a *Chersina* is ca. 3332 kJ/796 kcal (Thompson and Henshilwood, in revision).

Although the overall caloric return of ungulates is higher than for tortoises, there are many benefits to tortoise consumption. Hunted ungulates have many search and handling costs, while technological costs of tortoise processing are negligible. Time and energy investment could be made in searching for tortoises, but a more efficient method would be to simply collect them opportunistically as they are encountered. Encounter rates could also be increased by intentionally foraging for other resources in areas that are known to also contain tortoises. This would then mean that the only investments are in carrying and processing them: both minimally expensive tasks in terms of both caloric and time expenditure. In this sense they differ from other small prey (Bright et al., 2002) or mobile prey (Bird et al., 2009), which incur significant handling costs relative to their returns.

Live tortoises can be taken daily, but also be stored until the entire animal is ready to be eaten. They can then be cooked and consumed without having to prepare the remainder of the animal for future use. In contrast, the amount of group coordination required to hunt and process a large ungulate (or the coordination required to snare or net-drive smaller ungulates) presents a much more immediate, socially visible output of investment. Chelonian biomass is often very high relative to that of mammals in a given area (Iverson, 1982) and encounter rates are expected to be high relative to other slow-moving prey. Although the slow growth and reproduction of tortoises in general makes their populations susceptible to over-exploitation (Stiner et al., 2000), *Chersina* populations have a high inherent ability to rebound once intense predation pressure is removed (van Heezik et al., 1994). All of these factors make tortoises attractive food resources on the

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South African landscape, and they should have been taken upon encounter particularly by individuals within the group who were engaged in collecting activities.

5. Conclusions

Initial work on MSA subsistence took at face value that the faunal remains recovered in association with MSA artefacts were solely the result of human subsistence choices. Microscopic research at several MSA cave sites along the South African coast has shown there is more complexity in large mammal fossil assemblages (Marean et al., 2000; Thompson, 2010; Thompson and Henshilwood, 2011), but no comparable study had been done on a sizeable tortoise assemblage. Bone surface modification of the tortoise assemblage at BBC showed that MSA people were the main accumulators and modifiers of the tortoises in the M1 phase, and all other lines of evidence (taxonomic and skeletal element abundances) showed the same to be true for the M3 phase. Burning patterns in the M1 phase also demonstrated that tortoises were processed by being cooked upside down in their shells, which allowed for a general model of tortoise processing to be proposed. There is no evidence that tortoise shells were used as containers. A contributory factor might be the high degree of burning evident on the shells which would render them unsuitable for that purpose.

This study showed that analyses of skeletal element abundances based only on a single element are insufficient in the face of variable taphonomic processes even within the same site. *Chersina* taphonomy and ecology proved to be highly informative about aspects of MSA subsistence that have previously been undocumented. For example, the relatively small tortoise size noted by Henshilwood et al. (Henshilwood et al., 2001b) may be explicable in terms of a female-biased sex ratio. Other aspects of tortoise taphonomy that should be explored in more depth with modern collections are allometric body size relationships, relative proportions of butchery marks, and burning patterns on bushfire-produced tortoises.

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Figure captions

Figure 1 Modern distribution of *Chersina angulata* (Hofmeyr 2009), with fossil sites mentioned in the text. SRTM data are used for topography.

Figure 2 Layout and stratigraphy of Blombos Cave. Layers sampled for tortoise analysis and total NISP for each sample are indicated. Sampled areas of the cave are indicated, with a "1" where only M1 deposits were sampled, a "3" where only M3 deposits were sampled, and a filled circle where both were sampled.

Figure 3 Typical configuration of shell elements. Key to carapace (left): NE = Neural, NU = Nuchal, SP = Suprapygal, PY = Pygal, CO = Costal, and MA = Marginal.

Figure 4 Frequency histogram of the area of the epiplastron (light orange = females; medium blue = males; dark green = ambiguous). The box plot shows the median sizes for the three groups, with images of male and female epiplastra indicated with arrows. Scalebar = 1cm.

Figure 5 Relationship between NISP and MNE in the M1 and M3 phases.

Figure 6 The distribution and intensity of burning patterns on the shell, summed for all conjoining carapace and plastron units and divided by the MNE for those same conjoins.

Figure 7 (a) human chewing damage along margin of a carapace fragment showing smoothing and polish (white dots); (b) human chewing damage on a limb fragment showing smoothing, polish, and splintering (white dots); (c & d) human chewing damage on shell margin fragments showing randomly-oriented areas of crushing; (e) carnivore tooth marks showing subparallel scratching with a small indent near the top of the image showing the point of entry; (f) carnivore tooth marks showing subparallel puncture and drag characteristics; (g) single large carnivore puncture on shell margin; and (h) triangular indentations interpreted as raptor beak marks.

Figure 8 Stone tool cut marks on a tortoise limb (a), and scrape marks on the interior of a tortoise shell (b, c). Image at right is enlargement of left.

Figure 9 Percussion marks on the exterior of tortoise shell. Note the proximity of such marks to fracture edges or cracks indicating force applied to the area. Image at right is enlargement of left.

Figure 10 Proportions of shell and limb elements present at BBC by NISP and by MNE. Note that only identifiable elements are included, so as to make the data comparable to Sampson's (2000) data from the raptor accumulation at Volstruisfontein (VFT).

Table captions

Table 1 Summary of ages and material culture associated with the BBC stratigraphy.

Table 2 NISP and MNE for all fragments > 1cm in the maximum dimension from the two analysed phases.

Table 3 Completeness of carapace, plastron, girdle, and limb elements in each of the two phases. The p-value indicates the significance of the difference between the two ratios of complete: incomplete elements using Fisher's Exact Test.

Table 4 NISP:MNE Ratios for tortoise elements at BBC. Note that values below 1.00 are impossible, and should be interpreted as values of 1.00. They are an artefact of the compensation procedure described in the text.

Table 5 Distribution of burning across tortoise elements from BBC M1 compared to other Middle and early Late Pleistocene sites at which tortoises were consumed by people.

Table 6 Total counts of specimens bearing a tooth mark of any form (TM), cut mark (CM), or hammerstone percussion mark (PM) in the sample from BBC M1.

Supplementary Materials

Supplementary Materials 1 Surface modifications to tortoise shell elements not related to nutrient processing, including abrasion and polish (a, b) and root etching (c). Image at right is enlargement of left.

