The Alien Presence: Palaeoentomological Approaches to Trade and Migration

Gary Andrew King

PhD

2009

The Alien Presence: Palaeoentomological Approaches to Trade and Migration

Gary Andrew King

A thesis presented to the University of York in fulfilment of the thesis requirement for the degree of

Doctor of Philosophy

in

Archaeology

University of York

Department of Archaeology

September 2009

The alien presence: Palaeoentomological approaches to trade and migration

Abstract

This thesis addresses the potential of palaeoentomological remains to stand as evidence of past trade and culture contact. Three methodological tools are used to evaluate the effectiveness of insect subfossils as palaeoeconomic indicators: palaeoecology, biogeography, and isotopic analysis. Underpinning each of the methodological approaches is the premise that specific insect fauna are notably stenotopic in their distributional range. By superimposing the physiological and ecological habits of modern species over the archaeological record, they may effectively serve as analogues to interpret palaeoentomological evidence.

On that basis, the archaeological presence of stenotopic insects may reliably be employed as indicators of their associated habitats. Furthermore, the examination of the archaeological remains of the specific monophagous or oligophagous species that are known to feed on human exploitable resources may provide direct or indirect evidence towards the presence of those commodities. For example, *Sitophilus granarius* may stand as an indication of the presence of stored cereal grains.

In each of the methodological approaches, the palaeoentomological remains proved promising as a tool for suggesting probable socio-economic activity. However, the approaches differed in the precision and confidence of their results. The palaeoecological approach provided the most tentative assertions; where as the

isotopic method allowed for formulation of the most scientifically-grounded conclusions.

In addition to the three applied methodologies, the thesis explored the potential for palaeoentomological remains to yield assayable genetic sequences. Ancient DNA was recovered from preserved Roman and medieval specimens. If aDNA preservation is widespread in palaeoentomological remains, a phylogeographic method is conceivable as a means for assessing past trade and migration.

Table of Contents

Acknowledgements

I would like to thank my supervisor Mr. Harry Kenward for the support he has given me through each stage of the thesis research. His dedication and advice were invaluable to its completion. He was also kind enough to share his work environment and welcomed the invasion of beetle colonies into the laboratory. I am especially grateful for his unfailing encouragement as well as his unflappable willingness to always go the extra mile in support my endeavours.

I would also like to extend my appreciation to Dr. Allan Hall and Dr. Matthew Collins who offered valuable suggestions to improve my research. Moreover, Dr. Hall supplied a multitude of environmental samples for processing, and he was able to endure mishaps in the lab with a smile. Dr. Collins served as a catalyst for experiments conducted in association with the University of Copenhagen, the University of Glasgow, and Bradford University.

Dr. Tom Gilbert deserves a special mention, for without his patience and help I would never have been able to understand the procedures necessary to explore the potential of the genetic methodology. All the members of the laboratory in the Department of Ancient DNA and Evolution at University of Copenhagen were willing to help and address questions. My thanks extend to all of them.

A number of people and organisations assisted in providing specimens for this project. In particular, I would like to acknowledge Edith Schmidt for donating archaeological specimens from the German sites and Philippe Ponel for providing archaeological and modern individuals from sites in France. Laible Friedman of the Department of Zoology, Tel Aviv University and the team from Central Science

Laboratories deserve my thanks for providing numerous grain beetles from their respective museum collections. In addition, I am indebted to Laura Girven and Melanie Rousseau for their assistance processing and sorting the archaeoentomological samples.

I wish acknowledge the Palaeoecology, Archaeology, and Evolutionary Origins (PALAEO) research group for granting the Marie Curie Early Stage Short-term Training Fellowship. I am also grateful to the Department of Archeology, University of York for bestowing the Innovation and Research Priming Grant. The funding assisted with equipment fees, experiment costs, and travel.

Special thanks go to Emma Bradley and my parents, Gary and Bonnie King, for enduring cheerfully through the emotional roller-coaster of living with someone involved in such as long-term endeavour. They kept my spirits up through offering encouragement and advice and sometimes just by lending an ear.

Chapter 1

Introduction and Scope of Thesis

1.1. Trade and Migration: The Archaeological Viability

Throughout time, humans have migrated and interacted, and thus have both purposely and unwittingly carried animal species with them in their travels. While a few of the human-introduced animal species were able to permanently colonise these new geographical areas, numerous species failed to find suitable niches due to environmental or climatic restraints. The ability to distinguish the native species from the immigrants is archaeologically significant. However, the mapping of animal movement is not an end in itself rather it provides insight into the movement and interaction of past peoples. Additionally, the presence of man and the introduction of new animal species into a pre-existing ecosystem may lead to local extirpations, such as the pygmy hippopotamus in Cyprus (Simmons 1988) or the giant lemurs of Madagascar (Perez *et al.* 2005), and likewise the desertion of a region by man may have detrimental effects on strong synanthropes (Brothwell and Jones 1978). Given this, the study of faunal remains may shed light on past exchange and trade networks (e.g. Hodges 1982; Iregren 1988) as well as migration and population movement (Ashby 2004).

The ability to discern past exchange and trade patterns is archaeologically valuable. Exchange is an inclusive concept, which may be viewed as the spatial distribution of material items, ideas, and information between individuals and social groups (Earle 1982) with the payment being either immediate or delayed and indirect (Alden 1982). However, trade is a more narrowly defined and archaeologically visible index of exchange (Crabtree 1990) that refers specifically to material goods (Roslund 1992). The concepts are archaeologically interesting because commentators have postulated that exchange and trade were impetuses for urban and social development and cultural change (Hodges 1982; Wells 1980). With knowledge of

exchange and trade routes, inferences may be made concerning economic conditions, population pressures and settlement patterns (Hodges 1982).

Human movement through migration is another deep concern of archaeology. Although the archaeological visibility and legitimacy of migration have been questioned in the past (Clark 1966; Härke 1998), it has recently experienced resurgence (e.g. Anthony 1990, Burmeister 2000, Barrett *et al.* 2001). There are two main types of migration: immigration, a small-scale event, and population movement, a large-scale phenomenon. Migration as a small-scale event is difficult to infer archaeologically because the immigrants are assimilated into the local population (Burmeister 2000). However, population movement is made evident by the ensuing cultural change resulting from the absorption or forcing out of the local population by a large and powerful migrating body (Rouse 1986).

In past studies, the traditional methods for the identification of culture contact have too often resulted in the assumption that trade was the primary or sole mechanism for cross-culture interactions (Olausson 1988). The traditional methods include: polysemous contextual analysis (e.g. Hodder 1982), stylistic analysis (e.g. Lindstrom and Kristoffersen 2001), identification of raw materials (e.g. Rosenfeld 1965; Galloway *et al.* 1996), spatial distribution, and the presence or absence of a local precedent (Olausson 1988). Ethnographic comparisons have demonstrated that when applied individually, the traditional methods have severe limitations derived from assumptions that the imported objects will be:

- foreign in origin;
- valuable;
- unavailable in the local environment;
- limited in number (Olausson 1988).

These problems largely stem from the framework for analysis of culture contact and ethnicity being based in culture history, which unfortunately results in the identification techniques for foreign objects relying heavily on overly simplistic regional sequences of artefact development (Jones 1997). As Wells (1980) mentioned, style may signal acculturation, and the differences in function risk being mistaken for ethnic variation (Jones 1997). As archaeological cultures are not absolutes, direct correlations cannot be drawn with ethnic units (Jones 1997). It may be more effective to approach the study of culture contact through an index that reflects social and cultural relations but is less dependent on arbitrary cultural distinctions, i.e. ethnic expression (Jones 1997).

One method of countering these innate problems is through utilisation of holistic approaches. For example, stylist comparisons should be applied in addition to identification of raw materials (Hantman and Plog 1982) and contextual analyses (Hodder 1982). However, there are still other distortions in the interpretation of culture contact—it is disproportionately based on grave goods (e.g. Wells 1980) and may be skewed by artefact recovery based on the types of sites. This is made evident by studies of the Roman exchange in Europe, which are biased towards maritime trade because of the dominance of recovered amphora in the contexts (Pentz 1992). Faunal analysis is a promising area, which if applied to the study of human movement, would balance the evidence and avoid arbitrary cultural distinctions (Ashby 2001).

Ashby (2004; 2006) has approached the question of exchange and population movement from a zooarchaeological standpoint. In archaeology, animals are typically viewed in association with production and consumption rather than the realm of

exchange (Earle 1982). However, details of culture contact may be extrapolated using standard zooarchaeological methods:

- metric (continuous) variation;
- non-metric (discontinuous) variation;
- genetic analysis;
- species biogeography (Ashby 2004).

Metric and non-metric traits are beneficial for recognition of genotypes, age and sex of individuals, and bone shape variation (O'Connor 2000). Through examination of these variations, it is possible to ascertain information about phylogeny (e.g. Shigehara *et al.* 1993), the human factor in selection (e.g. O'Connor 2001), and trade (e.g. Murphy *et al*. 2000). Genetic work on the Pacific rat, *Rattus exulans*, has demonstrated the potential of DNA analysis in determining relationships between populations and thus provides insight into culture contact (Matisoo-Smith and Allen 1997; 2001; Matisoo-Smith and Robins 2004). Biogeography is essential to the understanding of animal movement (e.g. Barrett 1997) because it aids in the recognition of foreign species and may shed light on their original geographic region.

However, a zooarchaeological approach to culture contact is not without problems, notably taphonomy and inter-analyst variability. It is essential to consider the transposition of the living community into the archaeological assemblage, which is known as the taphonomic process (Efremov 1940). The final sampled and interpreted assemblage consists of the preserved remains of both autochthonous and allochthonous components. As the biotic assemblage proceeds through the various taphonomic stages, the ecological signal becomes distorted from its original state as increasingly more information is lost. The majority of taphonomic effects are beyond the control of the researcher, and the best that one may do is account for them in the

reports. However, problems with artefact recovery and inter-analyst variability are manageable through the standardization of methods and exercise of caution.

Although not entirely void of problems, the archaeological study of faunal remains and animal movement has proven capable of allowing inferences into identity and culture contact (e.g. Ashby 2006). An excellent example of the benefits of zooarchaeological analysis is illustrated by Rausling's examination of the presence of *Camelus bactrianus* bones in 11th century BC Mesopotamia (Rausling 1988), which implies a westward connection 1000 years before it is evidenced in documentary accounts.

While the applicability of animal remains to studies of culture contact has been investigated, most of the assessments have been restricted to vertebrate zooarchaeology with little attention given to invertebrate species. This is surprising given the strong ecological signal demonstrated by some insects (making them prime candidates for biogeographical study), the direct evidence that foreign product-associated species were transported on ships (e.g. Pals and Hakbijl 1992), and the discovery of import indicator species from archaeological sites (e.g. Osborne 1971). This thesis will focus on employing insect fossils for the purpose of inferring human movement and culture contact.

1.2. The Archaeological Significance of Insects

While insect fossils have been noted in archaeological sites for over a century (e.g. Roeder 1899; Bayford 1903), most of the advancements in the field of archaeoentomology have occurred since the 1970s. Insects have proven to be immensely valuable for the reconstruction of past climates (e.g. Coope *et al.* 1998) and environments (e.g. Hill 1994b). They have been employed in spatial

reconstructions of structures (e.g. Buckland *et al.* 1983) and interpretations of living conditions (e.g. Panagiotakopulu 2001). Recently, there has been a developing interest in the use of insects as archaeological indicators of human activity.

Reconstructing the level of human impact on an environment may be problematic especially after the onset of the Roman period (see Kenward in press). This is largely the result of the paucity of insect fossils collected from natural settings (e.g. Hill 1994b); however, sampling methods and taphonomy are also factors. Despite these caveats, Carrott and associates (1995a) have investigated a 'natural' layer beneath a *circa* 12th century strata at Keldergate, Beverly, which implies an occupational expansion into the area during that period. Also in the Period 3 samples (Hall and Kenward 1999a) from 16-22 Coppergate, York, there is evidence to suggest that the area was unoccupied (though used for rubbish deposits) prior to the construction of Anglo-Scandinavian tenements in Period 4 (Hall and Kenward 1999b; Kenward and Hall 1995). Some of the best evidence of human influence on the environmental is derived from the remains of drains, moats, and artificially constructed ponds. The invertebrate remains from the Higher Lane, Fazakerley, Merseyside site (Dobney *et al.* 1995) demonstrate the transition from the initial construction of an aquatic arena, to a stable aquatic body, and finally to a terrestrial area. The archaeoentomological field of human environmental impact is still in its infancy yet if properly applied, provides insight into human activity that may not be visible through traditional, material culture based approaches.

Additionally, archaeoentomology has demonstrated great potential in unveiling the human exploitation of resources through providing secondary evidence for the presence of livestock, cereals, vegetables, and other raw materials. Through scrutiny of the ecology of the various insect species, it is possible to ascertain insect

associations with certain materials that would have been utilised by the humans. At 16-22 Coppergate, York, the insect remains provide evidence for the availability of a number of resources. For example, the bark beetle *Leperisinus varius* was identified in forty-eight contexts (Kenward and Hall 1995) and indicates, through its ecological association, the presence of *Fraxinus* (ash) at the site. Indeed, this claim is supported by the recovery and identification of ash wood in 275 records from 16-22 Coppergate (Kenward and Hall 1995). At Nipáitsoq, Greenland (Buckland *et al*. 1983), the presence of taxa like *Byrrhus fasciatus* and *Simplocaria tesselata* imply that moss was employed at the site, possibly for floor-layers, bedding, or sanitary paper. When used in conjunction with other palaeoecological methods, the invertebrate remains provide another layer of evidence to substantiate the presence of certain resources.

Hall and Kenward (2003) have reviewed the potential of environmental remains as indicators of crafts and industries such as tanning, wool-processing, and dyeing. It has been postulated that insect remains may be used as signs of the tanning industry. *Trox scaber, Acritus nigricornis, Creophilus maxillosus, Teretrius fabricii*, and *Phymatodes testaceus* have all been suggested as a probable indicator group for tanning (Kenward in press). However, this association is tentative, and Hall and Kenward (2003) caution about using the species alone to discern tanning. Another craft indicator is the sheep ked *Melophagus ovinus*, which lives in wool, and has been argued as evidence for areas of wool production (Buckland and Perry 1989). Furthermore, the plant dyer's greenweed (*Genista tinctoria*) is believed to have been exploited in Anglo-Scandinavian York for its use as a dye. The existence of the dye industry is further supported at the 16-22 Coppergate site by the presence of the weevil *Apion* (*Exapion*) *difficile*, which is strongly associated with dyer's greenweed (Kenward and Hall 1995). The discovery of *Apion difficile* is more interesting still

because it is rare amongst the list of British beetles and is likely to be representative of another human activity, trade.

1.3. Aims of the Study

Studies of biological evidence from archaeological sites are providing a wealth of information about palaeoecology and human activities. Many commentators have noted that faunal remains are important and useful elements for inferences concerning resource exploitation, production, consumption, and industries. Recently, Ashby (2006) has demonstrated that an examination of faunal remains such as bone and antler may be used to ascertain information about identity and culture contact in the Viking Age. While the prospect of insect fossils as valuable indicators of culture contact has been proposed (e.g. Sadler 1988; Kenward in press), its potential has yet to be sufficiently addressed. The few attempts to connect insect transportation to human movement have been constructed on biogeographical grounds within the documented historic period (e.g. Lindroth 1957; Hammond 1974). However, these studies fail to provide a systematic index for the identification of transported insects or a means to substantiate their point of origin. In the present thesis, a systematic exploration of potential archaeoentomological approaches for discerning culture contact is undertaken.

1.4. Approaching a Methodology

Culture contact cannot be fully understood until its medium has been established. Thus, the first phase in analysis is to develop an index for determining which archaeoentomologically identifiable products were being distributed. While humans may have been engaging in the exchange of insect products (e.g. honey; silk),

knowledge of the ecological requirements of insect species provides secondary evidence of the human exploitation of resources [Section 1.2]. Therefore, the medium for culture contact can be established directly through evidence of the insect products themselves and indirectly through product-associated insect species.

Once the exchangeable products have been identified, it is necessary to determine their source. Insects may offer evidence of both short (at a local or regional level) and long-distance trade. Knowledge of the source of the resources is essential to developing an understanding of culture contact. Are the materials foreign in origin or locally accessible? If they were locally available, were the inhabitants electing to import the resources long distances? Why were the products being exchanged?

An understanding of insect morphology, physiology, and ecology is beneficial in distinguishing some of the foreign (alien) species from the natives or colonists. Through reconstruction of past climates and environments, the palaeoecology for a site can be established [Chapter 4]. Thus, it is possible to determine whether a species would be capable of surviving in a past ecosystem—ecological outliers being representative of imports. While this method serves to flag a few of the imported species, Lindroth (1957) and later Hammond (1974) have shown the problems of this method when sorting the natives from the aliens, and alternative approaches need be considered.

There are three main tools available to archaeoentomology which can be employed to trace the movement of faunal materials: species biogeography, isotopic analysis, and phylogeography. Species biogeography [Chapter 5] is essential to understanding animal movement without relying on chemical or genetic techniques (Barrett 1997; Buckland and Sadler 1989). Biogeography notes diachronic changes in species distribution as well as geographical ranges and thus allows for the tracking of

animal movement. Although stable isotope analysis [Chapter 6; Chapter 7] has largely been employed in climate studies (Schimmelmann and DeNiro 1986; Gröcke *et al.* 2006), it may be used to identify autochthonous and allochthonous components within and between sites. The oxygen isotope ratio, $^{18}O/^{16}O$, in meteoric water is quite regionally distinctive and may become fixed in the tooth enamel or chitin-layers of the inhabitants of those regions. Oxygen isotope analysis thus reveals the regional signal of the place in which the individual was living at the time of the chitin or enamel layer was formed. Hydrogen isotopes, D/H, function in the same manner as oxygen isotopes; however, they reflect hydrogen that was ingested as organic hydrogen or water hydrogen (Gröcke *et al.* 2006). By examining the isotopic signals preserved in alien chitin, it may be possible discern the origin of the associated imports. Phylogeography [Chapter 8] is the study of genetic relationships among populations of species, which sheds light on the length of time certain populations have been isolated from each other (e.g. Smith and Farrell 2005; Moya *et al*. 2004), and as such, serves as an index for discerning past culture contact.

