DERMESTES MACULATUS AND *PERIPLANETA AMERICANA*: BONE MODIFICATION CRITERIA AND ESTABLISHING THEIR POTENTIAL AS CLIMATIC INDICATORS.

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A Dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Master of Science.

Johannesburg, 2012

DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

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(Signature of candidate)

___15th___day of ____March_____2013___in_____Johannsburg_____

ABSTRACT

Various insect taxa are known to modify bone with their mandibles, including members of the orders of Dermestidae, Tenebrionidae, Calliphoridae, Tineidae and Termitidae. Despite bone modification being a known behavioural trait of many of these taxa, little work has been done to record the distinctive ways in which they modify the bone surface, and a lack of concise descriptions of modification suites inhibits decisive identification and interpretation. The most widely inferred causal agents in palaeontological literature are either termites or dermestid beetles, whilst cockroaches as potential bone modifying agents have not yet been considered. The primary aims of this investigation were to establish whether or not cockroaches and dermestids modify bone, and if so in what ways, develop an interpretative framework to aid future researchers in the identification and differentiation between the variously reported agents of bone modifications, test whether or not the agents will modify bone of varying densities (thin cortical, thick cortical, compact and cancellous bone) or in a particular state of preservation/condition (fresh, dry, weathered or fossilised), and investigate whether or not the occurrence of insect modifications on bone can be used as a proxy to establish a broad climatic signature based on their known thermal physiological limits. A single experimental trial of 18 bone specimens were exposed to the African cockroach *Periplaneta americana* for a period of six months and a further four experimental trials (totalling 80 bone specimens) were exposed to the Coleopteran *Dermestes maculatus* for periods of four months each under the absence or presence of substrate and variable feeding conditions. Experiments were conducted within an insectary at 28° C, 40 % humidity and 12 hour light/ 12 of darkness. Subsequently, all specimens were viewed using an Olympus SZX 16 Multifocus microscope fitted with a digital camera at

magnifications between 7 and 115x. Three modification types were identified for *P. Americana*, namely discolouration, destruction of bone and gnawing. A total of five modification types were established for *D. maculatus* including the occurrence of surface tunnels, destruction of bone, bore holes, surface pits (Classes 1–3) and gnawing. Three distinctive surface pits morphologies were identified; Class 1 pits are highly variable but most often semi-circular to elliptical shallow depressions with a U-shape profile with striations radiating around the outer circumference of the depression. Class 2 surface pits are semi-circular shallow depressions with randomly orientated striations occurring over the entire feature. Class 3 surface pits are irregular shaped depressions with complex profiles not associated to gnawing striations. Broad climatic signatures for both of these agents were developed based on their known physiological thermal limits. The indistinct modification signature of *P. americana* in combination with limited occurrence and frequency patterns may prove difficult to identify from an archaeological or palaeontological context. *Periplaneta americana* and *D. maculatus* do significant damage to aves bones, which could result in their under representation in the archaeological and palaeontological records. The highly distinctive signature as well as occurrence and frequency patterns of modifications produced by *D. maculatus* has enabled the reinterpretation of existing palaeontological analyses, suggesting that dermestids are in fact not responsible for reported instances in which they are suggested as the causal agent during the Mesozoic and Cenozoic.

Dedicated to my grandparents

Douglas Haig and Elsie Parkinson

and

William and Joyce Hunter

as well as

my parents

Ray and Joyce Parkinson

ACKNOWLEDGMENTS

I would like to thank Dr Job Kibii (Institute for Human Evolution – University of the Witwatersrand Johannesburg) for providing me with a National Research Foundation grant holder linked bursary (2011 and 2012), the Palaeontological Scientific Trust (PAST) for funding (2011 and 2012), the University of the Witwatersrand for giving me Post Graduate Merit Award (2011 and 2012) and Dr L.R. Backwell for providing me financial support to purchase various pieces of equipment used during my experiments. I am extremely grateful to both of my supervisors (Dr Lucinda Backwell and Dr Job Kibii) for all of their support, encouragement, enthusiasm, scientific expertise, input, guidance and direction they have provided me over the last two years. I am thankful to Dr Christine Steininger for providing me with unprovenanced and unidentifiable fossil specimens from Coopers D deposits, to the Cohen family for allowing me access to their property to collect specimens, to the Professor Marcus Byrne at the University of the Witwatersrand for providing me with a dedicated insectary to conduct all experiments, to Dr Jean-Bernard Huchet for the identification of the *Dermestes* species and to my brother-in-law Reo Botes for donating the fresh Gemsbok skeleton. Additionally, I would like to thank Luke Norton for his regular assistance in the feeding and maintenance of the dermestid colony in my absence. I am eternally grateful to my father Ray Parkinson and my fiancé Megan Botha for proof reading my early drafts. To Ray, Megan and my mother Joyce Parkinson for their constant encouragement and interest, as well as to my wonderful children Simara and Coben Botha for their love and support, and to the rest of my friends and family for not complaining during the endless amount of hours they had to listen to me go on about this project and my research.

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LIST OF ABBREVIATIONS

g	gram
kg	kilogram
kJ	kilojoule
mm	millimetre
Mn	manganese
MPa	megapascal
mya	million years ago
n	sample size
SD	standard deviation
µm	microns
Zn	Zinc

CHAPTER ONE - INTRODUCTION

Ichnology is the study of traces of organismal behaviour and has developed into two distinctive branches; Palaeoichnology, which deals with the study of trace fossils and neoichnology, which is the study of modern traces. Ichnology arose as an independent scientific discipline in the 19th century with the first descriptive studies of foot prints as well as invertebrate traces. However, the Renaissance artist Leonardo da Vinci was the first person to use trace fossils to interpret palaeoenvironmental conditions (see Baucon, 2008, 2010). da Vinci was clearly the founding father of ichnology and his work was soon followed by that of other 16th century researchers such as Aldrovandi, Bauchin and Gesner who all identified, described and interpreted various palaeoichnological traces (Baucon, 2008, 2010).

Historically, palaeoichnologists have mostly focused on resting, dwelling, feeding or movement traces created by everything from terrestrial tetrapods to marine invertebrates (Gautier, 1993). With regard to terrestrial invertebrates a significant amount of literature pertains to burrows, nests or galleries which appear to be associated with a particular maker such as ants, termites or other terrestrial invertebrates (Genise, 1997; Hasiotis, 2003; Hasiotis, 2004; Bordy *et al.* 2004; Duringer *et al.* 2007). In addition, a large body of literature exists which describe modifications to bone by terrestrial invertebrates, particularly insects including members of the orders of Dermestidae (Gabel, 1955; Coe, 1980; Hefti, 1980; Kitching, 1980; Rogers, 1992; Martin and West, 1995; Hasiotis *et al.* 1999; Paik, 2000; Chin and Bishop, 2004; Hasiotis, 2004; Laudet and Antoine, 2004; Bader, 2005; Robinson, 2005; West and Hasiotis, 2007; Britt *et al.* 2008; Fernández-Jalvo

and Monfort, 2008), Tenebrionidae (Zacher, 1929; McFarlane, 1971), Calliphoridae (Kitching, 1980; Huchet and Greenberg, 2010), Tineidae (Zacher, 1929; Hill, 1987; Gentry, 1987) and Termitidae (Derry, 1911; Thorne and Kimsey, 1983; Hill, 1987; Watson and Abbey, 1986; Wylie *et al.* 1987; Gautier, 1993; Kaiser, 2000; Kaiser and Katterwe, 2001; Dangerfield and Britt, 2005; Fejfar and Kaiser, 2005; Guapindaia, 2008; Huchet *et al.* 2009; Parkinson, 2010; Parkinson *et al.* 2010a, b; Backwell *et al.* 2012).

In terms of the archaeological and palaeontological record, insect bone modifications have been widely identified on all major terrestrial vertebrate groups ranging from therapsids (Schwanke and Kellner, 1999) to mammals (Kaiser, 2000; Fejfar and Kaiser, 2005), including more recently, hominids (Huchet *et al.* 2009; Backwell *et al.* 2012). However, due to the nature of preservation conditions, few instances have been recorded in which bone modifications and the associated agent(s) have been preserved (except Huchet *et al.* 2009; Kirkland and Bader, 2007). This has ultimately resulted in modifications primarily being described and their makers either being attributed to 'insects' in general or intuitively inferring a particular insect (Tobien, 1965; Kubiak and Zakrzewska, 1974; Wood, 1976b; Hendey, 1981; Denys, 1986; Jordy and Standford, 1992; Jerykiewics *et al.* 1993; Newman, 1993; Kirkland *et al.* 1998; Paik, 2000; Getty *et al.* 2003; Genise *et al.* 2004; Nolte *et al.* 2004; Makovicky *et al.* 2005; Bader, 2005; Kirkland and Bader, 2007; Roberts *et al.* 2007; Britt *et al.* 2008; Saneyoshi *et al.* 2011).

The application of neoichnology in combination with experimental taphonomy has proved very useful and has prompted a distinctive change in the focus of palaeoichnological research. Experimental studies have been conducted on a variety of modern organisms, including birds (Genise *et al.* 2009), reptiles (Hembree and Hasiotis, 2006), terrestrial arthropods (Davis *et al.* 2007; Hembree, 2009; Hembree *et al.* 2012), fresh water Ostrocods (Retrum *et al.* 2011), cicada nymphs (Smith and Hasiotis, 2008), termites (Parkinson, 2010; Backwell *et al.* 2012) and many others, in order to understand their associated traces and develop interpretive frameworks for use by palaeoichnologists. Such studies have also been used to greatly enhance ecological, environmental and taphonomic interpretations (Dall Vecchia, 2008; Dashtgard, 2011; Backwell *et al.* 2012). However, a number of potential limitations of such studies have been identified, such as a lack of standardised descriptive vocabulary, limited comparative case studies, localised applicability, insignificant sample sizes, unrepeatability, and use of single instead of multiple agents to gauge the frequency and intensity of different agents producing similar modification types (Fisher, 1995; Denys, 2002). Despite the increasing experimental neoichnological studies aimed at interpreting trace fossils, little has been done to establish criteria for the identification and differentiation of bone surface modifications created by terrestrial invertebrates, particularly within an African context. Termites, ants and dermestids are by far the most widely inferred agents of bone modification, however, cockroaches have never been considered nor investigated as potential agents despite reported observations on carrion (Byrd and Castner, 2009).

The destructive impact termites have on bones was first reported from Egypt (Derry, 1911), where crania were nearly completely destroyed. Subsequently reports from

China (Light, 1929) and more recently complete skeletal destruction from funerary urns were found within the Amazonian rainforests of Brazil (Guapindaia, 2008). The Research from the Australian sub-continent has resulted in a diversity of literature on the impact of termites on faunal remains (Wood, 1976a, b; Wylie *et al.* 1987), while other cases have been reported from Kenya (Behrensmeyer, 1978), Panama (Thorne and Kimsey, 1983) and Peru (Huchet *et al.* 2009). The first experimental work involving the study of termite impact on bone was conducted by Watson and Abbey (1978), however, more comprehensive work was recently undertaken (Huchet *et al.* 2009; Parkinson, 2010; Parkinson *et al.* 2010a, b; Backwell *et al.* 2012). Backwell *et al.* (2012) warrant special mention as their comprehensive work on termites suggested that micro-environmental conditions as well as the season of deposition of the modified remains can be inferred by correctly identifying the modifying agent. Furthermore, termites as agents of bone modification could potentially bias taxonomic and skeletal element representation, minimum number of individuals as well as age profiles inferred from faunal remains that have been subjected to termite damage (Backwell *et al.* 2012).

Ants have also be suggested as potential agents of modification but the complexities of maintaining an ant colony within controlled laboratory conditions as well as the difficulties of setting up field based experiments, since most ants are subterranean, has likely resulted in a paucity of comprehensive studies. However, due to the close ecological niches that ants and termites occupy, such studies are imperative to address the shortcomings, and prevent erroneous interpretations (Hill, 1980; Parkinson, 2010; Backwell *et al.* 2012). The conflicting nature of existing literature, as well as the more recently proposed usefulness and potential that the

identification of insect modifications can contribute to both broader taphonomic, ecological and environmental reconstruction suggested by recent studies on termites (Parkinson, 2010; Parkinson *et al.* 2010a, b; Backwell *et al.* 2012), prompted the current investigations in which the cosmopolitan cockroach *Periplaneta americana* and the Coleopteran *Dermestes maculatus* are investigated.

This study aims to test whether or not cockroaches and dermestids modify bone, if so, document how they modify bone, and describe any modifications recorded in detail at a macro- and microscopic scale as well as their associated distributional patterns on the bones themselves. Forensic scientists have used invertebrate activities to reconstruct the timing and sequence of events of skeletal remains post mortem for centuries (Smith, 1986; Benecke, 2001; Byrd and Castner, 2009) and many established forensic techniques can be useful to palaeontologists (Bader, 2005; Bader *et al*. 2009). As such, this study also aims to clarify key aspects of taphonomic enquiry such as the most likely conditions of faunal remains at point of modification. Furthermore, to gauge the usefulness of reported insect thermal physiological limits as an indicator of broad climatic conditions. Lastly, this project sought to produce a comprehensive comparative collection of bones modified by the two agents concerned, which could be used to aid other researchers in the future identification of insect modifications on faunal remains.

The following hypotheses are posited for cockroaches:

1. They will modify the surface of bones.

2. They will modify bones in all states of preservation/condition (Fresh, dry, weathered, fossil) and of varying densities (thin cortical, thick cortical, cancellous and compact bone).
3. The bone surface modification distribution and types produced are distinguishable from dermestid and termite modifications.

The following hypotheses are posited for dermestids

1. They produce a variety of modifications on the surface of bones.
2. They will modify bones in all states of preservation/condition (fresh, dry, weathered, fossil) and of varying densities (thin cortical, thick cortical, cancellous or compact bone).
3. Modification distribution and types are distinguishable from those produced by cockroaches and termites.
4. Experiment A – Presence or absence of substrate
    5.1 An absence of substrate as pupation medium will increase bone modification frequency and distribution, as a result of the dermestids seeking out a suitable substance into which they can successfully/safely pupate.
    5.2 An absence of substrate as pupation medium does not impact on the types of modifications produced on bone.
5. Experiment B – Food availability
    6.1 The availability of food impacts negatively on the frequency and distribution of bone modification.
    6.2 The availability of food does not impact on the types of modifications produced.

1.1. Cockroaches (Insecta: Blattodea , Blattidae)

1.1.1. Phylogeny and the fossil record

Cockroaches, mantids and termites form the order Dictyoptera based on the common cranial feature of having a perforation in the tentorium, as well as having ootheca, a specialised casing for their eggs (Thorne and Carpenter, 1992; Inward *et al.* 2007a). Their exact interrelations have been debated for many years, however, it is broadly recognised that both termites and mantids constitute a monophyletic group, and that termites are in fact eusocial cockroaches, most closely related to the wood-feeding genus *Cryptocercus* (Lo *et al.* 2000; Maekawa and Matsumoto, 2000; Robinson, 2005; Klass and Meier, 2006; Lo *et al.* 2007a, b; Inward *et al.* 2007a, b; Legendre *et al.* 2008, Lo and Eggleton, 2010). The earliest fossil evidence of cockroaches dates back to roughly 400 mya and today roughly 4000 species have been described (Laurentiaux, 1951; Kambhampati, 1995; Robinson, 2005).

1.1.2. Cockroaches as potential agents of bone modification

The investigation of cockroaches as potential agents of bone modification was prompted by the fact that termites and cockroaches are closely related and that termites have a well documented behavioural tendency to modify bone. In spite of this, cockroaches have never been identified in succession studies on carrion, however, have been known to scavenge on carrion in an indoor environment (Byrd and Castner, 2009). Additionally, they have been reported to gnaw on callused skin, fingernails and toenails, as well as on the eyelashes of

humans, particularly children whilst sleeping (Byrd and Castner, 2009). Lastly, infants left unattended in unsanitary conditions have been found with flesh wounds which suggest cockroach feeding (Robinson, 2005; Byrd and Castner, 2009). The lack of identification of cockroach involvement in carrion reduction may potentially relate to their nocturnal behaviour, as to date no known nocturnal succession carrion experiments have been undertaken. Nonetheless, cockroaches are considered highly flexible in their food selection and utilization which is largely driven by resource availability (Geissler and Rollo, 1987; Robinson, 2005).

1.1.3. Identification, life cycle and ecology

This experiment utilised *P. americana* (Linnaeus, 1758). The name is deceiving as this species has an African origin (Robinson, 2005). However, it had already reached cosmopolitan distribution by the time it was first described in 1758. Their global distribution is believed to relate to the increase in maritime trade, as their existence was recorded from a shipwreck discovered off the Bermuda coast dating to 1625. Their natural habitats include moist areas, preferably leaf litter, underneath bark, and under bracts of palm trees in forested or undisturbed areas with dense vegetation, however, they are also found in caves and cohabiting burrows with millipedes or rodents (Gier, 1947; Cornwell, 1968; Bell and Adiyodi, 1981; Robinson, 2005).

Periplaneta americana are large shiny red-brown cockroaches with a yellow area around the posterior margin of the pronotum (Figure 1). The adult males range between 34–53 mm in length and their wings extend well beyond the tip of their abdomen, whilst females are 29–36 mm in length and their wings merely overlap the abdomen. The tip of the female abdomen has a ventral keel with a slit running along the center of it, however, both sexes have a well developed cerci although only males have a pair of ventral styles on the last abdominal sternite (Cornwell, 1968; Robinson, 2005). An ootheca can contain 14–16 eggs and range between 8–10 mm in length (Picker *et al.* 2004; Robinson, 2005). Nymph development ranges from 7–13 instars during 5–15 months at 25–30° C (Gier, 1947). Only 50 % of nymphs hatch, whilst only an estimated 30 % will ever reach maturity (Gier, 1947; Robinson, 2005). Mandibles display variation, adult males predominately have one primary cusp with up to three auxiliary cusps (Figure 2).

The geographical distribution of *Periplaneta americana* is substantial they are known to occur in small isolated or restricted habitats in the Neoarctic and Palaeoarctic, but are widely distributed in the Neotropical, Oriental, Ethiopian, and Australian zoogeographical regions (Appel *et al.* 1983). Considering this geographical distribution they clearly have adapted to highly diverse thermal climatic ranges. However, they are known to prefer a warm moist environment in which the upper limit of behavioural activities is 33° C, but their preferred temperature is between 24–28° C, but they are known to be active at 21° C. They can

survive temperatures of 36–38° C, but most individuals die at 39° C, whilst in less humid conditions death is more frequent at 37–38° C. Nymphs are known to be more active at lower temperatures (24–26° C), whilst adults are active at slightly higher temperatures (28–30° C), but activities are possible between 15–31° C for nymphs and 17–31° C for adults. They are known to stop foraging at temperatures close to 17° C and completely immobile (chill coma) at temperatures of 3–7° C for nymphs and 5° C for adults (Bradfisch *et al.* 1982). Their maximum heat tolerance is 42° C, at which temperature they experience heat paralysis and die. Adult life span at 29° C is 90–706 days for females and only 90–362 days for males (Cornwell, 1968; Bell and Adiyodi, 1981; Robinson, 2005). Experiments have shown that once loss of locomotory capacity (chill-coma) is reached at 5-10° C (Bradfisch *et al.* 1982). To recover from chill-coma if temperatures rise to as much as 30° C they need to be kept at this temperature for as much as 20 hours before they become active again. Conversely, if kept at 30° C and then moved to 15° C it takes 2–3 days before they become acclimatised and begin to be moderately active (Cornwell, 1968).

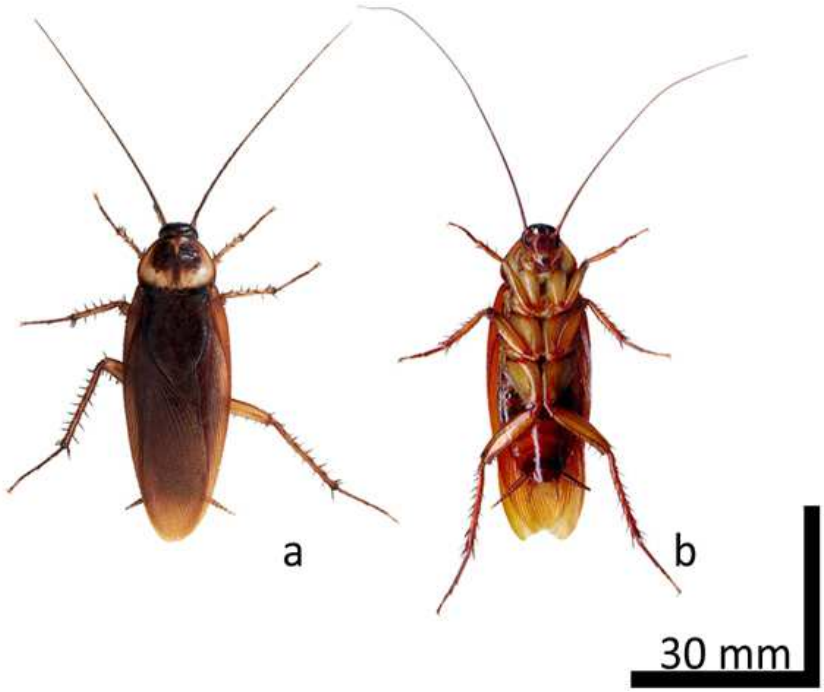

Figure 1: Adult male *P. americana* in dorsal (a) and ventral view (b).

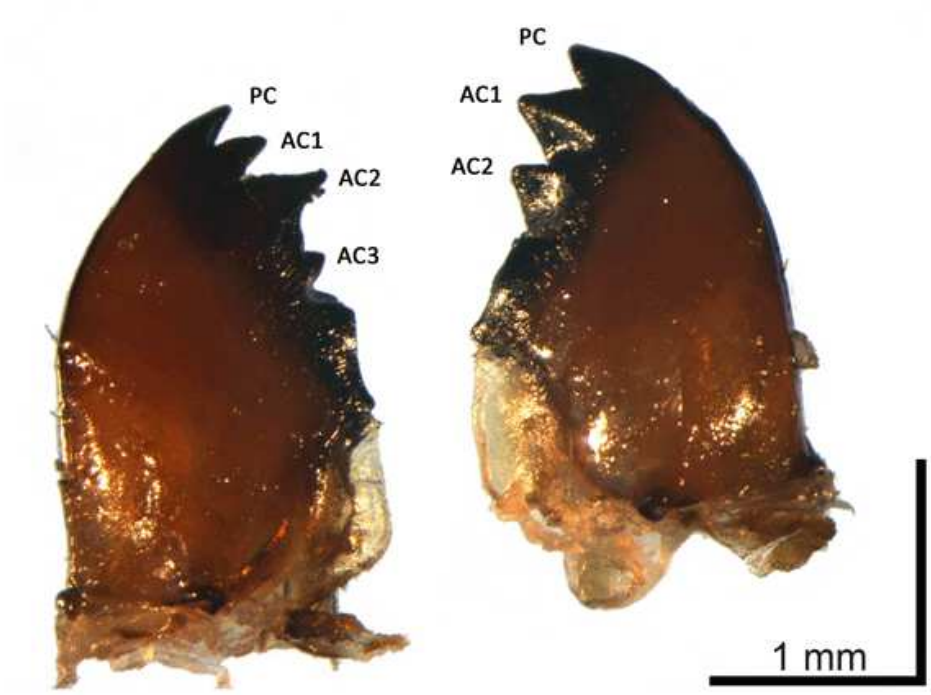

Figure 2: A pair of mandibles removed from an adult male *P. americana* displaying one primary cusp (PC) and two or three auxiliary cusps (AC1 – AC3).

1.2. Skin/Museum/Larder beetles (Insecta: Coleoptera, Dermestidae)

1.2.1. Phylogeny and the fossil record

The Family Dermestidae belongs to the Order Coleoptera, and the genus *Dermestes* was first described by Linnaeus in 1758. The oldest recognised Dermestidae date to Late Triassic deposits in Queensland, Australia (Dunstan, 1923), however, their associated dating is contentious (Kiselyova and McHugh, 2006; Kadej and Hava, 2011). Cretaceous specimens identified in Burmese amber are more reliably dated (Kiselyova and McHugh, 2006) and a phylogenetic analysis of extant larval morphology also supports a Late Cretaceous origin (Kiselyova and McHugh, 2006). Currently, Dermestidae comprise between 700–880 described species of which the vast majority are considered xerophilous necrophages, which distinguishes them from nearly all other insects (Kiselyova and McHugh, 2006; Zhantiev, 2009; Foottit and Adler, 2009).

1.2.2. Dermestids as potential agents of bone modification

The role of dermestid beetles in animal decomposition is well documented; they are known to consume soft sub-dermal tissue and skin, hence their name *Dermestes* derived from the Greek to “consume skin” (Cornaby, 1974; Smith, 1986; Byrd and Castner, 2009). There are also sporadic reports of them directly affecting human health by causing

papular urticaria (skin reaction), conjunctivitis or irritation of the respiratory system, through to ingestion of spicules which are shed by the larvae (Rustin and Munro, 1984). Their involvement in animal decomposition and associated consumption of dry and decomposing animal matter typifies members of the *Dermestes* genus. Due to this behaviour they are often used for stripping carcasses of meat for skeletal collections and are widely regarded as doing little damage to delicate bones (Howell, 1932; Borell, 1938; Voorhies, 1948; Hooper, 1950; Hefti *et al.* 1980; Timm, 1982; Weichbrod, 1987). However, despite actualistic references to them damaging bone (Fernández-Jalvo and Monfort, 2008), little direct evidence has been documented to suggest the ways in which such modifications occur, which would aid in their identification from an archaeological or palaeontological context. Existing literature can be divided into two primary bodies; one associated with the establishment, operation and maintenance of dermestid colonies for the cleaning of skeletal material, and the other palaeontological, in which articles describe insect modifications and infer dermestids as the most likely agent.

Cleaning of skeletal material

Howell (1932) and Borell (1938) state categorically that even skulls of minute sizes are cleaned without the slightest damage to the most delicate of processes. Howell (1932) goes on to state that the tympanic bullae of mouse-sized skulls are are infrequently eaten by the beetles, possibly in search of blood, processes are not broken off, delicate

structures are not destroyed, teeth do not fall out, and sutures do not gape even in the youngest of specimens. Voorhies (1948) states that after being exposed to dermestids for a number of weeks even delicate bat skulls (e.g. *Myotis*) are removed without any harm and cleaned to absolute perfection. However, experiments conducted by Hefti *et al.* (1980) found that once available food sources have been depleted the beetles begin to destroy specific areas, particularly the iliac crest of the pelvis as well as vertebrae but does not allude to which vertebrate group he is referring to. Hefti et al. (1980) goes on further to state that when bones are modified by dermestids that sufficient bone is removed and it is immediately obvious to the naked eye. Osuji (1975) states that *D. maculatus* larvae may bore into the flesh of dried fish, but do not bore into either their bones or skulls. More recently a forensic entomologist reported damage by *D. maculatus* larvae to both the humerus and the acetabulum of a human skeleton recovered from indoor conditions (Schroeder *et al.* 2002). However, unlike the vast body of palaeontological literature which suggests that dermestids modify bones in a number of distinctive ways, particularly the creation of pupation chambers or distinctive borings, the actualistic literature makes absolutely no mention to such features.

Roberts and Rogers (2003) conducted a study aimed at establishing modification criteria to bone by dermestids whilst measuring the influences of food availability, food type and substrata in increasing/decreasing bone modification. Tentative results suggested

that a wide variety of modification types were produced by dermestids, including oval-shaped borings into cortical bone and irregular excavations into trabecular (spongy) bone, however, preference was shown for marrow cavities of long bones. The most interesting observation was that the identified suite of modifications differed markedly from those attributed to dermestid beetles in the palaeontological literature (Roberts and Rogers, 2003). Furthermore, it was suggested that the identification of dermestid modifications could potentially serve as an indicator of a stressed habitat where food availability and nesting substrate are limited (Roberts and Rogers, 2003).

More recently, whilst investigating various skeletal preparation techniques it was established that *Dermetes sp.* can destroy bone, make grooves, holes and chew-marks (Fernández-Jalvo and Monfort, 2008). Despite providing scanning electron microscope images of the modifications identified, the qualitative descriptions provided by Fernández-Jalvo and Monfort (2008) are limited in their application for identification and particularly differentiation of dermestid modifications from other reported agents. Kenneth Bader, whist working with dermestid colonies, observed that dermestids often remove the periosteum from cortical bone. However, the majority of destruction occurred on softer cancellous bone, particularly Aves bones, but also on articular facets of mammal bones (Kirkland and Bader, 2010). However, to date no comprehensive descriptions of *Dermestes* modifications have been published that could be used to differentiate such modifications

when compared to those created by other potential terrestrial invertebrate agents.

Palaeontological literature of dermestid modifications to bone

Kitching (1980) described three long bone shaft fragments from Member 3 of the lime works at Makapansgat, dated to 2.90–3.32 MYA (Mcfadden *et al.* 2002), which displayed extensive bore holes. The bore holes ranged from 4–5 mm in diameter, and based on the limited literature available to aid in identification, he tentatively assigned the agent as a species of the family Dermestidae. Similarly, Paik (2000) identified borings on dinosaur bones from Korea, which ranged from a few millimetres to 10 mm in diameter, and proposed dermestid beetles as the most likely agent. It was further suggested that dermestid beetles played an important role as the last scavengers of dinosaur carcasses during the Early Cretaceous, and potentially that such activities may have negatively affected fossil preservation. Backwell *et al.* (2012) made similar suggestions in relation to termites affecting taxonomic and element representation in Plio-Pleistocene cave sites in Africa.

Bone modifications identified from the Upper Jurassic Morrison Formation were attributed to dermestids, and the modifications included grooves, both shallow and deep pits, shallow and deep borings and furrows. Furrows occurred primarily on spongy bone, which either damaged or completely destroyed the majority of the available articular surfaces (Britt *et al.* 2008). This study considered previous descriptions

of modifications to bone by termites, and tineid moths as not being comparable to the current suite of modifications represented in their sample. The authors concluded that dermestid beetles were the most likely agent, which was motivated by the modification striations appearing to be paired, suggesting that the agent in question had two apical teeth which came into contact with the bone surface. The occurrence of two apical teeth per mandible in extant *D. maculatus* (Figure 3) was then used to confirm the identification of dermestids as the responsible agent of modification (Britt *et al.* 2008).

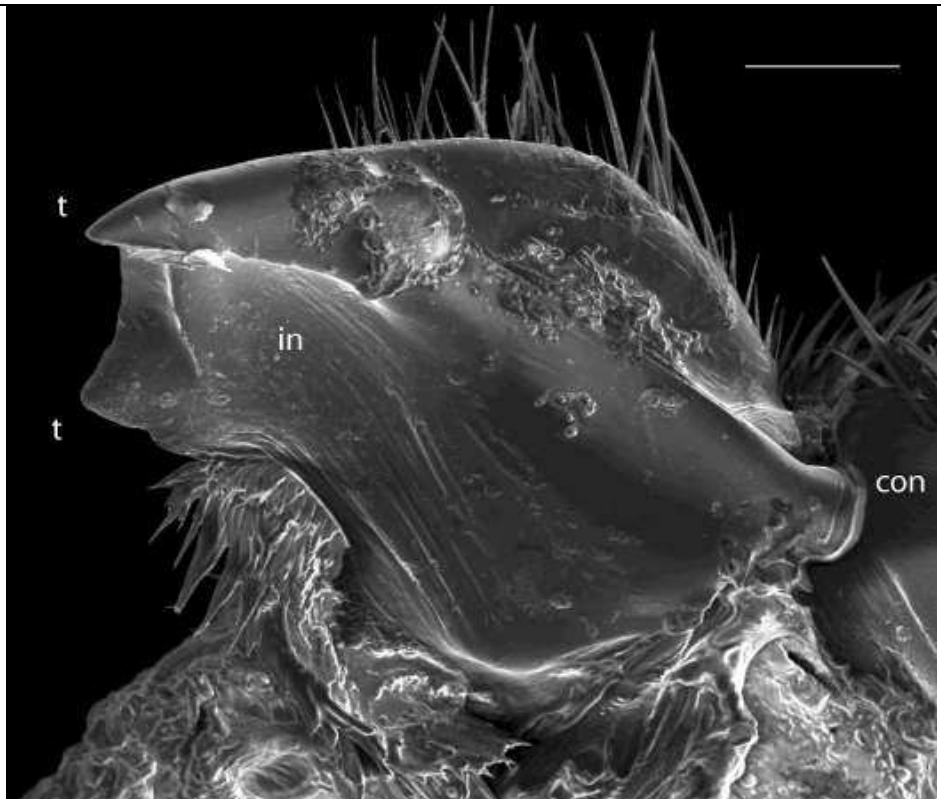

Figure 3: *D. maculatus* adult mandible in ventromedial view. The mandible is didentate with the two apical teeth separated by a concave incisor area. Scale bar = 100 µm (From Britt *et al*, 2008).