Table 1.docx

Phase	Age (ka)	Method	Dating Citations/Notes	
Sterile Sand	69 ± 5	OSL	Henshilwood, et al., 2002, Jacobs, et al., 2003a, Jacobs, et al., 2006, Jacobs, et al., 2003b	
	70 ± 5			
BBC M1	72.7 ±3.1	OSL	Jacobs, et al., 2003a, Jacobs, et al., 2003b	
	74 ± 5	TL	Tribolo, et al., 2006	
	78 ± 6			
BBC M2 Upper	76.8 ± 3.1	OSL	Jacobs, et al., 2006; Possible *terminus post quem* for Still Bay levels?	
Still Bay overall	ca. 75 – 72	OSL	Jacobs, et al., 2013; Possible t*erminus post quem* for Still Bay levels?	
BBC M2 Lower	84.6 ± 5.8	OSL	Henshilwood, et al., 2011, Jacobs, et al., 2006	
	78.9 ± 5.9		Jacobs, et al., 2013	
	78.8 ± 5.6			
BBC M3	ca. 100 to > 130	OSL	Henshilwood, 2012, Henshilwood, 2009, Henshilwood, et al., 2011, Henshilwood, et al., 2001b	(a)

Phase	Material Culture	Details	Material Culture Citations
Sterile Sand	None	Demonstrates separation between LSA and MSA layers	N/A
BBC M1	Still Bay points	Pressure-flaked bifacial foliate points made mainly on heat-treated silcrete	Mourre, et al., 2010, Villa, et al., 2009
	Worked bone tools	Formal and informal tools	d'Errico and Henshilwood, 2007, Henshilwood, et al., 2001a; Henshilwood & Sealy, 1997
	Engraved ochres	Pieces show clear engraved patterns	Henshilwood, et al., 2009, Henshilwood, et al., 2002
	Perforated *Nassarius kraussianus* shell beads with wear facets	Show differences in style of beading over time	d'Errico, et al., 2005, Henshilwood, et al., 2004, Henshilwood, 2009, Vanhaeren, et al., 2013
BBC M2 Upper	Still Bay points, worked bone tools, shell beads		As above

BBC M3	Basin shaped hearths and ochre, some engraved; Two *Haliotis midae* (abalone) shells with pigment mixture containing ground ochre, burnt bone, charcoal, ground quartz and associated with grindstones and hammerstones	Ochre-processing workshop and first recorded use of a container and a pigmented compound	Henshilwood, 2012, Henshilwood, 2009, Henshilwood, et al., 2011, Henshilwood, et al., 2001b (hearths and ochre); Henshilwood, et al., 2011 (ochre workshop)

(b)

Table 2.docx

		NISP M1	MNE M1	NISP M3	MNE M3	TOTAL MNE (Calculated)	TOTAL NISP (Phases Summed)	TOTAL MNE (Phases Summed)
CARAPACE	Carapace	101	N/A	7	N/A	N/A	108	N/A
	Neural	277	23	62	10	27	339	33
	Costal	900	31	145	6	37	1045	37
	Marginal	1118	53	186	8	56	1304	61
	Nuchal	66	46	24	12	57	90	58
	Suprapygal	37	31	0	0	31	37	31
	Pygal	56	52	11	7	59	67	59
PLASTRON	Epiplastron	154	65	12	6	72	166	71
	Entoplastron	77	74	5	5	80	82	79
	Hyoplastron	176	66	19	5	69	195	71
	Hypoplastron	180	51	21	6	57	201	57
	Hyo/Hypoplastron	181	N/A	2	N/A	N/A	183	N/A
	Xiphiplastron	145	62	15	5	67	160	67
	Plastron	170	N/A	3	N/A	N/A	173	N/A
	Carapace/Plastron	613	N/A	210	N/A	N/A	823	N/A
GIRDLE	Scapula	51	19	31	12	31	82	31
	Procoracoid	28	12	19	8	16	47	20
	Ilium	39	18	17	4	19	56	22
	Ischium	28	14	7	5	14	35	19
	Pubis	49	19	30	4	23	79	23
LIMB	Humerus	51	24	32	14	37	83	38
	Radius	20	9	21	0	9	41	9
	Ulna	18	9	12	0	9	30	9
	Femur	45	20	22	10	26	67	30
	Tibia*	29	14	26	13	26	55	27
	Fibula*	20	10	10	4	14	30	14
	Limb	60	N/A	33	N/A	N/A	93	N/A
CRANIAL, PEDAL, AND VERTEBRAL	Cranial	3	N/A	1	N/A	N/A	4	N/A
	Mandible	16	N/A	0	N/A	N/A	16	N/A
	Cervical Vertebra	1	N/A	0	N/A	N/A	1	N/A
	Neural Vertebra	70	N/A	46	N/A	N/A	116	N/A
	Caudal Vertebra	32	N/A	0	N/A	N/A	32	N/A
	Pedal	4	N/A	0	N/A	N/A	4	N/A
	Non-ID	2	N/A	0	N/A	N/A	2	N/A

*These elements are difficult to side, so this number is the MAU (all elements/2)

Table 3.docx

	NISP	M1	M3	M1	M3	p-value
Carapace	Complete	1044	110	42.5%	25.7%	< 0.0001
	Incomplete	1410	318			
	Total	2454	428			
Plastron	Complete	382	32	52.5%	44.4%	0.2166
	Incomplete	345	40			
	Total	727	72			
Girdle	Complete	143	82	73.3%	78.8%	0.3266
	Incomplete	52	22			
	Total	195	104			
Limbs	Complete	135	93	73.8%	75.6%	0.7894
	Incomplete	48	30			
	Total	183	123			
Carapace / Plastron	Complete	1426	142	44.8%	28.4%	<0.0001
	Incomplete	1755	358			
	Total	3181	500			
Girdle / Limbs	Complete	278	175	73.5%	77.1%	0.3837
	Incomplete	100	52			
	Total	378	227			

Table 4.docx

		Ratio NISP:MNE M1	Ratio NISP:MNE M3	Ratio NISP:MNE Total
CARAPACE	Neural	1.34	0.69	1.14
	Costal	1.61	1.34	1.57
	Marginal	0.96	1.06	0.97
	Nuchal	1.43	2.00	1.55
	Suprapygal	1.19	N/A	1.19
	Pygal	1.08	1.57	1.14
PLASTRON	Epiplastron	1.18	1.00	1.17
	Entoplastron	1.04	1.00	1.04
	Hyoplastron	1.33	1.90	1.37
	Hypoplastron	1.76	1.75	1.76
	Xiphiplastron	1.17	1.50	1.19
GIRDLE	Scapula	1.34	1.29	1.32
	Procoracoid	1.17	1.19	1.18
	Ilium	1.08	2.13	1.27
	Ischium	1.00	0.70	0.92
	Pubis	1.29	3.75	1.72
LIMB	Humerus	1.06	1.14	1.09
	Radius	1.11	N/A	2.28
	Ulna	1.00	N/A	1.67
	Femur	1.13	1.10	1.12
	Tibia	1.04	1.00	1.02
	Fibula	1.00	1.25	1.07