It is the aim of this thesis to define a methodology which is archaeologically applicable regardless of temporal or geographic boundaries. However, a comprehensive study of insect remains from all archaeological contexts is not feasible. Instead, case studies will be selected from the United Kingdom and Continental Europe.

1.5. Structure

While culture contact has been investigated utilising material culture and zooarchaeology, it has yet to be studied in an archaeoentomological framework. This thesis is divided into nine chapters. Following this brief introduction, Chapter 2 will

examine beetle morphology and ecology. A discussion of these issues is essential as they form the basis for any exploration into archaeoentomology. Form and function are the prerequisites for the success of an organism in its environment (Speight *et al.* 1999) and are essential to understanding an insect's ecological role. As such, Chapter 2 will discuss the concepts of habitats, ecosystems, and ecological associations. Elton (1927; 1966) examined several types of interactions between the same species, species of the same ecological niche, and species of different trophic levels. Through scrutiny of these ecological associations, it will be possible to ascertain connections between certain insect species and human-exploited materials or 'products'. Furthermore, palaeoecological factors like climate and environment will be employed to pin-point alien, foreign, species, which would have been unable to survive in the local area due to ecological constraints, and separate them from the native or successfully colonial species.

Having established the biological and ecological framework [Chapter 2], Chapter 3 will outline the methodological approaches taken in the project—palaeoecology, biogeography, isotopic analyses, and phylogeography. In addition to the information provided in Chapters 2 and 3, these methods are illustrated primarily through the use of case studies.

The techniques are applied in Chapters 4-8. Chapter 4 considers the insect remains from two case studies—Roman 7-15 Spurriergate, York and Anglo-Scandinavian 16-22 Coppergate, York—through a palaeoecological approach. The palaeoecological approach is employed to demonstrate the ability of archaeoentomological remains to stand as secondary evidence of commodities and materials that were used by humans in the past. Chapter 4 uses palaeoecology as a tool towards inferring culture contact. Chapter 5 presents a biogeographical

investigation of human migration and culture contact as evidenced through grain-associated insect species. In Chapters 6 and 7, stable-isotopic analyses of carbon-13, nitrogen-15, and deuterium are reviewed from modern and Neolithic insect specimens. Chapter 8 provides evidence towards the applicability of genetic analysis to insect fossils and discusses the potential of phylogeography as a palaeoeconomic tool. Following the presentation of the case studies and the results of the methodologies, their significance and meaning are discussed. While the functionality and practicality of the various methodologies are assessed, the emphasis is on culture contact. The thesis closes with general conclusions and comments concerning the applicability of archaeoentomology to culture contact and the potential for future research.

Chapter 2

Morphological and Ecological Concepts

2.1 Introduction

The formulation of hypotheses constructed from insect fossils is dependent upon the validity of the existing knowledge of the species. In this chapter, the published methods for insect species identification will be reviewed; followed by a discussion of the ecological principles inherent in the archaeological and palaeoenvironmental interpretations of the fossils. This presentation of the morphological and ecological concepts will form the basis for any archaeoentomological arguments that arise during the thesis as well as establishing the biological background for exploration of biogeography, isotopic analyses, and phylogeography.

2.2 Morphology

While this thesis is not primarily concerned with the form and structure of insects, a brief review of insect morphology is worthy of consideration because:

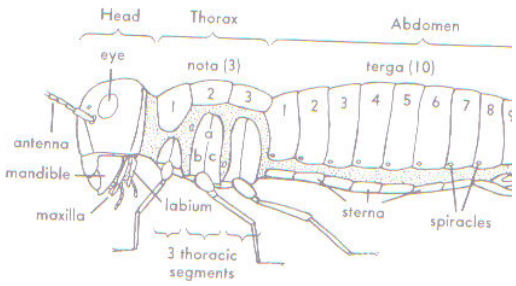
- it plays a significant role in the identification methods employed by both modern entomologists and palaeoentomologists;
- the ability of an organism to succeed in its environment is dictated by form and function; and,
- the biosynthesis involved in the formation of specific morphological components is a function of its environment.

Insects are six-legged, segmented invertebrates that possess the arthropod's characteristic articulated, external skeleton (i.e. exoskeleton). Taxonomic recognition of insect orders, families, and genera is often established through examination of the myriad anatomical features of the appendages—mouthparts, legs, wings, and abdominal apex, and moreover, species are almost exclusively denoted based on

anatomical distinctions. Because of the multitude of variations, it is only possible here to provide a basic overview of the external anatomy.

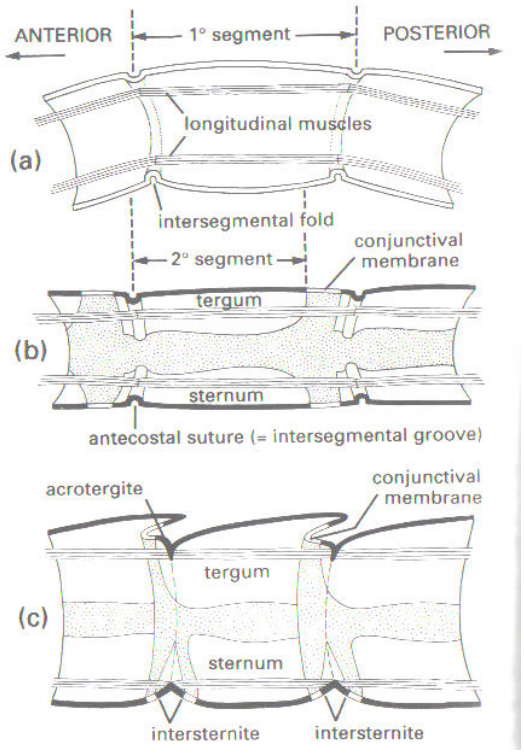
The basic structure of a typical adult insect [Figure 2.1] consists of three specialised sections called tagmata—a 6-segmented head for sensory perception and food gathering, a 3-segmented thorax for locomotion, and an 11-segemented abdomen for digestion and reproduction (Speight *et al.* 1999). While these external features have been amalgamated into functional units in adult and nymphal insects, the segmentation evidenced in the sclerotized adults and nymphs is not directly homologous with that of the unsclerotized larvae [Figure 2.2], which possess the distinctive metameric segmentation apparent in annelids (Gullan and Cranston 2000). In adults and nymphs, the sclerotization stretches beyond the primary segment, commencing in front of the fold and extending almost to the rear of the segment, which allows the muscles in the folds to attach to solid rather than soft cuticle (Gullan and Cranston 2000). In defined areas, the sclerotization

Figure 2.1 Insect Morphology



(Borror and White 1970, 30)

Figure 2.2 Types of Body Segmentation



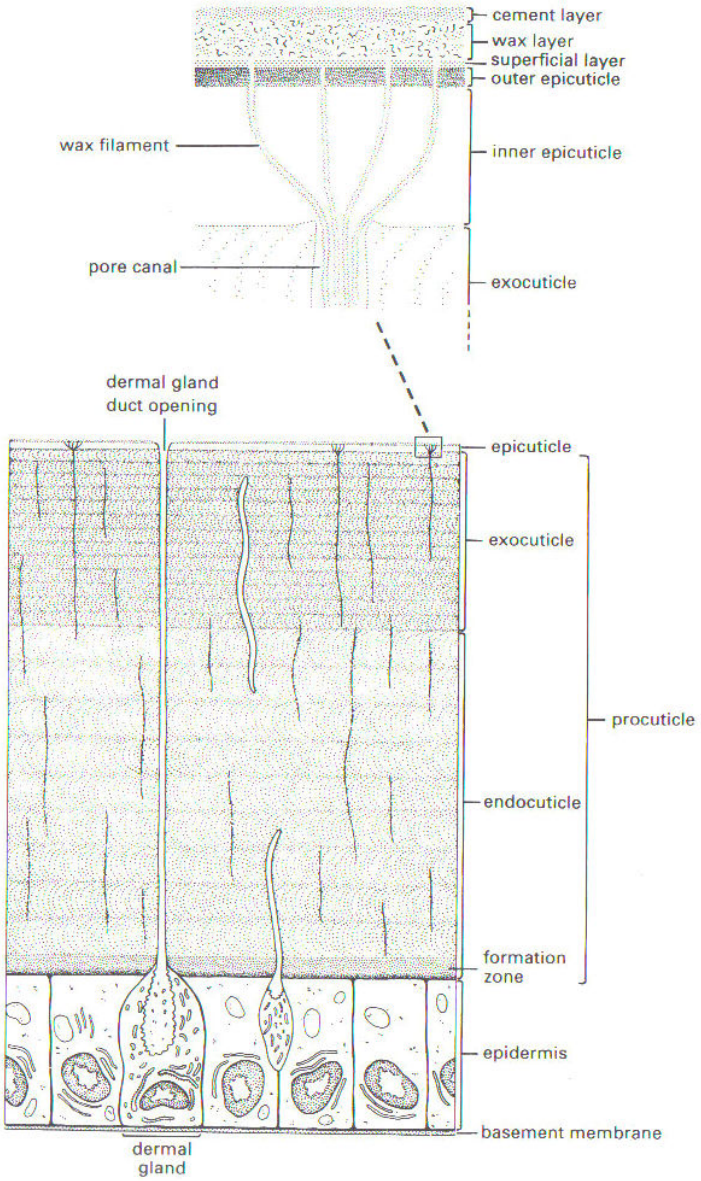
A) Primary segmentation evinced by soft-bodied larvae; B) Simple secondary segmentation; C) More derived secondary segmentation
(Snodgrass 1935)

process produces plates known as sclerites—the tergum (dorsal plate), the sternum (ventral plate), and the pleuron (side plate). In the head, all the sclerites are fused together into a rigid capsule. However, the abdominal pleura remain partially membranous, and on the thorax, they are sclerotized and linked to the tergum and sternum of each segment. During the sclerotization process, the progressive hardening of the proteinaceous structures is utilised by insects to stiffen and harden their exocuticle (Hopkins and Kramer 1992).

2.2.1 The Cuticle

The cuticle of insects functions both as an exoskeleton and a barrier between the living tissues and the environment and, to a large extent, determines the shape and appearance of insects. This thin layer of material consists of two main strata, a thin (0.1- 3 μm), outer epicuticle and a thicker (0.5- 10 μm) inner procuticle, which are secreted from an underlying single layer of cells, known as the epidermis [Figure 2.3]. As the outermost layer, the epicuticle serves to prevent dehydration and block invasive foreign matter. It consists of three layers, of which the innermost stratum, the cuticulin layer, is composed of lipoproteins and chains of fatty acids embedded in a protein-polyphenol complex. A monolayer of wax molecules, which are bipolar (i.e. with hydrophilic and hydrophobic ends), resides above the cuticulin layer and serves as the chief barrier to water passage in and out of the insect's body. In many insects, a third cement layer protects the waxy layer from abrasion and heat loss. Whereas the epicuticle acts as a barrier against external factors, the procuticle, which consists of a thick, pale endocuticle and a thin, often dark exocuticle, provides structural support. The procuticle is made primarily of chitin chains; its two layers

Figure 2.3 The Cuticle



(Hadley 1986)

being differentiated by the sclerotization of the exocuticle (Gullan and Cranston 2000).

While thin and flexible in many larvae, the adult cuticle is typically both rigid and armour-like (e.g. mandibles) and tough and elastic (e.g. abdomen) depending on its function and location in the body. The strength of the cuticle is derived from the extensive hydrogen bonding of adjacent chitin chains. Chitin is an amino-sugar

polysaccharide predominantly composed of β (1-4) linked units of N-acetyl-D-glucosamine (Gullan and Cranston 2000). Further rigidity is established in the exocuticle through the irreversible process known as sclerotization, which contributes to the proteins becoming water-insoluble. In the membranes between joints or segments, a solid cuticle is not conducive for the necessary flexibility, and an unsclerotized soft cuticle containing resilin is formed instead with a thicker endocuticle and a thinner, or absent, exocuticle. While the rigidity of the exocuticle is essential in certain parts of the insect's body, the benefit of a water-soluble soft cuticle is evidenced by the abdominal dilation permissible in the worker honeypot ant, *Camponotus inflatus*, which retains honey in its distensible abdomen as a colonial food store (Hadley 1986).

The procuticle lies directly on the epidermis, which is the single-celled stratum underlying the cuticle that is responsible for the production of the cuticular components, waxes, cements, and defence mechanisms (Gullan and Cranston 2000). The epidermis secretes cuticle through an organised array of microvilli upon its apical face. At the top of the epidermal microvilli, the cuticulin is deposed which then extends to form a continuous envelope. Through a different cellular process, the epicuticle is formed from the secretory discharge of epidermal vesicles (Payre 2004). Locke (2001) postulates that the laminae of chitin microfibers composing the procuticle are developed in an assembly zone located above the microvilli. The epidermal secretion process is the impetus in both the transformation and preservation of once living cellular material into the tough, durable cuticular layers.

It is the robustness of the cuticle layers that directly correlates to an insect's preservability in archaeological contexts. Therefore, Coleoptera (beetles) specimens are frequently archaeologically recovered due to the pronounced hardiness of their

cuticles whereas Lepidoptera (butterflies and moths) are rarely present. Sadler (1988, 14) claims that during the formation of the thanatocoenosis stage, "the soft parts of all insect families are lost… [and] in the poorly sclerotized groups, however, such as, the Lepidoptera, Diptera, Hymenoptera and many of the Anoplura and Siphonaptera, the majority of the animal is lost". Additionally, it is the more sclerotized portions, i.e. the head, the thorax, and the elytra, of the coleopteran specimens that survive taphonomically. While the preservation of morphological characteristics is crucial in the identification process, the survivability of Coleoptera, which do not moult in their adult stage, suggests that a cellular record of their complete adult life is retained in their subfossil remains allowing for the recovery of and experimentation with viable amino acids, isotopes, and ancient DNA.

2.2.2 The Chitin

Chitin is the principle structural component of the insect body and accounts for approximately 25-40 % of the dry weight of insect cuticle (Jeuniaux 1971). It consists predominantly of unbranched chains of β-(1, 4)-2-acetamido-2-deoxy-D-glucose (i.e. N-acetyl-D-glucosamine) and occurs in the procuticle but is absent from the epicuticle. Hackman (1964) suggests that chitin may be viewed as a derivative of cellulose in which the hydroxyl groups of the second carbon of each glucose unit have been replaced by acetamido (-NH (C=O) CH_3) groups.

During the pharate phase (the period of moulting when an insect has secreted a new cuticle but has not escaped the old cuticle) and immediately after ecdysis (the shedding of the integument) has taken place, chitin is synthesized most rapidly (Chippendale 1978). The chitin is produced in the epidermal cells from the sugar nucleotide, UDP-2-acetmido-2-deoxy-D-glucose. According to Chippendale (1978),

the synthesis of chitin from glucose in insects involves the series of reactions presented in Table 2.1.

Table 2.1 Steps leading to chitin synthesis

1.) ATP + D-glucose	=	ADP + D-glucose 6-phosphate (hexokinase)
2.) D-glucose 6-phosphate	=	D-fructose 6-phosphate (glucosephosphate isomerise)
3.) D-fructose 6-phosphate + L-glutamine	=	2-amino-2-deoxy-D-glucose 6-phosphate + L-glutamate (glucosaminephosphate isomerise)
4.) Acetyl-CoA + 2-amino-2- deoxy-D-glucose 6-phosphate	=	CoA + 2-acetamido-2-deoxy-D-glucose 6-phosphate (glucosaminephosphate acetyltransferase
5.) UTP +2-acetamido-2-deoxy-D- - Glucose 1-phosphate	=	pyrophosphate + UDP-2-acetamido-2-deoxy-D-glucose (UDPacetylgluco-samine pyrophosphorylase)
6.) UDP-2-acetamido-2-deoxy-D-glucose + [1, 4-(2-acetamido-2-deoxy-β-D-glucosul)]	=	UDP + [1, 4-(2-acetamido-2-deoxy-β-D-glucosyl)] (chitin synthase).

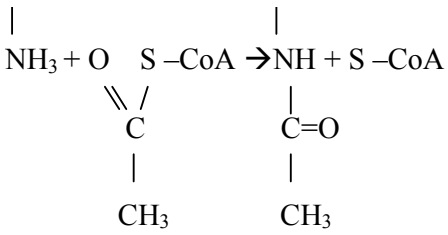
The metabolic reactions involved in the biogenesis of chitin directly impact the isotopic analyses that contribute to this research endeavour. The photosynthetic production of glucose, the building blocks of carbohydrates, in plants is a combination of atmospheric CO_2 and environmental water (i.e. precipitation).

$$6\ CO_2 + 6\ H_2O \rightarrow C_6H_{12}O_6 + 6\ O_2$$ **[Formula 2.1]**

Insects feeding on the plants, or plant products, ingest dietary carbohydrates, such as starch, which in turn are hydrolyzed by the enzyme endoamylase (1, 4-α-D-glucan glucanohydrolase). The enzyme attacks the interior glucosidic bonds of the starch producing a mixture of linear and branched oligosaccharides. The hydrolysis of the starch to absorbable glucose is completed in the intestine using the enzymes endoamylase, α-glucosidase, and oligo-1, 6-glucosidase. Afterwards, the nutrients are absorbed from the lumen of the intestine to the hemolymph through a rate that is controlled by two known limiting factors:

1.) the rate of release of fluid from the crop into the midgut;
2.) the rate of conversion of absorbed glucose into trehalose, i.e. a storage and transport sugar (Chippendale 1978).