Pupation chambers are often identified on palaeontological remains, and dermestid beetles are the most widely inferred agent of modification (Kitching, 1980; Martin and West, 1995; Hasiotis *et al.* 1999; Chin and Bishop, 2004; Hasiotis, 2004; Laudet and Antoine, 2004; Bader, 2005; West and Hasiotis, 2007). Even though the occurrence and identification of dermestid modifications on bone are not very common, it has been suggested that such modifications could be used to infer various taphonomic and climatic conditions (Martin and West, 1995). A wide variety of borings have been attributed to dermestid pupal chambers with little direct evidence to support such claims, other than simply intuitive inference. None the less, the pupation chambers are said to be flask shaped, almost exactly the size of the larvae's body, while the neck of the chambers are often short, and not deeply constructed (Martin and West, 1995).

While Martin and West (1995) infer that the distribution, shape and size of the burrows are consistent, and as such are a good criterion for the identification of dermestid pupation chambers/burrows, it was also highlighted that the size of chambers can be dependent upon climate, in that larger pupation chambers are indicative of warmer climate. It is suggested that should pupation chambers be comprehensively studied they may enable more specific climatic conditions to be inferred (Martin and West, 1995). However, factor which is not mentioned is the availability of food stuffs (see Roberts and Rogers, 2003), which also affects the size of the larval forms.

1.2.3. Identification, life cycle and ecology

Dermestes ater, D. carnivorus, D. frischii and *D. maculatus* are all known to consume bone (Gable, 1955; Robinson, 2005). In fact, the majority of species within the genus *Dermestes* are xerophilous necrophages, which scavenge on vertebrate carcasses, whilst few species are known to focus on invertebrate carcasses. Additionally, they are known to have specific carcass size preferences, ranging from very large animals to small reptiles, amphibians, birds or mammals however the mechanisms which drive such selection preferences have not been studied scientifically (Braack, 1987; Robinson, 2005). Coastal species will feed on both fish carrion and other aquatic animals (Zhantiev, 2009), however, it has been noted that *D. maculatus* prefers freshwater fish carrion, and that coastal fish carrion are usually completely unattractive to this particular species, which likely relates to the higher presence of salts (Picker *et al.* 2004; Robinson, 2005).

In sufficient numbers, dermestids have been known to reduce a human body to bones within as little as 24 days (Byrd and Castner, 2009). They are typically found on carcasses during the dry and skeletal stages of decomposition and are most active during the warmer months. Adult dermestid beetles are known to occupy carrion as early as the bloat stage of decomposition but in very low numbers whilst their numbers gradually increase during the decay stage and then peak during the dry stage (Smith, 1986; Braack, 1987; Byrd and Castner, 2009). Experiments by von Hoermann *et al.* (2011) have shown that benzyl butyrate is a

primary volatile responsible for the attraction of adult male *D. maculatus* during the bloat stage (9 days after death, T_{mean} = 27° C). This attraction event leads to the production of sexual or aggregation pheromones by males, responsible for the attraction of adult females (von Hoermann *et al.* 2011).

Following Howell (1932) experiments showed that within a roughly 30 day larval stage, the first 20 days are dedicated to constant eating associated with rapid growth (Russell, 1947), days 20–25 are spent excavating a site into either meat or wood to provide a safe place to pupate, and those forced to pupate in the open are susceptible to attack by other beetles apart from dermestids (Russell, 1947; Braack, 1987). Experimentation has shown that inter- and intra- specific cannibalism may be of pivotal importance favouring the use of protective pupation sites and that larva delay the onset of pupation when a secure pupation site cannot be located (Archer and Elgar, 1998). Larvae are, however, negatively phototropic, which limits the conditions under which they optimally feed (Smith, 1986; Weichbrod, 1987; Byrd and Castner, 2009). A complete reproductive cycle takes place over roughly 45 days, at 29°C, and is subdivided accordingly; egg three days, larva 30 days, pupa seven days, and five days as an adult before laying (Russell, 1947). However, this is dependent on both temperature and humidity (Weichbrod, 1987).

Dermestes maculatus, the species used during this investigation, was first described by De Geer in 1774 and now has a cosmopolitan distribution (Robinson, 2005; Byrd and Castner, 2009). The adults (Figure 4c, d) range from 5–10 mm in length, whilst fully grown larvae (Figure 4a) are between 10–14 mm. The adult beetles are black to reddish brown on their dorsal side and characterised by white and black markings on their ventral side, whilst the larvae are dark brown and display broad light brown to yellow bands extending lengthwise along their body. Adults can live up to 171 days, however, high temperatures and low humidity will negatively affect their life span. Females can produce between 200 and 800 eggs, hatching occurs within two to six days and larval development ranges from 19–50 days, with instars ranging between six and nine moults, all dependant on temperature (Smith, 1986; Osuji, 1975; Picker *et al.* 2004; Robinson, 2005; Byrd and Castner, 2009).

Pupal chambers (Figure 4b) are constructed after larvae have bored into a hard substrate (Robinson, 2005), however, when no suitable pupation medium is available dermestids often pupate in the open. When wood is used as pupation medium, chambers are said to be constructed quickly, and that the associated tunnels rarely intersect, however, when they do they are quickly abandoned and an alternative site is selected (Archer and Elgar, 1998).

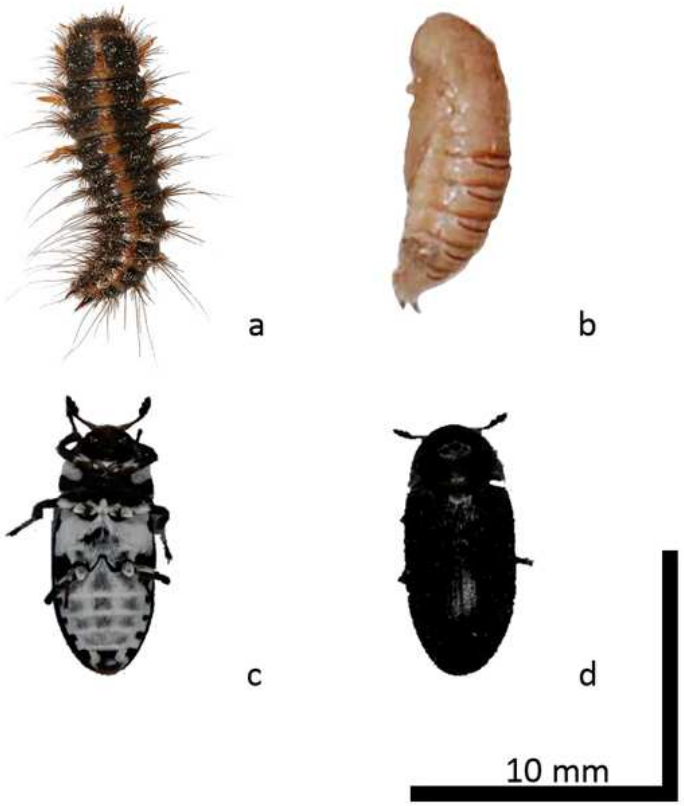

Figure 4: Developmental stages of *D. maculatus*. a – larva, b – pupal case, c – adult male beetle in ventral view, d – adult male beetle in dorsal view.

Optimal reproductive success for *D. maculatus* occurs between 30–35° C with a minimum temperature for foraging/feeding of 20° C, whilst for *D. frischii* optimal reproduction takes place between 31–34° C, and any foraging/feeding activities are halted below 22° C (Howe, 1965; Richardson and Goff, 2001). *Dermestes ater* eggs do not hatch at 15° C or below, whilst only 40 % hatch at temperatures of between 25–35° C, and 17 % at 37.5° C (Coombs, 1981). Similar temperature ranges have also been reported for *D. haemorrhoidalis, D. lardarius* and *D. peruvianus* (Coombs, 1978, 1979).

Hillerton *et al.* (1984) established using atomic absorption spectroscopy that the cutting edge of adult beetles, mandibles was dominated by the presence of Manganese (Mn) or Zinc (Zn). Manganese was shown to be dominate in the following species of *Desmestes; D. ater, D. frischii, D. haemorrhoidalis, D. lardarius, D. maculatus* and *D. peruvianus*. It is likely that the presence of Manganese provides additional hardness to the mandibles much like Zinc (Zn) is said to add to hardness to the mandibles of herbivorous insects (Hillerton *et al.* 1984).

1.3. Using insects modifications as a proxy for inferring prevailing climatic conditions

Insects are poikilothermic, so their metabolism and behavioural activities are dependent on prevailing environmental conditions. This has been widely recognised since the pioneering experimental work conducted during the 1930's on thermal thresholds in insects (Krogerus, 1932; Bertram, 1935; Mellanby, 1939). It is accepted that both extremely low and high temperatures can be damaging or even lethal, but even temperatures within those limits have a profound impact on performance and fitness (Elias, 1991; Hellqvist and Lemdahl, 1996; Huey, 2010; Gullan and Cranston, 2010; Hazell and Bale, 2011).

The relationship between climate and insect activities may prove useful if the exact agent of bone modification can be determined. The identification could then be augmented with a thorough understanding

of the particular species physiological thermal limits such as; chill coma as well as upper and lower lethal temperature limits. The combination of this data would be a good starting point from which broad climatic signatures could be inferred for the period during which bone modification took place.

The literature pertaining to thermal physiological limits of insects is extensive but recently Hazell and Bale (2011) stated that chill coma refers to a clearly defined physiologyical state whose onset includes a series of behavioural and physiological events. A brief summary of behavioural indicators of the various stages include; impairment of muscular function, loss of coordination [chill coma [4 & 3]], entry into chill coma is associated to jerking movements [chill coma [2]], chill coma itself is seen as the complete absence of movement [chill coma [1]] (Bradfisch *et al.* 1981; Hazell and Bale, 2011). The precise temperature at which chill coma occurs is variable between species but seems to be depends on the temperature to which the individuals/populations had previously been acclimated and the duration of exposure to low temperatures (Bradfisch *et al.* 1981). Furthermore, the process is reversible as long as the duration of chill coma is less than the critical limit beyond which survival becomes impossible, or that the temperature does not continue to fall to lethal limits (Hazell and Bale, 2011).

Insects could over a relatively short period of time acclimatise to variable conditions depending on the thermal history of the population

one example can be taken from Addo-Bediako *et al.* (2000) who stated that an insect was recorded to have switched from being freezing intolerant to freezing tolerant over a period of a year. Furthermore, it has been noted that the physiological responses by insects to temperature variability are often unpredictable (Gatson & Chown, 1999). Similarly, upper and lower lethal temperature limits are also variable and variations are often clear-cut between different species based on their associated thermal physiology (Gatson & Chown, 1999; Drodzicki & Caputa, 2005).

Exposure to temperatures resulting in chill coma or death can also be buffered by various thermoregulatory behaviours e.g. overwintering, habitat selection, altering geographical ranges or adjusting daily activity times (Elias, 1991; Hellqvist and Lemdahl, 1996; Parmesan *et al.* 1999; Huey, 2010; Gullan and Cranston, 2010; Hazell and Bale, 2011). An instance of alter geographical range was reported by Coope (1979) who showed that in response to frequent glacial/interglacial cycles during the Late Cenozoic Coleopterans changed their geographical ranges substantially and that this allowed them to keep the conditions in which they lived more or less constant. An understanding of overwintering strategies could allow winter to be excluded as a possible season of bone modification, for example temperate insect species are known to have some form of winter diapause. More specifically, winter diapause in univoltine species is obligatory but in multivoltine species it is

facultative being initiated by either abiotic or biotic triggers (Ward and Masters, 2007).

The above considerations of variation in thermal physiological limits (chill-coma, upper and lower thermal lethal limits) and variation in thermoregulatory behaviours, can either be seen as limitations or potentialities in terms of using insects as palaeo-climatic indicators. In some instances thorough research may be readily available on specific species of insects which could then in turn be used to better construct the prevailing climatic conditions during the period in which bones were modified. However, there is general scarcity of modern research on insect thermal limits and very little work in general has been done on African insects.

Lastly, the application of modern data in interpreting the fossil record should perhaps be restricted to no later than the Quaternary from which fossil insects are identical to living species (Coope, 1979). Though, it may be possible to push the application of modern data as far back as the Late Miocene as many species known from this period are most likely ancestral to living forms (Coope, 1979).

CHAPTER TWO - MATERIALS AND METHODS

All experiments used one or more trials comprising a variety of bone specimens representing bones of varying densities and in different states of preservation/condition to establish whether the insects where able to modify bones in all states. A total of 98 specimens were used and allocated specimen numbers ranging from 1 to 142. Note that not all number in this range has an associated bone specimen. The specimens were divided into 5 trials (C1, D1–D4). When more than one trial was used in a single experiment all bone specimens were specifically selected to be as comparable as possible in terms of size and skeletal element represented. Trial C1 was exposed to *P. americana* for 6 months. The particulars of each specimen (bone density, condition, element, etc.) are summarised in Table 1. Trials D1 and D2 were used during dermestid Experiment A and trials D3 and D4 were used during dermestid Experiment B, the particulars of the each specimen are summarised in Tables 2, 3, 4 and 5 respectively. Trials D1–D4 were placed within experimental tanks containing *D. maculatus* under different substrate/feeding conditions for a period of four months each.

Table 1: Specimens in trial C1 that were exposed to *P. americana* for a period of six months.

Spec. No.	Taxon	Element	Portion	Bone Density	Condition	Fig. No
125	Indet. bovid	Metapodial	Shaft fragment	Thick cortical	Fossil	5
126	Indet.	Indet.	Shaft fragment	Thin cortical	Fossil	5
127	Indet.	Tooth	Root fragment	Tooth	Fossil	5
128	Indet. bovid	Metacarpal	Shaft fragment	Thick cortical	Dry	5
129	Indet. bovid	Femur	Shaft fragment	Thin cortical	Dry	5, 12
130	Indet. bovid	Femur	Shaft fragment	Thick cortical	Weathered	5
131	Indet. bovid	Metapodial	Shaft fragment	Thin cortical	Weathered	5
132	Indet. bovid	Phalanx	Complete	Compact	Dry	5, 14, 15
133	Indet. bovid	M^2	Near complete	Tooth	Weathered	5
134	Indet. bovid	P_3	Complete	Tooth	Dry	5
135	Indet. bovid	Rib	Complete	Spongy	Weathered	5, 13, 17
136	Indet. bovid	Rib	Complete	Spongy	Dry	5
137	*D. pygargus*	Pelvis	Fragment	Thin cortical	Fresh	5
138	*D. pygargus*	Rib	Shaft fragment	Spongy	Fresh	5, 11
139	*D. pygargus*	Humerus	Shaft fragment	Thick cortical	Fresh	5, 10
140	*D. pygargus*	Tarsus	Complete	Compact	Fresh	5
141	*G. domesticus*	Humerus	Complete	Variable	Fresh	5
142	*G. domesticus*	Ulna	Complete	Variable	Fresh	5, 10, 16

Indet. – Indeterminate, D. – *Damaliscus,* G. – *Gallus*, M^2 – second molar, P_3 – third premolar. Variable = specimens with more than one bone density represented, Weathered = Stages 1-2 following Behrensmeyer, 1978.

Table 2: Specimens in trial D1 (Experiment A) that were exposed to *D. maculatus* in a tank without substrate for a period of four months.

Spec. No.	Taxon	Element	Completeness	Bone Density	Condition	Fig. No
1	*O. aries*	Scapula	Complete	Variable	Dry	6, 38
2a	*O. aries*	Radius	Complete	Variable	Dry	6
2b	*O. aries*	Ulna	Complete	Variable	Dry	6, 28
3	Indet. bovid	Tibia	Shaft fragment	Thick cortical	Dry	6
4	*O. aries*	Humerus	Shaft fragment	Thin cortical	Dry	6
5	*O. aries*	Tarsus	Complete	Compact	Dry	6, 26
6	*O. aries*	Rib	Complete	Spongy	Dry	6, 39
7	Indet. bovid	Vertebrae	Complete	Spongy	Weathered	6
8	Indet. bovid	Phalange	Complete	Compact	Weathered	6
9	Indet. bovid	Humerus	Distal epiphysis	Variable	Dry	6, 24
10	Indet.	Tibia	Shaft fragment	Thick cortical	Fossil	6
11	Indet. bovid	Indet.	Shaft fragment	Thin cortical	Fossil	6
12	Indet. bovid	Indet.	Enamel fragment	Tooth	Fossil	6, 34, 35, 40
13	*O. aries*	M^2	Complete	Tooth	Dry	6
14	*B. domesticus*	P^4	Complete	Tooth	Weathered	6
15	Antidae sp.	tibiotarsus	Complete	Variable	Dry	6, 22
16	Phocid sp.	Femur	Complete	Variable	Dry	6
17	*G. domesticus*	Femur	Complete	Variable	Fresh	6, 27
18	*D. pygargus*	Rib	Fragment	Spongy	Fresh	6
19	*D. pygargus*	Tibia	Shaft fragment	Thick cortical	Fresh	6
20	*D. pygargus*	Femur	Proximal epiphysis	Variable	Fresh	6, 22, 31

***O.* – *Ovis*, Indet. – Indeterminate, *B.* – *Bos*, *G.* – *Gallus*, *D.* – *Damaliscus,* M^2 – second molar, P^4 – fourth premolar. Variable = specimens with more than one bone density represented, Weathered = stages 1-2 following Behrensmeyer, 1978.**

Table 3: Specimens in trial D2 (Experiment A) that were exposed to *D. maculatus* in a tank with 50 mm of sterilised substrate for a period of four months.

Spec. No	Taxon	Element	Completeness	Bone Density	Condition	Fig. No
22	*O. aries*	Scapula	Complete	Variable	Dry	7, 29, 32, 33
23a	*O. aries*	Radius	Complete	Variable	Dry	7
23b	*O. aries*	Ulna	Complete	Variable	Dry	7, 36
24	Indet. bovid	Metapodial	Shaft fragment	Thick cortical	Dry	7
25	*O. aries*	humerus	Shaft fragment	Thin cortical	Dry	7
26	*O. aries*	Tarsus	Complete	Compact	Dry	7
27	*O. aries*	Rib	Complete	Spongy	Dry	7
28	Indet. bovid	Vertebrae	Complete	Spongy	Weathered	7
29	Indet. bovid	Phalange	Complete	Compact	Weathered	7
30	Indet. bovid	Humerus	Distal epiphysis	Variable	Dry	7, 23
31	Indet.	Indet.	Shaft fragment	Thick cortical	Fossil	7
32	Indet.	Indet.	Shaft fragment	Thin cortical	Fossil	7
33	Indet. bovid	Indet.	Enamel fragment	Tooth	Fossil	7
34	*B. domesticus*	P^4	Near complete	Tooth	Weathered	7
35	*O. aries*	M^2	Near complete	Tooth	Dry	7
36	Antidae sp.	Tibiotarsus	Complete	Variable	Dry	7
37	Phocid sp.	Femur	Complete	Variable	Dry	7
38	*G. domesticus*	Femur	Complete	Variable	Fresh	7, 30, 37
39	*D. pygargus*	Rib	Fragment	Spongy	Fresh	7
40	*D. pygargus*	Tibia	Shaft fragment	Thick cortical	Fresh	7
41	*D. pygargus*	Femur	Proximal epiphysis	Variable	Fresh	7

***O.* – *Ovis*, Indet. – Indeterminate, *B.* – *Bos*, *G.* – *Gallus*, *D.* – *Damaliscus*, P^4 – fourth premolar, M^2 – second molar. Variable = specimens with more than one bone density represented, Weathered = stages 1-2 following Behrensmeyer, 1978.**

Table 4: Specimens in trial D3 (Experiment B) that were exposed to *D. maculatus* in a tank with 50 mm of substrate, which received 100 g of canned meat twice a week for a period of four months.

Spec. No.	Taxon	Element	Completeness	Bone Density	Condition	Fig. No.
85	*O. aries*	Scapula	Complete	Variable	Weathered	8, 25
86	*O. aries*	Femur	Distal epiphysis	Variable	Dry	8
87	Indet. bovid	Metacarpal	Shaft fragment	Thick cortical	Dry	8
88	Indet. bovid	Metapodial	Shaft fragment	Thin cortical	Dry	8
89	*O. aries*	Tarsus	Complete	Compact	Dry	8
90	Indet. bovid	Rib	Fragment	Spongy	Dry	8
91	Indet. bovid	Rib	Fragment	Spongy	Weathered	8
92	Indet. bovid	Phalanx	Complete	Compact	Weathered	8
93	Indet. bovid	Tibia	Shaft fragment	Thick cortical	Fossil	8
94	Indet.	Metapodial	Shaft fragment	Thin cortical	Fossil	8
96	Indet. bovid	Tooth	Root fragment	Tooth	Fossil	8
97	*B. domesticus*	P_3	Near complete	Tooth	Weathered	8
98	*O. aries*	P_3	Complete	Tooth	Dry	8
99	Aves sp.	Humerus	Complete	Variable	Dry	8
100	Phocid sp.	Femur	Complete	Variable	Dry	8
101	*G. domesticus*	Femur	Complete	Variable	Fresh	8
102	*D. pygargus*	Rib	Shaft fragment	Spongy	Fresh	8
103	*D. pygargus*	Tibia	Shaft fragment	Thick cortical	Fresh	8
104	*D. pygargus*	femur	Distal epiphysis	Variable	Fresh	8

***O.* – *Ovis*, Indet. – Indeterminate, *B.* – *Bos*, *G.* – *Gallus*, *D.* – *Damaliscus*, P_3 – third premolar. Variable = specimens with more than one bone density represented, Weathered = stages 1-2 following Behrensmeyer, 1978.**

Table 5: Specimens in trial D4 (Experiment B), exposed to *D. maculatus* in a tank with 50 mm of substrate, which received 50 g of canned meat twice weekly for a period of four months.

Spec. No	Taxon	Element	Completeness	Bone Density	Condition	Fig. No
95	Indet. bovid	Tooth	Enamel fragment	Tooth	Fossil	9
106	*O. aries*	Scapula	Near complete	Variable	Dry	9
107	*O. aries*	Femur	Distal epiphysis	Variable	Weathered	9
108	Indet. bovid	Metacarpal	Shaft fragment	Thick cortical	Dry	9
109	*O. aries*	Metapodial	Shaft fragment	Thin cortical	Dry	9
110	*O. aries*	Tarsus	Complete	Compact	Dry	9
111	Indet.	Rib	Fragment	Spongy	Dry	9
112	Indet. bovid	Phalange	Complete	Compact	Weathered	9
113	Indet.	Indet.	Shaft Fragment	Spongy	Weathered	9
114	Indet. bovid	Tibia	Shaft fragment	Thick cortical	Fossil	9
115	Indet.	Indet.	Shaft fragment	Thin cortical	Fossil	9
116	*B. domesticus*	P_3	Complete	Tooth	Weathered	9
117	*O. aries*	P_4	Complete	Tooth	Dry	9
118	Phocid sp.	Femur	Complete	Variable	Dry	9
119	Aves sp.	Humerus	Complete	Variable	Dry	9
120	*G. domesticus*	Femur	Complete	variable	Fresh	9
121	*D. pygargus*	Rib	Shaft fragment	Spongy	Fresh	9
122	*D. pygargus*	Tibia	Shaft fragment	Thick cortical	Fresh	9
123	*D. pygargus*	femur	Distal epiphysis	Variable	Fresh	9

O. **– *Ovis*, Indet. – Indeterminate, *B.* – *Bos*, *G.* – *Gallus*, *D.* – *Damaliscus,* P_3 – third premolar, P_4 – fourth premolar. Variable = specimens with more than one bone density represented, Weathered = stages 1-2 following Behrensmeyer, 1978.**

The primary selection criteria for the bone specimens were condition (wet, dry, weathered, fossilised) and bone density (thin cortical, thick cortical, cancellous and compact bone). Certain specimens (e.g. complete long bones) display a variety of different bones densities and as such were classified as “variable”. When applicable, the distribution of modifications were described in terms of the area (periosteal, medulla, edge), and density in which they occurred, expressed as a percentage of the total available surface area of the bone specimen effected. Skeletal element, taxon, and bone portion were also recorded for each bone specimen. Skeletal elements included teeth, phalanges, ribs, pelves, humeri, tarsus and ulnae. Source taxa were primarily *Gallus domesticus* (chicken), *Damaliscus pygargus* (blesbok), *Ovis aries* (sheep), *Bos domesticus* (cow) and/or *Sus domesticus* (pig). Unidentified dry or fossil, large-sized bovid specimens are simply referred to as ‘bovid’, indicating animals in the range 23–84 kg (after Brain, 1974). The portion of bone was recorded as a complete or near-complete element, shaft fragment, proximal or distal epiphysis. All dry and weathered bone specimens were selected from field collections, fresh specimens were sourced from a local butchery or taken from a *D. pygargus* skeleton donated to the project as a result of a private hunting trip, and fossil specimens were sourced from unprovenanced and unidentifiable remains from the early hominin-bearing cave site of Coopers D, situated in the Cradle of Humankind, South Africa.

All experimental tanks used were kept within a dedicated insectary at the department of Animals, Plants and Environmental Sciences at the University of the Witwatersrand. The insectary maintained a temperature of 28 °C at 40 % humidity, with 12 hours of light and 12 hours of darkness.

The pre-experiment and analytical protocols documented below were standard across all experiments and are presented first. However, certain materials used and experimental protocols undertaken were particular to only a single experiment and as such have been detailed under dedicated subsections of this chapter.

Standard pre-experiment protocol

Prior to exposure to either *D. maculatus* or *P. americana*, all bone specimens were allocated a specimen number and labelled using a permanent marker. All specimens where photographed in both ventral and dorsal view on a high resolution flatbed scanner, and the resulting images printed in full colour. The specimens were scanned for two reasons; firstly to aid in the post experiment identification of the specimens, should the specimen numbers no longer be visible, and secondly, the printed images were used to record any existing surface modifications identified on the bones. Any existing features (e.g. a carnivore tooth mark on a dry bone) that could potentially be misinterpreted as insect modification were identified using a light microscope at magnifications between 7 and 115x, recorded on the printed images, and used for reference purposes during the data collection stage.

Standard analytical protocol

Initially all specimens were visually inspected to see if any macroscopic modifications were discernible, thereafter they were inspected using an Olympus SZX 16 Multifocus microscope at magnifications between 7 and 115x, fitted with a digital camera. All surface modifications were recorded on a Microsoft Excel spread sheet. A total of 123 digital micrographs of modifications displayed on specimens from trials C1, D1 to D4 were acquired. The data were then analysed and

modification types were established, qualitatively described and measured using 'analyse IT' image processing software linked to the Olympus SZX Multifocus microscope. All measurements were recorded in microns (µm) but the actual measurements taken depended on the feature being measured. All measurements were initially captured into a Microsoft excel spread sheet, and then put into IBM SPSS Statistics version 20 for statistical analysis. SPSS was used to determine descriptive statistics as well as to conduct Mann-Whitney U tests between the various samples. All raw data and test results obtained from SPSS have been included in Appendix A. Macroscopically visible modifications are considered modifications that can be seen with the naked eye, intermediate modifications can be seen at relatively low magnifications ranging from 7–20x, whilst microscopic modifications can only be seen at magnifications higher than 20x.

Definitions of terms used in the text

Modification Types

Bore holes – Deep semi-circular holes which may or may not have a discernible bottom. Penetrating through cortical or cancellous bone, and in to the medullary cavity or burrowing through the underlying trabecular bone.

Destruction – Obliteration of bone, completely destroying cancellous bone or articular facets, removal of cortical bone resulting in the roughening of the associated surface area or resulting in exposure of

	the underlying trabecular bone.
Discolouration –	Staining of the periosteal surface.
Gnawing –	Clusters of sub-parallel or parallel striations close to an edge, or clusters of irregularly orientated striations which cover a large surface area.
Surface pits –	Class 1: Highly variable in shape, however, most often semi-circular to elliptical shallow depressions with a U-shaped profile that have striations radiating from around the outer circumference of the depression. Class 2: Semi-circular shallow depressions with randomly orientated, often intersecting, striations occurring over the entire feature. Class 3: Irregular-shaped depressions with complex profiles not associated with striations.
Surface tunnels –	Shallow furrows with a U-shaped profile excavated across the surface of a bone. Bore holes may occur at either one or both ends of the furrow. Primarily occurring as a single furrow, however, occasionally as a complex of interconnected furrows.

Visibility Categories

Intermediate modifications –	Visible at low magnifications ranging from 7–20x.
Macroscopic modifications –	Visible with the naked eye.
Microscopic modifications –	Visible at magnifications greater than 20x.

Other descriptive terms

Modification distribution – The anatomical location of the modification types e.g. on the epiphysis or at the diaphysis-epiphysis junction.

Modification frequency – Number of modifications represented on a single bone specimen e.g. 4 bore holes recorded on one bone.

Modification occurrence – Modification types represented on a specimen of particular condition and bone density.

Modification type – Morphologically distinctive feature identified during the course of this investigation.

Substrate – Sterilised fine-grained river sand used at the base of experimental tanks, on top of which trials C1, D2, D3 and D4 were placed.

2.1. *Periplaneta americana* experiment

2.1.1. Materials

Trial C1 was used during this experiment and specimens were allocated numbers ranging from 125–142. The particulars of the specimens are summarised in Table 1, whilst the cortical thickness of bones identified as thin/thick cortical bone were measured and summarised in Table 6. A fish tank measuring 600x300 mm with 50 mm of substrate at its base was populated with thirty *P. americana*, provided with 100 g of bran and Pronutro© mixture as well as a bowl of water, whilst discarded egg boxes were used as housing. To allow sufficient air circulation, wooden

frames were constructed using 38x38 mm pine treated with creosote (wood preservative for protection against fungal decay and wood boring insects), and a double layer of 2 mm mosquito netting was used to cover the top of the tank to prevent escape.

2.1.2. Experimental protocol

Once all pre-experiment protocols had been completed the bone specimens were randomly scattered across the available surface area of the tank (Figure 5) and remained untouched by the experimenter for a period of six months. The only interference involved opening the tank to refill the water container, or to provide additional food. After the specimens were removed the standard analytical protocol was followed.

Figure 5: Layout of experimental specimens from trial C1 (125–142) at the start of the project, in a tank exposed to *P. americana* for a period of six months.

2.2. *Dermestes maculatus* experiment

2.2.1. Materials

A total of four fish tanks measuring 600x300 mm were used to facilitate Experiments A (presence of substrate) and B (food availability). Two fish tanks where used as breeding tanks to establish a colony of *D. maculatus*, whilst the other two tanks where used for experimentation purposes. Wooden framework lids where constructed using 38x38 mm pine branding, the wood was treated with creosote to prevent dermestids from boring into it and the top of the frames were covered with a double layer of 2 mm mosquito netting to prevent escape. Experiments A and B did not run concurrently, hence the same two fish tanks were used for both, and were populated with equal numbers of *D. maculatus*. In both experiments each trial (D1 through D4) was exposed to a total of 100 larvae (instars 4 or 5) and 35 adult beetles.

Trials D1 and D2 were used in Experiment A and trials D3 and D4 where used for Experiment B. The particulars of the specimens are summarised in Table 2, 3, 4 and 5, whilst the cortical thickness of bones identified as thin/thick cortical bone were measured and are presented in Table 6. The spatial arrangement of specimens (trial D1–D4) within the experimental tanks is shown in Figures 6, 7, 8 and 9.

2.2.2. Experimental protocol

The first priority was to establish a successful breeding colony. A single breeding tank was established with 50 mm of sterilised substrate placed at the bottom of the tank to allow for easy pupation. Fifteen larvae were placed in the tank, ranging in size between instars 3 and 4. It was noticed that the larvae tended to climb up the silicone used to glue the glass panels together in the inner corners of the tank. This facilitated their escape as they could easily squeeze through the 2 mm mosquito mesh used to cover the top of the tank. Hence the top 100 mm of the silicon on the inner corners of all tanks was removed, which prevented the larvae's escape.