Table 5.docx

	Total BBC M1	Burned BBC M1	BBC M1	Kebara Cave	Bolomor Cave	PP13B
Carapace/Plastron	562	371	66.0%	N/A	N/A	21.3%
Carapace	2289	1744	76.2%	10.2%	66.0%	13.7%
Plastron	1022	605	59.2%	4.0%	62.6%	21.0%
Girdle	166	57	34.3%	N/A	57.3%	18.9%
Limb	195	78	40.0%	9.0%	56.2%	18.4%
Vertebra	85	11	12.9%	N/A	63.6%	0.0%
Cranial	19	3	15.8%	N/A	N/A	0.0%

Table 6.docx

	Total	TM	%TM	PM	%PM	CM	%CM
Carapace/Plastron	562	42	7.5%	6	1.1%	9	1.6%
Carapace	2289	80	3.5%	51	2.2%	23	1.0%
Plastron	1022	53	5.2%	14	1.4%	4	0.4%
Girdle	166	14	8.4%	0	0.0%	0	0.0%
Limb	195	34	17.4%	0	0.0%	8	4.1%
Other	109	0	0.0%	0	0.0%	0	0.0%
Totals	4343	223		71		44	

	Total	TM	%TM	PM	%PM	CM	%CM
Carapace/Plastron	562	42	7.5%	6	1.1%	9	1.6%
Carapace	2289	80	3.5%	51	2.2%	23	1.0%
Plastron	1022	53	5.2%	14	1.4%	4	0.4%
Girdle	166	14	8.4%	0	0.0%	0	0.0%
Limb	195	34	17.4%	0	0.0%	8	4.1%
Other	109	0	0.0%	0	0.0%	0	0.0%
Totals	4343	223		71		44	

Figure 1
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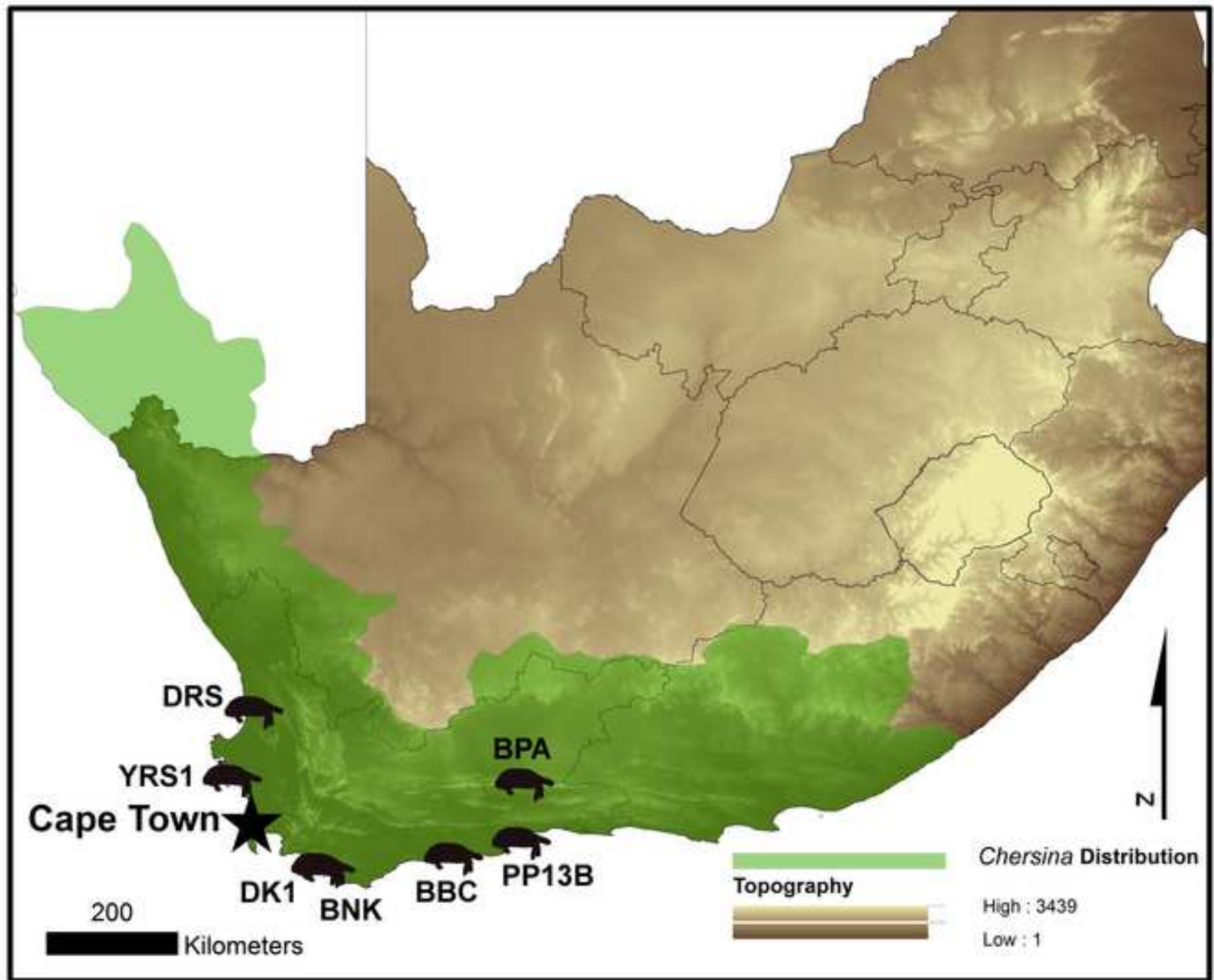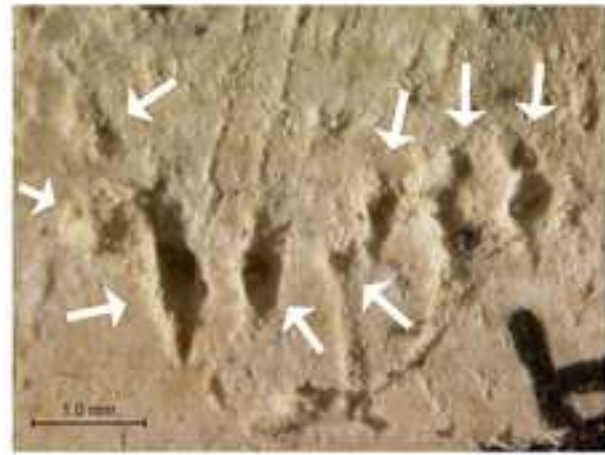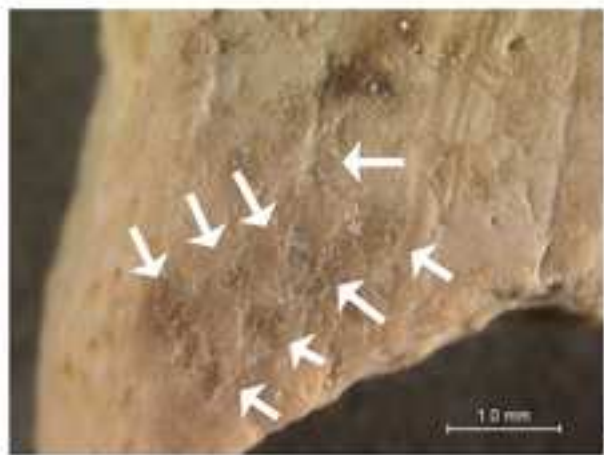
Figure 2
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Posterior