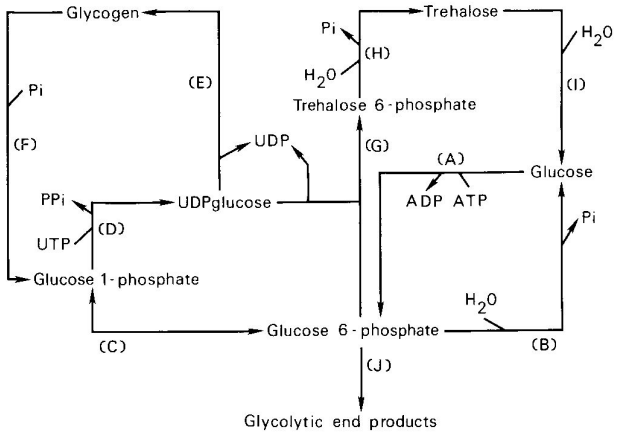
In the insect's body, the carbohydrates are stored as glucose, glycogen, or trehalose until used [Figure 2.4]. In regards to the chitin synthesis, the glucose is most likely the derivative of a trehalose precursor. During the biogenesis of chitin, hydrogen can be added to the carbon ring during two steps [see Table 2.1]. In step 3, the amino acid L-glutamine combines with D-fructose 6-phosphate resulting in 2-amino-2-deoxy-D-glucose 6-phosphate and permitting the NH_3 amino group to bond with the second carbon ring in order to add two new hydrogen atoms. In step 4, acetyl CoA (note that the hydrogen of acetyl CoA originates from glucose-derived pyruvate via the Embden Meyerhoff pathway) reacts with the amino group:



[Formula 2.2]

Of the ten carbon-bound hydrogen atoms contained in one unit of chitin ($C_8H_{13}NO_5$), seven were derived from the glucose produced during photosynthesis and three from pyruvate. The nitrogen-bound hydrogen is obtained from the L-glutamine, leaving two hydrogen atoms which are derived from an unaccounted source (Miller 1984).

Figure 2.4 The interactions of glucose, trehalose, and glycogen



(A) hexokinase (inhibited by glucose 6-phosphate; (B) glucose-6-phosephatase (activated by trehalose); (C) phosphoglucomutase; (D) glucose-1-phosphate uridylytransferase; (E) glycogen synthase (activated by glucose 6-phosphate; (F) glycogen phosphorylase (inhibited by ATP); (G) α, α-trehalose-phosphate synthase (activated by Mg^{2+}, inhibited by trehalose); (H) trehalose phosphatase; (I) α, α-trehalase; (J) glycolytic enzymes (control at phosphofructokinase and pyruvate kinase)

(Redrawn from Sacktor 1970 in Chippendale 1978, 33)

2.2.3 The Head

The head is the rigid capsule-like structure that constitutes an insect's anterior body region. The cranial capsule has only two openings, one to the mouthparts and the other through the occipital foramen to the prothorax. It is composed of six fused segments:

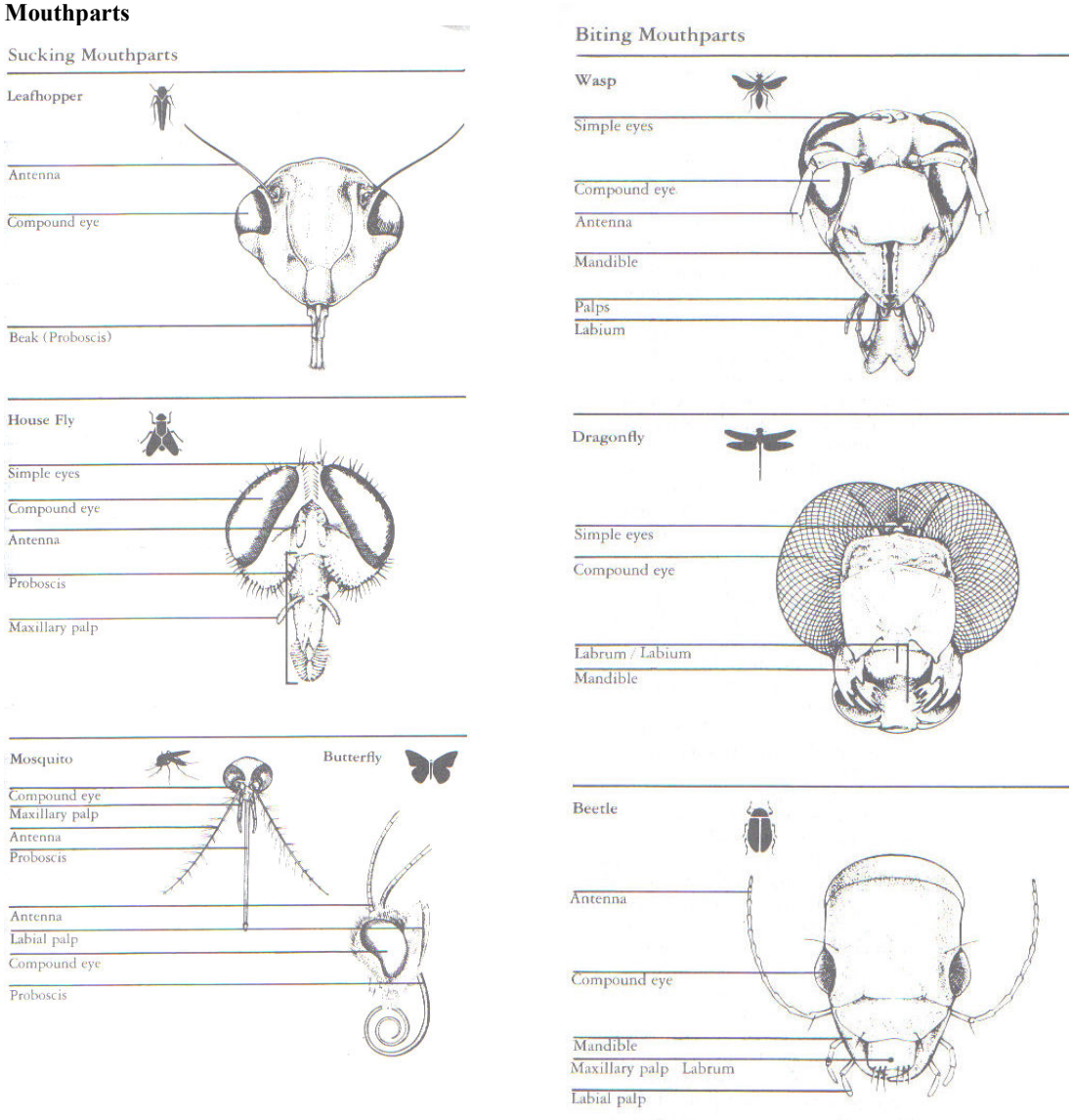
- labral;
- antennal;

- postantennal;
- mandibular;
- maxillary;
- labial (Gullan and Cranston 2000).

An insect's head is host to its mouthparts, eyes, and antennae. The mouthparts are constructed from all the head segments except the antennal, consisting of the upper (labrum) and lower (labium) lips, the jaws (mandibles), and two jaw-like appendages (maxillae) (Knopf 1980). Additionally, Gullan and Cranston (2000) list the hypopharynx, which is a tongue-like feature, amongst the basic mouth components. While the labrum and the labium form a preoral cavity, the hypopharynx divides the cavity into a food pouch and a salivarium. The mandibles and the maxillae assist in the processing of food. While the mandibles, which may possess an indentation hardiness of up to 30 kg mm^{-2} and a 3 on the Moh mineral hardness scale, cut and crush food, the maxillae hold and macerate the food (Gullan and Cranston 2000).

In addition to functioning as food acquisition and processing tools, insect mandibles feature prominently both as defence mechanisms and instruments for sexual selection. In some beetle species, like *Lucanus cervus*, the mandibles are analogous to antlers in elk and are similarly larger in males and employed by them in fights over females (Preston-Mafham 2005). Evolutionary adaptations for food processing, defence, or sexual selection have produced myriad mouthpart types based upon the basic components and design.

Figure 2.5 Types of Mouthparts



(Knopf 1980, 16-17)

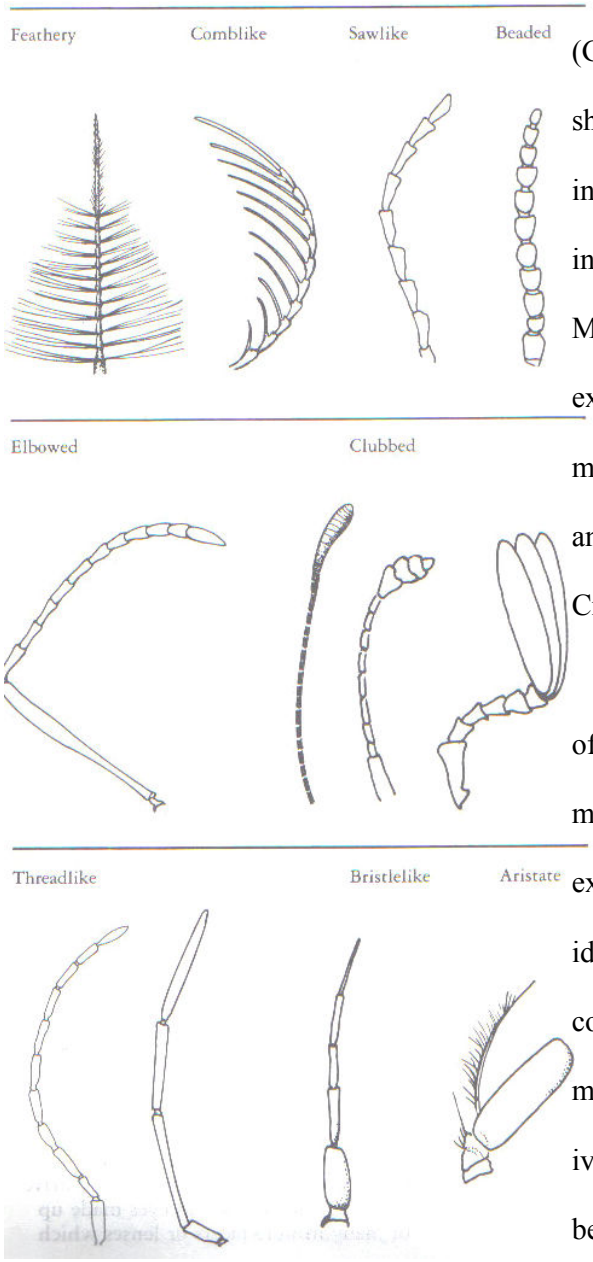
These modifications to mouthpart structures are exploited by phenotypic identification methods and serve as the foundation for ecological generalisations. The classification of mouthparts is typically categorised by feeding method [Figure 2.5] chewing, sucking, or piercing (Borror and White 1970). Chewing mouthparts are typically characterised by laterally moving mandibles that cut and crush the food; however, certain insects such as bees evince a chewing and lapping method. Gullan

and Cranston (2000, 27) define lapping as "a mode of feeding in which liquid or semiliquid food adhering to a protrusible organ, or 'tongue', is transferred from substrate to mouth." In bees, the mandibles are restricted to manipulation of wax, fighting, feeding larvae, and labour (Gullan and Cranston 2000). Most adult Lepidoptera (moths and butterflies) have evolved suctorial mouthparts in the form of an elastic proboscis, which pumps liquid food. While various modifications are indicative of piercing mouthparts, they largely consist of needle-like stylets or proboscis which specialise in breaking animal and plant tissue (Borror and White 1970). Afterwards, the piercing insects acquire their food through sponging the pre-existing liquids, e.g. Anoplura (sucking lice), or by extra-orally digesting any solids and sucking the resulting liquids, e.g. larval Neuroptera (net-winged insects), into the food canal (Gullan and Cranston 2000).

In addition to mouthparts, most insects have two kinds of eyes—simple and compound. Simple eyes, termed ocelli, are merely sensitive to light and are not designed for high-resolution vision (Knopf 1980). Generally, the ocelli reside in the triangular portion on the top of an insect's head, permitting the insect to respond to subtle changes in light (Gullan and Cranston 2000). The compound eye is the insect's most sophisticated visual organ, allowing coverage of nearly 360 degrees of space. Compound eyes are comprised of several minute lenses which provide the insect with panoramic images formed from apposed points of light (Gullan and Cranston 2000).

Further sensory structures exist in the form of paired mobile, segmented appendages called antennae, which insects use for smell, touch, and occasionally hearing (Knopf 1980). The antennae contain a multitude of hairs, pits, and cones that operate as sensory organs in the form of chemoreceptors, mechanoreceptors,

Figure 2.6 Types of Antennae



(Knopf 1980, 14)

thermoreceptors, and hygroreceptors (Gullan and Cranston 2000). Size, shape, and elaborateness vary between insects [Figure 2.6] and can be indicative of taxonomic groups. Moreover, antennae may often be examined to ascertain gender because male insects may have more elaborate antennae than females (Gullan and Cranston 2000).

The morphological variations of insect head features, especially the mouthparts and antennae, are often exploited for entomological identifications. As one of the more commonly recovered archaeoentomological fragments, the distinctiveness of the fossilised heads is often beneficial in the determination of taxonomic order and genera. However, analysis of thoracic and/or abdominal remains is occasionally necessary for species identification.

2.2.4 The Thorax

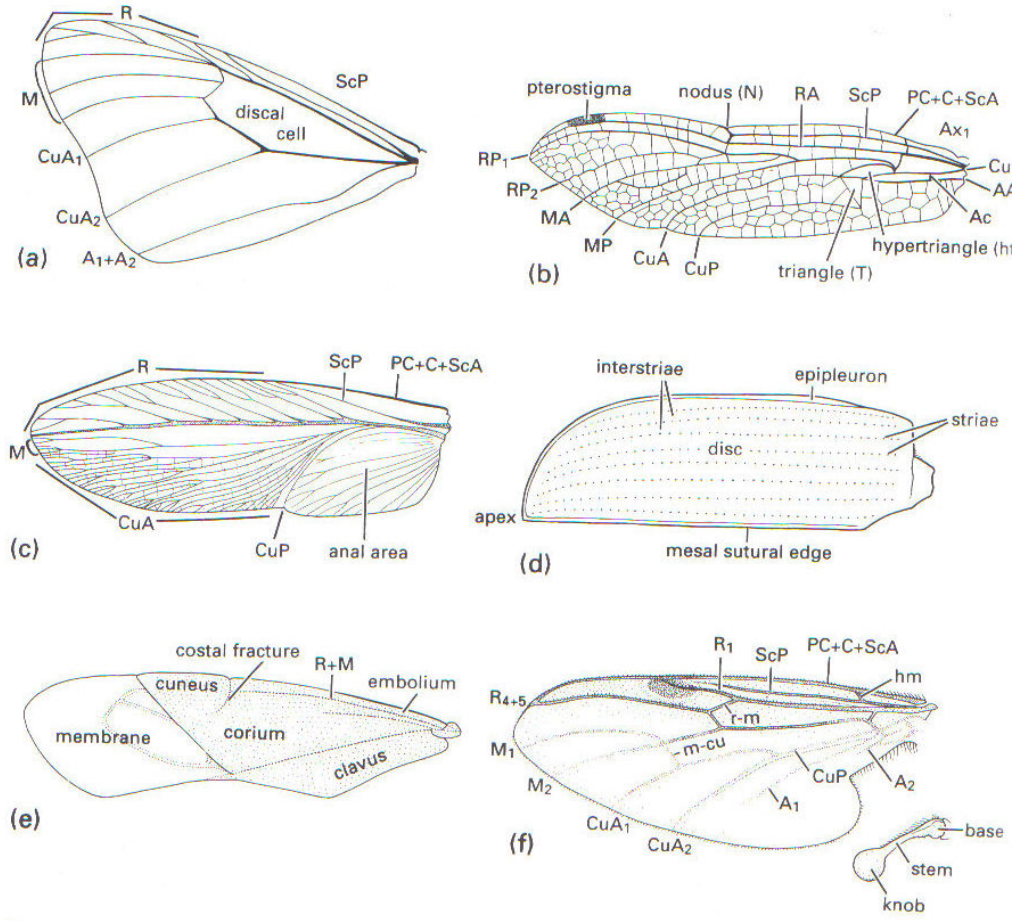
The thorax is made up of three segments: the prothorax, the mesothorax, and the metathorax. Each thoracic segment has one pair of six-segmented legs; in the case of winged insects, the mesothorax and usually the metathorax bear wings (Knopf 1980). The thoracic tergal plates are variously modified in pterygotic adults though remain rather simple in apterygotes and immature insects (Gullan and Cranston 2000). In beetles, mantids, grasshoppers, and some Orthoptera, the upper surface of the prothorax, the pronotum, is large, extending from the head to the wing base, and in cockroaches, it serves as a shield that covers part of the head and mesothorax (Knopf 1980). Because of its uniqueness, the preservation of the pronotum in the fossil record assists in the palaeoentomological identifications.