A single brand of canned meat was selected for use during both experiments; "TOP ONE – Corned Meat" which contains meat (beef, mechanically deboned poultry, beef and sheep hearts), water, soya protein, corn starch, salt, brown sugar, spices, flavour enhancers (MSG, E621, E635), an antioxidant (ascorbic acid E300) and curing agent (sodium nitrite E250). According to the packaging, its typical nutritional information per 100 g portion is protein 12.7 g, carbohydrates 9.7 g, total fat 7.8 g, salt 1.8 g and energy 658 kJ.

The canned meat was used as the primary food source during the establishment of the breeding colony as well as throughout the duration of the experiments. In reference to the breeding colony, the amount of food provided increased as the population density increased, from 100 g

twice a week to 300 g (full tin) every second day. Due to the high temperature within the insectary the surface of the canned meat dried out completely within 48 hours of exposure, and as such the food was replaced every three days. Dry cotton wool was placed in the tanks to serve a variety of functions (others authors have used paper tissues see Braack, 1987). Not only did the cotton wool slow down the drying out of the canned meat, it also provided an excellent medium for the larvae to hide and pupate, and for the adults to lay their eggs in. However, the use of cotton wool made the cleaning of the tanks difficult.

After a three month period the breeding population within the first tank had substantially increased making it impossible to physically count the number of larvae within the breeding tanks. At this time the population was divided between the initial tank and an additional breeding tank without substrate at the bottom using cotton wool as a pupation medium. After a further three months of running both breeding tanks their population density had reached overwhelming proportions. Due to the sheer size of the populations it became costly to provide them with canned meat as each tank could consume a complete tin of canned meat within 24 hours. During this time other food sources became available through the head veterinarian at the Johannesburg zoo, who donated a partially defleshed adult male lion and two still born day-old striped hyaena pups to the Bernard Price Institute for Palaeontological Research for their modern skeletal comparative collection. The defleshed lion bones dried as quickly as the canned meat, hence

frequent rehydration was needed by soaking the bones briefly in water and replacing them in the tank. The complete hyaena pups were completely stripped of all flesh or ligamentous remnants within seven days of exposure and did not require rehydration.

Experiment A

Hypothesis: An absence of substrate as pupation medium increases bone modification frequency and distribution.

Hypothesis: An absence of substrate as pupation medium does not affect the represented modification types, between the two trials.

Trials D1 and D2 were used during this experiment, and prior to exposure all bones were allocated specimen numbers (Trial D1: 1–20, Trial D2: 22–41). Two tanks were established, one tank had no substrate and trial D1 was scattered across the glass at the bottom of the tank (Figure 6), while the other tank had 50 mm of sterile substrate placed at the bottom of the tank, on top of which trial D2 was scattered randomly across the surface (Figure 7). Each tank was then populated with a total of 100 larvae (variable instar stages) as well as 35 adult beetles. The total exposure period was four months, which ensured at least three breeding cycles. The amount of food provided to the individual tanks remained constant throughout the exposure period with 100 g of canned meat provided twice a week to each tank.

Experiment B

Hypothesis: The lack of food increased the frequency and distribution of bone modification.

Hypothesis: The availability of food does not impact on the types of modifications produced.

Trials D3 and D4 were used during this experiment and prior to exposure all bone specimens were allocated specimen numbers (Trial D3: 85–94, 96–104, Trial D4: 95, 106–123). The two tanks used during Experiment A were emptied, thoroughly cleaned and reused during this experiment. The bottoms of both tanks were filled with 50 mm of sterilised substrate. The tanks were then populated with a total of 100 larvae (instars 4 or 5) as well as 35 adult beetles. Trial D3 was scattered across the surface of the substrate (Figure 8) and this particular tank received 100 g of canned meat twice a week, whilst trial D4 was scattered across the surface of the substrate at the bottom of the other tank (Figure 9) and received only 50 g of canned meat twice a week.

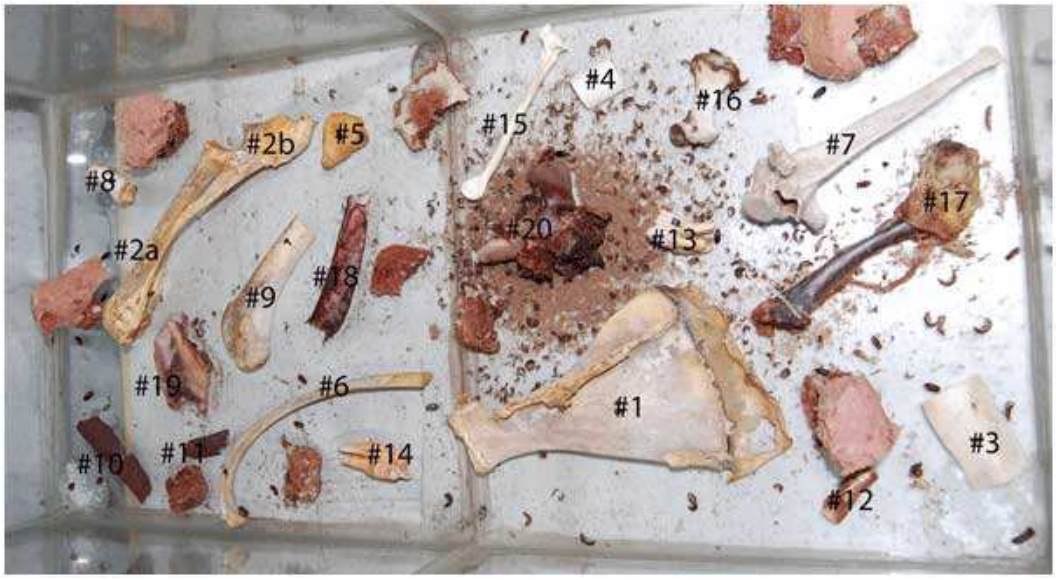

Figure 6: Layout of trial D1 (1–20) exposed to *D. maculatus* for four months, with no substrate at the bottom of the tank.

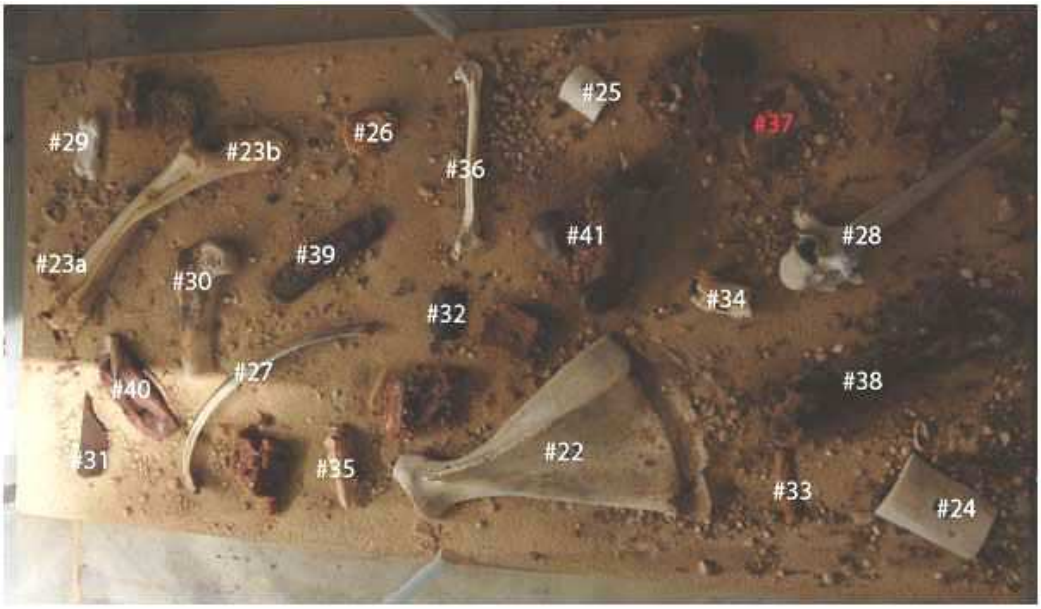

Figure 7: Layout of trial D2 (22–41) exposed to *D. maculatus* for four months, with 50 mm of substrate at the bottom of the tank, 37 disappeared from the lab and was not included in the final analysis.

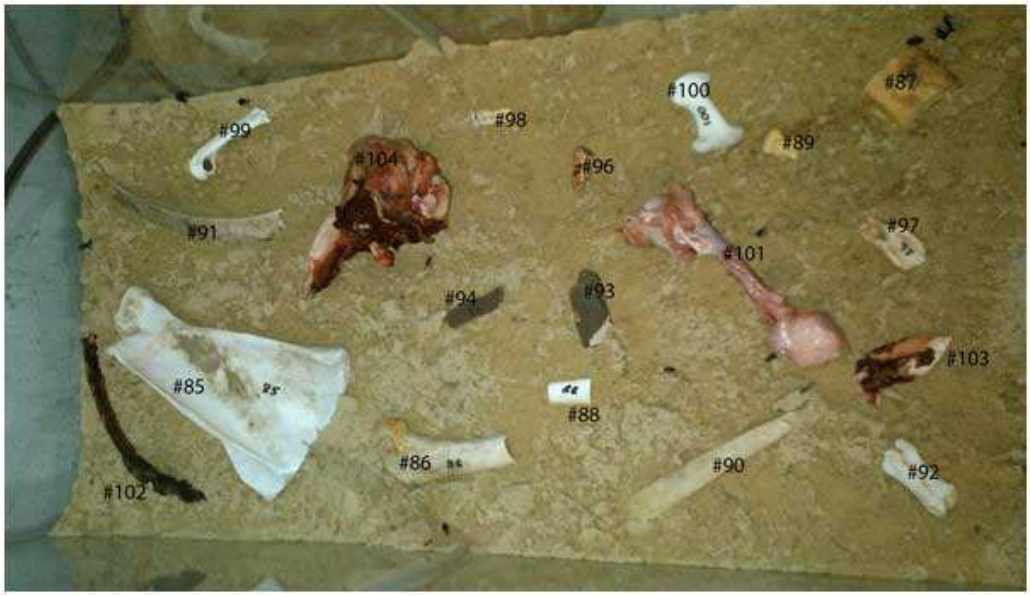

Figure 8: Layout of trial D3 (85–94, 96–104) exposed to *D. maculatus* for four months, whilst receiving 100 g of canned meat twice a week.

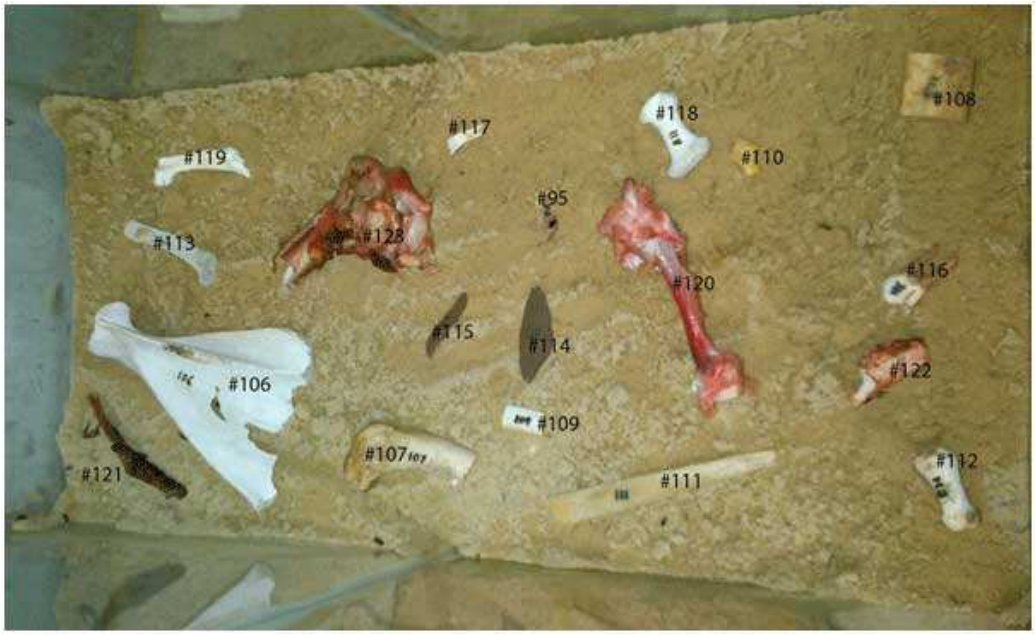

Figure 9: Layout of trial D4 (95, 106–123) exposed to *D. maculatus* for four months, whilst receiving 50 g of canned meat twice a week.

Table 6: Cortical thickness of all specimens recorded as either thin or thick cortical bone for all trials.

Trial	Specimen Number	Class	Thickness
C1	125	Thick	4–5 mm
	126	Thin	2.5–4 mm
	128	Thick	7.5 – 10 mm
	129	Thin	2.5 – 4 mm
	130	Thick	5.5 – 9 mm
	131	Thin	3.5 – 5 mm
	137	Thin	2 - 2.5 mm
	139	Thick	3.5 - 5.5 mm
D1	10	Thick	7 – 8 mm
	11	Thin	3 – 4 mm
	3	Thick	7 – 9 mm
	4	Thin	2 – 3 mm
D2	24	Thick	7 – 9 mm
	31	Thick	5 – 7 mm
	32	Thin	3 – 4 mm
	25	Thin	2 – 4 mm
D3	87	Thick	10 – 11 mm
	88	Thin	2 – 3 mm
	93	Thick	6 – 7 mm
	94	Thin	3.5 – 4.5 mm
	103	Thick	3 – 4 mm
D4	108	Thick	7 – 8 mm
	109	Thin	1.5 – 2.5 mm
	114	Thick	5 – 6 mm
	115	Thin	3.5 – 4.5 mm
	122	Thick	4 – 5.5 mm

CHAPTER THREE - RESULTS

3.1. *Periplaneta americana*

3.1.1. Behavioural observations during experimental run

Within seconds of exposure the cockroaches approached the fresh *G. domesticus* bone and *D. pygargus* shaft fragments (Figure 10). On the chicken bone they appeared to be consuming the remaining flesh, while on the *D. pygargus* shaft fragment they focused on the exposed marrow, consuming it from both ends and clambering on top of one another to get to it. This was the first time that they were not disturbed by the light, as on all prior occasions the moment the light was switched on they immediately scrambled into the egg box housing structures. The meat was attractive enough for them to risk being exposed in the light and remain unprotected. A single individual was seen scouting all the recently introduced bones, briefly eating meat on a fresh single chicken bone, and scouting the fresh rib and pelvic fragment before returning to the *D. pygargus* marrow cavity, a process that was repeated by this individual more than once.

Within 48 hours all the remnants of meat on fresh specimens had dried, but this didn't prevent the cockroaches from remaining on the specimens and feeding on the dried fleshy remnants. During the vast majority of visits to the insectary, which was every second day, cockroaches were spotted on a variety of fresh bone specimens, however, they were most frequently sighted on the specimen with marrow present, a fresh rib fragment (Figure 11), as well as the fresh chicken bones. Within six weeks of exposure the cockroaches seemed to be "sniffing" around the specimens, but were rarely seen consuming any of the exposed specimens. One thing that did become apparent was the constant movement of bone specimens which either slightly shifted or became partially buried in the substrate.

Figure 10: *P. americana* feeding on a fresh *D. pygargus* shaft fragment (specimen no. 139) and a *G. domesticus* long bone (specimen no. 142) within seconds of the specimens being place in the tank.

Figure 11: *P. americana* feeding on a *D. pygargus* rib (specimen no. 138) after six weeks of exposure.

3.1.2. Modification types created by *P. americana*

A total of three modification types were recorded, including discolouration, destruction and gnawing. Discolouration refers to the staining of the periosteal surface, so it is not strictly speaking a bone modification type, but rather a feature of cockroach activities. Destruction refers to the obliteration of bone (completely destroying cancellous bone and articular facets, or removal of cortical bone resulting in the roughening of the associated surface area), whilst gnawing refers particularly to clusters of sub- and parallel striations close to an edge. Discolouration and destruction were considered macroscopically visible whilst gnawing was microscopic in nature. Tables 7 and 8 shows the modifications recorded on trial C1.

A total of ten out of 18 specimens displayed no signs of modification after a period of six months. Specimen 127 was never recovered post experiment and hence has been excluded from any calculations, which brings the total number of specimens analysed to 17. Discolouration of the bone surface, recorded as a percentage of surface area cover, was identified to varying degrees on seven out of eight specimens (not 142), whilst only four (132, 136, 141 and 142) displayed destruction, and gnawing related striations were only identified on one specimen (135).

Table 7: Macroscopically visible modifications recorded on trial C1 after a period of six months exposure to *P. americana*.

Specimen no.	Macroscopic Feature							Macroscopic Modification						
	Discolouration	Location			Position	Degree of Visibility	Category % Cover	Destruction	Location			Position	Degree of Visibility	Category % Cover
		P	M	E					P	M	E			
125*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
126*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
127	X	X	X	X	X	X	X	X	X	X	X	X	X	X
128	Y	Y	-	-	X	Clr	<5 %	-	-	-	-	-	-	-
129	Y	Y	-	-	X	Mod	<20 %	-	-	-	-	-	-	-
130*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
131	Y	Y	-	-	X	Clr	<5 %	-	-	-	-	-	-	-
132	Y	Y	X	-	-	Ft	<5 %	Y	Y	X	-	Px	Ft	<10 %
133*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
134*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
135	Y	Y	X	Y	Ds, Px	Clr	<20 %	-	-	-	-	-	-	-
136	Y	Y	X	-	-	Ft	<5 %	Y	Y	X	-	Ds, Px	Ft	<5 %
137*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
138*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
139*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
140*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
141	Y	Y	X	-	-	Ft	<5 %	Y	Y	X	-	Ds, Px	Clr	<20 %
142	-	-	-	-	-	-	-	Y	Y	X	-	Ds, Px	Clr	<40 %

*** = Unmodified specimens, X – feature not available for modification, Y – present, P - Periosteum, M – Medullary cavity, E – Edge, Clr – Clear, Mod – Moderate, Ft – Faint, Px - Proximal, Ds – Distal. Specimen 127 was not recovered post experiment.**

Table 8: Microscopically visible modifications recorded on trial C1 after a period of six months exposure to *P. americana*.

Specimen no.	Microscopic Modification					
	Gnawing	Location			Position	Degree of Visibility
		P	M	E		
125*	-	-	-	-	-	-
126*	-	-	-	-	-	-
127	X	X	X	X	X	X
128	-	-	-	-	-	-
129	-	-	-	-	-	-
130*	-	-	-	-	-	-
131	-	-	-	-	-	-
132	-	-	-	-	-	-
133*	-	-	-	-	-	-
134*	-	-	-	-	-	-
135	Y	Y	X	Y	-	Mod
136	-	-	-	-	-	-
137*	-	-	-	-	-	-
138*	-	-	-	-	-	-
139*	-	-	-	-	-	-
140*	-	-	-	-	-	-
141	-	-	-	-	-	-
142	-	-	-	-	-	-

*** = Unmodified specimens, X – feature not available for modification , Y – present, P - Periosteum, M – Medullary cavity, E – Edge, Mod – Moderate. Specimen 127 was not recovered post experiment.**

3.1.2.1. *Macroscopically visible features*

Discolouration (specimen numbers 128, 129, 131, 132, 135, 136, 141).

A total of seven out of eight modified specimens displayed discolouration; 41 % of the total sample, or 88 % of the modified specimens. Whilst discolouration is not a modification type, it is certainly an identified feature. This feature was not recorded on the medullary cavity of any specimens, and was always found to occur on the periosteal surface. No independent control was put in place, therefore it is also a possibility that the bones may have discoloured as a result of another biotic mechanism and not the insects themselves (i.e. microbial activities). However, the sporadic distribution and variability of shape of the discolouration staining on the bones suggests that it does not relate to microbial action, but is more likely related to secretions produced by the cockroaches and as such has been included in the results and discussion of this dissertation.

In five instances discolouration was noted to occur on <5 % of the surface of the specimen. Four of the five specimens came from an indeterminate medium-sized bovid, but not the same individual, and included a dry thick cortical long bone shaft fragment, a weathered thin cortical long bone shaft fragment, a dry complete phalanx and a dry complete rib. The other specimen was a fresh complete *G. domesticus* humerus. The last two specimens which displayed discolouration were a dry thin cortical shaft fragment (Figure 12), and a weathered complete rib (Figure 13), both from an indeterminate medium sized bovid and displaying discolouration on <20 % of the available surface area. In three instances discolouration was considered clearly visible, once it was moderately visible, and considered faintly visible in the last three instances.

Figure 12: Discolouration caused by *P. americana* on a dry thin cortical indeterminate long bone shaft fragment (specimen no. 129) 7x magnification.

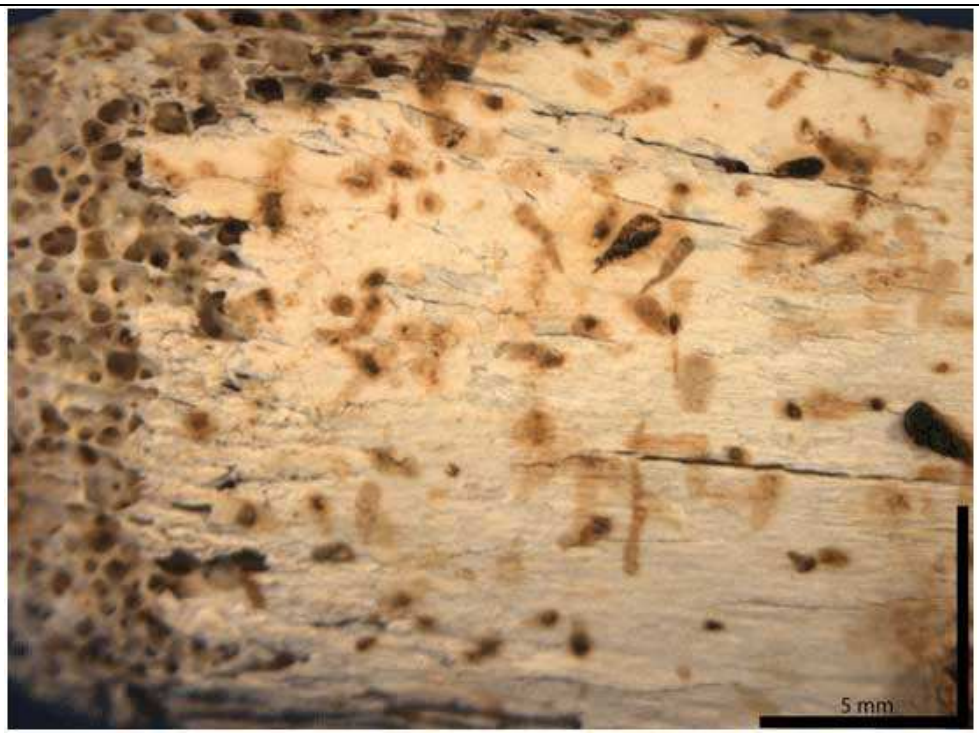

Figure 13: Discolouration caused by *P. americana* on a weathered complete rib from an indeterminate medium sized bovid (specimen no. 135) 7x magnification.

3.1.2.2. *Macroscopically visible modifications*

Destruction (specimen numbers 132, 136, 141, 142)

A total of four out of eight modified specimens displayed destruction; represented on 24 % of the total sample, or 50 % of the modified specimens. Destruction was only found to occur on the periosteum. All specimens that displayed destruction were complete skeletal elements, and in all but one instance (specimen 132), destruction occurred on both the proximal and distal ends of the elements. Visibility was considered clear on both fresh *G. domesticus* long bones; one of which displayed destruction on <20 % of the surface area (humerus), whilst the other displayed destruction on <40 % (ulna) (Figure 16). On the two remaining specimens destruction was only faintly visible, with a dry complete rib displaying destruction on <5 % of the surface area, whilst a dry complete phalanx displayed destruction on <10 % of the surface area (Figures 14 and 15), both skeletal elements were sourced from different indeterminate medium sized bovids.

Figure 14: Destruction by *P. americana* on a dry complete phalanx of an indeterminate medium sized bovid (specimen no. 132) 7x magnification.

Figure 15: Close up of destruction caused by gnawing by *P. americana* evident in Figure 14 on a dry complete phalanx of an indeterminate medium sized bovid (specimen no. 132) 40x magnification.

Figure 16: Destruction of epiphysis and cancellous bone by *P. americana* on a fresh *G. domesticus* ulna (specimen no. 142) 7x magnification.

Figure 17: Gnawing striations made by *P. americana* on a weathered complete rib from an indeterminate medium sized bovid (specimen no. 135) 40x magnification.

3.1.2.3. *Microscopically visible modifications*

Gnawing striations (specimen 135)

Only a single specimen out of the eight modified pieces displayed striations resulting from gnawing; represented on only 6 % of the total sample, or 13 % of the modified specimens. Only a single cluster of relatively parallel gnawing-related striations where identified. The cluster occurred along the edge of a weathered complete rib sourced from an indeterminate medium sized bovid (Figure 17).

3.1.3. Measurements of P. americana gnawing striations

Only gnawing striations could be quantified in terms of measurements. A total of eight striations were measured for the cluster displayed in Figure 17. The following descriptive statistics were obtained by entering in the length measurements into SPSS for analysis. Mean 468.25µm with a Std. error of 63.60, median 472.32µm, S.D. 179.89µm, minimum 179.43µm, maximum 726.94µm.

3.1.4. Occurrence patters of modification types

Occurrence (%) refers to a particular modification type being recorded on specimens as a percentage of the total sample size (Figure 18), or according to number of specimens of a particular bone density (Figure 19) or condition (Figure 20). Frequency refers to an *n* value, which for the modifications described could not be quantified, hence frequency has been omitted from these graphs.

Occurrence of modification types against total sample size

Figure 18 shows that the occurrence of discolouration was by far the greatest feature represented, present on just less than 40 % of the total sample. Destruction was recorded on slightly over 20 % of the total sample, and gnawing, the most distinctive modification type, was recorded on only 6 % of the total sample.

Occurrence of modification types according to density

Figure 19 shows that discolouration was found to occur on all specimens of different densities, except on teeth. Destruction was only recorded on compact and spongy bone as well as bones of varying densities, but was not recorded on purely thin or thick cortical bone, or on teeth. A single cluster of gnawing striations was recorded on a spongy bone specimen, represented on only 6 % of the total sample.

Occurrence of modification types according to condition

Figure 20 shows that discolouration was recorded on most bones, with the highest occurrence recorded on dry and weathered specimens, less regularly on fresh specimens, and not at all on fossil specimens. However, this is likely a result of the dark brown manganese dioxide coating on fossil specimens, which makes discoloration impossible to discern. Destruction was only recorded on dry and fresh specimens, and was marginally higher on dry specimens. The single cluster of gnawing striations was on a weathered specimen.

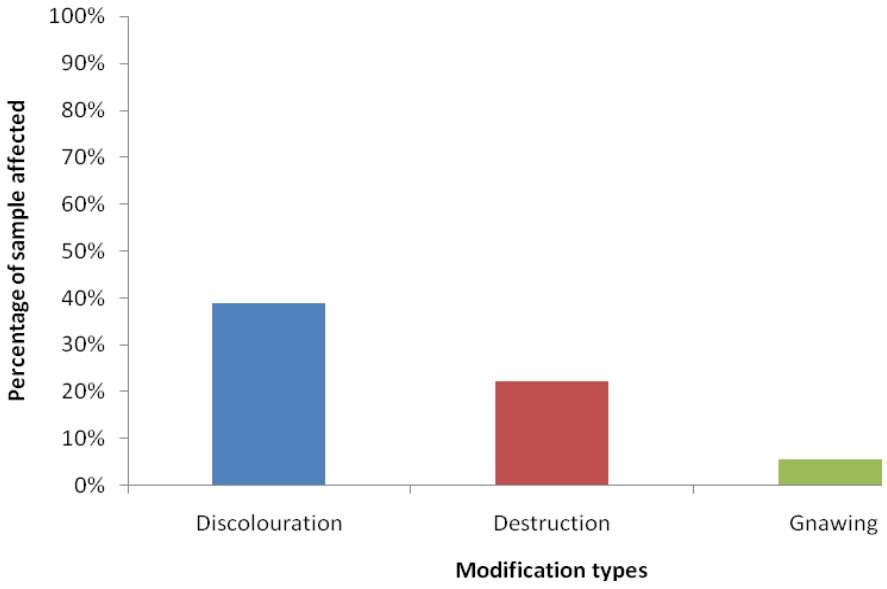

Figure 18: Occurrence of *P. americana* modifications in trial C1.

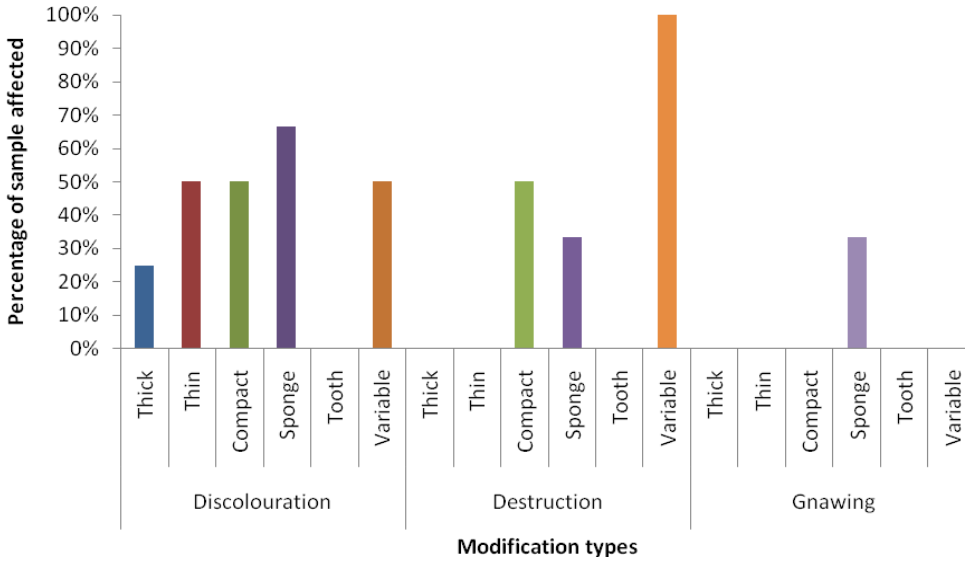

Figure 19: Occurrence of *P. americana* modifications on bones of different densities.

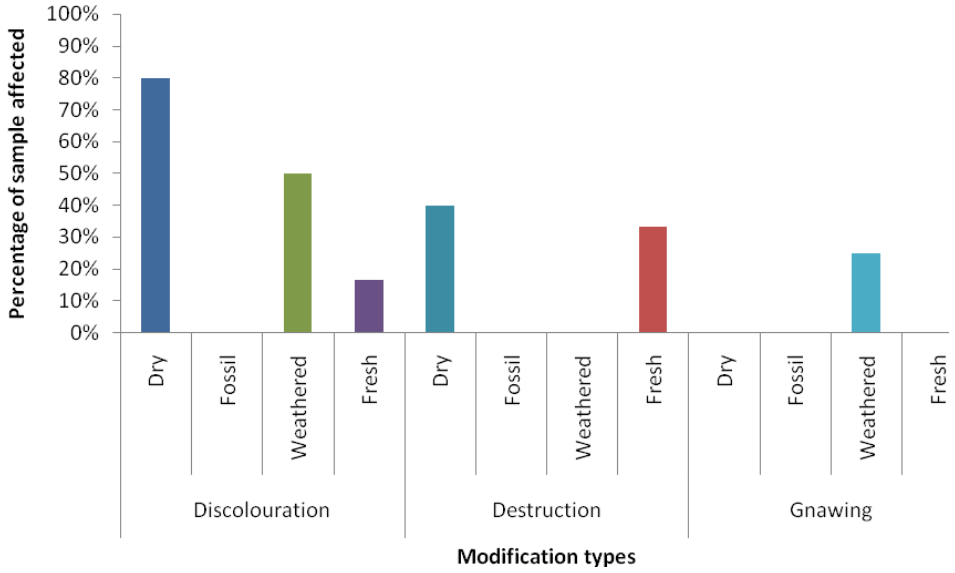

Figure 20: Occurrence of *P. americana* modifications on bones of different condition.

3.2. ***Dermestes maculatus***

3.2.1. Behavioural observations during experimental runs

Within minutes of placing the bone specimens in both experimental tanks (D1 and D2) adult beetles were observed on both fresh specimens and non-fresh specimens, although it was only in tank D2 that larvae were soon also spotted on fresh specimens. Whilst in tank D1 (no substrate present) the larvae took a number of minutes before they found the fresh specimens, and even after 30 minutes the larvae seemed to be more interested on escaping than on feeding or exploring their new surroundings. In tank D2, with substrate, the larvae were less interested in climbing walls and trying to escape, and adults were observed on fresh meat. Throughout the duration of both experiments adults and larvae burrowed into the available substrate (Figure 21).