PY
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CO-8-R SP CO-8-L MA-9-L
MA-9-R CO-7-R CO-7
NE-8
MA-8-R CO-6-R CO-6-L MA-8-L
NE-7
MA-7-R CO-5-R NE-6 CO-5-L MA-7-L
NE-5
MA-6-R CO-4-R CO-4-L MA-6-L
NE-4
MA-5-R CO-3-R CO-3-L MA-5-L
NE-3
MA-4-R CO-2-R NE-2 CO-2-L MA-4-L
NE-1
MA-3-R CO-1-R CO-1-L MA-3-L
MA-2-R MA-2-L
NU
MA-1-R MA-1-L

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Epiplastron Epiplastron

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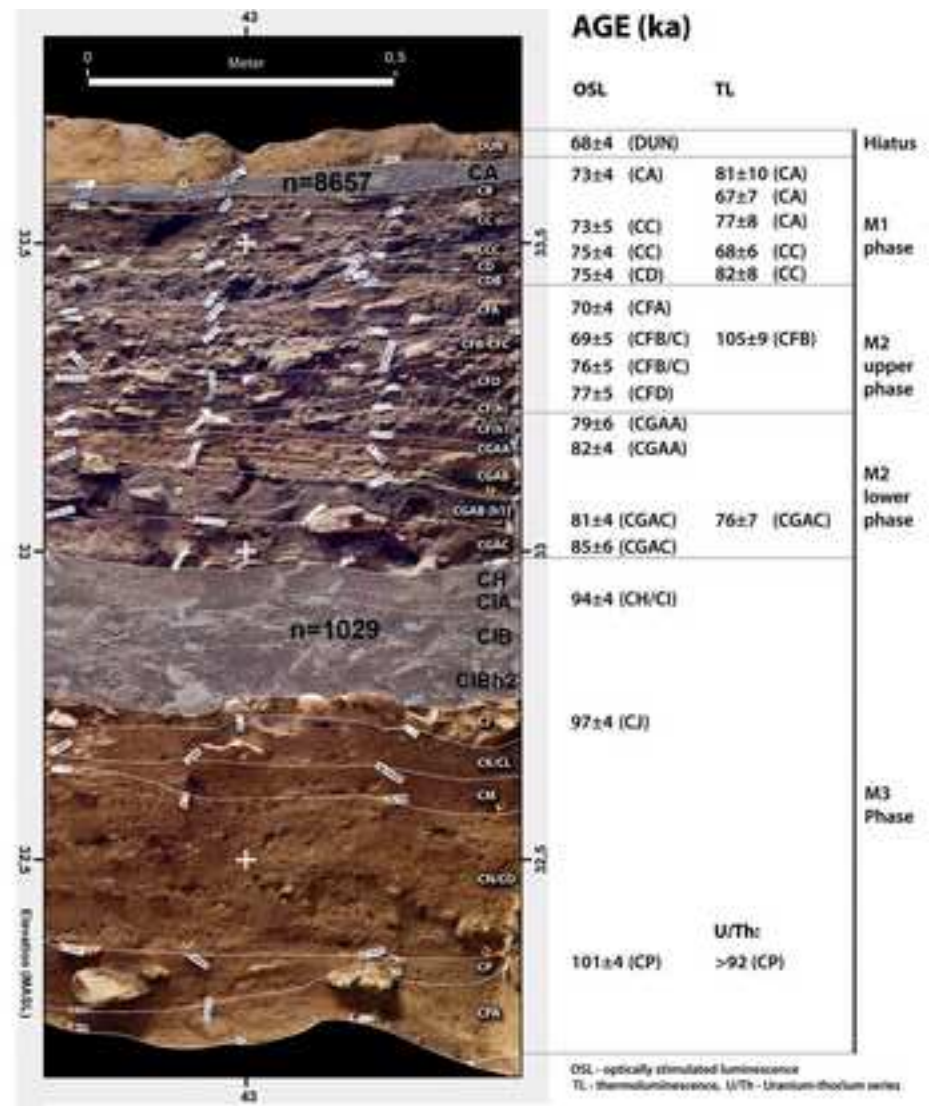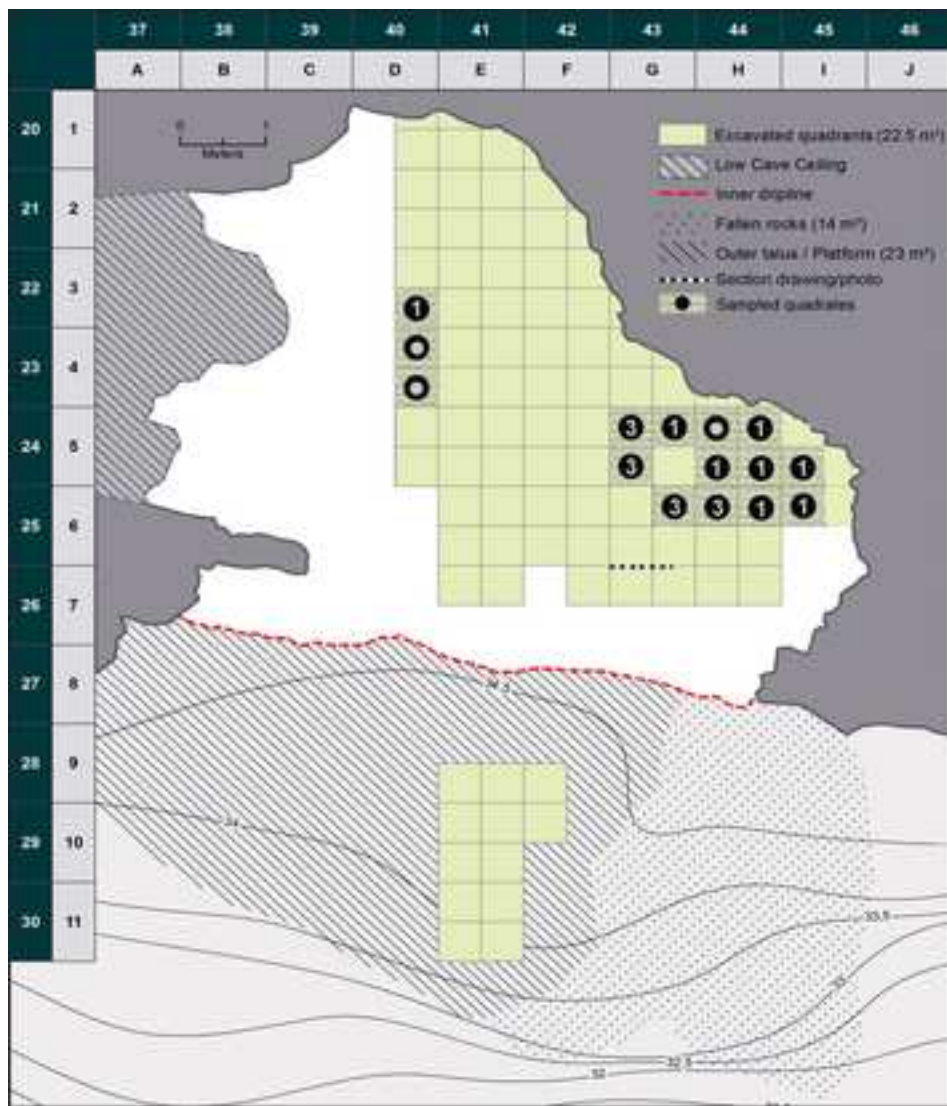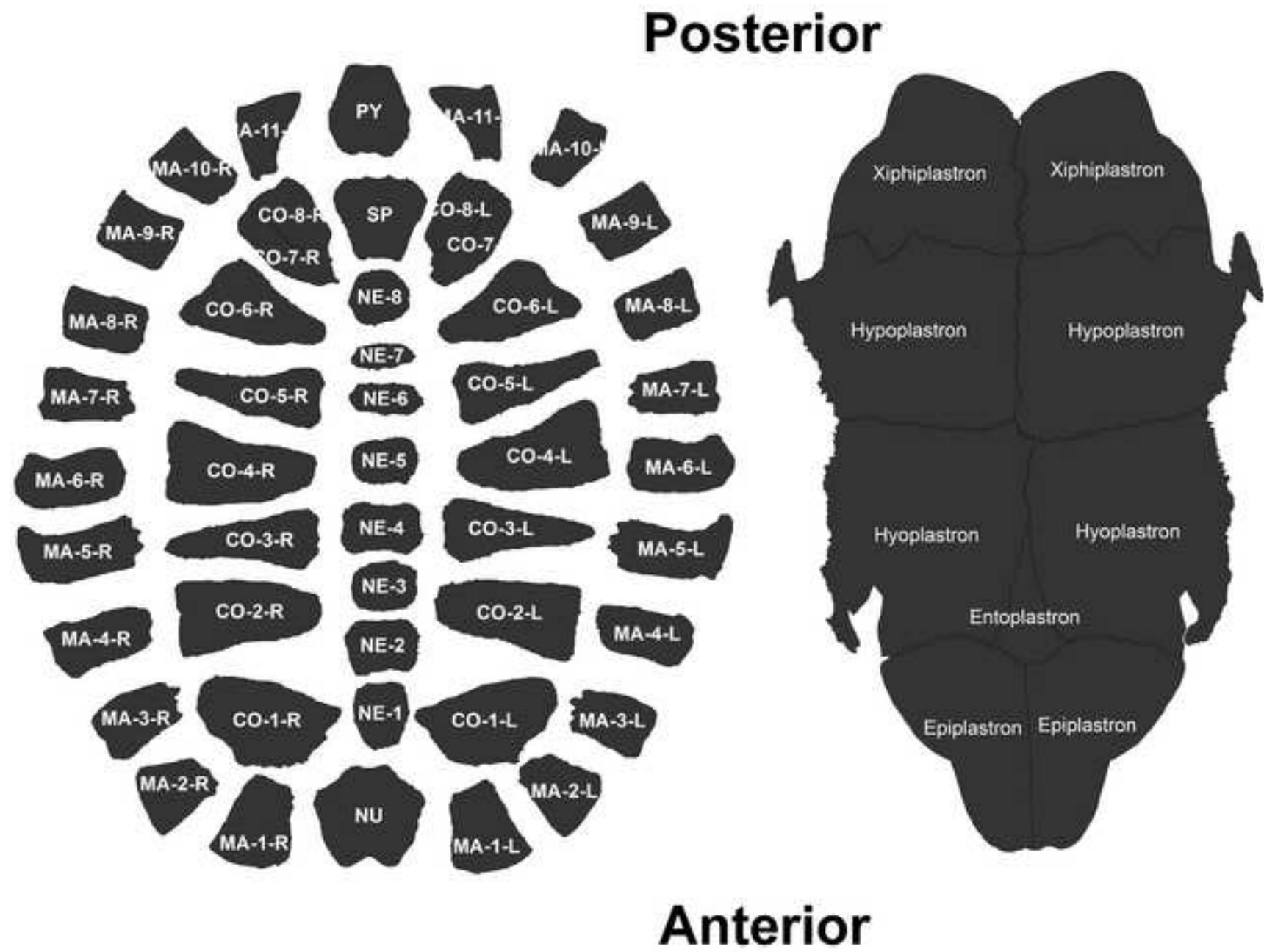