Insects have three pairs of legs—fore, mid, and hind—composed of five parts: the coxa, the trochanter, the femur, the tibia, and the tarsus (Knopf 1980). The apex of the tarsus usually wields a pair of claws and pad-like structures (Borror and White 1970). While the femur and the tibia are generally the longest leg segments, variations exist based on function (Gullan and Cranston 2000). These functional modifications may be indicative of behavioural specialisations such as the enlarged forelegs of mantids for snaring prey and the developed hind femora and tibiae of grasshoppers designed for leaping (Knopf 1980).

Further specialist adaptations are made evident by the thoracic wings. Although all winged insects are believed to share a homologous eight veined venation ground plan, venation patterns are only consistent within groups and further wing variations exist in shape, size, and degree of sclerotization [Figure 2.7] (Gullan and Cranston 2000). In the case of Coleoptera (beetles), the forewings have hardened into

protective wing cases, elytra, which secure the hind-wings when an individual is not in flight [Figure 2.7d]. Another wing modification is apparent in the Diptera (flies)

Figure 2.7 Wing Modifications



(a) Forewing of a butterfly; (b) Forewing of a dragonfly; (c) Forewing of a cockroach; (d) Forewing of a beetle; (e) Forewing of a mired bug; (f) Forewing and haltere of a fly
(Gullan and Cranston 2000, 38)

[Figure 2.7 f], in which the hindwings have been adapted as a balancer (Gullan and Cranston 2000). In adult insects, studying the positioning of wings helps distinguish between groups. For example, some members of Heteroptera and Coleoptera encase their membranous hindwings in their thickened forewings (i.e. elytra) when they are held flat against the back (Preston-Mafham 2005), suggesting convergent evolution between the taxonomic orders. However, in Heteroptera, the membranous wing-tips

overlap to create a triangular pattern while the coleopteran elytra are positioned in a straight line down the insect's back.

In recovered fossil specimens, the remains are often disarticulated and the membranous features are relatively rarely preserved. Regardless, because of their range of modifications and variations, the examination of fossilised pronota, elytra, and legs can result in the identification of insects to genus and species level.

2.2.5 The Abdomen

The typical insect abdomen is comprised of a maximum of eleven complete segments; however, one segment is occasionally incorporated into the thorax and the last segment is usually represented by appendages only (Gullan and Cranston 2000). Additionally, the fusing of abdominal segments is common in many insects. Each segment is composed of two principal sclerites, a dorsal tergum, and a ventral sternum (Borror and White 1970).

In most insects, the abdominal segments are void of appendages except for the posterior eleventh segment. When the terminal appendages are present, they may include a pair of dorsolateral cerci, a median epiproct, a pair of lateroventral paraprocts, and the genitalia (Borror and White 1970). The cerci generally are annulated and filamentous and may be modified into feelers (e.g. mayflies) and claspers (e.g. earwigs) (Gullan and Cranston 2000). On the eighth and ninth abdominal segments, the genitalia are usually formed and may be internally or externally present (Gullan and Cranston 2000). Moreover, the male genitalia are rather varied and often very complex (Borror and White 1970). As a result, the dissection of abdominal segments towards the examination of genitalia harbours

taxonomic implications for the recognition of modern and, where preserved, fossil insects.

2.3 Identification Methods

2.3.1 Modern Insects

Keys

The employment of entomological keys permits researchers to gradually narrow down species possibilities through the process of elimination based primarily on morphological differences of the exoskeleton. The keys are composed of a series of couplet stages, binary opposites, which progress to the name of the species examined, *i.e.* if the insect has feature A proceed to couplet 6; if not then go to couplet 27. For example,

> "1. Entire elytron uniformly pubescent, or at least with one row of setae or bristles along entire length of each (or every second) interval. …….2
>
> - Elytron glaborous, except for marginal setae and often setiferous "dorsal" punctures on intervals 2-3, or with only outer intervals pubescent. …….18"
>
> (Lindroth 1985, 24).

If the specimen matches the first alternative of couplet 1, then proceed to couplet two. However, if the insect matches the description in the second alternative of couplet one, then continue to couplet 18. The identification method progresses in this manner until a probable species is offered.

While the couplet method of identification is the most prevalent, a second method is available. Rather than being confronted with dichotomous alternatives,

table keys issue a single statement at each stage which if correct the researcher advances to the next sequential statement. If the statement is incorrect, an alternative bracketed number is listed for reference. The table style is exemplified by Joy's (1976) classification of Staphylinidae:

"1 (4). El. with strongly raised longitudinal keels.

2 (3). Segments of hind-body with 3 raised longitudinal keels on each, and ant. clubbed.

MICROPEPLINAE

3 (2). Hind-body simple, and ant. thickened to apex.

PSEUDOPSINAE

4 (1). El. without raised longitudinal keels.

5 (6). Eyes very large, and ant. clubbed characteristically.

STENINAE" (Joy 1976, 3).

While both types of keys provide a tabulated format for the recognition of insects based on humanly delineated phenotypic structures, caution is necessary in their application because insects, like humans, possess individual variations, resulting in a margin of error. Thus keys are best employed as means for quick identification of probable species. In order to more accurately verify an insect species, the specimen in question should be compared to previously identified species from credible entomological sources, *e.g*. museum collections.

Genetics

In order to compensate for the difficulties inherent in the traditional key methods, genetic methods have been developed that provide rapid and accurate identifications (Cainé *et al.* 2006). Genetic identification methods have proven proficient at species determination regardless of specimen damage or insect life stage (e.g. Wells and Sperling 2001). However, in order to genetically determine a species, it must have a pre-existing record in the databases, e.g. Genbank. This is established by extracting DNA signatures from positively identified species and generating a 'barcode' for that particular species (Murphy and Fraser 2006).

Processing DNA from a specimen identifies a genetic code which is unique to that species. By noting variations in the code, different species can be recognised. For example, the partial DNA signature, provided by the Barcode Life Project and corresponding with the mitochondrial CO1 gene, used to identify *Sitophilus granarius* is:

1 ATT CTC TAC AAA CCA CAA AGA TAT CGG CAC

31 ACT ATA TTT TAT TTT TGG AGC ATG ATC AGG

61 AAT AGT TGG AAC CTC TTT AAG ACT ATT AAT

91 TCG AGC AGA ATT AGG AAA CCC CGG CTC ACT

121 GAT TGG AAA TGA TCA AAT TTA TAA TAC TAT

151 CGT TAC TGC TCA CGC ATT TAT TAT AAT TTT

181 TTT TAT AGT TAT ACC TAT CAT AAT TGG AGG

211 ATT CGG AAA TTG ACT AAT TCC ATT AAT ATT

241 AGG AGC CCC AGA TAT AGC CTT CCC ACG ATT

271 AAA CAA TAT GAG ATT CTG ACT ACT TCC CCC

301 ATC TTT AAT TCT TCT ATT AAT AAG AAG ATT

331 TAT TGA AAA AGG TGC TGG AAC AGG GTG AAC

(Genbank ID DQ453486);

whereas the partial code for *Sitophilus oryzae* is:

1 ATT CTC TAC TAA CCA CAA AGA TAT CGG AAC

31 ATT ATA CTT TAT TTT TGG AAC ATG ATC AGG

61 AAT AGT AGG TAC ATC CTT AAG TTT GCT AAT

91 TCG GGC AGA ACT AGG AAA TCC TGG ATC ACT

121 AAT TGG AAA TGA CCA AAT TTA TAA TAC TAT

151 TGT CAC AGC ACA TGC ATT CAT TAT AAT TTT

181 CTT TAT AGT AAT ACC AAT TAT AAT TGG AGG

211 ATT TGG AAA CTG ATT AAT CCC ATT AAT ATT

241 AGG AGC CCC AGA TAT AGC ATT CCC CCG TTT

271 AAA TAA TAT AAG ATT TTG ATT ACT TCC ACC

301 CTC CTT AAC TCT TTT ACT AAT AAG AAG ATT

331 TAT TG AAA AGG GAG CAG GAA CAG GATG AAC

(Genbank ID AY131099).

Sitophilus granarius and *Sitophilus oryzae* are both species of the same genera; however, subtle differences are apparent in their genetic code. Although both of the gene sequences begin with "ATT CTC TAC," the first variation appears at the beginning of the fourth nucleotide triplet. In *Sitophilus granarius* the nucleotide adenine (A) is present while the sequence for *Sitophilus oryzae* has thymine (T). In these partial 360 nucleotide sequences, there are 51 base pair differences at the genetic level between these two closely related species. By analysing these notable distinctions, species determination is possible, and with the assistance of computer

processing, the genetic identification method is often quicker than the traditional entomological recognition methods.

2.3.2 Fossil Insects

Comparative Analysis

The study of Quaternary and late Tertiary insect remains in sediments was revitalised over forty years ago by G. R. Coope (Elias 1994) and is based largely upon the geological principle of uniformitarianism (the present is the key to the past) and the assumed relationship between the modern ecological community, the *biocoenosis*, and the fossilised death assemblage, the *thanatocoenosis*. The crux of this assumption centres on Coope's argument that in most temperate and arctic environments of the northern hemisphere, "it can be demonstrated that wherever fossils are available the Coleoptera show a remarkable degree of morphological stability throughout the Quaternary" (1977a, 324), and "the majority of species seems to have remained physiologically stable during this period" (1970, 107). Because of this theory of species constancy, palaeoentomologists are able to identify insect fossils based on comparative analysis with modern species and extract palaeoecological information in a similar fashion to anthropological analogies—superimposing the habitats of modern insects over the fossil record.

Coope (1970) stated that the traditional elimination method of the entomological keys towards the identification of modern species could not be utilised in the identification of fossil insect remains based on the premise that the complete specimen were rarely recovered. Because the fragmentation of the remains rendered the application of the keys redundant, some early entomologists erroneously claimed that fossilised insect species could not be identified. However, the concept of an

insect species, modern and fossilised, is reliant on morphological distinctions in the exoskeleton. The preservation of insect fossils, while often disarticulated, is such that in many cases, the heads, thoraces, and elytra retain morphological characteristics that permit examination of detailed microsculpture. Moreover, in contexts with excellent preservation, researchers have been able to recover and dissect fossilised insect abdomens in which genitalia and gut contents have been preserved (e.g. Matthews and Telka 1997). Because morphology is the primary criterion for the identification of modern specimens, comparative analysis of modern and fossil insects can be employed for recognition of the archaeologically recovered remains.

Although morphological characteristics are preserved, taphonomic alterations are occasionally evident in the fossilised remains, especially when dried, and must be considered in the identification process (Coope 1970). The original colouration of the specimens may be rendered bluish-black, brown, or completely devoid of colour, depending on the nature of the soil in which it was retained. In specimens in which colour remains, the colouration may have changed—red to green or green to blue. In dried fossils, deepened puncturations may develop, and prominences and hollows may become flattened (Coope 1970). While alterations may transpire in the post-mortem, comparative analysis of modern and fossil insects is successful if care is given to the consideration of taphonomic afflictions.

Another taphonomically imposed hurdle in the study of fossilised insect remains is the biases resulting from the taxonomic orders preserved, recovered, and documented. Coleoptera are the most commonly recovered and determinable insect fossils due to the robustness of their exoskeleton and the multitude of literature concerning the modern coleopterous fauna, which eases the identification and interpretation process. Because of the dominance of Coleoptera in the documentary

and fossil record, it will contribute much of the information discussed in this thesis. Although coleopteran remains often comprise the majority of recognisable fossils, dipteran (true flies) fragments are frequently recovered though often severely disarticulated. However, researchers have demonstrated that identification of dipteran remains can serve as an index for the reconstruction of past temperature regimes (e.g. Skidmore 1996). The heads and propodea of Hymenoptera (sawflies, bees, wasps, and ants) are common in archaeological assemblages and have been utilised for economic (e.g. Kenward and Hall 1995) and palaeoecological (e.g. Zazula *et al.* 2002) postulations. While Dermaptera (earwigs), Hemiptera (true bugs), and Trichoptera (caddis flies) are also common, they have been studied to a lesser extent and have not been employed to their full palaeoentomological potential. The recovery of the membranous wings of most insects and Mallophaga (louse flies) and Anoplura (sucking lice) specimens, which have thin flexible cuticles, is indicative of other preservational determinants, such as soil pH, though the cuticular thickness remains the primary factor. Although fossils of Orthoptera (cockroaches, crickets, and grasshoppers), Odonata (damselflies and dragonflies), and Lepidoptera (butterflies and moths) are occasionally archaeologically present, their rareness in the fossil record in comparison to the more robust fauna is not reflective of their abundance in the past.

Species constancy has permitted the identification of fossil insects through comparison with their modern counterparts. However, archaeologically recovered populations are biased because they provide insight into only a small point in space, which is further subjected to taphonomic distortions, from a complex occupational site. Thus while modern analogues are applicable for identification of fossil insects and the construction of pertinent ecological parallels, archaeological populations do

not truly resemble modern populations in regards to tabulating an accurate account of the frequency and abundance of a species.

2.4 Ecology

Charles Elton (1927) described ecology as scientific natural history, being reminiscent of researchers like Darwin and Linnaeus. However, the field of ecology progresses beyond the study and taxonomic classifications of species to encompass the examination of the "total relationships (interactions implied) of organisms with their environments, at the level of the individual (autoecology) or that of variously constituted groups (synecology—a community ecology)" (Huffaker *et al.* 1984). While ecology specialises in the analysis of ecosystems, it is an interdisciplinary amalgamation of concepts from:

- genetics (the investigation of mutation, recombination, selection, and diversity within taxa at the molecular level);
- physiology (the elucidation of mechanisms for cellular development and function towards the integration of specialised tissues and organs);
- behaviour (the study of how the physiological components, which directly interact the external environment, influence an individual's reaction to and interaction in an environment);
- evolution (the evaluation of an individual's current expression of genetic material in relation to the various historical influences which have acted upon its species) (Krebs 1972).

An ecosystem conceptualises the interplay between the biotic and abiotic world as a whole interlacing assemblage (cf. Tansley 1939). In this system, organisms and populations interact with one another whilst simultaneously

influencing the continuous cyclic transfer of energy and material. Evans (1956) delineates the dynamics of an ecosystem as:

> "the circulation, transformation, and accumulation of energy and matter through the medium of living things and their activities. Photosynthesis, decomposition, herbivory, predation, parasitism and other symbiotic activities are among the principal biological processes responsible for the transport and storage of materials and energy, and the interaction of the organisms engaged in these activities provide the pathways of distribution" (Evans 1956, 1127).

The fundamental concept of archaeoentomology is founded upon this ecological interplay having persisted in Quaternary insects unchanged. Underpinning this is the theory of species constancy, that under repeated conditions of change, insect communities will migrate rather than adapt through evolution (Coope 1978). Although there are studies of isolated island and mountain populations where migration is rare and speciation dominates (Elias 1994), extensive paleontological research has confirmed that some insects have remained physiologically and morphologically constant for up to 30 million years (Elias 1994). Based on this premise of stability, the ecological requirements of modern species may be analogously employed towards reconstructions of palaeoecology.

A discussion and understanding of the major ecological principles is particularly crucial to this thesis because it enables archaeoentomological researchers:

- to employ the insect fauna's ecological associations to reconstruct environments and climates of the past;

- to discern insect associated (directly or indirectly) materials used by past humans;
- to overlap species' thermal requirements in order to glean an understanding of a site's potential maximum and minimum temperatures, which may aid in identifying species that are ecological outliers, i.e. invasive.

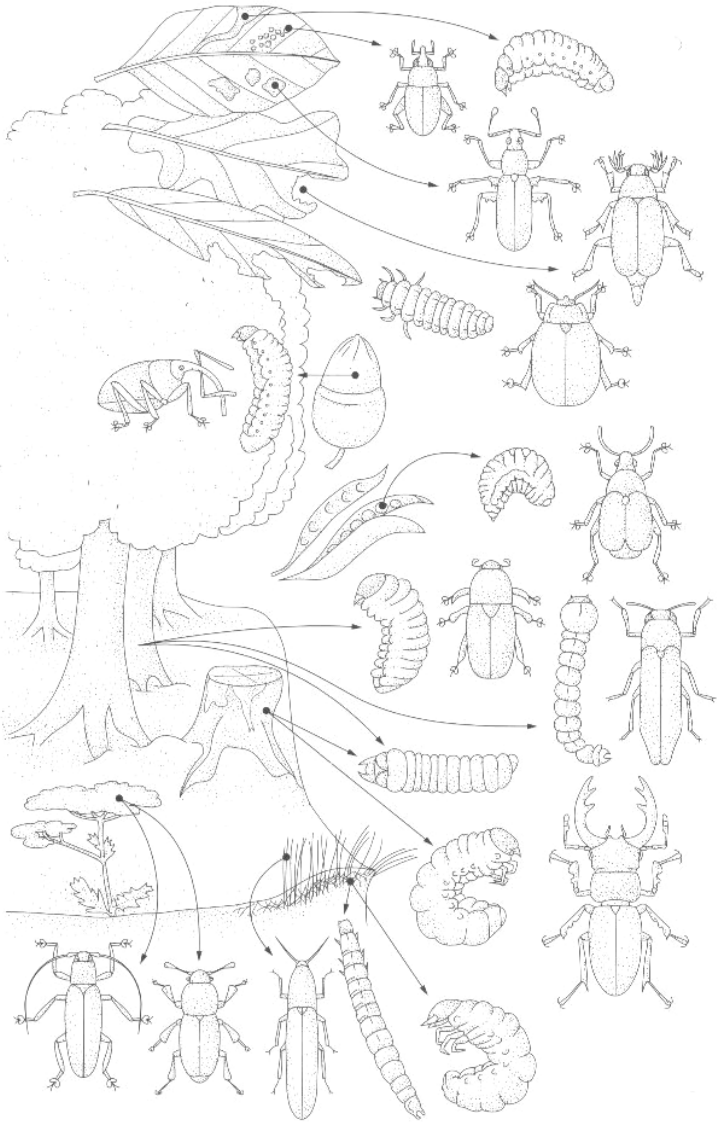
2.4.1 Components

As a system, an ecosystem is composed of myriad components of various levels of complexity. In a given locality, individual organisms comprise groups of potentially interbreeding individuals, called populations (Mayr 1963). Species are groups of individuals in a population that are capable of interbreeding and producing viable offspring. In turn, species may be categorised into guilds (species that exploit the same resource by similar means); guilds may form part of component communities (species associated with some microenvironment or resource, *e.g.* leaf litter); and component communities in the same area may interact to form compound communities, e.g. a pond (Price 1984). The interaction of these compound communities and their physical environment constitutes an ecosystem.