In both tanks adults were seen copulating within 20 minutes of being placed in the tanks. Pupal casings were regularly observed in tank D1 randomly scattered across the surface of the glass or lying under specimens (Figure 22). In tank D1, D3 and D4 both larvae as well as adults were regularly seen burrowing into the available substrate at the base of the tank and no pupal casings were ever observed on the surface of the substrate or under specimens.

The population densities of both tanks used during Experiment A (testing the influence of substrate) appeared visually comparable for the duration of exposure, whilst during Experiment B (testing the influence of food availability) the population densities between the two tanks appeared visually different, with a higher population density in tank D4, which received less food than tank D3. However, there was a greater difference in the rate of population increase in experimentation tanks when compared to tanks used for breeding purposes, which may relate to the presence of cotton wool as a pupation medium. This differential population increase is likely a result of the presence cotton wool, as this would have likely positively influenced the humidity levels, kept the available food sources moister for longer and provided darker conditions prompting longer periods of activity.

At feeding times, a few second after placing meat within the tanks adult beetles were seen feeding on the meat. Larvae often took a number of minutes before they moved onto the fresh food source. The surface of

the canned meat dried quickly, but larvae tended to remain on the dried remnants and frequently burrowed small pin prick-sized holes into the meat, whilst adults were seen less frequently on dry remnants. Similarly, even after exposure of four months in both experiments, previously fresh specimens were removed with remnants of both meat and marrow, which had remained un-eaten for the entire duration of the experiments. This was relevant to all trials but more so in relation to the trials used to test the influence of food availability (D3 and D4), suggesting that food was in excess, or had sufficiently dried for the remnants to become unattractive for consumption.

Figure 21: Adult *D. maculatus* burrowing through the available substrate at the bottom of tank D2.

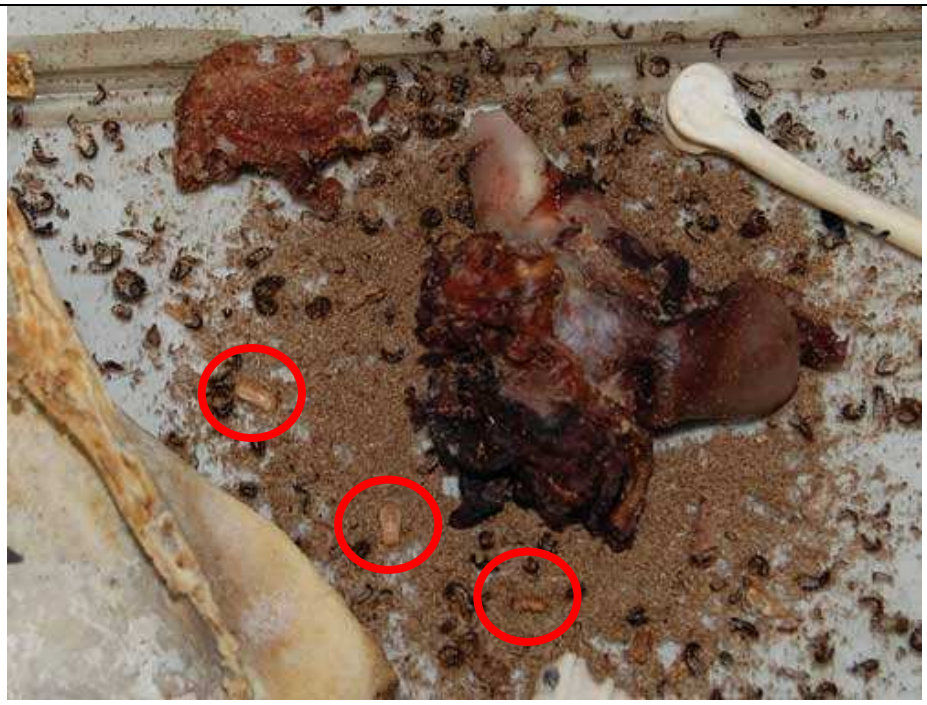

Figure 22: Three pupal cases (red circles) scattered across the bottom of tank D1.

3.2.2. Modification types created by *D. maculatus*

A total of five modification types were established across both experiments; surface tunnelling, destruction, bore holes, surface pits (Classes 1, 2 and 3), and gnawing. Only the occurrence of surface tunnelling was considered macroscopically visible, whilst destruction and the occurrence of bore holes was considered intermediately visible, and surface pits and gnawing were categorised as being microscopic in nature. Surface tunnels (Figures 23–25) are furrows with a U-shaped profile excavated across the surface of a bone, and bore holes often occur at either one or both ends of the furrow. Surface tunnels primarily occur as a single furrow, but occasionally as a complex of interconnected furrows. Destruction (Figures 26–28) refers to the

obliteration of bone, completely destroying cancellous bone or articular facets, and removal of cortical bone resulting in exposure of the underlying trabecular bone. Bore holes (Figures 29–30) are deep circular holes which may or may not have a discernible bottom, which penetrate through cortical or cancellous bone, and in to the medullary cavity or burrowing through the underlying trabecular bone. Class 1 surface pits (Figures 31–33) are highly variable in shape, however, most often semi-circular to elliptical shallow depressions with a U-shaped profile that have striations radiating from around the outer circumference of the depression. Class 2 surface pits (Figures 34–35) are semi-circular shallow depressions with randomly orientated striations occurring over the entire feature. Class 3 surface pits (Figures 36–37) are irregular-shaped depressions with complex profiles not associated with any striations. Lastly, gnawing (Figures 35–37) refers to clusters of irregularly orientated striations which cover a relatively large surface area. Tables 9–12 and 13–16 summarises recorded results for Experiment A (trial D1 and D2) and Experiment B (trial D3 and D4), respectively.

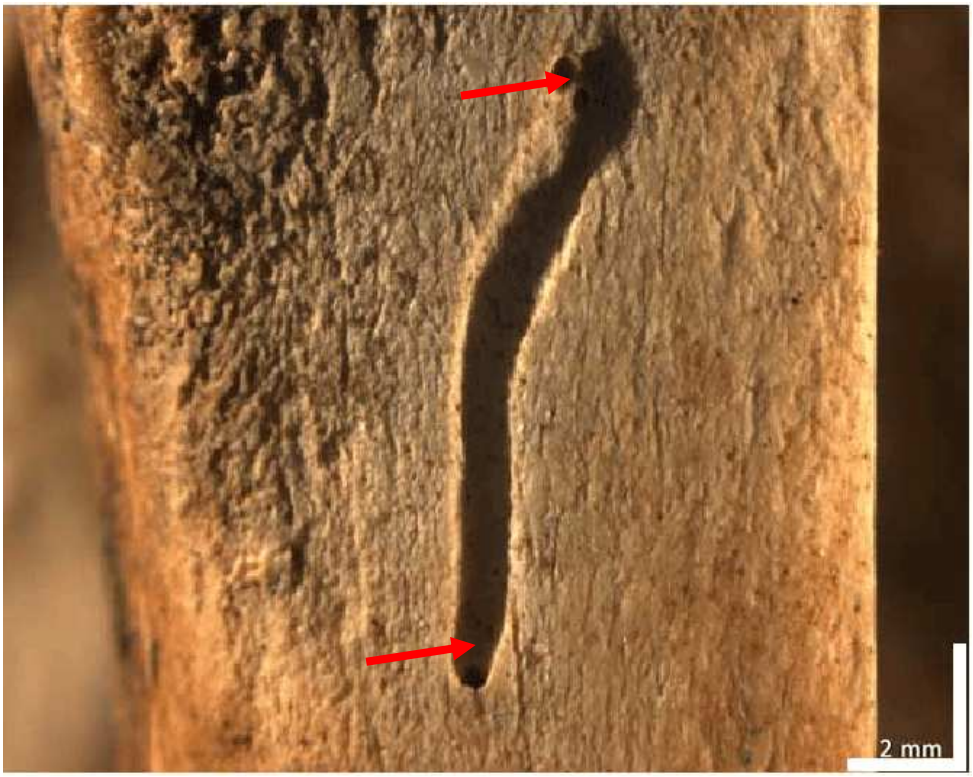

Figure 23: Single surface tunnel made by *D. maculatus,* displaying small bore holes at both ends in the cortical bone of the distal epiphysis of a dry unknown species of bovid humerus (specimen no. 30), 8x magnification.

Figure 24: Single surface tunnel made by *D. maculatus,* excavated into the trabecular bone of a proximal epiphysis of an unknown species of bovid humerus (specimen no. 9), 8x magnification.

Figure 25: Five small surface tunnels, displaying bore holes at either one or both ends, made by *D. maculatus* on a weathered *O. aries* scapula (specimen no. 85), 7x magnification.

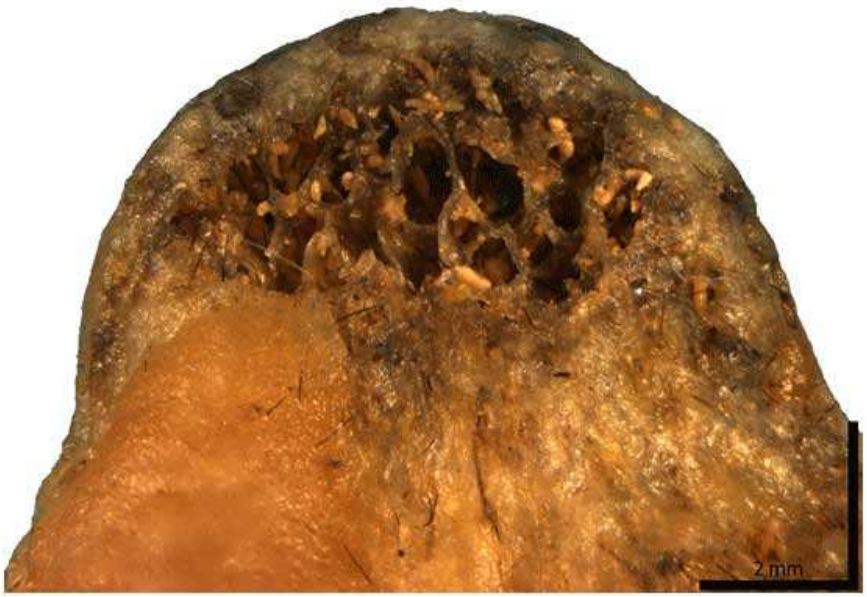

Figure 26: Destruction of bone by *D. maculatus* on a dry *O. aries* tarsus (specimen no. 5) exposing the underlying trabecular bone structure, 12.5x magnification.

Figure 27: Destruction by *D. maculatus* of the proximal epiphysis of a fresh *G. domesticus* femur (specimen no. 17), 7x magnification.

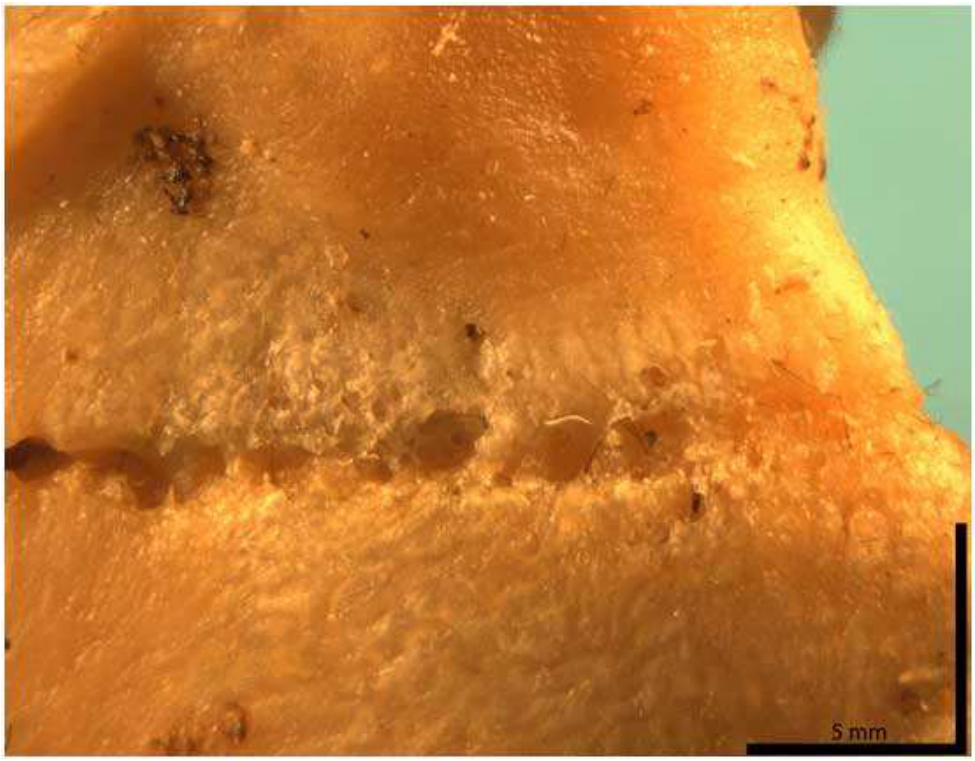

Figure 28: Destruction by *D. maculatus* at the diaphysis-epiphysis junction of a dry *O. aries* ulna (specimen no. 2b), 7x magnification.

Figure 29: Bore hole excavated into a dry *O. aries* scapula (specimen no. 22) with a *D. maculatus* larvae *in situ,* 20x magnification.

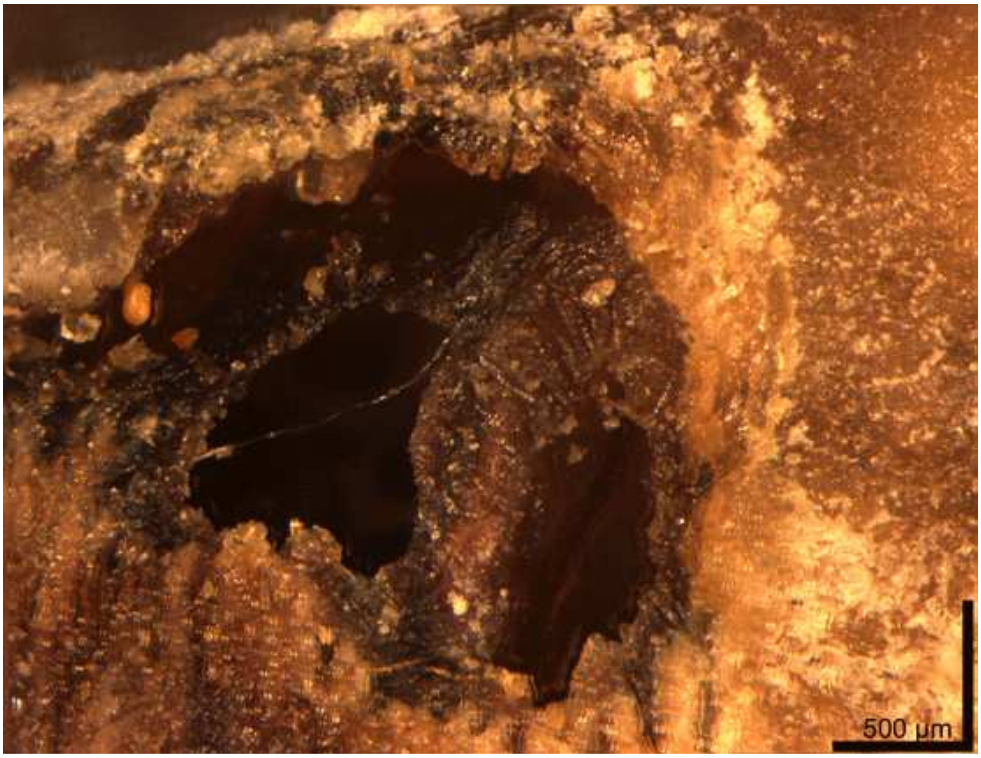

Figure 30: Bore hole excavated into a fresh *G. domesticus* femur (specimen no. 38), 40x magnification. This bore hole sought to enter the medullary cavity whilst a bridge remained unexcavated displaying numerous gnawing striations.

Figure 31: Four Class 1 surface pits excavated by *D. maculatus* into the diaphysis-epiphysis junction of a *D. pygargus* femur (specimen no. 20), 25x magnification.

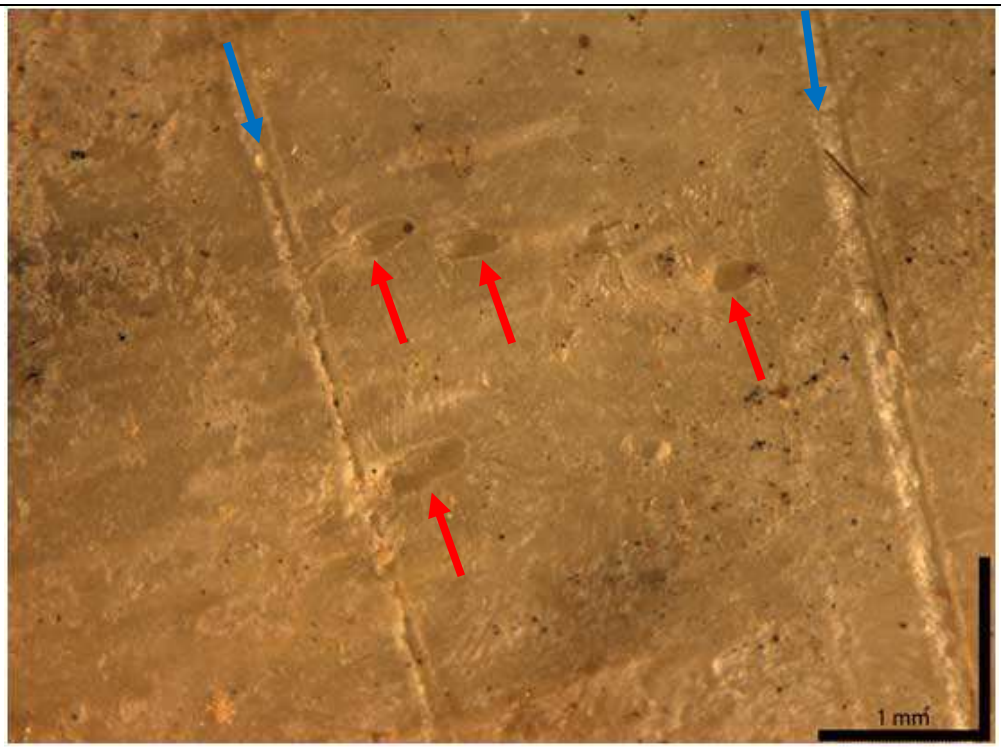

Figure 32: Four Class 1 surface pits excavated by *D. maculatus* into a dry *O. aries* scapula (specimen no. 22), 25x magnification. Note the striations radiating from the out circumference of the depressions and the blue arrows indicate existing damage recorded prior to exposure.

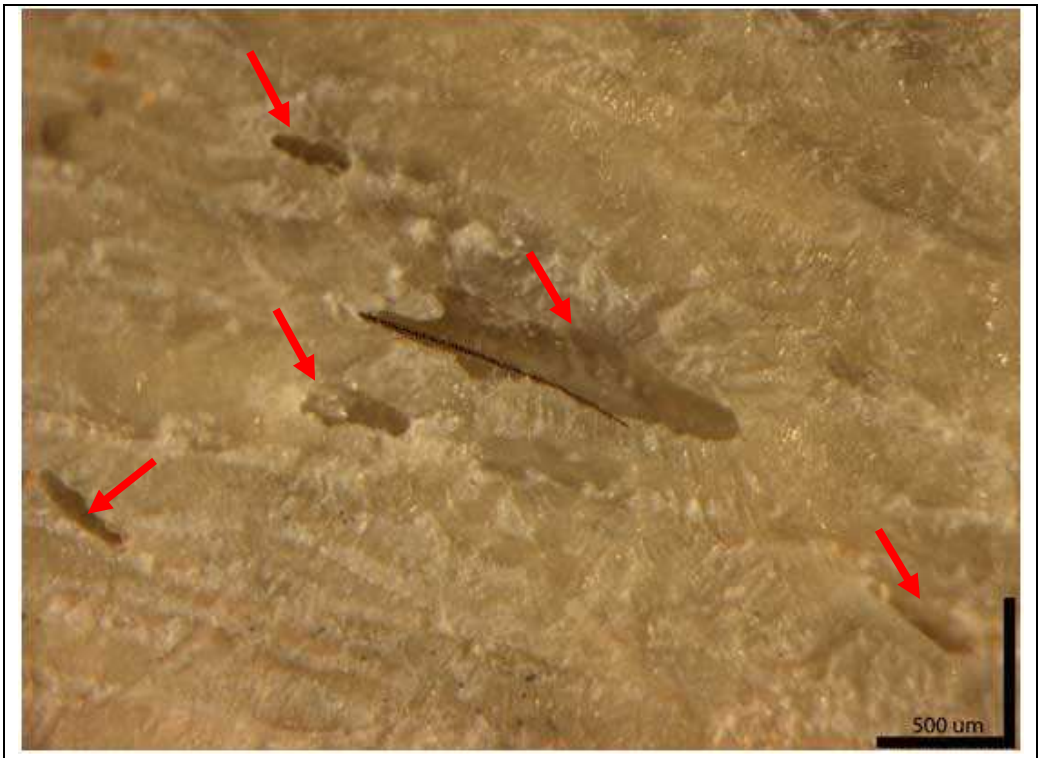

Figure 33: Five Class 1 surface pits excavated by *D. maculatus* into a dry *O. aries* scapula (specimen no. 22), 40x magnification.

Figure 34: Two Class 2 surface pits excavated by *D. maculatus* into a fossilised enamel tooth fragment from an unknown species of bovid (specimen no. 12), 8x magnification.

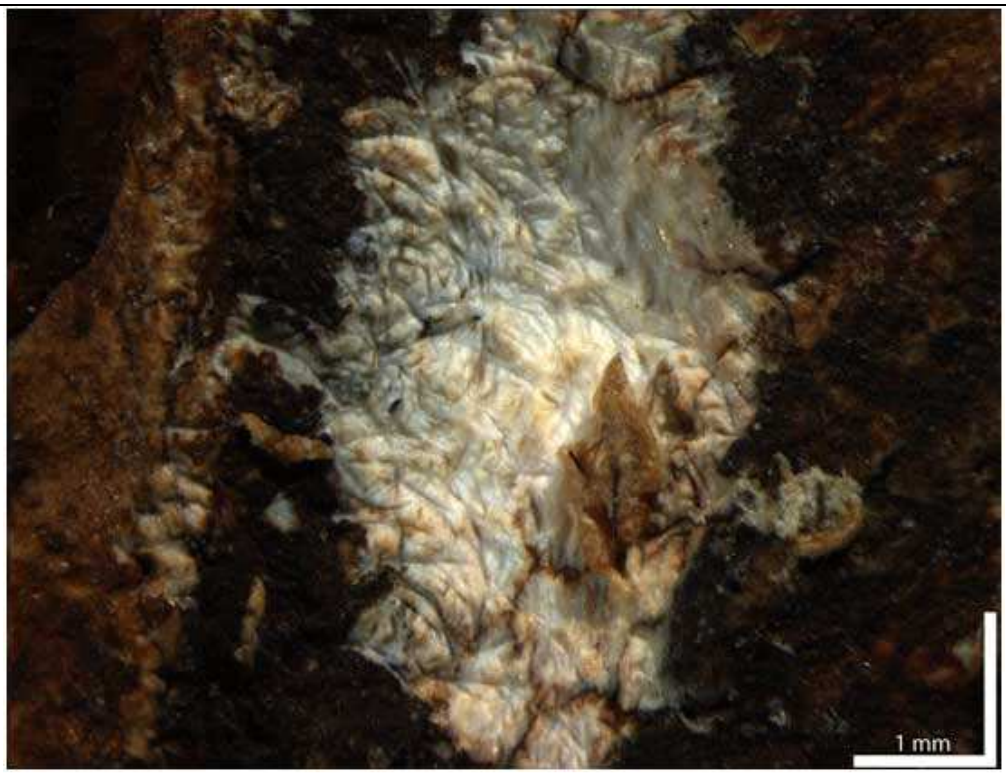

Figure 35: Class 2 surface pit excavated by *D. maculatus* into a fossilised enamel tooth fragment from an unknown species of bovid (specimen no. 12), 20x magnification. Note the randomly orientated individual striations occurring over the entire feature.

Figure 36: Two Class 3 surface pits excavated by *D. maculatus* into the proximal epiphysis of a dry *O. aries* ulna (specimen no. 23b), 20x magnification. Note the irregular-shaped holes/cavities with complex profiles and lack of associated striations.

Figure 37: A Class 3 surface pit excavated by *D. maculatus* into a fresh *G. domesticus* femur (specimen no. 38), 20x magnification.

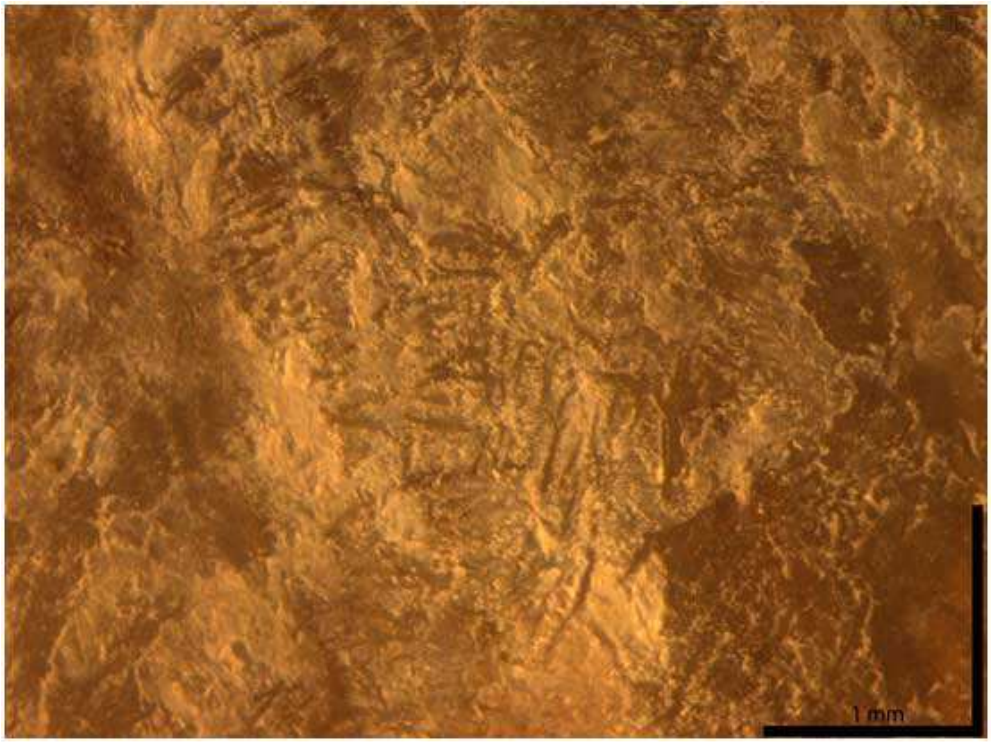

Figure 38: Gnawing striation cluster made by *D. maculatus* present on a dry *O. aries* scapula (specimen no. 1), 32x magnification.

Figure 39: Gnawing striations made by *D. maculatus* on the exposed trabecular structure of a dry *O. aries* rib (specimen no. 6), 50x magnification.

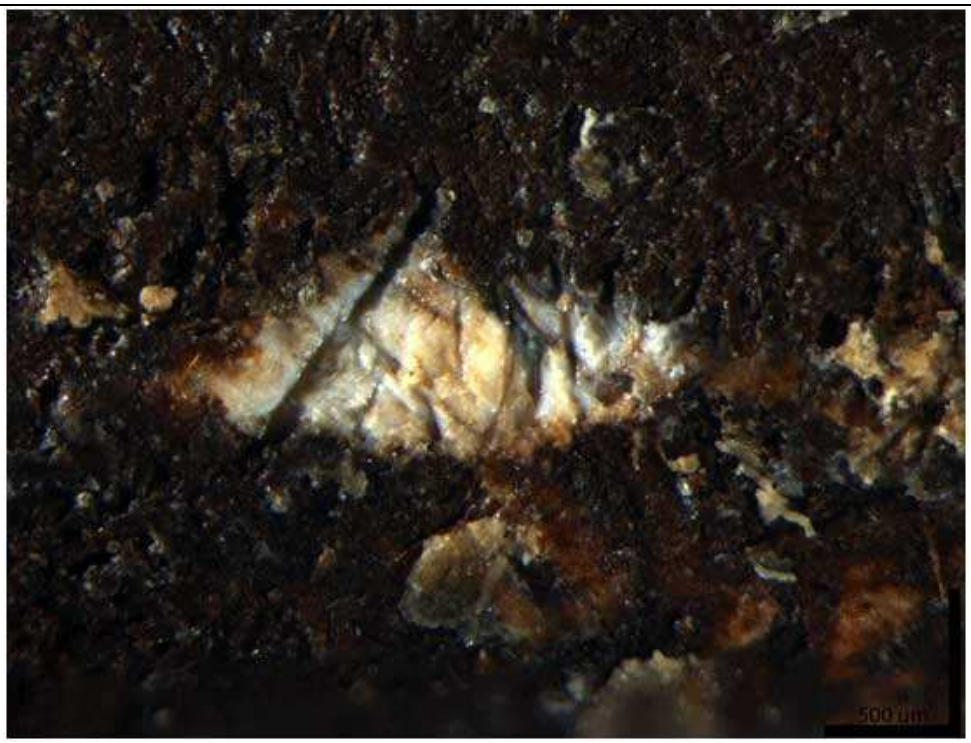

Figure 40: Isolated gnawing striations made by *D. maculatus* on a fossilised enamel tooth fragment from an unknown species of bovid (specimen no. 12), 40x magnification.