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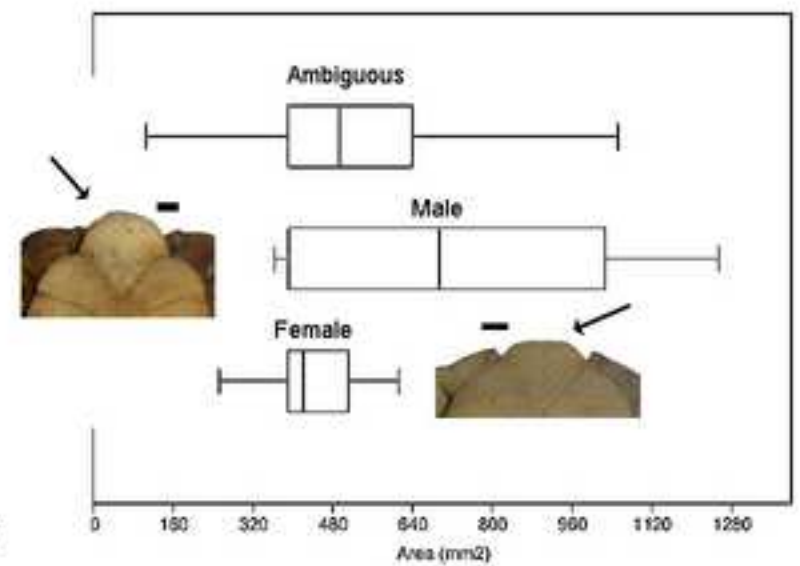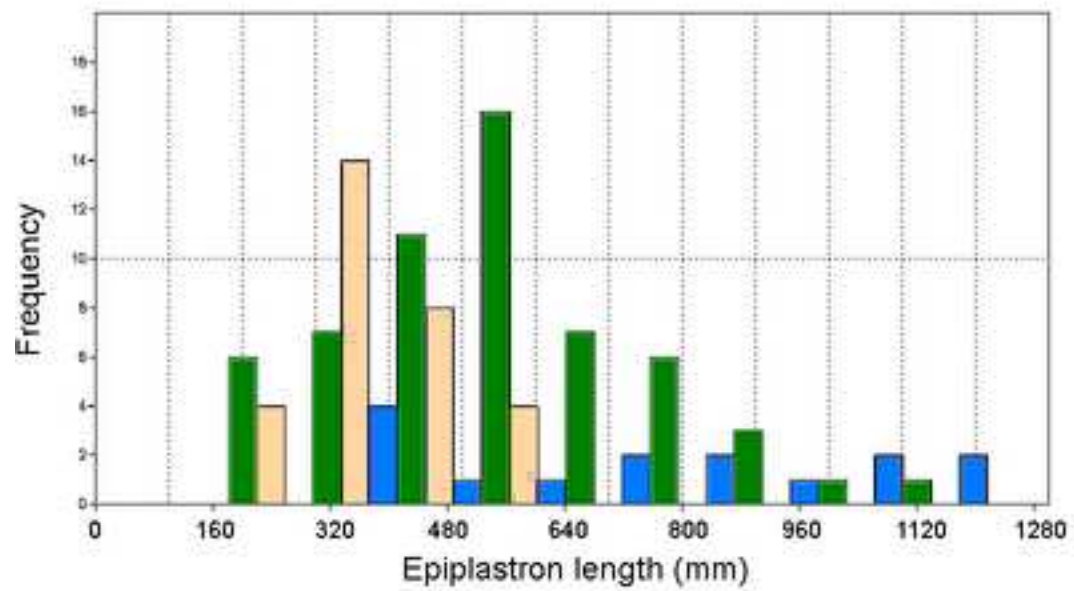
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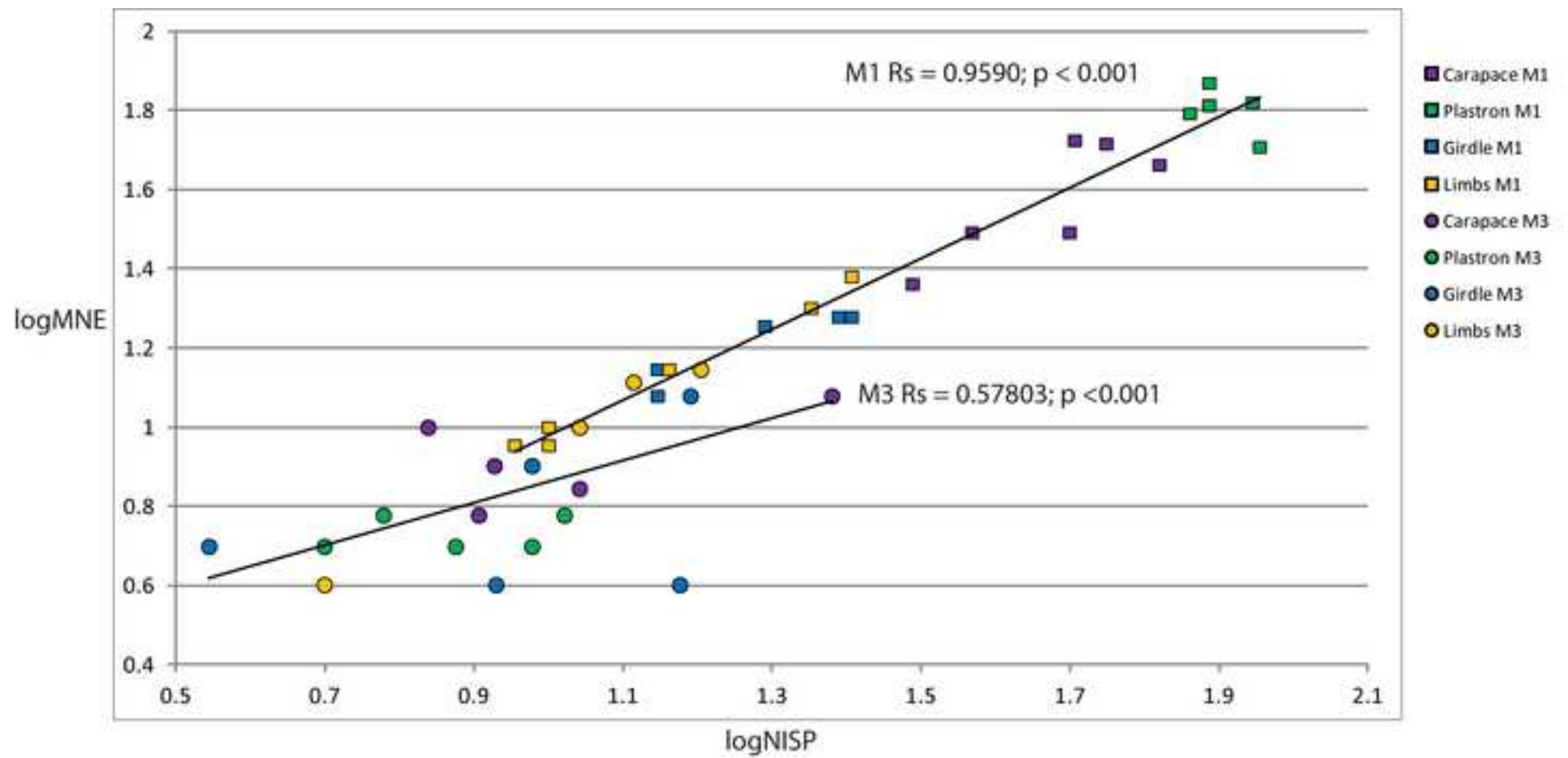
Figure 5