In an ecosystem, the relational position of a species or population, i.e. its niche, is controlled by habitat, resource availability, and trophic position (Elton 1927). Within a habitat [e.g. Figure 2.8], the members of the faunal community occupy certain roles—predator, herbivore, scavengers, etc. The occupation of these roles is best evinced in the relationship between aphids, ants, and ladybirds. On a rose, aphids suck sap from the phloem vessels and secrete a honeydew-like residue, and ladybirds prey upon the aphids as a food source. Additionally, ants living on the rose may try to

protect the aphids from the ladybirds in order to maintain their honeydew farm. Thus on the rose, there are herbaceous aphids, predatory ladybirds, and mutualistic

Figure 2.8 Diversity of beetles in a tree habitat



(Evans 1977, 232)

scavengers in the form of ants. This community is further monitored by resource availability in that if the ladybirds prey too heavily on the aphids, there will not be sufficient aphids to feed all the ladybirds and some may die. Likewise, if the plant dies, the aphids, which are dependent upon the rose for food, will die. While the

groundwork for these roles is omnipresent in various habitats, the animals may differ. For instance, instead of aphids, ladybirds, and ants on a rose, there may be sheep, wolves, and shepherds in a meadow. Within ecosystems, communities, and habitats, organisms and populations exist and interact and are able to survive by fulfilling a specific role, which is unique to them.

2.4.2 Synecology

The concept of an ecosystem is based on the interaction of its components. Price (1984) groups the interacting components into autotrophs, heterotrophs, and saprophages. Self-nourishing organisms, like plants, are autotrophic in that they capable of converting and utilising light energy and organic chemicals. Heterotrophs are organisms that feed directly or indirectly on autotrophs. If the organisms feed directly on the autotrophs (thus transferring the energy accumulated by the autotrophs directly into themselves), they are typically defined as herbivores, *i.e.* plant feeders. However, carnivores, which feed on the non-autotrophic organisms, still receive the autotrophic energy, though indirectly. Additionally, saprophages, or decomposers, are considered heterotrophic because they feed upon dead organic material; whether directly from the autotrophs or indirectly from other heterotrophs depends on the organism. These ecological associations may be mutually beneficial or involve the advancement of certain individuals, possibly at the expense of another.

The specific interactions evidenced by ecological associations are inter- or intraspecific as symbiosis, herbivory, and competition (Speight *et al*. 1999). Symbiotic relationships may categorised as mutualisms (a relationship in which both organisms benefit), commensalisms (an affiliation in which one organism benefits and other remains unharmed), or parasitisms (an association in which one species benefits

at the expense of another). Myrmecophytism is a type of mutualistic ant-plant association. During myrmecophytism, plants provide ants with food and shelter in return for defence. Vasconcelos and Casimiro (1997) have demonstrated the myrmecophytic relationship between plants in the genus *Cecropia* and *Azteca alfari* ants. The extrafloral nectaries of the *Cecropia* trees produce glycogen which may be broken down into glucose to provide *A. alfari* with a food source; however, the foliage of *Cecropia* is foraged by *Atta laevigata*, a leaf-cutting ant. Vasconselos and Casimiro (1997) observed that when *Cecropia* housed *Azteca alfari*, the predacious *A. alfari* deterred the foraging *Atta laevigata*, and the leaf-cutting ants selected other plants for harvesting. The association between *Cecropia* trees and *Azteca alfari* mutually benefited both species, the trees received protection and the ants acquired housing and food.

The relationship between the Ponerine ant *Gnamptogenys menadensis* and the Formicine ant *Polyrhachis rufipes* is indicative of a commensalistic interspecific interaction which provides benefit to one species while the other remains unaffected. *Gnamptogenys menadensis* foragers are reliant on chemical trails laid down between their nests and sugar sources. *Polyrhachis rufipes* exploit these trails to gain access to sugar sources. When a *Polyrhachis rufipes* worker encounters a *Gnamptogenys menadensis* forager, the *P. rufipes* exhibits aggressive antennal boxing to which *G. menadensis* reacts submissively (Gobin *et al.* 1998). By utilising the chemical trails 'blazed' by the Ponerine ants, the Formine ants are able to beneficially gain access to food resources while the Ponerine ants are neither benefited nor harmed by the association.

Unlike commensalisms, parasitic relationships aid one organism at the expense of another. Eggleton and Belshaw (1992) approximate ten percent of all

insect species are parasitic at some stage in their life cycle. Adult females of *Lysiphlebus testaceipes* deposit an egg into aphids. Two days after the egg is injected, it hatches and the larva begins to internally feed on its aphid host, resulting in the death of the aphid six to eight days later. Upon the aphid's death, the larva creates a hole in the bottom of the aphid in order to attach the aphid to a leaf with silk and glue and moults to the pupal stage. After four or five days, an adult wasp emerges from the aphid mummy (Knutson *et al.* 1993). Through its relationship with the aphid, the parasitic wasp is able to conduct its life cycle; however, the aphid does not gain any benefits and eventually dies as a result of the interaction.

Some ecological commentators have depicted herbivory as a means of parasitism (e.g. Price 1975). This theory is supported by the larvae of the European corn borer *Ostrinia nubilalis*, which burrows into corn stalks and devours the fruit tissue (Gullan and Cranston 2000). By feeding on the corn, the larvae reduce the reproductivity of the corn plant. However, it is not always the case that phytophagy inflicts harm on the autotrophic plants, *e.g*. the mutualism between *Azteca alfari* and *Cecropia* trees. Additionally, some researchers have proposed that herbivory may benefit plants. Pruning and mowing of plants by herbivores may advance the overall reproductivity of the plant through altering growth form and increasing quantity of seed sets (Gullan and Cranston 2000).

Unlike the specific interactions expressed by the different forms of symbiosis and herbivory, competition is an ecological association which is indicative of a negative-negative interaction. Begon *et al*. (1990) describe competition as an interaction between individuals, brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survivorship, growth, and/or

reproduction of the competing individuals concerned. It may be intra- and interspecific. Intraspecific competition exists between members of the same species, whereas interspecific competition refers to resource competition among members of different species. At the Roman age site of Park View School, County Durham, abundant fossil remains of the stored grain weevil, *Sitophilus granarius*, were recovered (King unpublished). During infestations of granaries with plentiful resources, a single weevil will inhabit a single grain at any given time. However, when resources are limited, more than one weevil will occupy the same grain simultaneously, i.e. intraspecific competition, often resulting in reduced growth. At the Park View School site, evidence for intraspecific competition was indicated by the presence of weevils of reduced size in addition to specimens of normal length (pers. comm. H Kenward 2007).

While the existence of intraspecific competition is apparent, interspecific competition is less discernable and in accordance with Gause's Axiom (Speight *et al.* 1999) not possible. Gause's Axiom proposes that two species cannot coexist if they have identical niches as any variation in the species may result in a competitive advantage permitting the displacement of the weaker competitor. Hence, although *Sitophilus granarius* and *Oryzaephilus surinamensis* are both commonly recovered pests of stored products in the same archaeological contexts, their niches may have overlapped but not been identical. *O. surinamensis* is able to process meal and other ground starches but is unable to cope with whole, dry grain unless it is damaged (Horion 1960). Therefore, *O. surinamensis* is not in direct competition with *S. granarius* regarding undamaged grains. Rather *O. surinamensis* commensally benefits from the interspecific association by processing the grains damaged by the grain weevils. Although an overlap exists, the interspecific competition is restricted

by subtle variations within the two coexisting species niches—the presence and availability of undamaged grains provides an unchallenged food resource for *S. granarius* while *O. surinamensis* is restricted to feeding upon the damaged grains and scavengery. In an ideal situation, as above, resource limitation is not an issue thus direct interspecific competition is not apparent. However, in the Park View School case, resource limitation was proposed as an impetus for intraspecific competition amongst *S. granarius*. Multiple individuals were thought to have simultaneously inhabited single grains. This would in imply that the grain weevils were not at liberty to abandon the damaged grains for undamaged grains as resources were limited. Hypothetically, *S. granarius* and *O. surinamensis* would have been in direct competition for the damaged grains, and *S. granarius* would have had the competitive advantage by being able to inhabit the undamaged grains first. In order to compete for the limited resources, *O. surinamensis* would have had to displace or coexist with the grain weevil. The fossil evidence from a Park View School sample tabulated an MNI of one for *O. surinamensis* and sixteen for *S. granarius*. The remains of both species indicated little decay suggesting that cuticle robustness would not have been a strong factor in influencing the MNI through preservation of the remains. The Park View School sample is likely to reflect the successful competition and displacement of *O. surinamensis* by *S. granarius* encouraged by overlapping niches and limited resources as the impetus for interspecific competition.

2.4.3 Ecological Constraints

Every species is limited in its distribution by biotic and abiotic factors. In a study of vegetational ecosystems, Holdridge and associates (1971) demonstrated that some species are distributionally constrained to a small part of the globe by factors

such as competition [see Section 2.4.2], climate, and environment, e.g. food availability. The ecological constraints that influence a species define its niche.

Climatic factors—temperature, photoperiod, and rainfall—impinge on the ecologies of insects. Although some species, *e.g.* bees and moths, are capable of elevating their body temperatures through rapid contractions of their flight muscles, all insects are poikilotherms (their body temperature and metabolism are functions of their surroundings) (Speight *et al.* 1999). Therefore, an insect's growth, development, and activity are dependent on temperature. For example, the saw-toothed grain beetle, *Oryzaephilus surinamensis*, is restricted in its distribution in the north as it is unable to complete its development at temperatures below 18 °C and does not flourish below 22 °C (Howe 1965).

Archaeoentomologists have employed modern species' temperature restrictions toward developing mechanisms for the reconstruction of palaeoclimates (e.g. Buckland 2000). If multiple temperature restrictions are calculated for fossilised insects at a site, temperature restrictions for the autochthonous species will overlap resulting in mutual minimum and maximum temperatures for the site at that period in time. Using Anglo-Scandinavian York, UK as an example, the insect evidence from 16-22 Coppergate, 6-8 Pavement, 5-7 Coppergate, and 1-9 Micklegate was utilised to calculated the mutual climatic range [MCR] with the assistance of the *BUGS Coleopteran Ecology Package* (Buckland and Buckland 2006). The MCR for each of the four sites indicated that York had a maximum temperature of 18 °C and a minimum temperature of -7 °C during the Anglo-Scandinavian period [see Table 4.5].

Like temperature, photoperiod, *i.e.* the length of daylight during a 24 hour day, is an impetus in the development of insects. Leimar (1996) postulates that photoperiod is used by insect larvae to ascertain information about seasonal change in

order to correlate growth and development rates with favourable conditions. The impact of day-length is considered in Nealis and others' (1996) examination of the parasitic wasp, *Cotesia melanoscela.* When exposed to day lengths greater than 18 hours, the larval wasps developed continuously to their adult stage; however, the larvae halted development in the cocoon prepupal stage by entering a diapause when they were subjected to less than 16 hours of daylight. Through monitoring photoperiod, the adult parasitoid *Cotesia melanoscela* arrive during the long days of summer when their hosts are most prevalent; thus improving their chances of depositing eggs and continuing the species. However, because of its reaction to photoperiod, *Cotesia melanoscela* is restricted ecologically. If the parasitic wasp was transported to an environment that constantly received less than 16 hours of daylight, it would never develop beyond its larval form.

Rainfall can directly and indirectly affect insects. Like the insect's relationship to photoperiod, seasonal changes in rainfall influences species abundance. This is reflected by some species being prolific during dry seasons and others during wet. Haggis (1996) demonstrated that outbreaks of the cereal pest *Spodoptera exempta* were related to amounts of rainfall, as severe outbreaks were often preceded by periods of drought. It was inferred that the wet conditions caused viral infections to afflict the larvae while the heat of the droughts destroyed the viruses allowing more of the larvae to survive to adulthood. Rainfall is also a factor in determining food availability for insects. The amount of rainfall affects the growth of plants and as such the food source for herbivores and the species that feed on the herbivores. In instances of drought, the plants may become stressed, which could result in limited resource availability, increased competition, and reduced survivability for the herbivores.

The availability of food sources in an environment is a fundamental determinant in the restriction of population size [see species competition in Section 2.4.2]. In the absence of food, an organism is confronted with three options: relocation, diapause, or death. Through the ingestion of food, the insects are able to obtain the energy and nutrients necessary for metabolic function, growth, development, and reproduction (Hagen *et al.* 1984). When subjected to limited food availability due to seasonal change, natural disasters, etc, insects will often relocate (through migration or short-range dispersal) or undergo a period of facultative diapause rather than starve. Insect species which are reliant on migration may be capable of:

- "changing behaviour to embark, such as young scale insects crawling to a leaf apex and adopting a posture there to enhance the chances of extended aerial movement;
- being in appropriate physiological and developmental condition for the journey, as in the flighted stage of otherwise apterous aphids;
- sensing appropriate environmental cues to depart, such as seasonal failure of the host plant of many aphids;
- recognizing environmental cues on arrival, such as new host plant, and making controlled departure from the current" (Gullan and Cranston 2000, 162).

An alternative to migration is diapause where the individual enters a state of arrested development as a direct response to unfavourable conditions. Diapause may be induced and/or terminated by environmental cues including photoperiod, temperature, food quality, moisture, pH, and chemicals (Gullan and Cranston 2000). In the case of food availability, the period of diapause may be ended by the

reappearance of the resource. In herbivores, the diapausal termination may be instigated by the plant's release of chemicals or pheromones, which the insect senses. However, one environmental cue may override another if conditions remain unfavourable in another respect. Thus if the food source reappears but the temperature and photoperiod remain inappropriate, the diapause will remain in effect.

In section 2.4, components, habitat and trophic level were delineated as two of the definitive measures of an ecological niche. In addition to the consideration given to where an organism lives and its role in that habitat, the ecological constraints that act upon a species set forth the full range of environmental conditions under which an organism can exist. In the absence of ecological constraints, organisms would be able to develop, grow, and reproduce to abundance without limitations. However, temperatures fluctuate, droughts occur, and food is both limited and the subject of competition. In order to assess a species' niche, its environmental limitations and its reaction to ecological stress must be considered.

2.4.4 The Ecology of Invasive Species

Although, as discussed above, organisms are established in a defined ecological niche, certain mechanisms, *e.g.* migration, wind or water dispersal, phoresy, and/or human transportation, occasionally unwittingly or wittingly act upon an individual or population such that it is removed from its original niche and supplanted in another location. If the ecological constraints of the new location are consistent with the limitations of niche, the relocated organism(s) may, with varying levels of difficulty, establish itself/themselves in the new location. If all other variables remain constant, the invasive species may face competition from indigenous organisms or if available, occupy a previously vacant niche.

Successful colonisation of new habitats requires that the first arrivals establish new viable, self-sustaining populations (Saki *et al*. 2001). The traits necessary for establishment vary in accordance to habitat-type: complex and established natural community (e.g. Elton 1927), human-disturbed habitat (e.g. Horvitz *et al.* 1998), and undisturbed natural island communities (e.g. Elton 1958). Saki and associates (2001) argue that a successful invasive species will exhibit a high fecundity rate as well as competitiveness.

The advantage of a species being able to quickly produce large numbers of offspring and out-compete competitors is apparent when confronted with an established natural community where breeding sites are already in use, food is already being eaten, and shelters are already occupied by other species. In order to survive, the invasive species must establish itself in a niche, often through the displacement of one or more organisms by means of interspecific competition. This is demonstrated in Elton's (1958) depiction of the introduction and spread of the Argentine ant, *Iridomyrmex humilis*, in Louisiana in 1891. The species multiplied immensely, and by 1905, it had spread throughout the southern United States and had invaded California. Smith (1935 in Elton 1958, 56) "often witnessed combats in the field between native and Argentine ants… The fact that the Argentine ant destroys practically all the native ants as it advances makes it comparatively easy to delimit an area infested by them." The Argentine ant successfully invaded the southern United States by rapidly reproducing and spreading and being able to out-compete the native ants for food and space, which lends credence to Saki *et al*.'s (2001) hypothesis concerning traits of successful invasive species.

However, alien species are not always faced with resistance from native species. In areas that have been modified or destroyed by human influence or natural

disasters, niches may be vacant. The modification or destruction of an area may temporarily 'empty' previously occupied niches by displacing or killing the organisms who resided in them. Moreover, major alterations to a habitat may result in the indigenous organisms being no longer suitably adapted to the area. When the European colonists arrived in the New World, they cleared forest and brush for the construction of settlements and the cultivation of crops. This land clearance displaced some of the indigenous species and created vacant niches for the invasive species. Lindroth (1957) tabulated 638 species of insects common to Europe and North America, and of these, he estimated that 242 were accidentally introduced through probable association with the materials employed as ship ballast. The European insect species, which inhabited the rubble and soil used as ship's ballast, would have been able to carve out a niche in the disturbed land around the colonial settlements and have faced little competition from the indigenous species which were displaced by the human-induced modifications. The successful establishment of Old World species in North America helped create what Crosby (2004) called Neo-European ecological spaces, which he proposed played a key role in early settlement viability.