Table 9: Macroscopic and intermediately visible modifications recorded from Experiment A trial D1 (no substrate present) after four months exposure to *D. maculatus.*

Specimen no.	Macroscopic Modifications								Intermediate Modifications													
		Surface Tunnels	Location			Position	Degree of Visibility	*n*		Destruction	Location			Position	Degree of Visibility	Category % Cover	Bore holes	Location			Position	Degree of Visibility	*n*
			P	M	E						P	M	E					P	M	E			
1	Y	Y	Y	X	-	Vn	Clr	3	Y	Y	Y	X	-	-	Ft	<5 %	Y	Y	X	-	Vn	Clr	1
2a	-	-	-	-	-	-	-	-	Y	Y	Y	X	-	Px	Ft	<10 %	-	-	-	-	-	-	-
2b	-	-	-	-	-	-	-	-	Y	Y	Y	X	-	Px	Ft	<10 %	-	-	-	-	-	-	-
3*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	Y	Y	Y	X	-	-	Mod	<5 %	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	-	Y	Y	Y	X	-	-	Mod	<5 %	-	-	-	-	-	-	-
7	-	-	-	-	-	-	-	-	Y	Y	Y	X	-	-	Ft	<5 %	-	-	-	-	-	-	-
8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	Y	Y	2	1	-	-	Ft, Clr	3	Y	Y	Y	Y	-	-	Clr	<40 %	Y	Y	-	-	Px	Clr	2
10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	-	-	-	-	-	-	-	-	Y	Y	-	Y	Y	-	Clr	<10 %	-	-	-	-	-	-	-
13*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	-	-	-	-	-	-	-	-	Y	Y	Y	X	-	Ds, Px	Mod	<5 %	-	-	-	-	-	-	-
17	Y	Y	Y	X	-	Ds	Clr	3	Y	Y	Y	X	-	Ds, Px	Mod	<40 %	-	-	-	-	-	-	-
18	Y	Y	Y	-	-	-	Ft	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	Y	Y	Y	-	-	Px	Ft, Clr	2	-	-	-	-	-	-	-	-	Y	Y	X	-	-	Mod	1

*** = Unmodified specimens, X – feature not available for modification, Y – present, P - Periosteum, M - Medullary Cavity, E - Edge, Vn - Ventral, Px - Proximal, Ds - Distal, Clr - Clear, Ft - Faint, Mod - Moderate.**

Table 10: Microscopically visible modifications recorded from Experiment A trial D1 (no substrate present) after four months exposure to *D. maculatus.*

Specimen no.	Microscopic Modifications																
		Surface Pits	Location			Position	Degree of Visibility	*n*			Gnawing	Location			Position	Degree of Visibility	Category % Cover
			P	M	E			Class 1	Class 2	Class 3		P	M	E			
1	Y	Y	Y	X	-	Vn, Dr	Ft	60	0	0	Y	Y	X	Y	Ds, Px	Ft	<60 %
2a	Y	Y	Y	X	-	Ds, Px	Ft	13	0	0	Y	Y	X	-	Ds, Px	Ft	<20 %
2b	Y	Y	Y	X	-	Px	Ft	16	0	0	Y	Y	X	Y	Px	Ft	<10 %
3*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Y	-	-	-	-	-	-	-	-	-	Y	Y	X	-	-	Ft	<5 %
6	Y	Y	Y	X	-	Px	Ft	6	0	0	Y	Y	X	-	Ds, Px	Ft	<20 %
7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	Y	-	-	-	-	-	-	-	-	-	Y	Y	X	-	Ds	Ft	<5 %
9	Y	-	-	-	-	-	-	-	-	-	Y	Y	-	-	-	Ft	<10 %
10	Y	-	-	-	-	-	-	-	-	-	Y	-	Y	-	-	Ft	<5 %
11*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	Y	Y	-	Y	-	-	Clr	0	2	0	Y	-	Y	Y	-	Clr	<10 %
13*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	Y	Y	-	-	-	Ds	Clr	0	0	1	-	-	-	-	-	-	-
17	Y	Y	Y	X	-	Ds	Ft	0	0	1	-	-	-	-	-	-	-
18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	Y	Y	Y	-	-	-	Mod	4	0	0	Y	Y	-	-	Px	Ft	<5 %

*** = Unmodified specimens, X – feature not available for modification, Y – present, P - Periosteum, M - Medullary, E - Edge, Vn - Ventral, Dr - Dorsal, Ds - Distal, Px - Proximal, Ft - Faint, Clr - Clear, Mod - Moderate.**

Table 11: Macroscopic and intermediately visible modifications recorded from Experiment A trial D2 (substrate present) after four months exposure to *D. maculatus.*

Specimen no.	Macroscopic Modifications								Intermediate Modifications													
		Surface Tunnels	Location			Position	Degree of Visibility	*n*		Destruction	Location			Position	Degree of Visibility	Category % Cover	Bore Holes	Location			Position	Degree of Visibility	*n*
			P	M	E						P	M	E					P	M	E			
22	Y	Y	Y	X	-	Vn	Mod	3	Y	Y	Y	X	Y	-	Ft	<40 %	Y	Y	X	-	Vn	Ft	6
23a	-	-	-	-	-	-	-	-	Y	Y	Y	X	Y	Ds, Px	Ft	<10 %	Y	Y	X	-	Ds	Clr	5
23b	-	-	-	-	-	-	-	-	Y	Y	Y	X	Y	Ds, Px	Ft	<10 %	-	-	-	-	-	-	-
24*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
26	-	-	-	-	-	-	-	-	Y	Y	Y	X	-	-	Clr	<10 %	Y	Y	X	-	-	Ft	1
27	-	-	-	-	-	-	-	-	Y	Y	Y	X	-	-	Ft	<20 %	Y	Y	X	-	-	Ft	1
28	-	-	-	-	-	-	-	-	Y	Y	Y	X	-	-	Ft	<5 %	-	-	-	-	-	-	-
29*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30	Y	Y	Y	-	-	-	Mod, Clr	3	Y	Y	Y	Y	-	-	Ft	<5 %	-	-	-	-	-	-	-
31*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
32*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
33*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
34*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
36*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
37	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
38	Y	Y	Y	X	-	Px	Clr	1	Y	Y	Y	X	-	Ds, Px	Clr	<40 %	Y	Y	X	-	Ds	Clr	1
39	-	-	-	-	-	-	-	-	Y	-	-	-	-	-	-	-	Y	Y	X	-	-	Ft	1
40*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
41*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

*** = Unmodified Specimens, X – feature not available for modification, Y – present, P - Periosteum, M - Medullary, E - Edge, Vn - Ventral, Ds - Distal , Px - Proximal, Mod - Moderate, Ft - Faint, Clr - Clear. Specimen 37 was not recovered post experiment.**

Table 12: Microscopically visible modifications recorded from Experiment A trial D2 (substrate present) after four months exposure to *D. maculatus.*

Specimen no.	Microscopic Modifications																
		Surface Pits	Location			Position	Degree of Visibility	*n*			Gnawing	Location			Position	Degree of Visibility	Category % Cover
			P	M	E			Class 1	Class 2	Class 3		P	M	E			
22	Y	Y	Y	X	-	Vn, Dr	Mod	44	0	0	Y	Y	X	-	Vn, Dr	Ft	<60 %
23a	Y	Y	Y	X	-	Ds	Ft	4	0	0	Y	Y	X	Y	Ds	Ft	<40 %
23b	Y	Y	Y	X	-	Px	Clr	8	0	2	Y	Y	X	Y	Ds, Px	Ft	<40 %
24*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
26	Y	-	-	-	-	-	-	-	-	-	Y	Y	X	-	-	Ft	<5 %
27	Y	Y	Y	X	-	-	Ft	9	0	1	Y	Y	X	-	-	Ft	<5 %
28	Y	Y	Y	X	-	-	Ft	1	0	0	-	-	-	-	-	-	-
29*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30	Y	-	-	-	-	-	-	-	-	-	Y	Y	-	-	Ds	Ft	<10 %
31*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
32*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
33*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
34*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
36*	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-
37	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
38	Y	Y	Y	X	-	Ds	Mod	0	0	2	Y	Y	X	-	Ds	Ft	<5 %
39	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
40*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
41*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

*** = Unmodified Specimens, X – feature not available for modification, Y – present, P - Periosteum, M - Medullary, E - Edge, Vn - Ventral, Dr - Dorsal, Ds - Distal, Px - Proximal, Mod - Moderate, Ft - Faint, Clr - Clear. Specimen 37 was not recovered post experiment.**

Table 13: Macroscopic and intermediately visible modifications made by *D. maculatus,* recorded from Experiment B trial D3 which received 100 g of canned meat twice a week.

Specimen no.	Macroscopic Modifications							Intermediate Modifications													
	Surface Tunnels	Location			Position	Degree of Visibility	*n*	Destruction	Location			Position	Degree of Visibility	Category % Cover	Bore Holes	Location			Position	Degree of Visibility	*n*
		P	M	E					P	M	E					P	M	E			
85	Y	Y	X	-	Dr	Mod	18	Y	Y	X	-	Vn, Dr	Ft	<10 %	-	-	-	-	-	-	-
86	Y	Y	-	-	Ds	Clr	3	Y	Y	Y	-	-	Ft	< 10 %	Y	Y	-	-	Px	Mod	2
87	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
88*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
89	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Y	Y	X	-	-	Ft	3
90	-	-	-	-	-	-	-	Y	Y	X	Y		Clr	<5 %	Y	Y	X	Y	-	Clr	3
91*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
92	-	-	-	-	-	-	-	Y	Y	X	-	-	Ft	<10 %	-	-	-	-	-	-	-
93*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
94*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
96*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
97*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
98*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
99*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
100	-	-	-	-	-	-	-	Y	Y	X	-	-	Ft	<5 %	-	-	-	-	-	-	-
101	-	-	-	-	-	-	-	Y	Y	X	-	Px, Ds	Mod	<20 %	Y	Y	X	-	Ds	Mod	2
102*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
103*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
104*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

*** = Unmodified Specimens, X – feature not available for modification, Y – present, P - Periosteum, M - Medullary, E - Edge, Dr - Dorsal, Vn - Ventral, Ds - Distal, Px - Proximal, Mod - Moderate, Clr - Clear, Ft - Faint.**

Table 14: Microscopically visible modifications made by *D. maculatus,* recorded from Experiment B trial D3, which received 100 g of canned meat twice a week.

Specimen no.	Microscopic Modifications															
	Surface Pits	Location			Position	Degree of Visibility	*n*			Gnawing	Location			Position	Degree of Visibility	Category % Cover
		P	M	E			Class 1	Class 2	Class 3		P	M	E			
85	Y	Y	X	-	Vn, Dr	Ft	7	1	0	Y	Y	X	-	Vn, Dr	Mod	<20 %
86	-	-	-	-	-	-	-	-	-	Y	Y	-	-	-	Ft	<10 %
87	-	-	-	-	-	-	-	-	-	Y		Y	-	-	Ft	<5 %
88*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
89	Y	Y	X	-	-	Ft	13	-	-	Y	Y	X	-	-	Ft	<5 %
90	-	-	-	-	-	-	-	-	-	Y	Y	Y	Y	-	Ft	<20 %
91*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
92	-	-	-	-	-	-	-	-	-	Y	Y	X	-	-	Ft	<5 %
93*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
94*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
96*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
97*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
98*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
99*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
101	Y	Y	X	-	Ds	Clr	-	-	1	-	-	-	-	-	-	-
102*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
103*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
104*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

*** = Unmodified Specimens, X – feature not available for modification, Y – present, P - Periosteum, M - Medullary, E - Edge, Vn - Ventral, Dr – Dorsal, Ds – Distal, Ft - Faint, Mod - Moderate, Clr - Clear.**

Table 15: Macroscopic and Intermediately visible modifications made by *D. maculatus,* from Experiment B trial D4 which received 50 g of canned meat twice a week.

Specimen no.	Macroscopic Modifications							Intermediate Modifications													
	Surface Tunnels	Location			Position	Degree of Visibility	*n*	Destruction	Location			Position	Degree of Visibility	Category % Cover	Bore Holes	Location			Position	Degree of Visibility	*n*
		P	M	E					P	M	E					P	M	E			
95*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
106	Y	Y	X	-	Vn	Mod	5	Y	Y	X	-	Vn, Dr	Ft	<5 %	-	-	-	-	-	-	-
107	Y	Y	Y	-	Ds	Clr	2	Y	Y	Y	-	Px	Ft	<5 %	-	-	-	-	-	-	-
108*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
109*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
110	-	-	-	-	-	-	-	Y	Y	X	-	-	Ft	<5 %	Y	Y	X	-	-	Ft	1
111	-	-	-	-	-	-	-	Y	Y	Na	-	Ds	Clr	<10 %	-	-	-	-	-	-	-
112	-	-	-	-	-	-	-	Y	Y	X	-	-	Ft	<10 %	-	-	-	-	-	-	-
113*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
114*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
115*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
116*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
117*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
118*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
119*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
120*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
121*	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
122*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
123*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

*** = Unmodified Specimens, X – feature not available for modification, Y – present, P - Periosteum, M - Medullary, E - Edge, Vn - Ventral, Dr - Dorsal, Ds - Distal, Px - Proximal, Mod - Moderate, Ft - Faint, Clr - Clear.**

Table 16: Microscopically visible modifications made by *D. maculatus,* recorded from Experiment B trial D4 which received 50 g of canned meat twice a week.

Specimen no.	Microscopic Modifications															
	Surface Pits	Location			Position	Degree of Visibility	*n*			Gnawing	Location			Position	Degree of Visibility	Category % Cover
		P	M	E			Class 1	Class 2	Class 3		P	M	E			
95*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
106	Y	Y	X	-	Ds	Ft	2	-	-	Y	Y	X	-	Vn, Dr	Ft	<10%
107	-	-	-	-	-	-	-	-	-	Y	Y	-	-	Ds	Ft	<5%
108*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
109*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
110	Y	Y	X	-	-	Ft	4	-	-	y	Y	X	-	-	Ft	<5%
111	-	-	-	-	-	-	-	-	-	Y	Y	X	-	-	Ft	<10%
112	-	-	-	-	-	-	-	-	-	Y	Y	X	-	-	Ft	<5%
113*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
114*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
115*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
116*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
117*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
118*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
119*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
120*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
121*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
122*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
123*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

*** = Unmodified Specimens, X – feature not available for modification, Y – present, P - Periosteum, M - Medullary, E - Edge, Ds – Distal, Vn - Ventral, Dr - Dorsal, Ft - Faint.**

Experiment A:

Modifications recorded during trial D1 with no substrate present

Out of 21 specimens, seven were not modified by *D. maculatus* after a period of 4 months; representing 33 % of the total sample. The unmodified specimens (3, 4, 11, 13–15 and 19) included two dry indeterminate shaft fragments (one thick and one thin cortical bone specimen), one fossilised thin cortical indeterminate long bone shaft fragment, a dry near complete *O. aries* molar, a weathered complete *B. domesticus* premolar, a dry complete *Antidae* sp. tibiotarsus, and lastly a wet thick cortical bone indet. long bone shaft fragment from a *D. pygargus*. The remaining 14 specimens all displayed either one or a combination of modification types. Only five out of the 14 remaining specimens had macroscopically visible modifications, while ten out of 14 displayed intermediate modification categories, and 12 out of 14 displayed microscopic modifications.

3.2.2.1. *Macroscopically visible modifications (Experiment A: Trial D1 – No substrate)*

Surface tunnelling (specimen numbers 1, 9, 17, 18, 20)

A total of 12 surface tunnels were identified on five different specimens; represented on 24 % of the total sample, or 36 % of the modified specimens. The surface tunnels occurred on the periosteal surface of the specimens, but in one of the three specimens in which a medulla was immediately available without having to bore through the outer cortical lamella to gain

access to it, a single tunnel was recorded. Specimen 1 displayed three surface tunnels on the periosteal surface that were clearly visible. Specimen 9 displayed a further three surface tunnels; one on the periosteum was complex, with multiple interconnected furrows leading from a primary furrow. The other one on the periosteum was only faintly visible, while the third was clearly excavated into the trabecular bone (Figure 24). Specimen 17 displayed three clearly visible surface tunnels, two at the distal end and one on the mid shaft. Specimen 18 had a single faintly visible surface tunnel, whilst specimen 20 had one clear and one faint surface tunnel on the articular surface.

Surface tunnelling was found to occur with all other modification categories in only a single instance (1), whilst it was found to occur with destruction (1, 9 and 17), surface pits (1, 17 and 20), and gnawing (1, 9 and 20) in three instances, and with bore holes (1 and 9) in only two instances.

3.2.2.2. *Intermediately visible modifications (Experiment A: Trial D1 – No substrate)*

Destruction (specimen numbers 1, 2a, 2b, 5, 6, 7, 8, 9, 10, 12, 16, 17, 18, 20)

Ten of the 14 modified specimens displayed varying degrees of destruction by *D. maculatus*; represented 48 % of the total sample, or 71 % of the modified specimens. Destruction

primarily occurred on epiphyses or at the diaphysis-epiphysis junction. Destruction of cancellous bone was visibility obvious, and was not associated with gnawing striations. In only two instances, destruction was recorded on less than 40 % of the bone surface, whilst the balance of specimens had destruction on either less than 5 or 10 % of the bone surface. If the exact state of each specimen had not been known prior to exposure, in most instances it would have been very difficult to differentiate between existing damage or *D. maculatus* damage. However, destruction which that occurred on bone densities other than cancellous, which ultimately exposed the underlying trabecular bone structure, was associated with extremely faint striations on the trabecular at high magnifications (50x or more, see Figure 39).

In two specimens (9 and 12) in which the medulla was exposed, both showed signs of destruction. Specimen 9 displayed clear destruction on <40 % of the periosteal surface, whilst specimen 12 displayed damage on <10 % of the medullary surface, with no destruction recorded on the periosteum. Specimens 1 and 7 both showed faint destruction on less than 5 % of the periosteum. Specimens 5 (Figure 26) and 6 had moderately visible destruction on <5 % of the bone, whilst in 16 the destruction was on the epiphysis. Specimens 2a and 2b (Figure 28) both showed faint destruction on less than 10 % of the

bone. Specimen 17 (Figure 27) displayed moderate destruction on less than 40 % of the bone, primarily on the proximal and distal epiphyses.

Destruction was found to occur with all other modification categories in only a single instance (1), whilst it was found together with surface tunnels in three instances (1, 9 and 17), bore holes in two instances (1 and 9), surface pits (1, 2a, 2b, 6, 12, 16 and 17) and gnawing (1, 2a, 2b, 5, 6, 9 and 12) in seven instances each.

Bore holes (specimen numbers 1, 9, 20)

Only three of the 14 specimens modified by *D. maculatus* displayed a combined total of four clearly visible bore holes; represented on 14 % of the total sample, or 21 % of the modified specimens. Specimen 1 displayed a single bore hole on the periosteal surface. Specimen 9 displayed a further two bore holes. Specimen 20 had a single bore hole excavated into a fresh proximal epiphysis. Bore holes were not recorded within the exposed medullary cavity, but rather penetrated cortical or cancellous bone to either enter the medullary cavity or excavate through the underlying trabecular bone structure.

Bore holes occurred in both instances with surface tunnels (1 and 9), destruction (1 and 9) and gnawing (1 and 9), whilst occurring with surface pits (1) in a single instance.

3.2.2.3. *Microscopically visible modifications (Experiment A: Trial D1 – No substrate)*

Surface pits

Three distinctive surface pit classes were identified. Ninety-nine pits were recorded on eight of the 14 specimens which displayed modifications made by *D. maculatus*; represented on 38 % of the total sample, or 57 % of the modified specimens. Surface pit Classes 1, 2 and 3 were not all present on the same specimen and hence their occurrences are listed separately below.

Class 1 (specimen numbers 1, 2a, 2b, 6, 20)

This class was by far the most common surface pit recorded; occurring on five of the eight specimens displaying surface pits made by *D. maculatus*. Specimen 1 was the most highly modified specimen used in Experiment A; 60 faint surface pits were recorded over the ventral and dorsal surfaces of the specimen. Specimen 2a displayed 13 faint surface pits; seven on the proximal and six on the distal ends. Specimen 2b recorded a further 16 faint surface pits on the proximal

end. Specimens 2a and 2b were fused to each other and in both instances pits occurred primarily on the epiphysis or close to the diaphysis-epiphysis junction. Specimen 6 recorded an additional six faint surface pits; two on the proximal and four on the distal end. Lastly, specimen 20 (Figure 31) recorded four moderately visible surface pits.

Class 1 surface pits were found to occur with surface tunnelling, destruction, bore holes and gnawing in a single instance (1), with gnawing in all five instances (1, 2a, 2b, 6 and 20), with destruction in four cases (1, 2a, 2b and 6) and with surface tunnels in two instances (1 and 20).

Class 2 (specimen number 12)

Only two surface pits of this type were recorded on a single specimen (12). Both pits were clearly visible and occurred on the inner surface of a fossilised piece of tooth enamel from an indeterminate bovid. (Figures 34 and 35)

Class 2 surface pits were found to occur with destruction and gnawing.

Class 3 (specimen numbers 16, 17)

This type of surface pit was only observed on two of the eight specimens, which recorded surface pits of varying types. Specimen 16 displayed a single clearly visible pit on the distal articular facet. Specimen 17 displayed an additional faintly visible pit on the distal end.

Class 3 surface pits were found to occur with destruction in one instance (16), whilst with destruction and surface tunnelling in another (17).

Gnawing (specimen numbers 1, 2a, 2b, 5, 6, 8, 9, 10, 12, 20)

This feature was recorded on 10 of the 14 specimens modified by *D. maculatus*; represented on 48 % of the total sample, or 71 % of the modified specimens. Gnawing and associated striations were considered as always faint (except specimen 12), and never as singular striations (except specimen 10), but rather occurred as distinct areas or clusters of multiple striations across an extended surface area.

Specimen 1 (Figure 38) had gnawing striations over ~80 % of the ventral surface area and only <40 % of the dorsal surface area. Specimens 2a and 6 (Figure 39) had striations on the distal and proximal ends, covering <20 % of the total surface area of each specimen. Specimen 2b displayed gnawing striations on the

proximal end, which covered <10 % of the total surface area of the specimen. Specimen 5 displayed very faint striations on < 5 % of the surface area of the specimen. Similarly, specimen 8 had very faint striations on <5 % of the surface. Specimen 9 displayed gnawing striations on <10 % of the surface area. Specimen 10 displayed only three isolated striations on the medullary surface. Specimen 12 (Figure 40) showed clearly visible striations along the inner surface of the enamel fragment. Lastly, specimen 20 displayed faint gnawing striations on <5 % of the surface area.

Gnawing was found to occur with surface tunnels in three instances (1 and 9) and with surface pits in six cases (1, 2a, 2b, 6, 12 and 20).

Modification recorded during trial D2 with 50mm of substrate present

A total of 11 out of 21 specimens were not modified at all by *D. maculatus* after a period of 4 months; representing 52 % of the total sample. Specimen 37 was removed from the microscope laboratory without the experimenter's knowledge and hence reduced the total number of specimens analysed to 20. However, all other specimens were accounted for and as a result of the photographs taken; no specimens could have been mistaken for one another nor have been mixed up during the analysis process. Hereafter, all percentages consider the sample size to be 20 and not 21. The unmodified

specimens (24, 25, 29, 31–36, 40 and 41) included two dry long bone shaft fragments, one thick cortical and one thin cortical piece, from an indeterminate bovid long bone, two fossilised shaft fragments, one thick cortical and one thin cortical from an indeterminate bovid long bone, a single fresh thick cortical shaft fragment belonging to a *D. pygargus* long bone, three weathered specimens, a dry complete phalanx from an indeterminate bovid, a near complete *B. domesticus* premolar and a near complete *O. aries* molar, a fossilised enamel fragment from an indeterminate bovid, a dry complete tibiotarsus from an *Antidae* sp., and a proximal epiphysis of a fresh femur from a *D. pygargus*. The remaining nine specimens all displayed one or a combination of modification categories. Only three out of the nine remaining specimens had macroscopically visible modifications, whilst all nine displayed intermediate modifications categories, and eight out of nine recorded microscopic modifications.

3.2.2.4. Macroscopically visible modifications (Experiment A: Trial D2 – Substrate)

Surface tunnels (specimen numbers 22, 30, 38)

A total of seven surface tunnels were found distributed over three specimens; represented on 15 % of the total sample, or 33 % of the modified specimens. Specimen 22 displayed three moderately visible surface tunnels. Specimen 30 (Figure 23) displayed a further three surface tunnels which were either

clearly or moderately visible. Lastly, specimen 38 displayed a single clear surface tunnel on the proximal end of a long bone.

Surface tunnels were found to occur with destruction and gnawing in all instances (22, 30 and 38), with bore holes in two instances (22 and 38), with surface pits (Class 3) in one case (38) and a Class 1 pit in another (22).

3.2.2.5. Intermediately visible modifications (Experiment A: Trial D2 Substrate)

Destruction (specimen numbers 22, 23a, 23b, 26, 27, 28, 30, 38)

This modification was recorded on a total of eight specimens; represented on 40 % of the total sample, or 89 % of the modified specimens. Destruction primarily occurred on the epiphysis or at the diaphysis-epiphysis junction. Destruction of cancellous bone was the most obvious, but was not associated with any gnawing striations. In only two instances (26 and 38) was the destruction recorded as being clearly visible, whilst the six other occurrences were considered only faintly visible. Specimens 22 and 38 displayed destruction on <40 % of the surface area. Specimens 23a, 23b, 26 and 27 all had destruction on <10 % of the surface area and were all *O. aries* elements, but not from the same individual. Specimen 28 and 30 had destruction on <5 % of the surface area.

Destruction was found to occur with all modification types in a single instance (22), with surface tunnels in three instances (22, 30 and 38), with bore holes in five instances (22, 23a, 26, 27 and 38), with surface pits in six instances (22, 23a, 23b, 27, 28 and 38) and with gnawing in all but one instance (28).

Bore holes (specimen numbers 22, 23a, 26, 27, 38, 39)

A total of 15 bore holes made by *D. maculatus* were recorded on six different specimens; represented on 30 % of the total sample, or 67 % of the modified specimens. Specimens 22 (Figure 29), a scapula, recorded the highest frequency of bore holes (totalling six) that were all considered faintly visible. Specimen 23a recorded a further 5 bore holes which were considered clearly visible on the distal end of the long bone. The remaining specimens (26, 27, 38 and 39) all recorded a bore hole per specimen, most of which were considered faint, except for the bore hole in specimen 38, which was located on the distal end and was considered clearly visible.

Bore holes were found to occur with all other modifications types in a single instance (22), with surface tunnels in two instances (22 and 38), with destruction and gnawing in all but one instance (39), and with surface pits in four instances (22, 23a, 27 and 38).

3.2.2.6. *Microscopically visible modifications (Experiment A: Trial D2 – Substrate)*

Surface pits (specimen numbers 22, 23a, 23b, 27, 28, 38)

A total of 71 surface pits of the varying classes (1, 2 and 3) were recorded on six different specimens; represented on 30 % of the total sample, or 67 % of the modified specimens. Unlike in trial D1, the various surface pit classes were found to co-occur and as such their occurrences will be described together.

Specimen 22 (Figure 32 and 33) recorded the highest occurrence of moderately visible surface pits (totalling 44) scattered over the dorsal and ventral sides of the scapula specimen. Specimens 23b and 27 both had 10 pits each, 23b had eight class 1 and two class 3 pits (Figure 36), whilst specimen 27 had nine class 1 and one class 3 surface pits. Specimen 23a displayed 4 faint class 1 surface pits. Specimen 28 displayed a single class 1 pit. Lastly, specimen 38 displayed two class 3 pits (Figure 37) both on the distal end.

Surface Pits of varying classes were found to occur with all other modification types in two instances (22 and 38), with surface tunnels in two instances (22 and 38), with bore holes in four instances (22, 23a, 27 and 38) and with gnawing in all but one instance (28).

Gnawing (specimen numbers 22, 23a, 23b, 26, 27, 30, 38)

Faint gnawing striations made by *D. maculatus* were recorded on seven of the nine modified specimens; represented on 35 % of the total sample, or 78 % of the modified specimens. Specimen 22 had gnawing striations on ~60 % of the total surface area of the specimen. Specimens 23a and 23b had gnawing striations on ~40 % of the surface area. Specimen 30 had striations on less than 10 % of the surface area. Specimens 26, 27 and 38 had striations on <5 % of their total surface area.

Gnawing was found to occur with all other modifications types in two instances (22 and 38), with surface tunnels in three instances (22, 30 and 38), with destruction in all cases, with bore holes in five instances (22, 23a, 26, 27 and 38) and with surface pits of varying classes in five instances (22, 23a, 23b, 27 and 38).

Experiment B:

Modifications recorded during trial D3 which received 100 g of canned meat bi-weekly

Eleven out of 19 specimens were not modified by *D. maculatus* after a period of four months; representing 58 % of the total sample. The unmodified specimens (88, 91, 93–94, 96–99, 102–104) included thin cortical bone specimens from metapodial shaft fragments, one dry and one fossil, two tibia shaft fragments made of thick cortical bone, long bone shaft fragments from an indeterminate fossil bovid and a fresh *D.*

pygargus, a fossil tooth root fragment from an indeterminate bovid, a weathered *B. domesticus* premolar, a dry complete *O. aries* premolar, a dry Aves humerus of indeterminate affiliation, a weathered rib fragment from an indeterminate bovid, two fresh specimens from a *D. pygargus*, one a rib shaft fragment and the other the distal section of the femur. The eight remaining specimens displayed either one or a combination of modification types; only two out of eight had macroscopically visible modifications, whilst seven out of eight had either intermediately or microscopically visible modifications.

3.2.2.7. *Macroscopically visible modifications (Experiment B: Trial D3 – 100g food)*

Surface Tunnelling (specimen numbers 85, 86)

A total of 21 surface tunnels made by *D. maculatus* were identified on two specimens; representing 11 % of the total sample, or 40 % of the modified specimens. Surface tunnels were only found to occur on the periosteal surface of the specimens. Specimen 85 displayed the most surface tunnels recorded across all bone specimens from all trials (D1 – D4). A total of 18 moderately visible surface tunnels where recorded on the dorsal side of a weathered scapula from an *O. Aries.* Specimen 86 displayed a further three surface tunnels on the distal end of a dry epiphysis of an *O. aries* femur. The average size of the surface tunnels where visibly smaller when compared to those recorded during experiment A (trial D1 and D2).

Measurements are provided and discussed below in section 2.4.3, page 102.

Surface tunnelling was found to occur with destruction and gnawing striations in both instances, and with bore holes in one case (86) and with surface pits in the other (85).

3.2.2.8. *Intermediately visible modifications (Experiment B: Trial D3 - 100g food)*

Destruction (specimen numbers 85–87, 89, 90, 92, 100, 101)

Destruction by *D. maculatus* was identified on six different specimens; 32 % of the total sample, or 75 % of the modified specimens. Destruction was recorded primarily on the periosteal surface, but in a single instance damage was recorded within the medulla of a dry *O. aries* distal femoral epiphysis, representing 10 % of the total surface area of the specimen. Two other specimens also showed faintly visible damage on <10 % of the available surface area, including a weathered *O. aries* scapula on both the ventral and dorsal surfaces, as well as a weathered phalanx from an indeterminate bovid. A dry *Phocid sp.* femur displayed faintly visible damage on <5 % of the available surface area, as did, a dry rib fragment from an indeterminate bovid, however, the bovid damage was considered clearly visible. A fresh *G. domesticus* femur displayed

moderately visible destruction on <15 % of the available surface area particularly on both the distal and proximal epiphysis.

Destruction was found to occur in combination with surface tunnels (85 and 86) and surface pits (85 and 101) in two instances, with bore holes in three instances (86, 90 and 101) and with gnawing striations in four instances (85, 86, 90 and 92).

Bore holes (specimen numbers 86, 89, 90, 101)

A total of 10 bore holes were recorded on four specimens; represented on 21 % of the total sample, or 50 % of the modified specimens. Bore holes were located only on the periosteal surface. In two instances the bore holes were considered moderately visible, which included two bore holes on a dry distal epiphysis of an *O. aries* femur and two bore holes recorded on a fresh *G. domesticus* femur. A further three bore holes were faintly visible on a dry *O. aries* tarsus, while the last three bore holes were clearly visible on a dry rib fragment from an indeterminate bovid.

Bore holes were found to occur in combination with both destruction (86, 90 and 101) and gnawing striations (86, 89 and 90) in three instances, with surface pits in two instances (89 and 101) and with surface tunnels in a single instance (86).

3.2.2.9. *Microscopically visible modifications (Experiment B: Trial D3 – 100g food)*

Surface Pits

A total of 20 Class 1 and two Class 3 surface pits made by *D. maculatus* were recorded on three specimens; represented on 16 % of the total sample, or 38 % of the modified specimens. Only a single Class 3 surface pit was considered clearly visible, occurring on the distal epiphysis of a fresh *G. domesticus* femur. All other surface pits were considered faintly visible, including 13 Class 1 surface pits recorded on a dry *O. aries* tarsus, as well as the remaining eight surface pits recorded on a weathered *O. aries* scapula (four Class 1 and one Class 3 on the ventral surface, and three Class 1 on the dorsal surface). No Class 2 surface pits were recorded in this trial.

Surface pits were found to occur in combination with destruction (85 and 101), bore holes (89 and 101) and gnawing striations (85 and 89) in two instances, whilst occurring in combination with surface tunnels in a single instance (85).

Gnawing (specimen numbers 85–87, 89, 90, 92)

Gnawing striations made by *D. maculatus* were identified on six specimens; represented on 32 % of the total sample, or 75 % of the modified specimens. Gnawing was only considered moderately visible in a single instance; a weathered *O. aries*

scapula on which <20 % of the ventral and <10 % of the dorsal surface was covered with striations, which resulted in the roughening of the out cortical lamellae. A dry rib fragment from an indeterminate bovid displayed gnawing striations on <20 % of the bone surface including along edges and the medullary wall. A dry distal section of an *O. aries* femur displayed faint gnawing on <10 % of the surface area, a dry metacarpal from an indeterminate bovid displayed faint gnawing on both the periosteal surface and medullary wall, covering <5 % of the available surface area. Lastly, a dry *O. aries* tarsus and a weathered phalanx from an indeterminate bovid displayed faint gnawing striations on <5 % of the surface area.

Gnawing striations were found to occur in combination with surface tunnels (85 and 86) and surface pits (85 and 89) in two instances, with bore holes in three instances (86, 89 and 90) and with destruction in four instances (85, 86, 90 and 92).

Modification records during trial D4 which received 50 g of canned meat bi-weekly

Fourteen out of 19 specimens in this trial did not display any modifications; representing 74 % of the total sample. The unmodified specimens (95, 108, 109, 113–123) including a weathered *B. domesticus* premolar, a dry *O. aries* premolar, a fossil enamel fragment from an indeterminate bovid, thick cortical bone specimens, including a dry

metacarpal shaft fragment and a fossilised tibia shaft fragment, both from indeterminate bovids, a fresh tibia shaft fragment from a *D. pygargus,* a thin cortical metapodial shaft fragment from an *O. aries*, a weathered cancellous bone shaft fragment and a fossilised shaft fragment, both from an indeterminate skeletal element and species, a dry *Phocid sp.* femur, a humerus from an indeterminate bird, and three fresh specimens, including a *G. domesticus* femur, a rib shaft fragment and the distal section of a *D. pygargus* femur.