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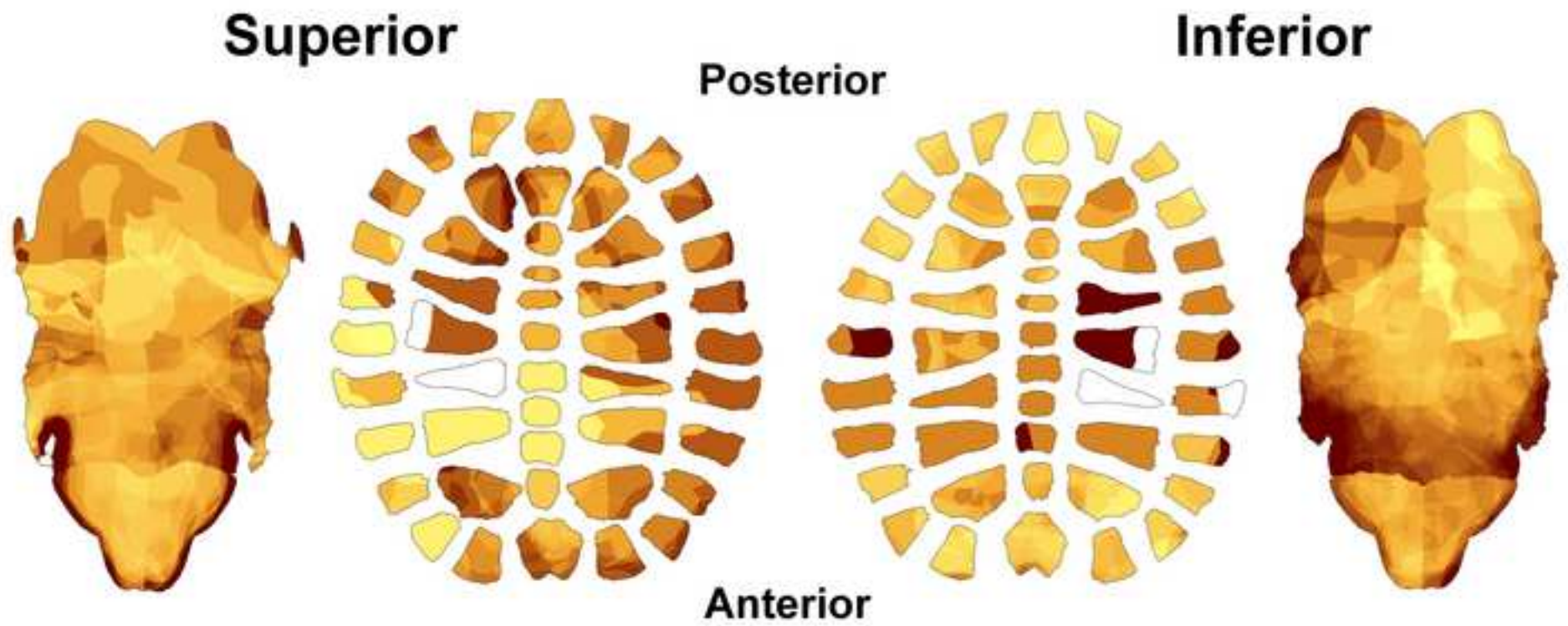
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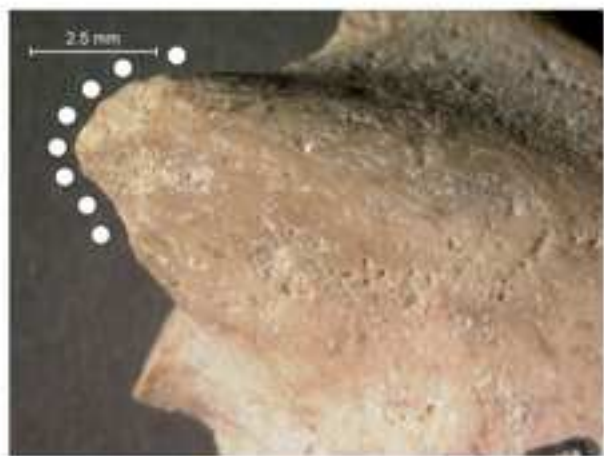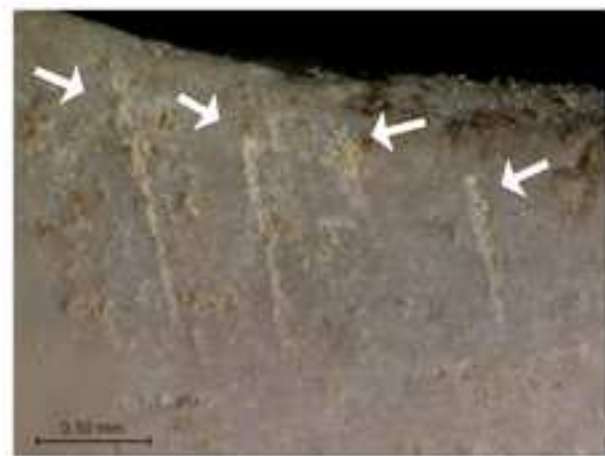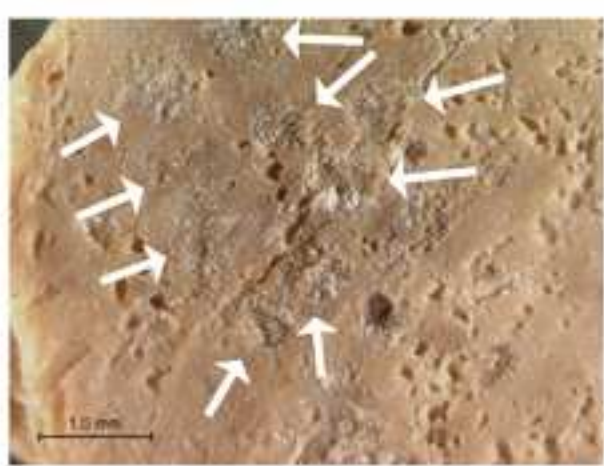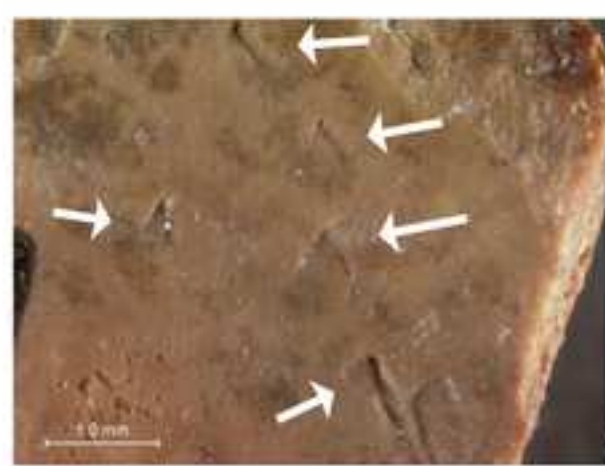
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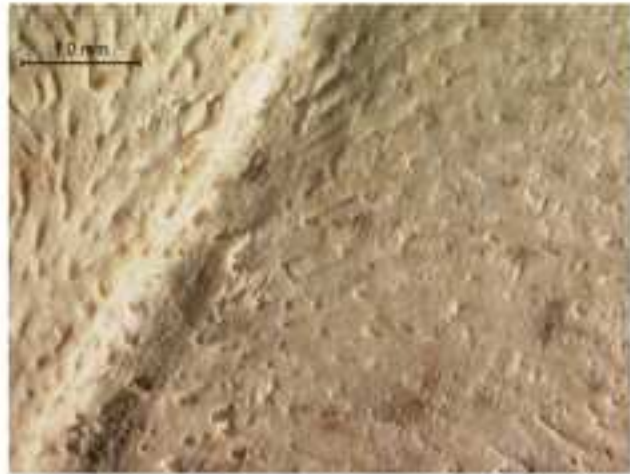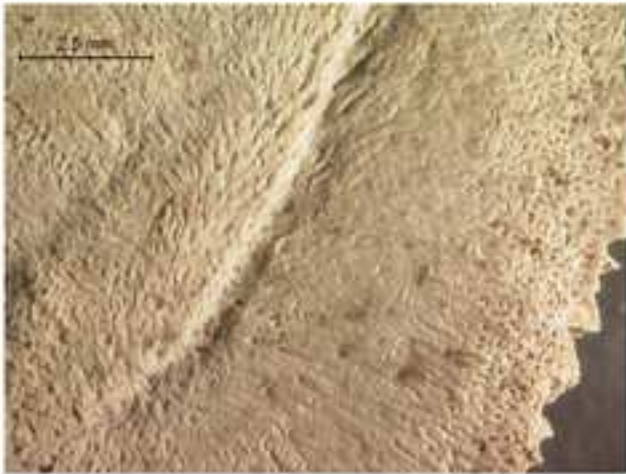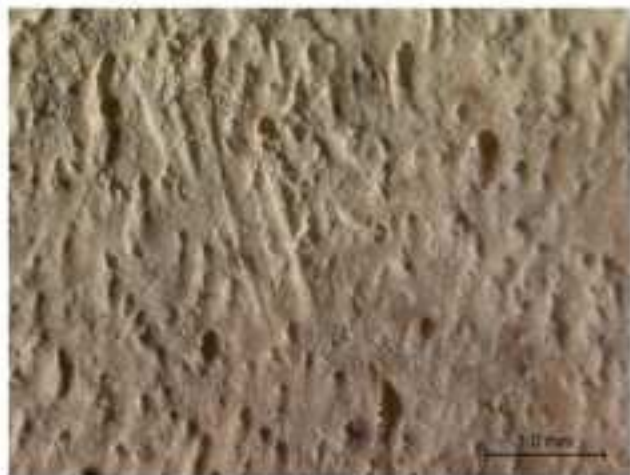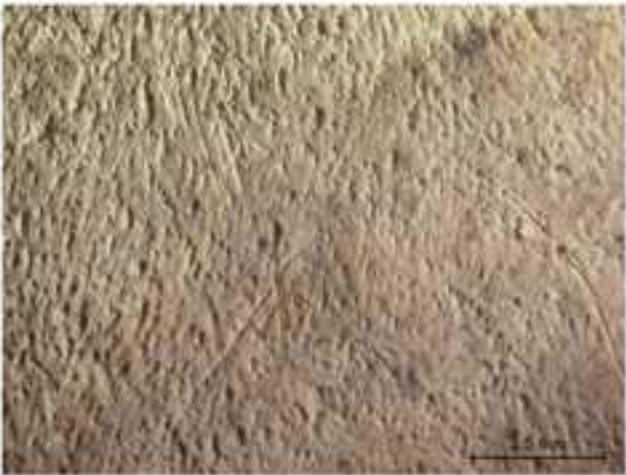Click here to download high resolution image