Elton (1958) has demonstrated the susceptibility of remote islands to invasive species. The early ecological surveys of Easter Island detected only five endemic invertebrate species: a land snail, a water beetle, a weevil, a fly, and a green lacewing; in comparison to the 44 types of invertebrates, 2 lizards, 2 species of bird, and rats that are known to have been introduced (Elton 1958). Because of their remoteness, island populations are isolated. Unlike continents where several dense populations are in constant interaction, the 'native' fauna of remote islands is likely to be composed of a few species that arrived haphazardly over time from the nearest land masses, possibly through wind or water dispersal. As a result, competition for

resources and space is minimal and vacant niches exist. The only conflicts with which an invasive species is confronted concern the ecological constraints inherent to that species.

The ecology of invasive species and population dynamics are major components in the present thesis. In order to elucidate culture contact through utilisation of insect fossils, the archaeological contexts are examined for evidence of foreign species. However, do ecological, morphological, and genetic variations between the native and foreign organisms exist, and are they visible in the fossil record?

Chapter 3

Methodological Review

3.1 Introduction

Building upon the entomological principles discussed in the previous chapter, Chapter 3 will outline the specific analytical methods of the thesis. The means for data collection, processing, and recording will be reviewed, and each of the four research approaches will be detailed. First, the palaeoecological method, incorporating habitat association and Mutual Climatic Range, is summarised. This is followed by an outline of the biogeographical approach for assessing species movement and the importance of absence. A review of the isotopic method comes next. The chapter is concluded with a section discussing genetic applications and phylogeography.

3.2 Data Collection

As already noted, the aim of this investigation is to explore various methods of using insect fossils to help trace human migration and trade. The thesis will diachronically and synchronically focus on material from Neolithic and Roman England and Europe. An Anglo-Scandinavian site will also be considered in Chapter 4. Thus, the study comprises the following components:

- A survey of the published insect remains from Mediterranean sites broadly dated to the Neolithic and Roman periods;
- Application of palaeoecology and modern analogues to identify specific human transported species beyond their natural geographic ranges;
- Comparison of British and European material to facilitate the recognition of patterning, and thus allow one to infer the effects of trade, migration, and acculturation.

3.3 Processing Methods

Although the early methods, prior to the mid-1960s, of processing samples for insect remains involved splitting sediments along the bedding planes and searching the exposed areas for fossils (Coope 1959), the method proved to be time consuming and had a tendency for bias as it led to the more conspicuous insect remains being over represented. In 1968, Coope and Osborne (cf. Coope 1986a) presented an alternative procedure based on a wet sieving method. Once their technique was modified to include a flotation stage designed to concentrate the cuticle, it has since proven effective. While the paraffin flotation method is both cheap and efficient, it is not without problems and several amendments aimed at increasing fossil recovery have been presented (Kenward 1974; *et al.* 1980; 1985). However, these modifications differ only slightly from the original methodology employed by Coope and Osborne (1968). Rousseau (2009) has systematically tested the paraffin approach and provides a detailed discussion of its efficiency, or rather its inefficiency.

3.4 Palaeoecology

3.4.1 Theoretical Perspective

As discussed in Chapter 2, organisms are established in a defined ecological niche which in turn is regulated by habitat, resource availability, and trophic position (Elton 1927). When an organism is transported to a foreign location, its survivability is dependent upon factors such as ecological constraints and competition. In studying the past, palaeoentomologists have relied on the analysis of modern insect species which firstly, produces ecological data on specific species and species groups, and secondly, can be used as controls to be contrasted with the fossil species associations.

Additionally, the work of Kenward (1975a; 1976; 1985) on the 'background' component of modern death assemblages has served to emphasise the need for caution in interpreting fossil insect assemblages. Through modern analogues, palaeo-entomologists are able to ascertain information about ecological components, species associations, and behavioural characteristics of various species and apply the knowledge to the fossil remains.

3.4.2 Background to the Methodology

Ecological Categorisation

In order to assess the potential of archaeological insect assemblages in the reconstruction of products and exchange patterns, invertebrate remains must have been retrieved from the sites and their associated ecology delineated. By assigning the insect fauna to broad ecological categories, it is possible to separate the autochthonous species from those individuals that may have been transported on materials from other habitats (Kenward 1974). The broad grouping method can be problematic with insects because of regional variations in species, differences in ecological niches based on the life-cycle stages of a single species, and habitat seasonality (Hill 1994b). While Hill (1994b) cautions about the disadvantages of using broad ecological classifications, it is applied in this study to help identify the indigenous species that would not have been imported. Once the autochthonous individuals have been recognised, it will be possible to examine the remaining insect species for associations with specific products and habitats, which could be utilised to detect exchange patterns.

A variety of schemes exist concerning the ecological grouping of archaeologically recovered insect remains. Kenward (1978ab) and Hall *et al.* (1983)

employed an ecological grouping system based on a limited range of categories. Kenward (1978a) emphasised the importance of coding for outdoor species and aquatic and aquatic-marginal fauna, and Kenward (1979) incorporated categories of species exploiting decomposing matter. Hall and Kenward (1980) and Hall *et al.* (1983) formalised the system through its use in categorising a large insect assemblage. Kenward (1988) and Hall and Kenward (1990) added further ecological groups including wood and bark, with stored grain, with living plants, and with heathland/moorland. Furthermore, a synanthrope group was incorporated and utilised by Kenward (1997).

Robinson (1981; 1983) designated ten species ecological groupings: aquatic, pasture/dung, probable meadowland, wood and trees, marsh/aquatic plants, bare ground/arable, dung/foul organic material, Lathridiidae, synanthropes, and species especially associated with structural timbers. Later, an eleventh group was added, i.e. species on roots in grassland (cf. Robinson 1991). A similar system was employed by Hellqvist (1999), and Hill (1993) produced a classification closely modelled upon Robinson's. Hill (1993) specified the following groups: eurytopic, aquatic, synathropic/urban, arable/disturbed ground, pasture/dung, marsh/fen, heath/moorland, decomposers/litter dwellers, associated with trees, true woodland species, and uncoded. The true woodland species category was further subdivided into predators, deadwood (saproxylic), phytophagous, bark beetles, fungus feeders, litter dwellers, ant associates and dung beetles.

A number of other classification systems have been employed by palaeoentomological researchers (e.g. Girling 1980; Hakbilj 1989; Smith 1996ab), which does not allow for the existence of a unified, common, ecological coding system in the discipline at this date. While a number of the classification systems

have their merits, they tend to be designed to meet the needs and the whims of their users. For example, Bain (1998) employed a limited number of high-level groups: pests, compost and dung dwellers, carrion beetles, and mould and fungus feeders; whereas, Boswijk and Whitehouse (2002) used an ecological coding classification that subdivided the species groups into a finer level of detail than any of the systems discussed above. The narrower the resolution, the more equipped the system is at detecting subtle environmental changes within and between contexts.

Palaeoclimatic Reconstruction

Fossil beetle assemblages have been used for more than 25 years towards reconstructing past temperature conditions (e.g. Coope 1977a; Atkinson *et al.* 1987; Elias 1994). The Mutual Climatic Range (MCR) method is one of the leading methods through which these reconstructions are carried out. Under this method, reconstructing the climatic conditions associated with a fossil beetle assemblage involves three steps:

1. Modern distributional and climatic data are utilized to measure the climatic ranges or envelopes of the species present in the fossil assemblage. These climate envelopes are usually two dimensional; one dimension is the mean temperature of the warmest month (TMAX) and the other is either the mean temperature of the coldest month (TMIN) or the difference between TMAX and TMIN (TRANGE);
2. The climatic conditions are determined using the overlap of these climatic envelopes where the overlap itself contains a range of climatic conditions;
3. The range is issued single values of TMAX and TMIN (or TRANGE). This conversion is founded on linear regression models relating observed modern

values of these variables to the corresponding midpoints of the ranges found through application of the first two steps to the modern data.

3.4.3 Methodology

The palaeoecological aspect of this thesis is two-fold; firstly modern analogues will be used to tabulate the behaviour, habitat, and associations of the fossil entomofauna in order to reconstruct the palaeoenvironment of a site, and secondly, the MCR method will be employed to estimate the palaeotemperature of a site [Chapter 4]. The utility of any individual species which is intended to be employed as a palaeoecological indicator is reliant upon the ecological parameters which limit its distribution in time and space. Consequently, stenotopic insects are of greater value than eurytopes as they have narrower habitat restrictions.

Because of their narrow habitat restrictions, certain stenotopic insects can be used as indicators of the presence of associated material or conditions in the environment. Moreover, as this study is concerned with human activity, the number of stenotopic fauna assessed can be further reduced with the consideration of only synanthropic insects (species which are unable to maintain breeding populations without the ameliorated conditions provided by human buildings and/or human activity). On this basis, the fossil material will be surveyed to identify insect species that are strongly associated with potentially tradable commodities such as cereals. Once the potential trade indicator species have been highlighted, MCRs will be calculated for the corresponding sites as well as a selected range of similarly dated sites. The TMax and TMin for each site will be compared to the temperature requirements, especially the optimal range, necessary for the associated insect species to complete their development. It is hypothesised that insect species whose

temperature requirements fall outside the MCR determined temperature range for a site will represent hitchhikers introduced to the site through the importation of goods. While these species may have been able to survive within the artificial microhabitats of human structures, if the conditions in the surrounding natural environment presented ecological constraints on their development, it is unlikely that they would have been natives.

3.5 Biogeography

3.5.1 A Brief Literature Review

As the study of living things in space and time, biogeography addresses issues such as the distribution of species throughout time, the mechanisms behind the distribution, and the human influence upon these patterns of species distribution (Cox and Moore 2000). To a limited degree, some previous applications of biogeographical concepts and palaeoentomology have been attempted. The bulk of these studies have been concerned with the context of North Atlantic faunal connections (e.g. Buckland 1988; Buckland *et al*. 1995; Coope 1986b; Sadler 1991a; 1991b; Sadler and Skidmore 1995; Kenward 1997). However, while all these investigations emphasise the benefits of utilising biogeography, they restrict its use to a single site or region, note probable invasive species, and as a result, offer tentative speculations about their origins based on historical documentary accounts. Although these accounts have primarily hypothesised about the origins of the invasive species, they were proficient at noting the presence and absence of species through the different chronological periods of the site or region.

Kenward (1997) attributes the limitations of the field to a paucity of securely dated material and palaeoentomological evidence, particularly outside of the United

Kingdom; however, efforts have been made to apply biogeography on a larger scale (to a limited extent Buckland 1981, and to a larger degree Buckland and Sadler 1989; Kislev *et al.* 2004). While palaeoentomological surveys may not have been conducted extensively outside the United Kingdom, an investigation of both the published and grey literature on the subject permits the mapping of species' distribution and movement through time on a broader scale.

3.5.2 Approaching the Problem

Before biogeographical analysis can begin in earnest, a number of preliminary tasks need to be undertaken. As the investigation is ultimately intended to address the issue of human movement and trade in the past, it will not be realistic to attempt to apply the method to every insect species. Rather the project relies upon the ability to target synanthropic species associated with human transported materials.

Once the applicable insect species have been selected, an exploration of the literature will ensue in order to document the presence and absence of the species temporally and geographically [Chapter 5]. This information will be recorded and assessed for each species. As the existing documented material presumably represents only a fraction of the original biocoenosis in the past and does not account for the thanatocoenosis of future sites, it must be understood that the biogeographical mapping of palaeoentomological remains only provides a provisional reflection of the past. With that in mind, the resulting biogeographical interpretation will indicate the geographic presence of each species at archaeologically dated points in time. As the species are strongly synanthropic, their movement will hypothetically reflect human movement rather than geographic range shifts resulting from climate change or seasonal migration.

3.6 Isotopic Analyses

3.6.1 History

In recent years, isotopes, especially deuterium and oxygen, have proven beneficial in paleotemperature estimates especially from deep-sea sediments (e.g. Shackleton and Opdyke 1973; Bauch and Erlenkeuser 2003), ice cores (e.g. Dansgaard *et al.* 1989; Grootes *et al.* 2002), and calcium carbonate rich lake sediments (e.g. Oeggl and Eicher 1989; Talbot 1990). Given the success of isotopes in these past studies and the application of beetles in climate reconstructions using MCR, researchers (e.g. Gröcke *et al*. 2006; Hardenbroek 2006; *et al*. 2007) have sought to use stable isotopes from beetle chitin to ascertain palaeoclimatic information.

Stable-isotopes have also been employed towards the tracing of animal and human diet. This is particularly evidenced in studies investigating marine versus terrestrial foodwebs. The stable-isotope composition of marine biomes tends to be more enriched relative to terrestrial C_3 or freshwater foodwebs (Peterson and Fry 1987; Schaffner and Swart 1991; Hobson *et al.* 1997; Hebert *et al*. 2009). Carbon-13, nitrogen-15, and sulfur-34 are especially evidenced by this pattern and are commonly analysed; however, deuterium and oxygen-18 have also shown enrichment in marine systems compared to terrestrial (Fry and Sherr 1984; Schaffner and Swart 1991). In terrestrial ecosystems, analysis of stable-isotopic carbon provides insight into plant resources within a foodweb. Differences in plant photosynthetic pathways result in distinct isotopic differences between C_3, C_4, and Crassulacean acid metabolism (CAM) plants (Peterson and Fry 1987; Tieszen and Boutton 1988).

Moreover, isotopic analyses may prove invaluable as indicators of geographic origin. Hobson and associates (1999) have used deuterium and carbon-13 to trace the migration of the Monarch butterflies to their natal origins through examination of variation in continental gradient evidenced through the deuterium, and carbon-13 and nitrogen-15 have been shown to be linked to altitude and humidity (Körner and Diemer 1987; Körner *et al.* 1988; Körner *et al*. 1991). Migratory connectivity over a large geospatial scale has been investigated using stable carbon, sulfur and hydrogen for migrant birds and insects (Chamberlain *et al.* 1997; Hobson and Wassenaar 1997; Wassenaar and Hobson 1998; Rubstein and Hobson 2004). Recently, applications have been developed to assist in systematically determining the origins of isotopes through the creation of basemaps from the interpolation of precipitation isotope values, and the methods been employed towards studies in wildlife forensics (Bowen *et al.* 2005).

3.6.2 Theoretical Basis

The stable isotope deuterium is a rare component of the water molecule (H_2O) and enters organisms through means of the hydrological cycle [Figure 3.1; Figure 3.2]. The deuterium/hydrogen (D/H) ratio of meteoric water is a function of temperature or climate (Dansgaard 1964), and varies with respect to geographical parameters such as

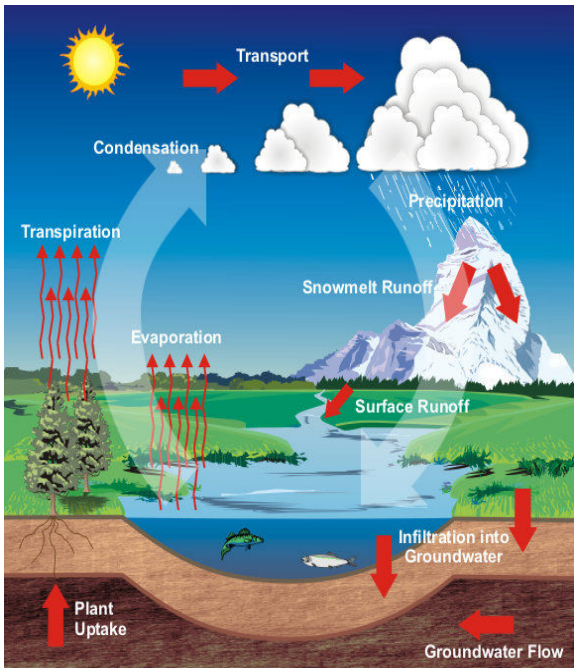
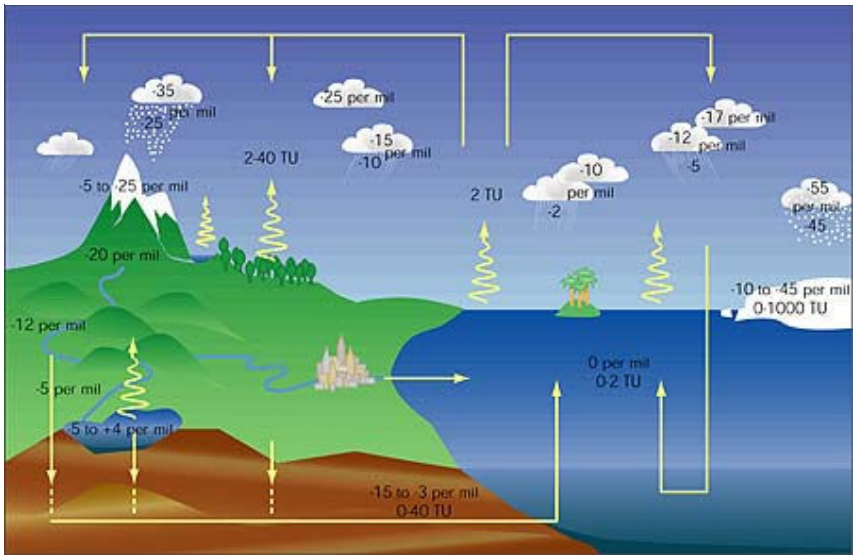