The remaining five specimens displayed either one or a combination of modification types; only two out of five remaining specimens showed macroscopically visible modifications, whilst all five showed both intermediate and microscopically visible modifications.

3.2.2.10. *Macroscopically visible modifications (Experiment B: Trial D4 – 50g food)*

Surface Tunnels (specimen numbers 106, 107)

A total of seven surface tunnels made by *D. maculatus* were identified on two separate specimens; represented on 11 % of the total sample, or 40 % of modified specimens. They included a weathered distal portion of an *O. aries* femur, which recorded two clearly visible surface tunnels, one on the periosteal surface and one excavated into the trabecular bone within the exposed medullary cavity, as well as a dry *O. aries* scapula that displayed five moderately visible surface tunnels on the ventral surface.

Surface tunnels were found to occur in combination with gnawing striations and destruction in both instances, whilst occurring with surface pits only once (106) and were not found to co-occur with bore holes.

3.2.2.11. *Intermediately visible modifications (Experiment B: Trial D4- 50g food)*

Destruction (specimen numbers 106, 107, 110–112)

Destruction by *D. maculatus* was recorded on five different specimens; represented on 26 % of the total sample, or 100 % of the modified specimens. It was considered clearly visible only on a dry rib fragment from an indeterminate species, which was evident on <10 % of the total surface area. Destruction of the medullary wall was only faintly visible on a weathered distal section of an *O. aries* femur on <5 % of the surface area, whilst a weathered phalanx from an indeterminate bovid displayed very faint destruction on <10 % of the available surface area. The remaining two specimens showed faint destruction on <5 % of the available surface area, which included a dry *O. aries* scapula on the lateral articular facet and a dry *O. aries* tarsus.

Destruction was found to occur in combination with gnawing striations in all five instances, with surface tunnels (106 and 107) and surface pits (106 and 110) in two instances, and with bore holes in a single instance (110).

Bore holes (specimen 110)

Only one specimen recorded a single bore hole; representing 5% of the total sample, or 20 % of the modified specimens. The faintly visible bore hole was recorded on the periosteal surface of a dry *O. aries* tarsus.

The single bore hole was found to occur in combination with gnawing, surface pits and destruction.

3.2.2.12. *Microscopically visible modifications (Experiment B: Trial D4 – 50g food)*

Surface pits (specimen numbers 106, 110)

A total of six class 1 surface pits were identified on two separate specimens; 11 % of the total sample, or 40 % of the modified specimens. A dry *O. aries* scapula showed two very faint surface pits on its dorsal surface, whilst a dry *O. aries* tarsus displayed the remaining four faintly visible surface pits.

Surface pits were found to occur in combination with gnawing and destruction in both instances, whilst with bore holes (110) and surface tunnels (106) in a single instance each.

Gnawing (specimen numbers 106, 107, 110–112)

Gnawing made by *D. maculatus* was identified on five separate specimens; represented on 26 % of the total sample, or 100 % of

the modified specimens. In all five instances gnawing striations were considered faintly visible and were not identified within the medullary cavity. Gnawing was evident on <10 % of the available surface area in two instances, which included a dry *O. aries* scapula as well as a rib fragment from an indeterminate species. The remaining three specimens displayed gnawing on <5 % of the available surface area of the following specimens; a weathered distal section of an *O. aries* femur, a dry *O. aries* tarsus and a weathered phalanx of an indeterminate bovid.

Gnawing striations were found to occur in combination with destruction in all five instances, with surface tunnels (106 and 107) and surface pits (106 and 110) in two instances and with bore holes in a single instance (110).

3.2.3. Measurements of modification types

All measurements were obtained from digital micrographs using 'analyse IT' image processing software linked to the Olympus SZX Multifocus microscope. All measurements were recorded in microns (μm) and captured in a Microsoft excel spreadsheet. Descriptive statistics and non-parametric tests were obtained using IBM SPSS Statistics version 20. The raw data and non-parametric test results are all included in Appendix A.

Borehole measurements

Two measurements were taken from each bore hole; length and breadth. Length was considered the larger of the two measurements whilst breadth was taken as the smaller of the two.

Experiment A

The measurements were put into SPSS and the following descriptive statistics were obtained from the four boreholes measured from trials D1 & D2. Width; mean 1206.02µm with a Std. error of 759.51, median 472.37µm, S.D. 1519.03µm, minimum 395.75µm, maximum 3486.59µm. Breadth; mean 823.66µm with Std. error of 567.35, median 283.75µm, S.D. 1134.71µm, minimum 204.79µm, maximum 2522.38µm.

Experiment B

The measurements were put into SPSS and the following descriptive statistics were obtained from the four boreholes measured from trials D3 & D4. Width; mean 449.33µm with a Std. error of 68.25, median 424.84µm, S.D. 167.18µm, minimum 214.84µm, maximum 688.58µm. Breadth; mean 376.62µm with a Std. error of 76.09, median 326.13µm, S.D. 186.38µm, minimum 148.73µm, maximum 639.21µm.

Measurement comparisons of borehole form Experiment A & B

A non-parametric Mann-Whitney U test was conducted to examine the distribution of both width and breadth between data from experiment A and B. The test results produced P values of 0.476 (width) and 1.000 (breadth) suggesting that there is no statistically significant difference in the size of boreholes between the two experiments.

Surface pit class 1 measurements

Two measurements were taken from each surface pit class 1; length and width. Length was taken as the widest measurement across the feature and width was taken as the greatest measurement perpendicular to the length.

Experiment A

The measurements were put into SPSS and the following descriptive statistics were obtained from the 16 class 1 surface pits measured from trials D1 & D2. Length; mean 526.82µm with a Std. error o f 91.22, median 377.47µm, S.D. 364.91µm, minimum 165.26µm, maximum 1381.45µm. Width; mean 255.74µm with a Std. error of 37.71, median 182.90µm, S.D. 150.86µm, minimum 115.68µm, maximum 550.30µm.

Experiment B

The measurements were put into SPSS and the following descriptive statistics were obtained from the two class 1 surface pits measured from trials D3 & D4. Length; mean 119.62µm with a Std. error of 9.37, median 119.62µm, S.D. 13.25µm, minimum 110.25µm, maximum 129.00µm. Width; mean 81.80µm with a Std. error of 18.73, median 81.80µm, S.D. 26.49µm, minimum 63.07µm, maximum 100.54µm.

Measurement comparisons of class 1 surface pit form Experiment A & B

A non-parametric Mann-Whitney U test was conducted to examine the distribution of both length and width between data from experiment A and B. The test results produced P values of 0.013 (length) and 0.013 (width) suggesting that there is a statistically significant difference between the distribution of these measurements between the two experiments. However, this is likely a result of only two class 1 surface pits being measured from experiment B as opposed to the 16 class 1 surface pits measured from experiment A.

Surface Pit Class 2 measurements

Only two class 2 surface pits were identified during the course of the investigation. Two measurements were taken from each surface pit class 2; length and breadth. Length was the taken as the widest

measurement across the feature and breadth was taken as the greatest measurement perpendicular to the length. The measurements were put into SPSS and the following descriptive statistics were obtained from the two class 2 surface pits measured from trial D1. Length; mean 5260.76µm with a Std. error of 72.82, median 5260.76µm, S.D. 102.98µm, minimum 5187.94µm, maximum 5333.58µm. Breadth; mean 2974.35µm with a Std. error of 102.56, median 2974.35, S.D. 145.04µm, minimum 2871.79µm, maximum 3076.92µm. Due to the size of the sample no comparative statistics were possible.

Surface Tunnel measurements

Two primary measurements were used for the purpose of statistical analysis of surface tunnels; length and width. In situations in which the width varied across the length of the feature, up to 5 width measurements were taken at regular intervals. Length was then taken as the greatest measurement across the feature, and width was taken as the average measurement perpendicular to the length. Surface tunnels were also subdivided into two size classes; those with a length <5000µm and those with a length >5000µm to establish if there is any statistically significant difference between these two size classes.

Experiment A

The measurements were put into SPSS and the following descriptive statistics were obtained from the 16 surface tunnels measured from trials D1 and D2. Length; mean 7290.12µm with

a Std. error of 1154.70, median 6183.56µm, S.D. 4618.83µm, minimum 1500.31µm, maximum 17093.04µm. Width; mean 482.85µm with a Std. error of 92.32, median 329.02µm, S.D. 369.31µm, minimum 108.69µm, maximum 1405.48µm.

Experiment B

The measurements were put into SPSS and the following descriptive statistics were obtained from the 13 surface tunnels measured from trials D3 and D4. Length; mean 4228.65µm with a Std. error of 1015.00, median 2212.17µm, S.D. 3797.78µm, minimum 953.57µm, maximum 13997.93µm. Width; mean 590.31µm with a Std. error of 103.46, median 475.85µm, S.D. 387.13µm, minimum 192.54µm, maximum 1618.39µm.

Measurement comparisons of surface tunnels from Experiment A and B

A non-parametric Mann-Whitney U test was conducted to examine the distribution of both length and width between data from experiment A and B. The test results produced P values of 0.034 (length) and 0.224 (width) suggesting that there is a statistically significant difference between the length of surface tunnels between the two experiments, but no statistically significant difference in width between the two experiments.

Surface tunnels with a length <5000µm

The measurements were put into SPSS and the following descriptive statistics were obtained from the 15 surface tunnels measured from trials D1 - D4. Length; mean 2318.43µm with a Std. error of 284.98, median 1971.02µm, S.D. 1103.74µm, minimum 953.57µm, maximum 4479.08µm. Width; mean 388.35µm with a Std. error of 64.02, median 360.97µm, S.D. 247.95µm, minimum 108.69µm, maximum 1108.41µm.

Surface tunnels with a length >5000µm

The measurements were put into SPSS and the following descriptive statistics were obtained from the 15 surface tunnels measured from trials D1 - D4. Length; mean 9404.44.90µm with a Std. error of 935.65, median 9284.83µm, S.D. 3623.79µm, minimum 5087.51µm, maximum 17093.04µm. Width; mean 677.64µm with a Std. error of 111.10, median 537.20µm, S.D. 430.29µm, minimum 193.73µm, maximum 1618.39µm.

Measurement comparisons of surface tunnels with a length <5000µm or >5000µm.

A non-parametric Mann-Whitney U test was conducted to examine the distribution of both length and width between surface tunnels with a length <5000µm or >5000µm. The test results produced P values of 0.000 (length) and 0.041 (width), suggesting that there is a statistically significant difference in both length and width between the two sizes classes.

3.2.4. Occurrence and frequency patterns of modification types

Occurrence and frequency of modification types – Experiment A (D1 and D2)

Figure 41 represents the occurrence (%) of specimens that displayed a particular modification type for each trial. Surface tunnels, bore holes and surface pits made by *D. maculatus* could be physically counted. In the absence of substrate, both the occurrence of modifications (%) as well as the frequency of modifications made by *D. maculatus* (*n* value) is higher than in the presence of substrate. The only exception to this is bore holes, for which both the occurrence and frequency are higher in the presence of substrate.

Occurrence and frequency of modification types according to bone density – Experiment A (D1 and D2)

Figure 42 depicts the occurrence (%) of modification types made by *D. maculatus* on specimens of varying bone density for each trial in Experiment A. Figure 42a shows that surface tunnels in the presence of substrate where limited to specimens of varying density. However, these modifications did not occur on cortical bone, but rather on less dense bone located at the diaphysis-epiphysis junction. In the absence of substrate the occurrence of these modifications increased, and were also recorded on specimens classified as purely spongy in nature. Destruction (Figure 42b) was recorded in equal proportions on compact bone, spongy bone and bones of variable densities across both trials, however, in the absence of substrate, destruction was also recorded on

an enamel tooth fragment. In the absence of substrate bore holes (Figure 42c) only occurred on bones of varying density, whilst in its presence they were recorded on compact and spongy bone, as well as more frequently on specimens of varying densities. Surface pits (Figure 42d) made by *D. maculatus* occurred less frequently on spongy bone in the absence of substrate, whilst more frequently on bones of varying densities, but it was only in the absence of substrate that surface pits were recorded on an enamel tooth fragment. Gnawing striations (Figure 42e) occurred in equal proportions in both trials on spongy bone and bones of variable density. However, in the absence of substrate they were more frequently recorded on compact bone specimens, and were recorded on an enamel tooth fragment and on thick cortical bone specimens.

Occurrence and frequency of modification types according to bone condition – Experiment A (D1 and D2)

Figure 43 depicts the occurrence (%) of modification types made by *D. maculatus* on specimens of varying condition for each trial in Experiment A. Figure 43a shows that surface tunnel occurrence was relatively consistent on dry bone specimens for both trials, but that in the absence of substrate the occurrence and frequency of surface tunnels was much higher on fresh specimens. Figure 43b shows that the occurrence of destruction on both dry and fresh specimens was relatively consistent for both trials, but marginally higher on weathered

specimens, and only recorded on fossil specimens in the absence of substrate. Bore hole (Figure 43c) occurrence and frequency was markedly higher on fresh and dry specimens in the presence of substrate, and only represented on dry specimens in the absence of substrate. Surface pits (Figure 43d) occurred relatively consistently on dry specimens, but their frequency was slightly higher in the absence of substrate. Only a single borehole occurred on a weathered bone specimen in the presence of substrate and on fossil specimens in the absence of substrate. Lastly, the occurrence and frequency of surface pits in the absence of substrate on fresh specimens was markedly higher. Gnawing striations (Figure 43e) occurred equally on fresh specimens, were marginally higher on dry specimens in the presence of substrate, and were only recorded on weathered and fossil specimens in the absence of substrate.

Occurrence and frequency of modifications types – Experiment B (D3 and D4)

Figure 44 represents the occurrence (%) of specimens that displayed a particular modification type for each trial. The graph shows that in the absence of sufficient food (D4) the occurrence of modifications (%) as well as the frequency of modifications (*n* value) is lower than when food was more regularly supplied. However, surface tunnel (see Figures 41 and 44) occurrence was identical for both trials, but the frequency (*n* value) was markedly higher when more food was available ($n = 21$), as opposed to when food availability was limited ($n = 7$). Nonetheless, the

general trend is clear in that food availability impacts both on the occurrence and frequency of modifications and that apart from surface tunnels, both are increased in the presence of sufficient food.

Occurrence and frequency of modification types according to bone density – Experiment B (D3 and D4)

Figure 45 depicts the occurrence (%) of modification types made by *D. maculatus* on specimens of varying bone density for each trial in Experiment B. Figure 45a shows that the occurrence of surface tunnels is comparable between the two trials on specimens of variable density, but that the frequency is much higher under normal feeding conditions. The occurrence of destruction (Figure 45b) on spongy bone specimens was comparable between the two trials, but was markedly less on variable bone specimens under stressed feeding conditions, and markedly higher on compact bone specimens. Bore holes (Figure 45c) were only recorded on variable and spongy bone specimens under normal feeding conditions, whilst on compact bone occurrence was comparable, but frequency was marginally higher under normal feeding conditions. Similarly, surface pit (Figure 45d) occurrence was comparable on compact bone specimens, but frequency was markedly higher under normal feeding conditions, whilst both occurrence and frequency was higher on variable bone specimens under normal feeding conditions. Lastly, gnawing (Figure 45e) occurrence was comparable on compact, spongy and variable specimens, but was only recorded on thick cortical bone specimens under normal feeding conditions.

Occurrence and frequency of modification types according to condition – Experiment B (D3 and D4)

Figure 46 depicts the occurrence (%) of modification types against the number of available specimens of varying condition for each trial in Experiment B. Figure 46a shows that the occurrence of surface tunnels on dry and weathered specimens is comparable between the two trials. However, frequency is much higher on weathered specimens under normal feeding conditions, whilst marginally higher on dry specimens under stressed feeding conditions. Destruction (Figure 46b) occurrence is comparable on both dry and weathered specimens across both trials but was only recorded on fresh bone specimens under normal feeding conditions. Bore hole (Figure 46c) occurrence and frequency was markedly higher on dry specimens under normal feeding conditions when compared to stressed feeding conditions, and were only recorded on fresh specimens under normal feeding conditions. Similarly, surface pits (Figure 46d) were only recorded on fresh and weathered specimens under normal feeding conditions. However, their occurrence was higher under stressed feeding conditions, but not their frequency. The occurrence of gnawing striations (Figure 46e) was comparable on weathered bones and only slightly higher on dry specimens under normal feeding conditions.

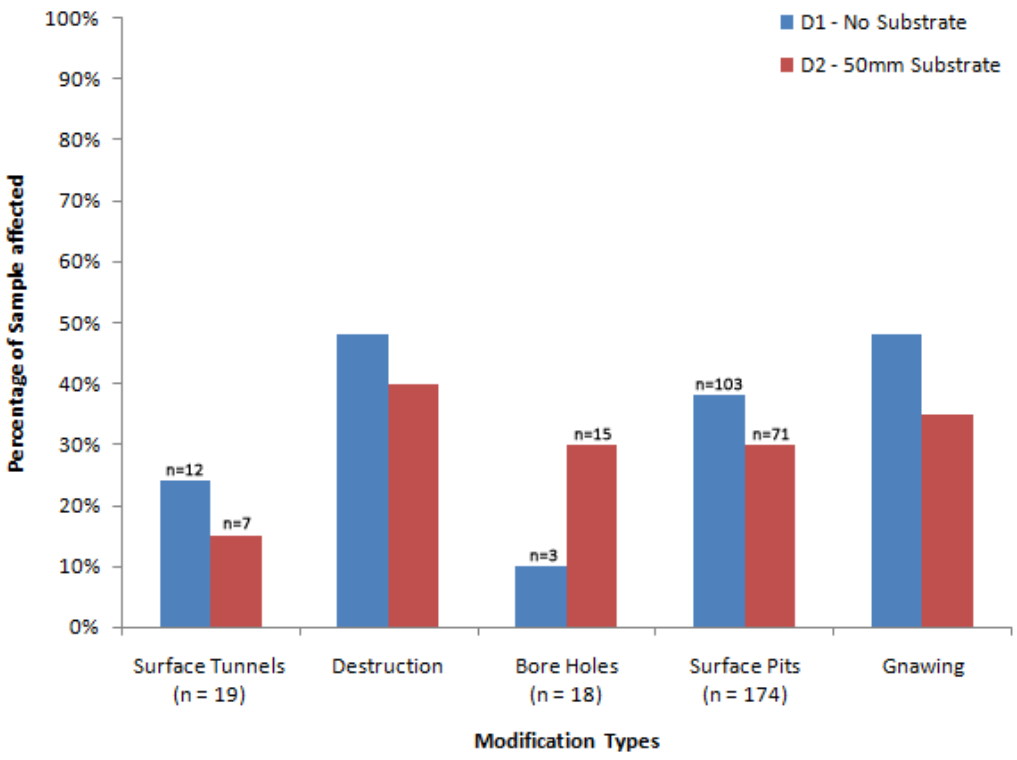

Figure 41: Frequency of bone modification types made by *D. maculatus*, made in the absence or presence of substrate. Note: *n* value refers to the physical amounts of modifications counted e.g. Trial D1 recorded 12 surface tunnels in total, however *n* values do not apply to the modification types; destruction or gnawing.

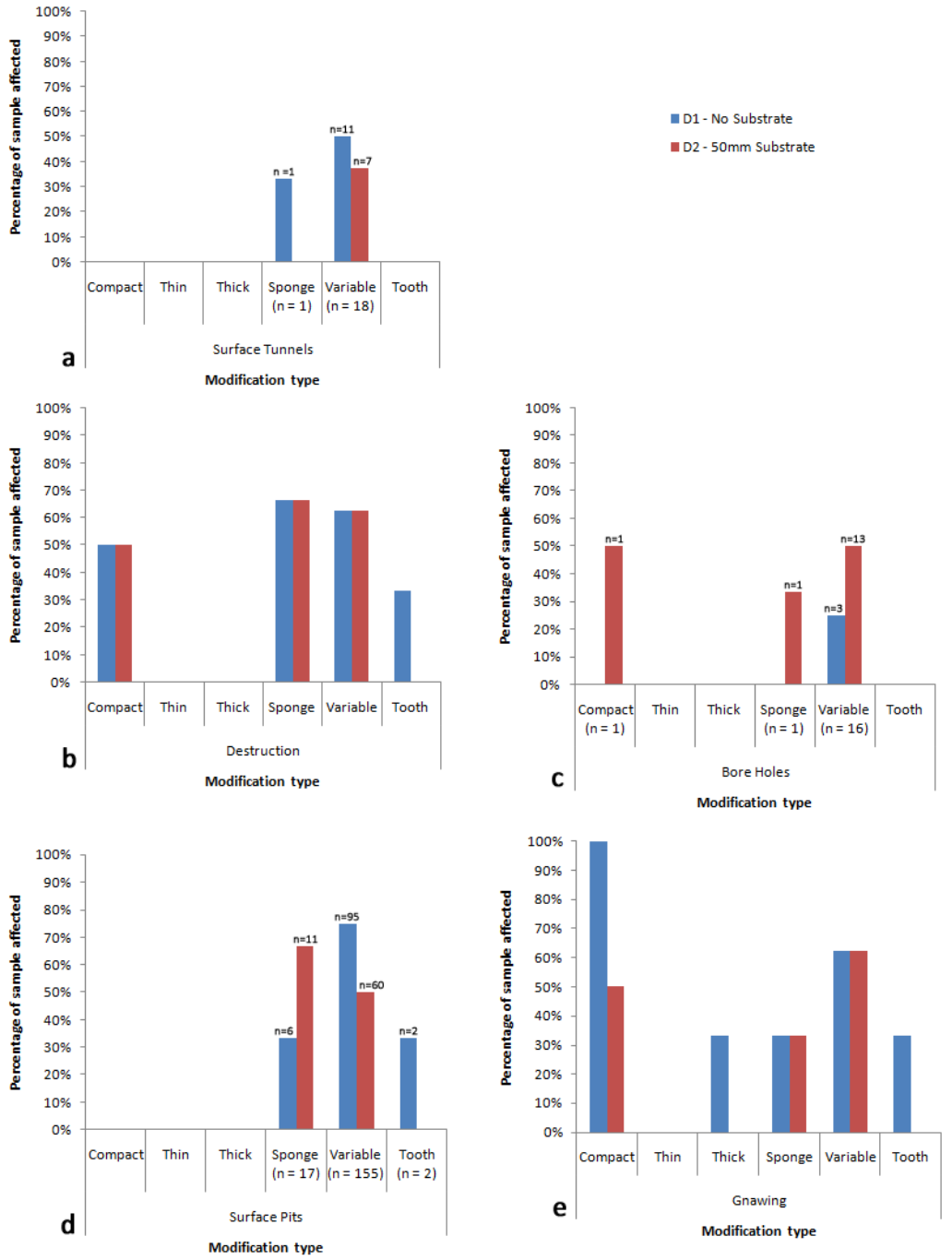

Figure 42: Frequency of bone modification types made by *D. maculatus*, made in the absence or presence of substrate. Note: *n* value refers to the physical amounts of modifications counted e.g. Trial D1 recorded 11 surface tunnels on bones of variable density which were distributed over 50% of the sample, however *n* values do not apply to the modification types; destruction or gnawing.

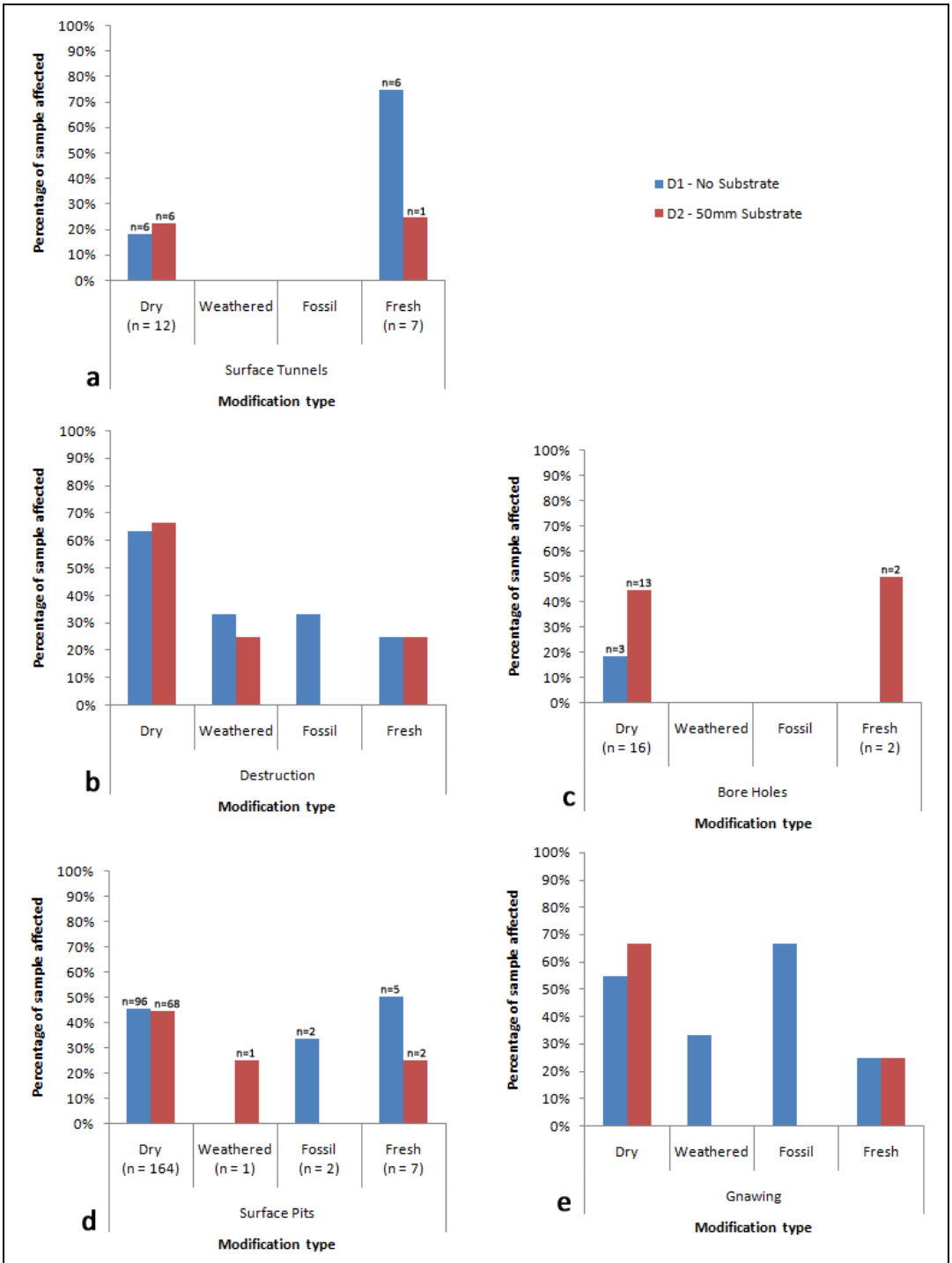

Figure 43: Frequency of bone modification types made by *D. maculatus*, made in the absence or presence of substrate. Note: *n* value refers to the physical amounts of modifications counted e.g. Trial D1 recorded 6 surface tunnels on dry bones which were distributed over 18% of the sample, however *n* values do not apply to the modification types; destruction or gnawing.

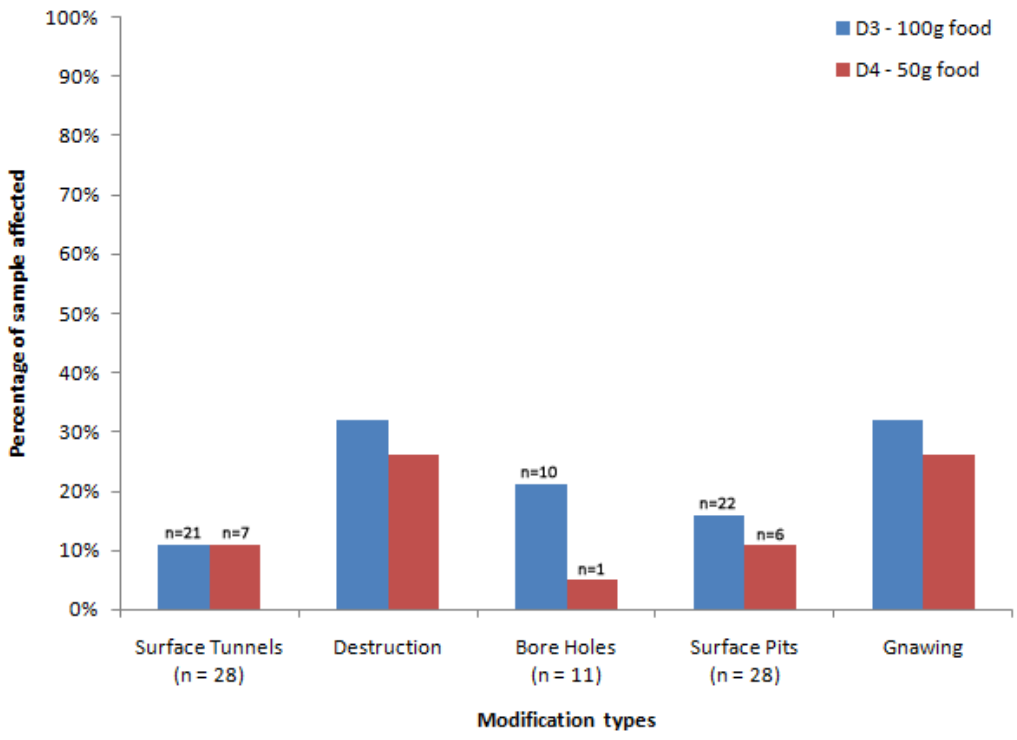

Figure 44: Frequency of bone modification types made by *D. maculatus*, under normal and reduced feeding conditions. Note: *n* value refers to the physical amounts of modifications counted e.g. Trial D3 recorded 21 surface tunnels in total, however *n* values do not apply to the modification types; destruction or gnawing.

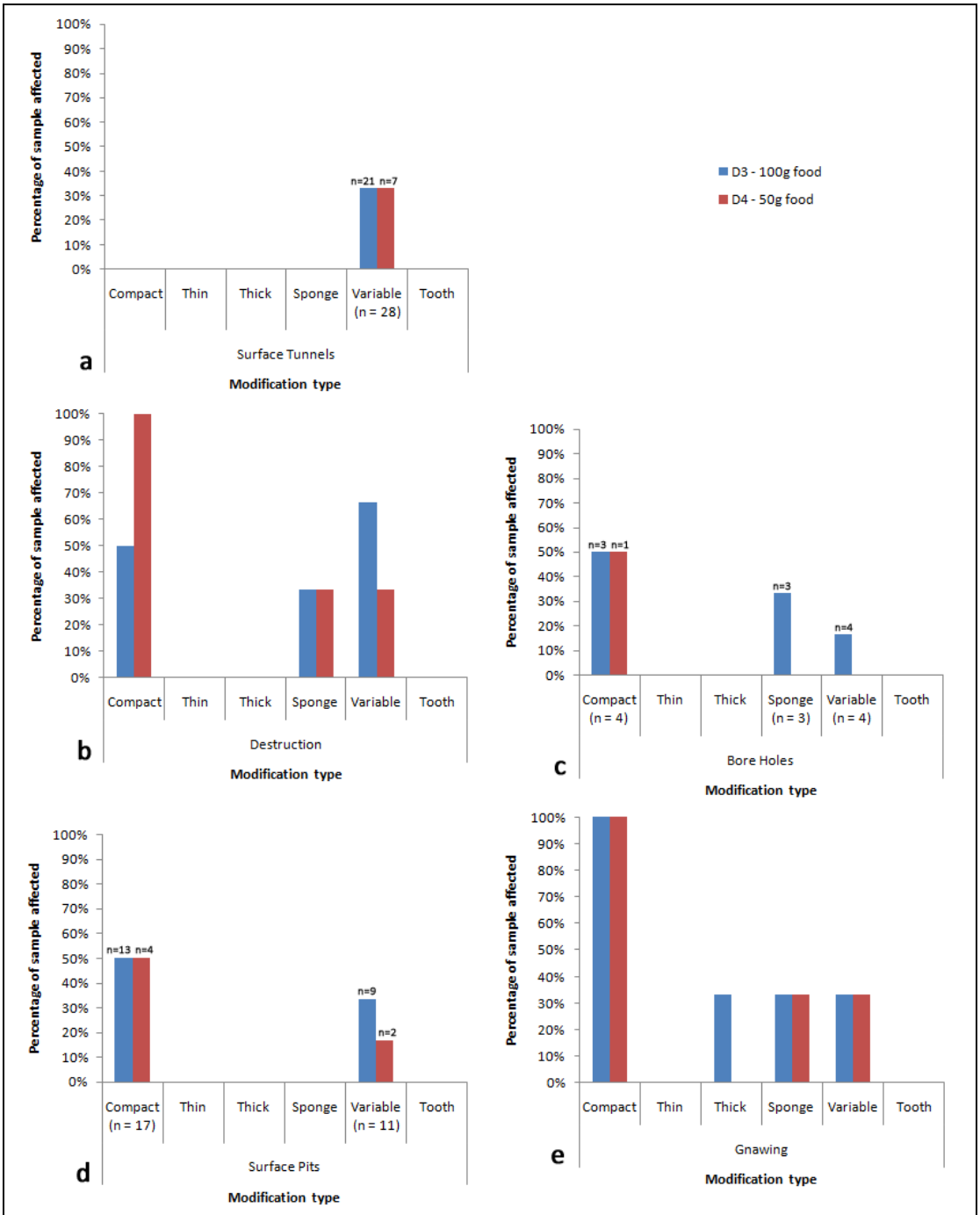

Figure 45: Frequency of bone modification types made by *D. maculatus*, under normal and reduced feeding conditions. Note: *n* value refers to the physical amounts of modifications counted e.g. Trial D3 recorded 21 surface tunnels on bones of variable density which were distributed over 35% of the sample, however *n* values do not apply to the modification types; destruction or gnawing.