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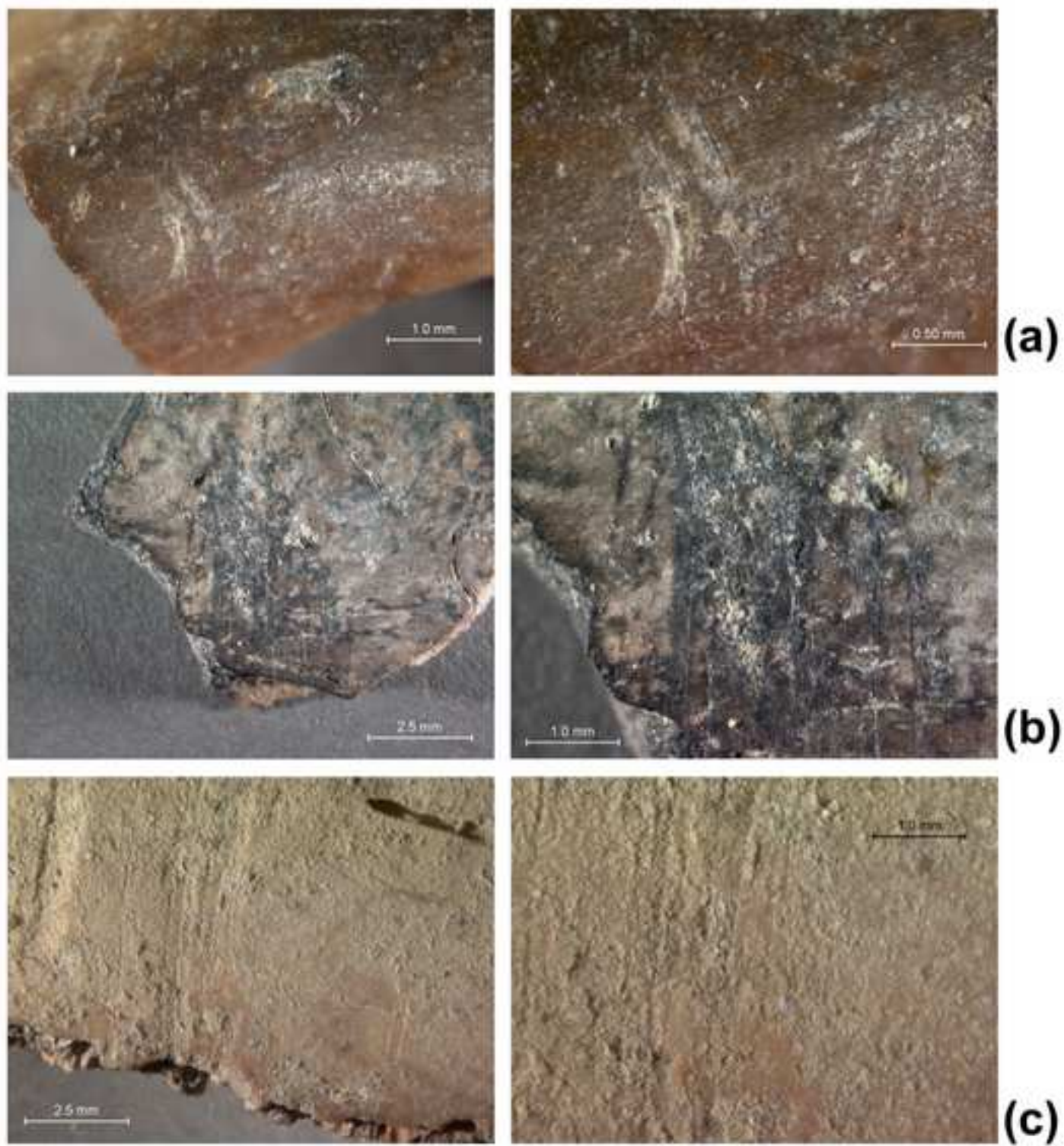
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Figure 10

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