Figure 3.1 The hydrological cycle

(National Weather Service n.d.)

latitude, altitude, continentality, and intensity of precipitation as well as ecological parameters such as trophic level. The geographical variation is the result of the Raleigh distillation, which reflects changes in the degree of rain-out of moisture from

Figure 3.2 Isotopes in hydrological cycle



(IAEA 2000)

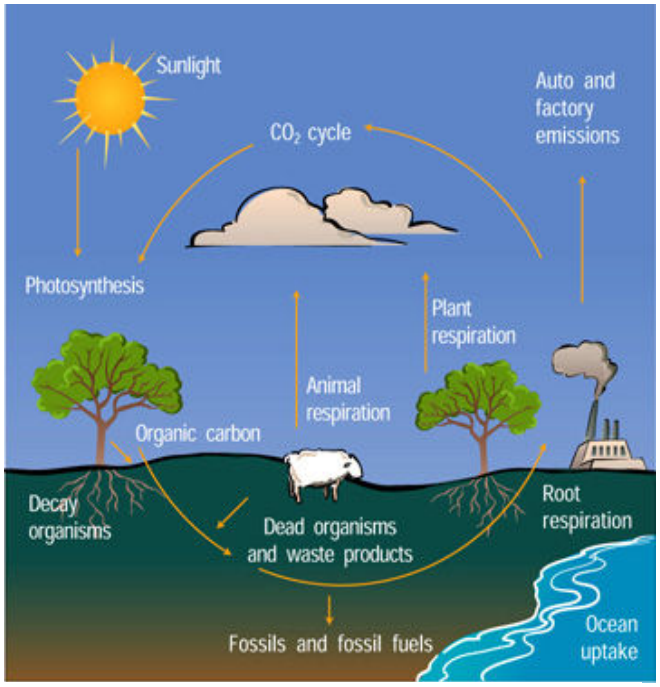
an air mass (Yurtsever and Gat 1981). The water vapour that forms precipitation is depleted in heavy isotopes, such as deuterium, relative to ocean water. As condensation forms raindrops from a cloud, the heavy isotopes condensate first, creating isotopically enriched rain, as the cloud becomes isotopically depleted by rain-out (IAEA 2000). This means that successive rainfall events from an air mass become isotopically lighter. At middle and high latitudes, isotopes are closely correlated with temperatures, and thus seasonality, with winter precipitation being more enriched than summer precipitation. At lower latitudes, the isotopic content is a function of the volume of the precipitation. During periods of increased precipitation, the isotopes are more depleted in the precipitation. The intensity of the precipitation is also a factor as lighter rains are more enriched than harder rains (IAEA 2000).

The isotopic variation apparent in a region's meteoric water is transferred to organisms living within that region via the food web. The relationship of the D/H

ratio of chitin and the D/H signature of the meteoric water in an insect's habitat has been documented (e.g. ladybirds in Ostrom *et al.* 1997, and Monarch butterflies in Wassenaar and Hobson 1998). The stable isotopic signature contained in a terrestrial insect's chitin is dependent upon its diet during the formation of its exoskeleton. Thus the hydrogen isotopes present in the chitin of predatory beetles will be based upon the isotopic values of their prey, and herbivorous insects will reflect the corresponding isotopic signature present in the vegetation upon which they feed. As such, a region's isotopic indicator is transferred from the meteoric water to the locally grown vegetation to the herbivores to the predators.

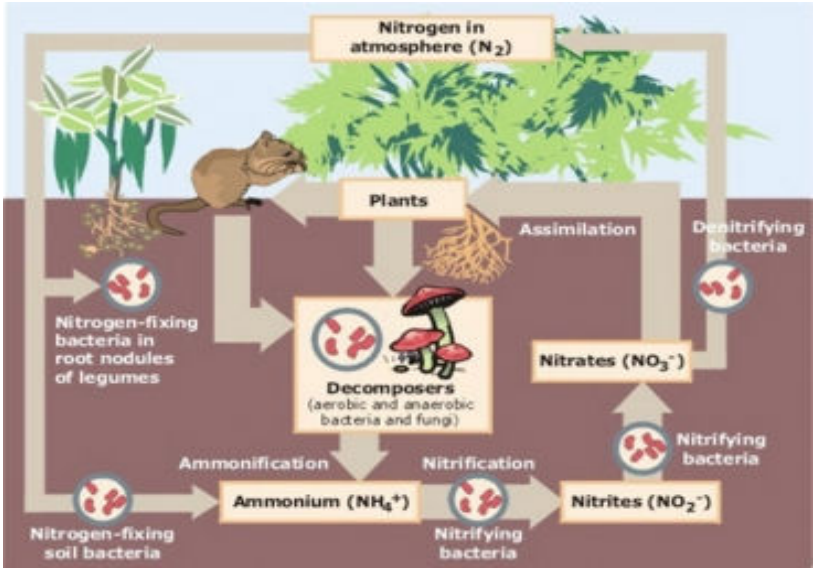
A similar process occurs in regards to stable-isotopic carbon and nitrogen. Carbon-13 is transferred to organisms through the carbon cycle [Figure 3.3], and nitrogen-15 is introduced via the nitrogen cycle [Figure 3.4]. As with deuterium, carbon-13 and nitrogen-15 vary in relation to geographic and ecological parameters. The insect species consuming food from a specific locality will acquire the carbon and nitrogen signature of that food and that region. However, fractionation occurs within the carbon and nitrogen isotopic ratios relative to trophic level. For example, the isotopic values are enriched in carnivores relative to herbivores within a food web.

Figure 3.3 The carbon cycle



Gardiner 2008

Figure 3.4 The nitrogen cycle



(Wojciechowski and Mahn 2006)

The potential of isotopes as geographic indicators is significant. If a locally grown plant is transferred outside of its original region through means such as trade, then herbivores feeding upon it at other destinations will display the isotopic signature of the plant's host region. Similarly, predators feeding on those herbivores will carry that plant's isotope value. By comparing the stable isotopes of beetles that are known to feed upon local vegetation (e.g. trees and grasses) and beetles suspected of feeding on potentially non-local plants (e.g. cereals), it is hypothesised that imported materials can be identified.

3.6.3 Methodology and Objectives

In order to explore the potential of beetles as isotopic indicators of trade, modern and fossil material were analysed. The modern aspect of the experiment was two-fold; involving laboratory-reared granary weevils [Chapter 6] and beetles retrieved from traps in the wild [Chapter 7]. The laboratory experiments used a

parent population (G1) of the granary weevil *Sitophilus granarius* L. as a control. Ten individuals of G1 were placed in tubes containing separate cereals and seeds from various regions with known isotopic records. In order to breed and lay eggs, the granary weevils were left in the tubes for ten days at 28 °C. Afterwards, G1 was removed from the tubes and individuals were held in the freezer for isotopic analysis. After 3-5 weeks, the second generation adults (G2) emerged from the cereals and seeds in the tubes. At this stage, two G2 individuals from each tube were frozen for isotopic analysis (G2a) and five G2 individuals from each culture were placed in separate containers with grain from another isotopic region (G2b). At 10, 15, 20, 25, and 30 days, an individual from G2b was removed from the containers and frozen for evaluation. It is hypothesised that the G2 specimens will reveal the respective isotopic signature of the cereals in which their exoskeleton was formed and not that of the G1 generation. Additionally, it is suspected that the transfer of G2b to another cereal source will not impact its isotopic value, and that the G2b specimens will not differ from the corresponding individuals, G2a, from their original tubes.

Similarly, ten individuals of G1 were placed in tubes containing a mixture of 25% barley, 25% wheat, 25% oats, and 25% buckwheat kernels. The G1 specimens were allotted ten days at 28 °C to oviposition and were then removed from the tubes. As the G2 individuals emerged after 3-5 weeks at 28 °C, they were frozen for isotopic evaluation [see Chapter 6.3.2].

Pitfall traps were employed to collect modern beetle species from the reconstructed Anglo-Saxon village located at West Stow, UK. The wax (lipids) and proteins were removed from the remains; thus isolating the chitin. $\delta^{2}H$, $\delta^{13}C$ and $\delta^{15}N$ analyses were performed on the chitin. The stable-isotope ratios were compared between the species and trophic level variations considered. The West Stow

specimens were investigated for recognition and classification of species considered to represent local and imported materials.

In regards to the fossil material [Chapter 7], recovered archaeological insect remains were investigated from the Neolithic sites of Eythra, Plaußig, and Erkelenz-Kückhoven, Germany. Deuterium, carbon-13, and nitrogen-15 isotopic assays were conducted on the chitin isolated from the individual species. The resulting isotopic predictions were compared at intra- and inter-site levels to determine the presence of patterns in results and to identify isotopic outlier species, which may indicate human activity.

The objective of incorporating isotopic analyses into this assessment of trade and migration is to devise a way of differentiating between potentially tradeable perishable goods from those locally supplied, and secondly to begin to trace the origins of tradeable products through the mapping of their inherent stable isotope values of their respective regions in the past.

3.7 Phylogeography

3.7.1 The History of Ancient DNA

In 1984, Russ Higuchi and associates published a revolutionary finding—that traces of deoxyribonucleic acid (DNA) from a museum specimen of the Quagga, *Equus quagga*, (an Equid believed to have gone extinct in the late 19th century) remained in the specimen over 150 years after the death of the individual and that the DNA could be extracted and sequenced (Higuchi *et al.* 1984). Svante Pääbo expanded upon Higuchi's discovery and demonstrated that the procedure could be replicated in mummified human samples dating back several thousand years (Pääbo 1985a; 1985b; 1986).

However, until the development of the Polymerase Chain Reaction (PCR) (Mullis and Faloona 1987; Saiki *et al.* 1988) in the late 1980s, the field of ancient DNA (aDNA) progressed slowly. The introduction of PCR heralded a series of papers claiming authentic DNA could be extracted from specimens that were millions of years old. The majority of the claims were founded on the retrieval of DNA from amber-preserved specimens. Preserved insect DNA was reported from amber-encased fossils dating to the Ogliocene (25-35 mya), e.g. stingless bees (Cano *et al*. 1992a; Cano *et al.* 1992b), termites (DeSalle *et al*. 1992; DeSalle *et al*. 1993), and wood gnats (DeSalle and Grimaldi 1994), and the Cretaceous (120-135 mya) periods, e.g. Lebanese weevils (Cano *et al*. 1993).

Moreover, aDNA retrieval was not limited to amber. Golenberg and collaborators (1990; Golenberg 1991) extracted DNA from sediment-preserved plant remains dating to the Miocene. Additionally, DNA sequences were investigated from dinosaur bone, which dated over 80 million years ago (mya) (Woodward *et al.* 1994), and Cretaceous egg (An *et al.* 1995; Li *et al.* 1995). These sequences of DNA stretching millions of years into the past were referred to as Antediluvian DNA (Lindahl 1993b).

Unfortunately, despite these exciting and potentially revolutionary claims, a critical review of ancient DNA literature indicates that few recent studies have succeeded in amplifying DNA from remains older than several hundred thousand years (cf. Willerslev *et al.* 2003). Since the early studies may reflect the amplification of contaminated material, they should be regarded carefully. However, recent investigations of sub-glacial deposits in Greenland (Willerslev *et al.* 2007) and insect carapaces from museum collection samples (less than one hundred years old, e.g.

Zakharov *et al.* 2000; Junquiera *et al.* 2002; Gilbert *et al.* 2007) have yielded DNA fragments with no indication of contamination.

3.7.2 The Extraction of Ancient DNA from Samples

Although the methods utilised to extract DNA from ancient specimens vary in accordance to the tissue, the majority of aDNA studies employ one of two procedures. These techniques call for an initial digestion of the tissue to release DNA followed by a purification step involving either organic solvents or the DNA binding properties of silica. The experiments carried out for the purpose of this thesis will rely on the silica method for purification.

To remove any surface contaminants, a specimen is typically 'pre-prepared' post-sampling using a range of decontamination techniques. In non-destructive methods (as employed in this study), the material is not ground. Instead the fossil and modern specimens are placed in tubes, fully immersed in digestion buffer (400 µl), and incubated overnight at 55 °C with gentle agitation. As in Gilbert *et al.* (2007), the digestion buffer is modified from Pfeiffer *et al.* (2004) to consist of 5 mM $CaCl_2$, 1 % sodium dodecyl sulphate (SDS), 40 mM dithiotreitol (DTT), 2.5 mM ethylenediamine tetraacetic acid (EDTA), 250 mg/ml proteinase K, 10 mM Tris buffer pH 8, and 10 mM NaCl (final concentrations). After incubation at modest temperatures (50-60 ºC) with gentle agitation for 16-20 hours, the nucleic acids are purified from the solution.

Silica-based DNA extractions

DNA extractions involving silica (Boom *et al.* 1990; Höss and Pääbo 1993) require the extraction of DNA in high concentrations of salts such as guanidinium

thiocyanate (GuSCN). The salts have the ability to lyse proteins and simultaneously act as a chaotropic agent facilitating the binding of DNA to silica particles.

After the period of incubation and gentle agitation, 2 ml of Phosphate Buffer (PB) buffer (the protein-lysing salt) are added to the 400 µl digestion buffer and vortexed gently. Once mixed, 650 µl aliquots are added to the spin column, spun at 6000 g for 1 minute. Then collection tube is emptied. This step is repeated three times to ensure that the extraneous non-DNA material has been separated and removed and that the remaining DNA has sufficiently bound to the silica filter. 500 µl PE buffer (containing ethanol to wash the filter) is added to the column and spun for 1 minute at 10000 g in order to rinse the filter. Afterwards, the collection tube is emptied and the column spun again at maximum speed for 3 minutes to dry the filter. The filter is then transferred to a clean new 1.5 ml Eppendorf Biopur tube and 50 µl of AE Elution buffer is placed on the filter and left for 5 minutes to initiate the release of the DNA from the silica filter. Finally, the column is spun again at >10000 g for 1 minute to allow the solution to migrate to the base of the new tube.

Analyses incorporating PCR

PCR is a reiterative process that depends on the annealing of sequence specific oligonucleotide probes ('primers') to complementary DNA sequences. Two primers per reaction are typically used, each approximately 20 base pairs (bp) in length and designed to bind to the 5' end of the target sequence. Deoxyribonucleotide bases (dNTPs), a DNA polymerase enzyme (e.g. HiFi), 10x PCR buffer, and 2.5 mM $MgCl_2$ are added to a mixture of DNA, primers, and bovine serum albumin (BSA). The specific DNA sequence can be exponentially amplified through a cyclical process

involving the repeated denaturation of templates, the binding of primers to DNA targets (annealing), and strand replication by the enzymes (elongation).

A PCR, in theory, should result in the sole amplification of the target regions of DNA specified by the selected primers. However, because of the likelihood of sequence modification resulting from *post mortem* DNA damage and contamination, PCR reactions occasionally amplify multiple DNA sequences, which can result in unreadable sequence data or conflicting base calls. By cloning the PCR products, it is possible to avoid these problems.

The molecular cloning of ancient DNA

Through molecular cloning techniques, sequence heterogeneity can be detected within a single PCR reaction. Amplicons are inserted into bacterial plasmids, which are transformed into *Escherichia coli* cells. The resulting colonies can be identified through blue/white screening as a result of disruption to one of a range of subunits of the plasmid's b-galactosidase gene, which metabolises X-gal (5-bromo-4-chloro-3-indolyl-b-D-galactopyranoside) into a blue product. Because each clone will have incorporated a single amplicon, post-mortem DNA damage, jumping, and contamination can be assessed by screening multiple clones.

3.7.4 Ancient DNA Authentication Criteria

Because of the risk for contamination and the occasional lack of result reproducibility prevalent in the early Antediluvian DNA investigations, a list of suggested criteria has been published to help limit the effect of sample contamination. Based on the criteria proposed for forensic studies (Carracedo *et al.* 2000), this list is

designed to help minimise some of the field's errors (Handt *et al*. 1994; Cooper and Poinar 2000). The list is as follows:

1) Isolation of work areas in an effort to avoid contamination by separating the environments used for the handling of samples and extraction of DNA from the PCR amplified products;

2) Negative control extractions and amplifications to monitor for contaminants infiltrating the process at any stage;

3) Appropriate molecular behaviour – because of DNA degradation, aDNA investigations should be suspicious of the successful amplification of large DNA fragments;

4) Reproducibility – multiple PCR and extractions should generate consistent results;

5) Cloning of products to screen for damage, contamination and jumping PCR;

6) Independent replication – the generation of consistent results by independent research groups;

7) Biochemical preservation – preservation of other biomolecules that correlate with DNA survival (e.g. collagen, amino acid racemisation) should be indicative of good sample preservation;

8) Quantification - through competitive PCR or real-time PCR to give an estimate of the number of starting templates in the reaction;

9) Associated remains – are associated remains equally well preserved, and do they show indicate contamination?

3.7.5 Targeting Mitochondrial DNA: The Aims of the Project

Mitochondria are endosymbiotic organelle that resemble free-living eubacterium similar to modern α-Proteobacteria (Gray *et al.* 1999; Lang *et al.* 1999)

and act as a cell's respiratory source for the generation of ATP. There are thousands of mitochondria in each cell, and its presence in copy numbers is approximated to range between 1,000-10,000 times that of single-copy nuclear DNA (Taanman 1999). As a result, given similar rates of degradation, mitochondrial DNA will remain present in a cell longer than nuclear DNA. In addition to this, mitochondrial DNA (mtDNA) undergoes a fairly rapid rate of evolution (Lang *et al.* 1999) and is inherited maternally which makes it exceedingly useful in population studies.