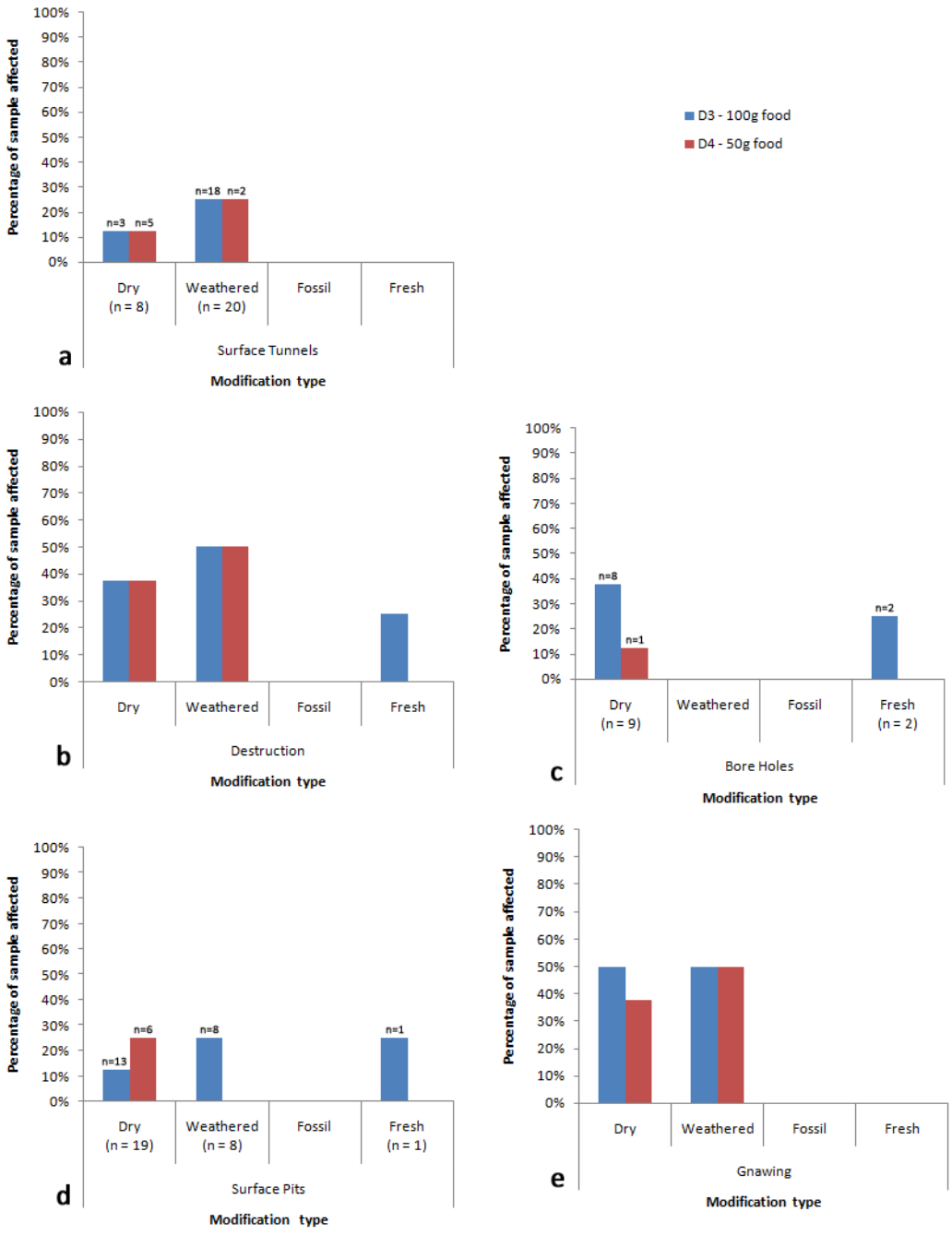

Figure 46: Frequency of bone modification types made by *D. maculatus*, under normal and reduced feeding conditions. Note: *n* value refers to the physical amounts of modifications counted e.g. Trial D3 recorded 3 surface tunnels on dry bones which were distributed over 10% of the sample, however *n* values do not apply to the modification types; destruction or gnawing.

CHAPTER FOUR - DISCUSSION

4.1. *Periplaneta americana*

Results show that *P. americana* certainly do modify bone, but the low frequency of modifications, and microscopic size may make the future identification of such modifications from an archaeological or palaeontological context difficult. *Periplaneta americana* were found to destroy/obliterate bone, particularly cancellous bird bone. There is no evidence to suggest that they are able to penetrate cortical bone, but they do gnaw on it, resulting in the roughening of the outer cortical lamellae. A single cluster of relatively parallel gnawing striations were identified, but their occurrence and frequency is very low. Discolouration of the bone surface is not a modification type but rather a feature of *P. americana* activities, and it was the most obvious, widely distributed and frequent modification type recorded. Importantly, *P. americana* modification signature in terms of occurrence, frequency and distribution is different from that of *D. maculatus* as well as *Trinervitermes trinervoides* (Backwell *et al.* 2012). Therefore, these three agents should be easily distinguishable from one another when identified in the archaeological or palaeontological record.

Periplaneta americana has a cosmopolitan distribution but this experiment has shown that the levels of modification on exposed specimens are extremely low (Figure 18), compared to *D. maculatus* or *Trinervitermes trinervoides* (Backwell *et al.* 2012). Additionally, *P.*

americana may be either not attracted to or unable to modify denser bone, such as compact, thin or thick cortical bones (Figure 19), and the distribution of modifications according to condition (Figure 20) does not indicate any distinct selection preference. The random selection of specimens in bone type and state of preservation is likely related to exploratory behaviour, but a larger sample size may show evidence of selection.

The future identification of cockroach modifications from an archaeological or palaeontological context may be hampered by an inability to observe discolouration of the bone surface, a key feature associated with cockroach activities, but one that is probably limited in terms of preservation potential. Discolouration may be confused with tiny burn marks on the bone, but it is not consistent with heating in terms of distribution and colour. Under ideal conditions fecal remnants might possibly be found attached to the bone specimen. The longevity of discolouration needs to be tested under different preservational conditions and an experimental control established to ensure that discolouration does not relate to other biological processes. Until such time the occurrence of discolouration will most likely not be interpreted as a feature of *P. americana* activities.

Destruction of bone by cockroaches leaves a definite trace, as do gnawing striations, but the latter are unfortunately limited in occurrence and frequency. While destruction and gnawing are traces

now known to be produced by cockroaches, these features alone are limited in providing comprehensive criteria for the identification of *P. Americana* modification. However, observations during experiments suggested that *P. americana* are attracted to fresh bones with meat. Despite their ability to modify less dense bone, the infrequency of modifications on bone indicates that perhaps they are more interested in the soft tissue rather than the bone itself. Cockroaches are likely involved in consuming meat on corpses at an early stage of decomposition, and have likely not been previously considered as agents in this role because of their primarily nocturnal foraging behaviour.

4.1.1. Modification interpretation

Discolouration likely relates to secretions produced by cockroaches, which stains the bone surface. However, the lack of an experimental control limited it applicability as it may relate to other decomposition processes. None the less, discolouration was not associated to changes on the bone surface in the form of a depression or recess. Apart from the visual discolouration it appears not to have physically altered the bone in any way and as a result its preservation potential and future identification is potentially limited. It was identified on all bone densities (except on teeth) as well as on specimens of all condition (except fossil).

Destruction by *P. americana* was most distinct on *G. domesticus* long bones, but was also found to occur on articular facets or the diaphysis-

epiphysis junction. The distribution of destruction on the various specimens suggests that either *P. americana* chooses not to or are physically unable to substantially modify dense cortical bone. Destruction or obliteration of bone was not associated with any other distinctive trace morphologies, such as gnawing striations. Most often destruction was identified as the removal of the outer cortical lamellae to expose the underlying trabecular bone structure on cancellous skeletal elements (particularly bird bone), or the roughening of the outer cortical lamellae on more dense skeletal elements. Without prior knowledge of the condition of the bone before exposure, it would prove difficult to identify such modifications as being those created by *P. americana*. It is likely that this type of damage in the fossil record would be interpreted as differential preservation or the result of other pre- or post- depositional processes, like sedimentary abrasion.

The occurrence of gnawing striations was only identified on a single cancellous bone specimen. The morphology of the individual striations was distinct in that they displayed a single, smooth-bottomed arrowhead shape; wide at one end and extremely narrow at the other. After an exposure period of six months the frequency of striations was very limited. Nonetheless, gnawing striations may prove useful in the future identification of *P. americana* damage.

The gross morphology, distribution and orientation of striations provide potential insight into the associated behaviour. In that, striations are

perpendicular to the edge with their narrowest side furthest away from the edge and widen towards the edge of the bone (Figure 17). This may be explained in terms of the need for leverage; one mandible is anchored to the edge of the bone whilst the other mandible creates the striation. At the point of contact the least pressure is exerted resulting in the narrow side of the gnawing striation and through the bringing together of the mandibles both the associated pressure and bone penetration by the primary apical tooth increases resulting in widening of the striations toward the point of occlusion. This reaffirms conclusions drawn about *Trinervitermes trinervoides* (Parkinson, 2010; Backwell *et al.* 2012) and those about *D. maculatus*, in that the primary apical tooth is likely responsible for the creation of the gnawing striation, and despite the presence of secondary or tertiary apical teeth they do not appear to play a role in the creation of gnawing striations but this requires further testing.

4.1.2. Identification criteria

Despite the limited potential for long term preservation of discolouration, and relatively low rates of occurrence of the described modification types, the following is proposed to aid in the identification of *P. americana* modifications on bones recovered from an archaeological or palaeontological context.

The occurrence of gnawing striations should be found on, but not restricted to cancellous skeletal elements such as ribs or vertebrae, as

well as areas of long bones which have less dense bone, such as at the diaphysis-epiphysis junction. Gnawing striations are likely to occur near to or on an edge, oriented approximately perpendicular to it, and as a group of similarly oriented individual striations, distributed sub- or parallel to one another (see Figure 17). However, establishing modification criteria based on a single cluster of striations is limiting in that a larger sample size may further indicate a higher degree of variability in terms of position and distribution on bones. It is likely that bone surface morphology and overall bone shape are influential in determining the orientation of striations as such the above are merely general guidelines.

Similarly, destruction will also primarily be restricted to cancellous skeletal elements, or areas of a bone that are less dense, like articular facets and the edges of epiphyses. On long bones, destruction should take the form of removal and roughening of the outer cortical lamellae (Figures 14–15), and exposure of trabecular bone at the diaphysis-epiphysis junction (see Figure 16).

It should be borne in mind that the identification of *P. americana* modifications should not be based on the identification of a single modification type, but rather on the described suite of modifications. Most importantly, these modifications should be in accordance with their described rates and distribution patterns of the associated modifications. Therefore, the co-occurrence of destruction, gnawing

striations, discolouration and their associated occurrence and distribution patterns should all be considered prior to attributing cockroaches to the damage observed.

4.1.3. Climatic Interpretation

Periplaneta americana are well studied in terms of their thermal physiology but the usefulness of this data in terms of palaeo-climatic reconstruction is limited. This is primarily due to the extremely high variability in thermal limits to which they are known to have adapted (Appel *et al.* 1984). None the less, if one considers the upper and lower thermal lethal limits of most populations of *P. americana* it could be infer that the prevailing climatic regime would likely to have had a mean maximum temperature of between 39 - 45° C with a mean minimum temperature of no less than -15° C (Strang, 1992; Cornwell, 1968).

In terms of determining the climatic conditions during the period of modification this would be dependent on the temperatures at which chill coma occurs i.e. 10° C (Bradfisch *et al.* 1981) and at which behavioural activities are seized i.e. <18° C (Strang, 1992). However, the variability of these specific limits, the potential of regional environmental acclimatisation as well as the fact that temperatures can fluctuate tremendously within a day, any attempt to infer more specific microclimatic conditions would simply result in the over simplification of the facts.

4.2. Dermestes maculatus

The general consensus in the actualistic literature is that dermestids infrequently damage bone and that when modifications do occur they are immediately obvious to the naked eye (Howell, 1932; Borell, 1938; Voorhies, 1948; Hooper, 1950; Hefti *et al.* 1980; Weichbrod, 1987). However, this study has shown that dermestids do in fact frequently modify bone in a number of distinctive ways, but that most modifications are only microscopically visible. The only macroscopically visible modification is surface tunnelling, but at magnifications from 7–20x bore holes and destruction of bone becomes more apparent. At magnifications higher than 20x surface pits of varying classes as well as microscopic gnawing striations become immediately obvious.

This study reaffirms the tentative conclusions drawn by Roberts and Rogers (2003) that the suite of modifications created by extant dermestids are not comparable to those attributed to them in the palaeontological literature. The modifications that are described in the palaeontological literature are often only superficially comparable to one another. The most pressing issue in ichnology is a lack of comparative material in the form of insect traces created by known agents. Another problem is the high variability in terminology usage, and a lack of comprehensive qualitative descriptions thereof.

Experimentation has shown that frequency of specific modification types are influenced by food availability or presence of substrate, but

that the type and distribution of modifications is relatively consistent despite conditions. Frequency patterns are thus vital in interpreting the taphonomic history and sequence of events recorded in modern and fossil faunal assemblages. Lastly, the diversity of trace modification types produced by dermestids (Surface tunnels, bore holes, surface pits of varying classes, destruction and gnawing striations) as well as association occurrences, distribution and frequency patterns should facilitate ease in identification of such modifications from archaeological or palaeontological faunal remains. The described suite of modifications identified during the course of this study shows that *D. maculatus* modifications are distinguishable from those made by *P. americana* and *Trinervitermes trinervoides* described by Backwell *et al.* (2012). Being able to reference only two other insect taxa highlights the need for additional experimentation using an expanded sample of insects which are assumed to modify bone.

The potential impact that termites may have on taxonomic and element representation, minimum number of individuals and age profiles in faunal assemblages (Backwell *et al*. 2012), and similar assertions made by Paik (2000) with particular reference to dermestids during the early Cretaceous, is unlikely to be as relevant in respect to *D. maculatus* activities as a result of the relatively minor impact they have on bone. The distribution of *D. maculatus* modifications, particularly on epiphysis and at the diaphysis-epiphysis junction is likely to result in increased separation and fragmentation of skeletal elements, which will make

them more prone to destruction, affecting skeletal element and in due course taxonomic representation. Destruction or obliteration of dense bone through gnawing was obvious, but by no means prolific. However, dermestids may be able to do enough damage to particularly small vertebrates or Aves remains within a relatively short period of time, and as such may be one of the factors which influence their under-representation in the fossil record but by no means are they the only factor affecting their underrepresentation.

It should be noted that four Aves skeletal elements (15, 36, 99 and 119), one from each trial, remained completely unmodified. These particular skeletal elements were collected on the beach along the north coast of Natal and therefore were likely to have had a high salt (sodium chloride) content, this potentially made them unattractive to *D. maculatus*, as reported by Picker *et al.* (2004) and Robinson (2005). Similarly, four Phocid femurs were also recovered from the coast; specimen 118 remained unmodified, specimen 37 was lost in transit, specimen 16 displayed only a single faint class 1 surface pit, and specimen 100 displayed minimalistic faint destruction on <5 % of its surface area. The few modifications on specimen 16 and 100 can likely be explained in terms of exploratory behaviour, despite them originating from the coast and also having a potentially unattractively high salt content. All other Aves bones showed high degrees of modification by *D. maculatus*, which was also noted by Kirkland and Bader (2010). *Periplaneta americana* as well as *Trinervitermes trinervoides* (Backwell *et al.* 2012) do significant

damage to Aves bones and therefore it is posited that invertebrates may be partially responsible for the under-representation of Aves bones in archaeological and palaeontological deposits.

4.2.1. Modification interpretation

Results show that *D. maculatus* certainly do modify bone in a number of different ways which include the creation of shallow furrows displaying a U-shaped profile excavated across the surface of a bone, regularly displaying small bore holes at either one or both ends of the furrow (surface tunnels), concentrated obliteration of bone (destruction), semi circular bore holes which do not have a discernible bottom, surface pits which are highly variable from semi circular to elliptical shaped shallow depressions with U-shaped profiles, with associated gnawing striations radiating around the outer circumference of the depression (Class 1), large semi- circular shallow depressions with randomly orientated striations over the entire feature (Class 2), individual striations are lens shaped which intersect and cross cut one another and are found in large clusters (see Figures 34 and 35), irregular shaped depressions with vertical walls and complex profiles not associated with gnawing striations (Class 3), and lastly clusters of randomly orientated gnawing striation which cover a large surface area.

Non parametric statistical tests were conducted to examine the differences in length and width of surface tunnels recorded during experiment A and B. Results show that surface tunnels recorded from

experiment A were significantly longer ($p = 0.024$) whilst the width measurements were comparable ($p = 0.224$).The consistency of width likely relates to the head width of the larvae responsible for the creation of this feature, whilst length may be attributed to the seeking out of less dense bone in order to penetrate into the medulla or underlying trabecular structure. This is further supported by the occurrence of tiny bore holes at the terminus of surface tunnels in that once less dense bone is located the dermestids bore through the cortical bone and do not choose to extend the surface tunnel further. Additionally, no bore holes were located in the middle of a surface tunnel but were either completely absent or located at either one or both end of the feature. A failed attempt to immediately penetrate cortical bone may result in the creation of surface tunnels as they explore the surface of the bone seeking out less dense bone in order to penetrate through the cortical bone. The highest frequency (*n* value) of surface tunnels was recorded in the absence of substrate, whilst the frequency of surface tunnels was markedly lower when substrate was present. The creation of surface tunnels potentially relates to the larvae seeking a suitable medium into which they can pupate, but the sheer lack of suitably sized bore holes to act as pupation chambers potentially suggests that dermestids are unable or have little interest in expending energy in order to create complete or even partial pupation chambers in bone, however, this remains to be tested. There appeared to be a substantial difference between surface tunnels which could be classified as either having a length of <5000µm or >5000µm. To test whether or not these were

significantly different groups non parametric tests were conducted. Results suggested that these two groups are significantly different both in terms of length ($p = 0.000$) and width ($p = 0.041$) which may suggest that two different stages of instars are responsible for the creation of these two size classes of surface tunnels.

The may be that dermestids are unable/choose not to expend the required energy to penetrate dense cortical bone. Supported by the fact that surface tunnels were never recorded on purely thin, thick or compact cortical bone specimens, but only found to occur on either cancellous or bone specimens of varying densities. In the instances in which tunnels were recorded on bone specimens of variable bone density the surface tunnels, as with all other modification types, tended to be located either on the epiphysis or close to the diaphysis-epiphysis junction and not on the dense cortical bone areas of the relevant specimens. Lastly, Surface tunnels were never recorded on either weathered or fossil specimens and were only found to occur on dry and fresh specimens (Refer to Figures 41–46).

Destruction by dermestids was more frequently recorded in the absence of substrate and specimens in all states of preservation were modified, including fossil specimens, whilst in the presence of substrate destruction was recorded only on dry, weathered and fresh specimens. Additionally, the absence of substrate increased the frequency of destruction of weathered bone, whilst levels of destruction of dry and

fresh specimens were comparable. Destruction was not recorded on either thin or thick cortical bone specimens, but was found in comparable proportions on compact and cancellous bone specimens displaying variable bone densities. Destruction of compact bone was confined to areas in which the cortical bone thickness was not substantial, and existing surface roughness and/or cracking allowed for further destruction of already exposed underlying trabecular bone (Figure 26). It was only in the absence of substrate that a fragment of fossilised tooth enamel showed signs of destruction, suggesting that the absence of substrate prompts more exploratory behaviour in terms of feeding.

The increased bone densities and varying condition which are modified in the absence of suitable substrate for pupation, probably reflects the increased exploration of specimens, potentially seeking out a suitable substance into which a pupation chamber could be bored. However, no distinctive pupations chambers were identified during current investigations of dermestid activities. In the absence of substrate, pupal casings were regularly observed on the surface of the glass at the base of the tank, or underneath bone specimens. However, in the presence of substrate pupal casings were never observed, and are assumed to have been created in the available substrate (Figure 21). The lack of the occurrence of pupation chambers in bone can perhaps be explained in terms of time and energy availability, by examining the known behaviour and life cycle of dermestids. The first 20 days of a larvae's life

is dedicated to constant eating, whilst days 20–25 are spent finding a suitable place to pupate (Howell, 1932; Russell, 1947), but dermestids have been known to delay the onset of pupation when a suitable/safe location cannot be found (Acher & Elgar, 1998). This poses a number of questions, such as is five days sufficient time for a larva to bore a pupation chamber into a bone, and is too much time and energy needed to do so, with the result that larvae are forced to pupate in the open or select a site with little or no protection, like under a bone. The lack of pupal chambers in bone, as well as the finding that dermestids chose to pupate either in the open or under minimal protective conditions suggests that the creation of pupation chambers in bone is not habitual. Though the fact remains that the palaeontological literature suggests that dermestids do pupate in bone but the currently study does not support such assertions.

Bore holes tended to be slightly elliptical in shape and did not occur as frequently as one would expect by examining existing palaeontological literature. Bore holes are markedly smaller than the average size of the adult beetles, which suggests that the larvae are responsible for their creation. Bore holes could represent another class of surface pit, but for the purposes of this classification they have been separated from other classes of surface pits because bore holes have no discernible bottom. Due to the size (diameters ranging between 148.73 – 688.58μm) and infrequency of bore holes it is not likely that they are related to the creation of pupation chambers, but rather represent surface pits which

successfully managed to penetrate the surface of bone, entering into the medulla and excavating through the underlying trabecular structure. Bore holes are the only modification types which do not conform to the patterns represented by the other modification type distributions, as they were more frequently recorded in the presence of substrate. In the presence of substrate, bore holes were recorded on both fresh and dry specimens, as well as on compact and cancellous bone, and on specimens of variable bone density. However, in the absence of substrate bore holes were only recorded on dry specimens of variable bone density. The distribution of bore holes potentially relates to the exposure and exploitation of underlying haversian canals that contain nerves, and blood and lymph vessels, and provide an easy route to marrow (White & Folkens, 2005). No statistically significant difference in bore hole size was found between experiment A and B.

Three distinctive classes of surface pits were established, but Class 1 are perhaps the most distinctive and most diagnostic of dermestid related activities. Class 1 pits occur in very high frequency, unlike classes 2 and 3, which were markedly less frequent. Class 2 surface pits were the largest of all modification types identified, and due to the distinctiveness in both size (diameter ranging from 2871.79 – 5333.58µm) and morphology of this modification type it is likely that adult beetles are responsible for their creation, whilst both Class 1 and 3 surface pits are more likely created by larvae. Class 3 pits may simply represent an area of concentrated destruction, and as such may not

warrant the establishment of a distinctive modification type. The increased occurrence of surface pits on bone of different types and conditions in the absence of substrate suggests again that a lack of suitable pupation medium results in more exploratory behaviour by the dermestids (Refer to Figures 41–46).

Lastly, a higher frequency of gnawing related striations were found in the absence of substrate. Thus striations were recorded on all bone densities (except for thin cortical bone specimens), as well as specimens displaying all condition including fossil, dry, fresh and weathered. The frequency of striations in the presence of substrate were slightly higher on dry specimens, in equal proportions on fresh specimens, but were not recorded on either weathered or fossil specimens. In the absence of substrate, gnawing striations occurred much more frequently on compact bone specimens than when present, but occurred in equal proportions on cancellous and bones of varying densities. Gnawing striations were only recorded on fossil teeth and thick cortical bone specimens in the absence of substrate (Refer to Figures 41–46). Once again the high occurrence of gnawing striations in the absence of substrate suggests increased exploratory behaviour by the dermestids under such conditions. Unlike the gnawing striations created by *P. Americana*, those created by *D. maculatus* were not limited to bone edges. This suggests that unlike *P. americana,* dermestids do not require leverage to create striations as they were found to have absolutely random distribution and orientation.

In sum, the distribution and frequency of modification types suggest that the absence of substrate not only increases the rate of modification by dermestids, but also results in the exploration of a wider range of skeletal elements of varying densities and conditions, which in the presence of substrate were unattractive. Despite the constant availability of food throughout the duration of this experiment, dermestids still modified bone, which is in contradiction to the suggestion that dermestid only modify bone when available food sources have depleted (Hefti *et al*. 1980). The reasons for modifying bone may thus not be strictly diet related, but could relate to the exploration of available media for the creation of pupation chambers. The absence of substrate clearly increased which bones were more readily explored as a pupation medium, but in no instance were pupation chambers like those described in the literature observed (Kitching, 1980; Martin & West, 1995; Hasiotis *et al.* 1999; Chin & Bishop, 2004; Hasiotis, 2004; Laudet &Antoine, 2004; Bader, 2005; West & Hasiotis, 2007). In fact, the modifications identified and described in the literature which have been attributed to dermestid beetles are markedly different from the findings of this investigation, as well as the preliminary conclusion reached by Roberts and Rogers (2003).

4.2.2. Identification criteria

The identification of *D. maculatus* modifications should not merely be based on any single modification type described in this study, but rather on the identification of the described basket of modification types, as

well as their associated occurrence, frequency and distributions patterns. This cautionary approach is advisable as the reality remains that not all invertebrate agents have yet been investigated, and that the potential of individual modification types being mimicked by different agents is very possible. Nonetheless, the co-occurrence of surface tunnelling, destruction of bone, infrequent bore holes, surface pits of varying classes and broad areas of gnawing striations can be used as an indicator of *D. maculatus* activities. Only surface tunnels are macroscopically visible, whilst bore holes and destruction is intermediately visible with the naked eye or at <20x magnification. The occurrence of surface pits of varying classes as well as broad areas scattered with randomly oriented gnawing striations are visible at magnifications higher than 20x.

Boreholes alone are not necessarily indicative of *D. maculatus* modifications as neither do they display distinctive trace morphology or any other characteristic/diagnostic feature (i.e. associated gnawing striations), which would attribute them to dermestids. Additionally, bore holes are not frequently created and it is likely they could easily be interpreted as exposed haversian canals or secondary osteons. Nonetheless, the infrequent occurrence of this modification type in combination with the others described in this study can be used to identify *D. maculatus* as the causal agent.

Similarly, the identification of destruction of primarily cancellous bone will also prove difficult to identify in the fossil record, the reasons being that destruction is not associated with any other indicative trace morphology (i.e. gnawing striations), and without prior knowledge of the condition of the specimens at the time of deposition, the destruction of epiphysis, cancellous bone or destruction occurring in the region of the diaphysis-epiphysis junction may simply be interpreted as the result of differential preservation and/or other pre- or post-depositional processes.

The most characteristic modification type created by *D. maculatus* are certainly surface pits of varying classes, but unfortunately apart from Class 2 pits, they are also the most microscopic in nature. Class 1 surface pits, which have fine striations radiating from them, are by far the most frequently recorded and distinctive modification type identified in this study. Whilst Class 2 pits may not have been frequent, they certainly are highly distinctive, with their largely randomly oriented striations across the base of the pit, a feature that is potentially diagnostic of *D. maculatus* activities. Despite the small size, frequency and distinctiveness of Class 1 pits, their preservation potential may be limited because they are so fine and superficial, but larger and deeper Class 2 and 3 surface pits are likely to have a high preservation potential.

Gnawing striations do not appear to have any distinctive morphology and are variable in length, width, orientation and position. The high

variability is likely a result of the variation in size of the larvae and/or adult beetles responsible for their creation. However, striations are rarely found as isolated clusters but rather distributed over a larger surface area. Lastly striations are not deeply excavated into the surface of the bone which may also resulted in their long term preservation potential being limited.

4.2.2.1. Experiment A – Identification of a lack of substrate

From a palaeontological perspective, the most likely scenario in which a carcass is to end up under conditions in which little/no substrate is available in the immediate vicinity is in a cave. Bone preservation in cave sites is facilitated by accumulators such as carnivores, rodents and other cave dwellers, as well as by rainfall, gravitational processes and death trap situations. Bones may not come to rest on substrate, but rather a rocky cave floor. Whilst death on the landscape on rocky terrain is likely uncommon in nature, the chances of preservation are extremely low. The identification of dermestid modifications under conditions by which little/no substrate is available in the nearby vicinity for pupation should be best tested on large comparative samples from various accumulations within a cave environment.

An absence of substrate can be identified in the fossil record in terms of occurrence of all modification types, excluding bore holes. Surface tunnels and surface pits would be far more

frequent in the absence of substrate than in its presence, whilst bore holes would be markedly less frequent. The distribution of all modification types should broadly conform to the standard distribution patterns (restricted to cancellous bone, epiphysis or at the diaphysis-epiphysis junction), but the occurrence of gnawing striations, destruction and bore holes are likely also to be recorded on compact bone or thick cortical bone, though at relatively low frequency.

If one considers a death trap scenario it is likely that multiple individuals will fall to their death over a period of time, which means that various attraction events would take place and as such various stages of decomposing skeletons would be available to dermestids. In single deposits in which various taphonomic signatures are presented such as a composition of both weathered and un-weathered bones, or in terms of a dolomitic cave deposit in which both calcified and un-calcified substrates occur, it is likely that modification did not occur as a result of a single attraction event but rather as various waves of modifications which may prompt modifications of exposed fossil or partially fossilised remains, such as the example in which a piece of fossilised tooth enamel was modified during the course of this study.

It should be noted that the modification of either weathered or fossil remains is highly unlikely to occur without an attraction event (i.e. introduction of a fresh corpse into an area which has existing dry, weathered or partially fossilised remains), nor is it likely that either weathered or fossil bones will be modified under conditions in which substrate is available for pupation. Therefore, under normal environmental conditions the most likely condition of the bones at the point of modification is either fresh or dry.

4.2.2.2. Experiment B – Identification of stressed feeding conditions

It is difficult to imagine a scenario on a natural landscape in which dermestids are put under stressed feeding conditions. Thus, once again a cave environment is the most likely place for this to occur, in that the supply of new carrion might not be regularly replenished, resulting in the long term in all available resources being utilised.

The occurrence of destruction, gnawing, surface tunnels and surface pits is relatively consistent, however, their frequencies are markedly reduced under stressed feeding conditions. Hence, the identification of modifications taking place under conditions of reduced food resource availability could potentially be identified in terms of a lack of surface tunnelling, bore holes and surface pits. Although it should be kept in mind that various

other factors are likely to impact on modification type frequency such as cooler climatic conditions or predation pressures.

Stressed feeding conditions would result in limited energy availability and potentially explain the associated reduction in the frequency of modifications which may require greater energy expenditure to produce i.e. surface tunnels, bore holes and surface pits. The only occurrence of boreholes and surface pits on dry bone were under stressed feeding conditions, however, there frequency was much higher under normal feeding conditions. Additionally, the occurrence of destruction is likely to be highest under stressed feeding conditions, indicative of the dermestids seeking to penetrate into the medulla in order to locate and utilise any of the remaining nutrients.

Much like the requirements for testing the lack of substrate, it is however, also advisable that one have a large comparative sample of multiple deposits within a single cave system. This would enable successful comparison of the occurrence and frequency signatures of the various trials to establish any significant differences in signature, which could then potentially indicate either condition. In testing for either condition (lack of substrate and stressed feeding conditions) it would not be advisable to attempt to identify such conditions within a single accumulation or without multiple sets of comparative data.

However, in cases where other proxy data (taphonomic, geological, stratigraphic) or other lines of evidence can be used to support this deduction, then one may be able to suggest that either one of these taphonomic conditions prevailed at the time of modification.

4.2.3. Climatic interpretation

D. maculatus behavioural activities are halted at temperatures below 20° C whilst optimal reproductive success takes place between 31–34° C, but this is also dependent upon humidity (Howe, 1965). High temperature and low humidity will negatively affect reproduction, but high temperatures at high humidity are more conducive to reproduction (Howe, 1965). Dermestids are highly dependent on food availability to provide optimal conditions under which they can successfully reproduce. *Dermestes maculatus* will undergo a complete life cycle within an average of 45 days, whilst larvae can remain on a decaying carcass for up to six months (Smith, 1986; Byrd and Castner, 2009).

Reproductive success plays a vital role in the creation of modifications, as upon the death of an animal in the landscape, initially only adult male dermestids arrive, and soon after attract females, copulate and produce off spring. The resulting larvae are primarily responsible for the reduction of carrion. Hence the potential for creation and future detection of modifications is increased by the associated larval population density, which occupies and consumes a carcass after death

(Howe, 1965; Richardson and Goff, 2001; Robinson, 2005; Byrd and Castner, 2009).

Dermestes maculatus have a lower thermal lethal limit of -23° C and an upper thermal lethal limit of 60° C (Strang, 1992) as such these two variables can be used to infer a very broad signature of the dominate climatic regime. However, the usefulness of this information is probably negligible and any further attempts to infer prevailing microclimatic conditions during the period of modification would merely be an over simplification of the facts.

Nonetheless, the physiological links between body temperature, activity and prevailing climatic conditions are highly indicative of dermestid activities, in that during the winter months carrion reduction by dermestids is markedly reduced or altogether halted, which means that winter is a period in which modifications do not take place (Howe, 1965; Strang, 1992; Richardson and Goff, 2001; Robinson, 2005; Byrd and Castner, 2009).

4.2.4. Implication for the fossil record

The regularity of cases and proposed associated agents of bone modification from the Mesozoic into the Cenozoic are disparate. During the Mesozoic the primary purported agent is the dermestid. The increase number of reported cases of bone modifications, attributed to dermestids, through the Mesozoic suggested that the associated

behaviour of bone modifications became more widespread and prolific; with instances reported from the Triassic (Schwanke and Kellner, 1999), Jurassic (Hasiotis *et al.* 1999; Chin and Bishop, 2004; Hasiotis, 2004; Bader, 2005, 2008; Dangerfield and Britt, 2005; Britt *et al*. 2008;) and Cretaceous (Rogers, 1992; Jerykiewicz *et al.* 1993; Kirkland *et al.* 1998; Paik, 2000; Getty *et al.* 2003; Genise *et al.* 2004; Nolte *et al.* 2004; Makovicky *et al.* 2005; Kirkland & Bader, 2007; Roberts *et al.* 2007).

For the Cenozioc relatively few cases are made to dermestids as agents of bone modifications (except Kitching, 1980; Martin and West, 1995; Laudet and Antoine, 2004; West and Hasiotis, 2007; Dominato *et al*. 2009), but ever increasing reference is made termites as agents of bone modification (Hill, 1987; Kaiser, 2000; Kaiser and Katterwe, 2001; Fejfar and Kaiser, 2005; Backwell *et al*. 2012), and such reports continue into historical times (Watson and Abbey, 1986; Wylie *et al*. 1987; Guapindaia, 2008; Huchet *et al*. 2009), whilst inferences to dermestid modifications dwindle (Kitching, 1980; Martin & West, 1995; West and Hasiotis, 2007).

One of the most common modifications that are described and attributed to being associated with dermestids is the occurrence of bore holes, which are suggested to act as pupation chambers (Kitching, 1980; Martin and West, 1995; Hasiotis *et al.* 1999; Hasiotis, 2004; Laudet and Antoine, 2004; Chin & Bishop, 2004; Bader, 2005; West & Hasiotis, 2007). It has been proposed that the occurrence of pupation chambers,

if further investigated, could potentially be used to infer more specific micro-palaeoclimatic information (Martin and West, 1995). However, no comparable modifications of this nature were identified during the course of the current investigation, and neither the presence nor absence of substrate for pupation or variable feeding conditions resulted in the creation of large borings to act as pupation chambers. This highlights the disparity between modern actualistic findings (Howell, 1932; Borell, 1938; Voorhies, 1948; Hooper, 1950; Hefti *et al.* 1980; Weichbrod, 1987) and those reported in the palaeontological literature.

The neoichnological data presented in this study clearly suggest that the assumption that dermestids bore into bone to form pupation chambers, does not find credence when tested using extant dermestids under controlled conditions. These finding have significant implications for the fossil record and its interpretation. Table 18 summarises a total of 42 published cases of insect modifications and the proposed causal agents, and the key criteria (where possible) on which the identification was based. Figure 47a presents the distribution of cases according to the proposed causal agent through time. The three primary agents are presented separately, which include unknown (indeterminate), dermestids and termites, whilst the few reported instances of moth, wasp and ant modifications were grouped as 'other'.

The first instance of assumed terrestrial insect modifications to bone is from the Triassic. Interestingly, the bulk of reported dermestid modifications occur during the late Jurassic, which predates their Cretaceous body fossil record (Kiselyova and McHugh, 2006). Only one case from the early Cretaceous and another from the late Cretaceous are reported, whilst the majority of remaining reports come from the Pliocene or Pleistocene. The cases of unknown causal agent have a similar distribution; first case from the Triassic peaking in the Late Cretaceous and only beginning to markedly reappear from the Pliocene through to the Pleistocene. In light of the results of this study, which shows that dermestids do not create pupation chambers in bone, the proposed identifications of the associated causal agent needs to be re-examined. A total of 12 reported cases of proposed dermestid modifications are presented in Figure 47a, nine of which are based on the occurrence of pupation chambers. Additionally, within the unknown category there are a total of 18 reports three of which describe the occurrence of pupation chambers.

Table 17: Publications detailing fossil insect modifications and attributed agents.

Geological Time Period	Gnawing Striations	Surface Pits	Bore holes/ Surface tunnels	Surface Tunnels	Pupal Chambers	Taxon	Author
Triassic	-	-	X	-	-	Unknown	Schwanke & Kellner, 1999
Late Jurassic	-	-	-	X	-	Unknown	*Bader, 2005
Late Jurassic	-	X	-	-	X	Dermestids	*Bader, 2005
Late Jurassic	-	X	-	-	-	Termites	Dangerfield *et al.* 2005
Late Jurassic	-	-	X	-	X	Dermestids	Chin and Bishop, 2004
Late Jurassic	-	X	-	-	X	Dermestids	Hasiotis *et al.* 1999
Late Jurassic	-	X	-	-	X	Dermestids	Hasiotis, 2004
Late Jurassic	X	X	X	X	-	Dermestids	Britt *et al.* 2008
Early Cretaceous	X	-	X	X	-	unknown	Nolte *et al.* 2004
Early Cretaceous	-	-	X	-	-	Dermestids	Paik, 2000
Late Cretaceous	-	-	-	X	-	Unknown	Genise *et al.* 2004
Late Cretaceous	-	-	-	-	-	Unknown	Getty *et al.* 2003
Late Cretaceous	-	-	X	-	-	Unknown	Jerykiewicz *et al.* 1993
Late Cretaceous	-	-	X	-	-	Unknown	Kirkland *et al.* 1998
Late Cretaceous	-	-	X	-	-	Solitary Wasps	Kirkland *et al.* 1998
Late Cretaceous	-	-	X	X	-	Unknown	Makovicky *et al.* 2005
Late Cretaceous	X	-	X	-	X	Unknown	*Roberts *et al.* 2007
Late Cretaceous	X	X	-	X	-	Unknown	*Roberts *et al.* 2007
Late Cretaceous	-	-	X	-	-	Unknown	*Roberts *et al.* 2007
Late Cretaceous	-	-	X	X	-	Dermestids	Rogers 1992
Late Cretaceous	-	-	-	-	X	Unknown	Kirkland & Bader, 2007
Oligocene	X	-	-	-	-	Termites	Fejfar & Kaiser, 2005
Oligocene/Miocene	-	X	-	-	X	Dermestids	Laudet & Antoine, 2004
Pliocene	-	X	-	-	-	Unknown	Denys, 1986
Pliocene	X	X	-	-	-	Termites	Fejfar & Kaiser, 2005
Pliocene	-	-	-	X	-	Tineid Moths	Gentry, 1987
Pliocene	-	-	-	X	-	Unknown	Hendey, 1981
Pliocene	X	-	-	-	-	Termites	Kaiser & Katterwe, 2001
Pliocene	X	X	X	-	-	Termites	Kaiser, 2000
Pliocene	-	X	X	-	X	Dermestids	Kitching, 1980
Pliocene	-	X	-	-	X	Dermestids	*Martin & West, 1995
Plio-Pleistocene	-	-	X	-	X	Tineid Moths	*Hill, 1987
Plio-Pleistocene	-	X	-	-	-	Termites	*Hill, 1987
Plio-Pleistocene	X	X	-	-	-	Ants	*Hill, 1987
Plio-Pleistocene	-	-	X	-	-	Unknown	Newman, 1993
Plio-Pleistocene	-	X	-	X	X	Unknown	Tobien, 1965
Pleistocene	-	-	X	-	-	Unknown	Kubiak & Zakrzewska, 1974
Pleistocene	-	X	X	-	X	Dermestids	*Martin & West, 1995
Pleistocene	X	-	-	-	-	Termites	Watson & Abbey, 1986
Pleistocene	-	-	X	-	-	Unknown	Jordy & Standford, 1992
Pleistocene	-	X	-	-	X	Dermestids	West & Hasiotis, 2007.
Pleistocene	X	X	X	-	-	Termites	Backwell *et al.* 2012

*** multiple citations to a single paper refers to instances in which disparate suites of modifications are described and attributed to multiple causal agents within a single publication.**

If one eliminates dermestid modifications based on the occurrence of pupation chambers, and group them with the three reported instances of unknown agents associated with pupation chambers, then a total of 12 instances of insect modifications are associated with pupation chambers. Whilst the reported instances of unknown causal agents not associated with pupation chambers drops to 15. The three remaining reports of dermestid modifications not based on the occurrence of pupation chambers are Rogers (1992), Paik (2000) and Britt *et al.* (2008), which are all prior to the Cretaceous-Tertiary extinction event (KT boundary) with no reported instances of dermestid modifications in the last 65 million years.

However, both Paik (2000) and Roger's (1992) modifications are limited to a few isolated borings without any other diagnostic features to make an identification with any certainty, and the authors themselves propose that if it is not dermestids, then it is likely another 'dermestid-like' carrion feeding insect. Current findings that bore holes are not frequently made by dermestids, and that they are primarily very small in nature when they are, could be used to motivate for the elimination of these two cases from being attributed to dermestids, and added to the "unknown category, without associated pupation chambers". Finally, Britt *et al.* (2008) provided a very strong motivation for their identification of the causal agent based on mandibular morphology; on the occurrence of the gnawing striations being paired, which was supported by extant dermestids have a primary mandibular cusp followed by a secondary marginal cusp. It was thus suggested that during the creation of the modification, both the primary

and secondary cusp come into contact with the bone surface and thus create a pair of parallel striations with every bite. Britt *et al*. (2008) drew this conclusion by examining adult *D. maculatus* mandibles (Figure 4), but despite extant *D. maculatus* beetles having both a primary and secondary cusp, the creation of a pair of parallel striations during bone modification was not observed/recorded during the course of the current investigation. Therefore, it is unlikely that both cusps are in contact with bone during the creation of modifications. *Trinervitermes trinervoides*, were shown to have both a primary and secondary marginal mandibular cusp and it was also suggested that the secondary marginal cusps do not come into contact with the bone during modification (Parkinson, 2010; Parkinson *et al*. 2010a, b; Backwell *et al.* 2012). Therefore, the primary motivation provided by Britt *et al.* (2008) for the identification of dermestids as the causal agent of bone modification does not find support when experimentally tested. As such, the three remaining cases (Rogers, 1992; Paik, 2000; Britt *et al.* 2008) of reported dermestid modifications, based primarily on the occurrence of large borings, is not sufficiently supported by this study, and should be reassigned to the category of "unknown causal agent without the association of pupation chambers".

Based on the above argument, Figure 47b presents a re-interpretation of insect modifications through time, and despite the total elimination of dermestids as agents of bone modification (as reported from the palaeontological literature), it highlights a significant finding. A macro consideration of Figure 47b shows there is likely an absolute minimum of

two agents that are involved in the carrion reduction process during the Mesozoic that leave identifiable traces on bone; one leaves pupation chambers whilst the other does not. Cases of bone modification originate in the Triassic and peak during the Late Cretaceous. However, post the KT extinction event there is a complete paucity of reported cases of bone modifications in the fossil record for nearly 60 million years, until the onset of the Pliocene. From the Pliocene reported instances of insect modification become more regular and consistent, and the number of potential agents diversifies, with termites being the most commonly cited agent of bone modification.

It is therefore hypothesised that the carrion community was drastically affected by the KT extinction event, which prompted a number of extinctions within the carrion reduction niche. However further work is required and may result in this impacting being measurable through a thorough consideration of the paleontological record of insect-bone interactions as well as the more comprehensive body fossil record. A number of variables need to be considered, such as the immediate effect of the impact event, the subsequent climatic changes, the impact such events had on the food web, the reduction in the availability of large carcasses, and whether or not other insect communities were affected.

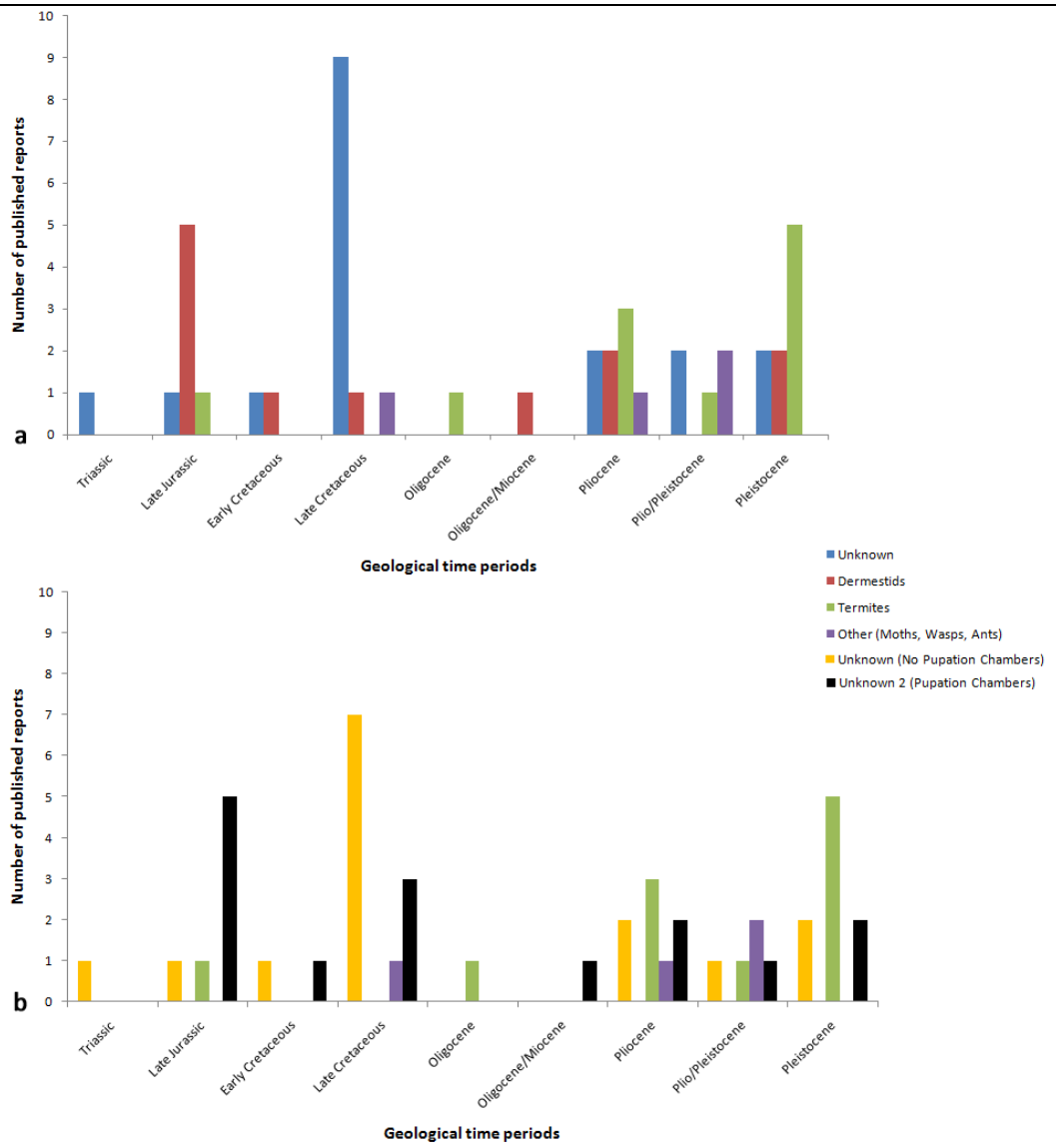

Figure 47: (a) Reflects the distribution of published reports of insect modification to bone and the inferred causal agents through time based on information presented in Table 18, (b) displays the reclassification of dermestids as causal agents based on the identification criteria established for them during this study. Note that dermestids are no longer represented, but two other groups become evident; a modification suite associated with pupation chambers and one which is not associated with pupation chambers.

It has been proposed that the KT extinction event was prompted by an extra terrestrial impact. If one accepts that the KT extinction event was prompted by the Chicxulub impact event in the Yucatán Peninsula off the coast of Mexico (Hildebrand *et al.* 1991; Sharpton *et al.* 1992; Morgan *et al.* 1997), then the results of this impact had to have been devastating in terms of producing a completely unbalanced food web for at least 1–2 million years after the initial impact, which ultimately resulted in instability and opportunism in a dramatically simplified ecological landscape (Wilf *et al.* 2006). The impact would have prompted the onset of an 'impact winter' which resulted in an estimated solar transmission reduction to a meagre 10–20 % of the norm, for a period said to be between 8–13 years (Pope *et al.* 1994). This would ultimately produce a decade of freezing or near freezing temperatures, followed by several decades of moderate warming. It has been proposed that the prolonged nature of the impact winter would be a major contributing factor that drove tetrapod extinction (Pope *et al.* 1994; Kring, 2007).

In considering that carrion as a food resource is temporary, unpredictable and inconsistent in terms of availability and locality, it can be seen as a rather ephemeral resource with no long-term prospects for existence (Braack, 1987). Besides the post impact environment there would have likely been an exponential burst of readily available carrion of large bodied individuals, but that within a relatively short period of time the availability of large bodied carrion would have been highly reduced and eventually carrion would be limited to small corpses. In terms of immediate onset of

the impact winter it is likely that the carrion reduction process would have been completely halted, and that any significant drop in average minimum temperature, and the associated mean minimum winter temperature, would have had the greatest impact on the carrion feeding community. If the impact winter resulted in a significant drop in temperatures then it is also likely that it may have pushed the mean minimum temperatures of specific regions below the thermal lethal limit of various populations of carrion feeding insects which culminated in regional extinctions. Additionally, colder more variable ambient temperatures not only impact on overall physiological performance but also population growth rates, whilst with shorter growing seasons and restrictive rates of population growth, these factors would greatly increase insect vulnerability to extinction (Huey, 2010). Extended periods of near freezing conditions would have potentially resulted in death of vast population of carrion feeding insects by either starvation, or simply by halting the reproductive cycle whilst existing population reaching the end of their life span ultimately prompting a relatively abrupt extinction.

Therefore, the suggested decade of freezing or near freezing conditions worsened by a complete lack of any significantly sized carrion on the landscape must have become a restrictive factor in the long term survival of any carrion dependant invertebrates, and dramatically impacted on the carrion community, which is evident during the late Cretaceous from the reported instances of insect-bone interactions.

The above are the most likely factors which prompted the extinction of the variously reported causal agents of bone modification, evident in the Mesozoic bone trace fossil record. It is also likely that these conditions prompted extinctions affected other members of the carrion dependant community which do not leave an associated trace fossil record. Lastly, preservational potential of invertebrates who occupy corpses is low and would ultimately result in a limited body fossil record.

Interestingly, it took close on 60 million years for this once heavily occupied niche of bone modifying agents to become evident again in the fossil record. Bone modification may simply have reappeared potentially as a result of convergent evolutionary behaviour. The disappearance and potentially associated extinctions of causal agents have been well documented within the insect-plant association fossil record particularly across the KT Boundary (Labandeira *et al.* 2002; Labandeira, 2005). However, this is the first time in which the carrion community of invertebrates has been considered as contributing evidence of extinction through the examination of the fossil record of insect-bone interaction.

The lack of correlation between extant *D. maculatus* modifications and those described in the palaeontological record, does not categorically prove that dermestids are not responsible for the creation of the palaeontological modifications. The current investigations only examined a single species of the genus *Dermestes*, but the possibility remains that other species of *Dermestes* may produce slightly variable modification types and

distributions to those described in this study. To test whether or not dermestids are responsible for Mesozoic modifications one could quite easily conduct further experiments using the other dermestid species that are known to consume bone; *D. ater*, *D. carnivorus* and *D. frischii* (Gabel, 1955; Robinson, 2005).

The aims of future research should focus on establishing whether different *Dermestes* species produce different modification suites or whether they mimic one another based on similarities in feeding behaviour and/or mandibular morphology. Lastly, the influence of predation pressures by other arthropods, birds or even lizards should be tested to establish whether or not predation affects represented modification types and/or their associated distribution patterns. A lack of predation pressure during the course of this investigation may have resulted in pupation chambers not being constructed and could very well have influenced other behavioural phenomena observed.

CHAPTER FIVE - CONCLUSION

This study has shown that both *P. americana* and *D. maculatus* modify bones in a number of different ways. The identification of these causal agents should be made in terms of modification type, morphology, associated occurrence and frequency patterns. Distribution patterns are similar for both agents, with modifications primarily restricted to cancellous bone, epiphysis or in less dense regions of bone such as the diaphysis-epiphysis junction. Both modification signatures are disparate from those described for the termite *Trinervitermes trinervoides* (Backwell *et al.* 2012), highlighting firstly that their traces are diagnostic and recognisable, and secondly that far too little empirical data for other invertebrate agents of bone modification are available, so there is a need for invertebrate-bone modification research. Like termites, *P. americana* and *D. maculatus* both do substantial damage to bird bones, which suggests that invertebrates may be one of the reasons for their under-representation in archaeological and palaeontological records.

Periplaneta americana produce a small suite of bone modification types; destruction, gnawing striations and discolouration, though the latter is more a feature than a type, and its preservation potential is low. Given that destruction damage lacks a distinctive morphology and that gnawing striations occurred in low frequencies, the future identification of *P. americana* modifications from either an archaeological or palaeontological context may prove difficult. No distinct selection preference could be established as modification occurrence

and frequency appeared random, suggesting either that bone modification is not habitual, or that cockroaches select bones in all states of preservation.

The establishment of this suite of modification types and patterns of occurrence and frequency has laid the foundation for this interpretative framework. Thou further experimental work is required including larger samples of varying bones to statistically show selection preferences and determine the degree of consistency between represented modification types and their associated frequency and distribution patterns. However, at this stage it is not advisable to base the identification of *P. americana* modifications on the occurrence of a single modification type described in this study but rather adopt a cautionary approach until further tests/experiments have been conducted. However, once definitive identification of *P. americana* modifications has been confirmed their associated ecology and known physiology can be used to infer very broad climatic conditions. In that *P. americana* could not have been exposed to temperatures during summer months above 39° C and conversely during winter months temperatures below -15° C as either of these conditions would have resulted in death.

D. maculatus produce a highly diverse suite of modification types which are distinctive in terms of morphology and associated patterns of occurrence, distribution and frequency. Experiments have shown that the lack of substrate for pupation affects the occurrence and frequency patterns of modification, but does not affect the represented modification types. Similarly, a lack of sufficient food also affects the occurrence and frequency of modification, but not

represented modification types. Under the conditions of a lack of suitable substrate for pupation, *D. maculatus* modify a higher diversity of bone of varying densities and conditions, including both weathered and fossil bones, which likely represents exploratory behaviour by the dermestids seeking out a suitable medium for pupation. However, without the impetus of an attraction event it is unlikely under normal conditions that they will select such a diversity of specimens for the purposes of pupating, and as such under normal conditions modifications are most likely to have occurred on either fresh or dry skeletal elements, which have not undergone diagenesis. Lack of available food reduced the frequency of modification types and may relate to energy availability. In that under stressed feeding conditions there would be an associated lack of available energy resources, which results in a reduction in the frequency of modification types that require the most amount of energy to create (surface tunnels, bore holes, and surface pits).

Under natural conditions it would be rare that either a lack of substrate or lack of food would be encountered. However, the most likely scenario in which either one or both of these conditions could be regularly encountered would be within a cave environment. To test for either one of these conditions it is preferable to have large comparative samples from different accumulations within a cave system in order to establish significant differences in occurrence and frequency distribution signatures, an exercise that would require data from other proxies (geological, stratigraphic, biological or taphonomical indicators).

The identification of dermestids as agents of bone modification should not be based on the single occurrence of a single modification type, but rather be based on representation of the described suit of modifications, both in terms of modification morphology and the associated occurrence, distribution and frequency patterns. Once thorough consideration of all of these factors has been taken into account, then the identification of dermestids as the causal agent of bone modification should be conclusive. Once identification has been established very broader climatic data can be inferred. *Dermestes maculatus* could not have been exposed to temperatures below -23° C and as high as 60° C as either condition would result in death.

Perhaps the most significant finding of this study is the fact that *D. maculatus* did not bore into bone for the purposes of pupation, which is in contradiction with the palaeontological literature. This finding alone has allowed for the reinterpretation of existing literature, and has resulted in the hypothesis, which requires further testing, that an absolute minimum of two unknown carrion feeding insects (one which created pupation chambers and one that did not) were prolific during the Mesozoic, and likely went extinct shortly after the KT boundary event as a result of dramatic climatic, environmental and ecological change.

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7. Appendix A

Table A1: Length measurements of gnawing striations created by *P. americana* on specimen no. 135, trial C1.

n	Length (µm)
1	669.16
2	489.29
3	511.85
4	422.47
5	726.94
6	179.43
7	291.54
8	455.36

Table A2: Length and breadth measurements of bore holes created by *D. maculatus*

Specimen No.	Experiment	Length (µm)	Breadth (µm)
#9	A	3483.59	2522.38
#1	A	504.72	358.27
#39	A	395.75	209.23
#22	A	440.03	204.79
#110	B	429.50	263.15
#89	B	688.58	639.21
#90	B	358.97	290.60
#89	B	420.18	361.66
#110	B	583.91	556.37
#110	B	214.84	148.73

Table A2 – Length and ave. width measurements of class 1 surface pits created by *D. maculatus*

Specimen No.	Experiment	Length (µm)	Ave. Width (µm)
#20	A	366.98	362.66
#20	A	207.23	142.47
#20	A	846.21	505.13
#20	A	772.92	511.14
#20	A	387.97	343.61
#20	A	615.32	550.30
#1	A	189.97	116.57
#1	A	190.01	143.06
#1	A	293.58	164.06
#22	A	361.10	162.76
#22	A	275.32	156.78
#22	A	490.64	209.76
#22	A	165.26	115.68
#22	A	1381.45	201.74
#22	A	1166.02	258.38
#22	A	719.16	147.76
#110	B	110.25	100.54
#110	B	129.00	63.07

Table A3 Length and width measurements of class 2 surface pit made by *D. maculatus*, specimen no. 12 from trial D1.

n	Length (µm)	Width (µm)
1	5333.58	3076.92
2	5187.94	2871.79

Table A4: Length and ave. width measurements taken from surface tunnels created by *D. maculatus*.

Specimen No.	Experiment	Class	Length (µm)	Ave. Width (µm)
#20	A	2	5916.18	193.73
#18	A	1	2936.11	234.11
#17	A	2	8731.12	717.99
#17	A	1	4479.08	580.96
#9	A	2	5087.51	319.22
#9	A	2	9284.83	316.43
#9	A	2	6450.94	537.20
#1	A	1	1971.02	108.69
#1	A	1	1500.31	144.51
#30	A	2	9945.52	338.83
#22	A	1	4174.53	185.07
#30	A	2	11579.84	1094.48
#30	A	2	12833.38	270.21
#9	A	2	12613.40	1405.48
#9	A	2	17093.04	856.98
#22	A	1	2045.12	421.78
#106	B	2	5261.91	748.88
#107	B	1	4082.72	1108.41
#107	B	2	9411.56	1618.39
#85	B	1	1610.71	458.57
#85	B	1	1889.60	192.54
#85	B	1	1990.70	481.40
#85	B	1	1444.09	239.83
#85	B	1	1308.95	513.69
#85	B	1	953.57	324.51
#85	B	1	2433.65	470.30
#85	B	1	1956.34	360.98
#86	B	2	5508.27	517.15
#86	B	2	7351.17	352.64
#86	B	2	13997.93	877.09

Class 1 – surface tunnels have a length <5000µm, Class 2 – surface tunnels have a length >5000µm.

Hypothesis Test Summary

	Null Hypothesis	Test	Sig.	Decision
1	The distribution of Width is the same across categories of Exp.	Independent-Samples Mann-Whitney U Test	.476[1]	Retain the null hypothesis.
2	The distribution of Breath is the same across categories of Exp.	Independent-Samples Mann-Whitney U Test	1.000[1]	Retain the null hypothesis.

Asymptotic significances are displayed. The significance level is .05.

[1]Exact significance is displayed for this test.

Figure A1: Mann-Whitney U Test results of width and breadth of bore holes created by *D. maculatus* during experiment A and B. Results show no significant difference in length or width between the two experiments.

Hypothesis Test Summary

	Null Hypothesis	Test	Sig.	Decision
1	The distribution of Length is the same across categories of Exp.	Independent-Samples Mann-Whitney U Test	.013[1]	Reject the null hypothesis.
2	The distribution of Width is the same across categories of Exp.	Independent-Samples Mann-Whitney U Test	.013[1]	Reject the null hypothesis.

Asymptotic significances are displayed. The significance level is .05.

[1]Exact significance is displayed for this test.

Figure A2: Mann-Whitney U Test results of length and width of class 1 surface pits created by *D. maculatus* during experiment A and B. Results show a significant difference in length and width between the two experiments. However it should be noted that only two class 1 surface pits from experiment B are included hence the results should be adopted with caution.

Hypothesis Test Summary

	Null Hypothesis	Test	Sig.	Decision
1	The distribution of Length is the same across categories of Exp.	Independent-Samples Mann-Whitney U Test	.034[1]	Reject the null hypothesis.
2	The distribution of Width is the same across categories of Exp.	Independent-Samples Mann-Whitney U Test	.224[1]	Retain the null hypothesis.

Asymptotic significances are displayed. The significance level is .05.

[1]Exact significance is displayed for this test.

Figure A3: Mann-Whitney U Test results of length and width of surface tunnels created by *D. maculatus* during experiment A and B. Results show a significant difference in length but no significant difference in width between the two experiments.

Hypothesis Test Summary

	Null Hypothesis	Test	Sig.	Decision
1	The distribution of Length is the same across categories of Class.	Independent-Samples Mann-Whitney U Test	.000[1]	Reject the null hypothesis.
2	The distribution of Width is the same across categories of Class.	Independent-Samples Mann-Whitney U Test	.041[1]	Reject the null hypothesis.

Asymptotic significances are displayed. The significance level is .05.

[1]Exact significance is displayed for this test.

Figure A4: Mann-Whitney U Test results of length and width of surface tunnels with a length <5000µm (class 1) or >5000µm (class 2) created by *D. maculatus* across all trials (D1 to D4). Results show a significant difference in length and width between the two class sizes of surface tunnels.