Animal mitochondria span 16-20 thousand base pairs in length, containing the same 37 genes coding for small- and large-subunit rRNAs, 13 proteins, and 22 tRNAs (Hoy 2004) and at least one noncoding (control) region (Boore and Brown 1998). In insects, this noncoding region is rich in adenine (A) and thymine (T) and regulates replication and transcription (Hoy 2003). In modern phylogeographic studies, researchers have primarily focused on the cytochrome oxidase I (COI) (specifically the variable portion corresponding with sites 2410 and 2665 in the *Drosophila yakuba* mitochondrial genome) and cytochrome oxidase II genes (e.g. Juan *et al.* 1998, Moya *et al.* 2004; Smith and Farrell 2005).

Given the suitability of the mitochondrial genome for phylogenetic investigations, the present study aims to investigate the retrievability of genetic information from archaeologically recovered insect remains of the cereal pest beetle *Sitophilus granarius* L. from waterlogged contexts dated to the Roman and medieval periods and seeks to investigate the variation presented in the intraspecific mitogenomes towards the potential mapping of geographic relationships between populations of various trade-indicator species past and present. This initial investigation will involve the application of PCRs in order to amplify key regions of the COI and COII genes in order to pinpoint variation within species.

By conducting population studies on trade-related species, this investigation hypothesises that following concepts can be assessed:

- The mapping of past trade patterns through a genetic evaluation of population movement and relationships;
- The conceptualisation of the intensity of trade—the presence of high or low initial genetic diversity;
- The trade continuity—in the case of limited genetic diversity, the presence or absence of evidence of founder effect possibly resulting from maintained trade with a singular source over time.

Chapter 4

The Palaeoecological Approach:

An Assessment of Two Case Studies

4.1 Introduction

In Chapter 4, palaeoecological reconstructions are formulated from the insect fossils recovered from two urban archaeological sites that were excavated in the city centre of York, UK: 7-15 Spurriergate and 16-22 Coppergate. The palaeoenvironmental reconstructions roughly follow Robinson's (1981; 1983) ecological coding system. The following species groups are employed:

Group 1: Aquatic

This category includes all beetle species that can spend most of their adult life under water, e.g. *Helophorus* sp.;

Group 2: Pasture/dung

Species Group 2 is composed of dung beetles which mostly occur in or under the dung of large herbivores. The species are more common with dung in the field than manure heaps. It is usually comprised of species from the genera *Geotrupes*, *Copris*, *Aphodius*, and *Onthophagus*;

Group 3: Probable meadowland

This category is comprised of species which mostly feed on leaves and stems of vetches, clovers, and other grassland flora, e.g. *Mecinus pyraster* and *Sitona* sp.;

Group 4: Wood and trees

Beetles which are found in the wood, leaves, bark, and fruits of live trees and shrubs as well as species which feed on wood that is undergoing various stages of decay, e.g. *Magdalis carbonaria*;

Group 5: Marsh/aquatic plants

These are species of beetles which feed exclusively on marsh or aquatic plants, e.g. *Notaris acridulus*;

Group 6: Disturbed ground/arable

This category includes Coleoptera that inhabit bare ground, arable soils, and weedy disturbed ground, e.g. *Amara* sp.;

Group 7: Dung/foul organic material

This group consists of species which live in different types of foul organic matter such as decaying vegetation, dung, compost, carrion, and manure heaps. The beetles are primarily decomposers, e.g. *Megasternum obscurum* and *Cercyon* sp.;

Group 8: Lathridiidae

This classification comprises a family of beetles which primarily feed on fungi and mould on decaying plant material, e.g. *Lathridius minutus* group;

Group 8: Synanthropes

This category consists of species which are associated with human-made environments. It is comprised of species that usually inhabit or are associated with human-made structures, e.g. *Ptinus fur* and *Typhaea stercorea*;

Group 10: Species especially associated with structural timbers

Coleopteran species, such as *Anobium punctatum* and *Lyctus linearis*, which live in dry dead wood and are able to reproduce in structural timbers, are categorised in this species group; and,

Group 11: On roots in grassland

This species group includes Scarabaeidae and Elateridae which as larvae feed on the roots of grassland herbs, e.g. *Hoplia philanthus* and *Phyllopertha horticola*.

The palaeoenvironmental reconstructions serve to provide insight into the flora, fauna, and geography in the vicinity of the site. By examining the habitat and

diet of the insect fauna, it is also possible to identify indicator species of commodities, which may have been exploited by humans in the past. Several of these commodities were not likely to have been autochthonous to the sites and may indicate palaeoeconomic activities such as long-distance trade or exploitation of the hinterland resources. Mutual Climatic Reconstruction models (MCRs) are used to build palaeoclimatic reconstructions. The MCRs are compared to the thermal requirements of individual insect species to help identify ecological outliers, i.e. species that may not have been indigenous to or capable of surviving in the wild of the United Kingdom. The application of MCRs in conjunction with specific 'economic' indicator taxa is hypothesised to aid in the ability to recognise the occurrence of local and long-distance trade.

4.2 Case Study 1: 7-15 Spurriergate, York (site code: 2000:584)

4.2.1 Introduction

Biological samples were collected during archaeological work on 7-15 Spurriergate, York by MAP Archaeological Consultancy Ltd. in 2000 and 2005. The deposits were of early Roman (1st century AD) to medieval date with preservation ranging from good to exceptional (cf. Hall *et al*. 2000; Carrot *et al.* 2005). Figure 4.1 shows the location of the site to the northeast of the River Ouse near Micklegate Bridge.

4.2.2 Processing Methods

Six samples were selected from the early Roman context 6063 for palaeoecological evaluation, primarily of insect remains. The procedures outlined in

Figure 4.1 Location of 7-15 Spurriergate site northeast of the River Ouse [red icon]. York Minister is shown at the top of the photo and Clifford's Tower is present in the bottom right corner (Google Earth 2009).

Kenward and associates (1980; 1985) were followed for the recovery of insect fossils from the samples using paraffin floatation. The insect remains in the resulting residue and washover were sorted using low-power binocular microscopes with the assistance of M. Rousseau, and identification was performed through comparison with modern reference material in the collection of the former Environmental Archaeology Unit, University of York. The identifications were cross-checked through the kindly assistance of H. Kenward.

4.2.3 Results and Analysis of the Data

The species identifications have been listed in Table 4.1, giving the minimum number of individuals [MNI] represented by remains of each species for each sample. The nomenclature follows Kloet and Hinck's (1964; 1976; 1977; 1978) revised

Table 4.1Species list for 7-15 Spurriergate, York

Taxon	2000.584 6063 MNI per Sample						Ecology
	4	6	7	10	12	16	
Carabidae indet.	1				1		N/A
Dyschirius globosus (Hbst.)		1					on sandy loamy, clayey and muddy banks, swamps, bogs, brick pits, moist arable fields, loamy gardens, in leaves, moss, detritus, flood debris, rotting vegetation, compost (Koch 1989a).
Trechus obtusus/quadristriatus (Er./Schr.)		1		1			*T. obtusus:* in moist deciduous woodland and on river banks, swamps, moist shaded meadows. High mountains raised bogs. Littoral wash zone. Under leaves and moss, in detritus and *Sphagnum* sp. *T. quadristriatus*: frequently synanthropic, loamy arable fields, moist weedy areas, gardens, woodland margins, hedges, shaded banks, dunes, caves. In hay stacks and barns, under rotting vegetation, in detritus and compost (Koch 1989a)
Pterostichus melanarius (Ill.)						2	prefers thick vegetation; loamy arable fields, flood plains, meadows, woodland margins; hedges and gardens; brick pits; gravel pits. Littoral - wash zones. In decaying vegetation and flood debris; under loose bark (Koch 1989a)
Hydraena testacea (Curtis)					1		in muddy streams or stagnant drainage ditches (Duff 1993)

Taxon	2000.584 6063 MNI per Sample						Ecology
	4	6	7	10	12	16	
Helophorus aquaticus/grandis (L./Ill.)	1						*H. aquaticus:* in temporary pools and muddy or weedy margins of ponds and lakes in spring and autumn (Brown 1940). *H. grandis:* in stagnant freshwater, preferring eutrophic, more or less open and often temporary pools with clayey and grassy bottom (Hansen 1987)
Helophorus sp.	1				1	1	Aquatic
Cercyon haemorrhoidalis (F.)	1	1	1			1	very eurytopic, in all kinds of decaying organic matter, mainly in cow, horse and sheep dung, but also frequently in rotting plant debris, especially compost heaps, also old mushrooms, flood debris on wetter habitats, carrion, at sap, e.g. on birch, in nests of various birds (Hansen 1987)
Cercyon unipunctatus (L.)		1		1			in all kinds of decaying organic matter, distinctly synanthropic, in various debris around farm buildings, e.g. compost heaps and barn manure (Hansen 1987)
Cercyon atricapillus (Marsham)	4	1	2	4	1	1	in fields, weedy places, cow pastures, river meadows, heaths, gardens and stables, especially in fermenting materials (compost, root heaps, stable manure, heaps of rotting vegetation), fresh dung and carrion (Koch 1989a)
Cercyon terminatus (Marsham)			3				in herbivore dung or decaying grass (Duff 1993)

Taxon	2000.584 6063 MNI per Sample						Ecology
	4	6	7	10	12	16	
Cercyon tristis (Ill.)	1						associated with muddy detritus and decaying plant litter in well vegetated stagnant waters, including fens, marshes and swampy overgrown canals, borrow pits and ditches (Merritt 2006)
Cercyon analis (Payk.)	2	3		3	1	1	in almost all rotting vegetation, in flood debris and litter (Koch 1971)
Megasternum obscurum (Marsham)	1	1	1	1	2		in decaying grass and herbivore dung (Duff 1993)
Cryptopleurum minutum (F.)			1			1	in all kinds of decaying organic matter, usually very abundant, mainly in compost heaps, rotting grass, in dung and at carrion, also among various plant debris near water (Hansen 1987)
Acritus nigricornis (Hoff.)			1				in fields, meadows, gardens, weedy places, woodland margins and pine heaths; especially in the lower layers of old stable dung heaps, in dung, rotting vegetation, compost and rootcrop heaps, tannery waste, wood debris and barn straw (Koch 1989a)
Omalium caesum (Grav.)				1			in grass tussocks, including cereal crops, or in haystack refuse and leaf litter (Duff 1993)
Xylodromus concinnus (Marsham)		1	1	1	1		in fields, river meadows, woodland margins and woods. In straw in barns and stalls in hay and compost heaps; occasionally also in woods in wood mould and in nests in hollow trees (Koch 1989a)

Taxon	2000.584 6063 MNI per Sample						Ecology
	4	6	7	10	12	16	
Carpelimus bilineatus (Steph.)	2	1	3	3	2	2	on sandy-muddy banks, fields, gardens, woodland margins. Littoral: wash zone. On mud, under detritus and flood debris, in wet compost, straw and stable manure heaps (Koch 1989a)
Oxytelus sculptus (Grav.)	2	1	2	3		1	in fields; cattle pastures; weedy places; gardens; woodland margins; stables. Littoral - dunes. In dung stable manure; in debris of *Phragmites* sp.; in rotting hay (Koch 1989a)
Anotylus rugosus (F.)	1		1	1			in rotting vegetation, also in fungi, in mouldering leaves, litter and flood debris, in game bird food debris, in compost, straw and stable manure, in dung of cattle and man, in bird nests and underground animal burrows, on mud and in *Sphagnum* sp. (Koch 1989a)
Anotylus sculpturatus (Grav.)					1	1	in more or less fresh dung; in carrion; in stable manure and compost heaps; in rotting vegetation (Koch 1989a)
Anotylus nitidulus (Grav.)	1	1	3		2	1	on damp soil, banks, swampy and wet meadows, river meadows, copses and gardens. Alpine - in pastures and green alder zones. In rotting vegetation, also in fungi, in stable manure and compost heaps (Koch 1989a)
Anotylus tetracarinatus (Block)	1				1	1	in rotting vegetation, also fungi; in dung and carrion; in compost and stable manure heaps; in rotting straw in barns and ricks (Koch 1989a)

Taxon	2000.584 6063 MNI per Sample						Ecology
	4	6	7	10	12	16	
Platystethus arenarius (Geoff.)	2		3		3		in herbivore dung and damp decaying vegetation (Duff 1993)
Platystethus degener (Muls. and Rey)			1		1		in mud and damp litter near water (Duff 1993)
Platystethus cornutus (Grav.)				1			in mud and damp litter near water (Duff 1993)
Platystethus nitens (Sahl.)			1	1			in mud and damp litter near water (Duff 1993)
Lithocharis ochracea (Grav.)			1		1		in meadows, woodland margins, woods, fields and gardens. In rotting vegetation, in straw debris, in straw and chaff in field barns and heaps (Koch 1989a)
Leptacinus intermedius (Donis.)						1	in woods, woodland margins, heaths, especially in nests of *Formica* sp (Koch 1989a); in some numbers in haystack bottom (Donisthorpe 1939)
Leptacinus pusillus (Steph.)						1	on field margins; weedy places; gardens; woodland edges. Especially in old stable manure heaps, in compost and rotting vegetation; in rotting root crops; in rotting marginal straw in barns and heaps (Koch 1989a)
Philonthus sp.	1		1	1	1	1	N/A
Tachinus laticollis (Grav.)	1	1					in rotting vegetation, in compost and stable manure heaps, in mouldy straw from barns and heaps, in carrion and dung (Koch 1989a)
Kateretes sp.	4	3	4	5	2	3	N/A

Taxon	2000.584 6063 MNI per Sample						Ecology
	4	6	7	10	12	16	
Monotoma picipes (Hbst.)						1	on field and meadow edges; gardens; weedy places; rubbish dumps; In rotting and mouldy vegetation, compost, stable manure, hay, straw; occasionally on fungi, under dry cattle dung and with ants (Koch 1989a)
Monotoma longicollis (Gyll.)	1	1		1	2		in gardens; rubbish dumps; barns and stalls; field and meadow edges; also woodland margins and river meadows (Koch 1989a)
Oryzaephilus surinamensis (L.)	8	5	6	18	10	6	in cereals and cereal products (Koch 1989a)
Cryptolestes ferrugineus (Steph.)	9	8	9	17	19	9	in cereals and their products; also in dried fruit and peanuts; more rarely under more or less dry bark of decaying and fallen trunks of *Fagus, Carpinus, Quercus,* and *Salix viminalis*, but also on conifers; occasionally in mouldy straw in heaps and in leaf litter at the foot of trees. Feeds on debris and mould fungi; also in deciduous and mixed woodland; parks; river meadows; woodland margins; field margins (Koch 1989b)
Cryptophagus scutellatus (Newman)	1	1	4	2		1	in stables, barns and cellars, gardens, field and meadow edges, more rarely in stream and river meadows (Koch 1989b)

Taxon	2000.584 6063 MNI per Sample						Ecology
	4	6	7	10	12	16	
Ephistemus globulus (Payk.)		1			1		in rotting hay and straw, as well as in stable manure and compost heaps, also in rotting vegetation, beet heaps, fresh grass cuttings, game food debris, dry dung and wild animal droppings, more rarely in woodland litter, detritus, grass tussocks and flood debris, as well as at sap flows on trees (Koch 1989b)
Lathridius minutus (grp.) (L.)	9	8	10	8	3	5	mycetophagous, in mould fungi; often synanthropic, in barns, cellars, etc, in houses on damp walls, in granaries & warehouses, in rotting provisions, corn etc. In the wild, among mouldy leaves, vegetation, near fungi and tree fungi, *Polyporus* sp. (Horion 1961)
Enicmus sp.	1		1	2	1	4	Mycetophagous
Corticaria sp.	1	1	1	1	1	4	Mycetophagous
Typhaea stercorea (L.)		1	1	2	1	2	mostly synanthropic, in cellars, stalls, barns, etc. in mouldy rotting materials, wood, hay, straw, leaves, etc., often in provision stores on corn etc in mills etc. Not a pest but a mould feeder. In the wild, less common, on tree fungi, in decaying fruit trees, amid rotting leaves, etc. (Horion 1961)
Palorus ratzeburgi (Wiss.)	4	1	2	7	4	1	in mills and bakeries, also in deciduous woods and woodland margins. Above all in cereals, meal and bran supplies; also noted under rotting bark of old deciduous trees, particularly *Fagus* (Koch 1989b)

Taxon	2000.584 6063 MNI per Sample						Ecology
	4	6	7	10	12	16	
Tenebrio obscurus (F.)				1			in cellars, stalls, corn stores and mills, more rarely in deciduous woodland, parks and gardens. Above all in cereals and their products, also in pigeon lofts and nests of *Passer domesticus*, occasionally in hollow deciduous trees, mostly in association with old bird nests, under rotting bark, in mouldy stumps (Koch 1989b)
Aphodius contaminatus (Hbst.)						1	in sandy pastures, river floodplains and woods, especially in fresh cattle and horse dung, also in human faeces (Koch 1989b)
Aphodius fimetarius (L.)				1			in all dung, more rarely in compost and stable manure heaps and rotting vegetation, especially cabbage stalks, and human faeces (Koch 1989b); known to be a pest of potatoes and cultivated mushrooms (Jessop 1986)
Aphodius granarius (L.)	2	1			2	1	in cattle pastures; fields; stream and river meadows; vineyards and gardens; woodland margins; heaths. in rotting and fermenting vegetation, rotting beets, cabbage stalks, grape husks, also in silage heaps, compost and stable manure heaps, as well as in dung of pets and humans; occasionally on carrion (Koch 1989b)
Phyllopertha horticola (L.)						1	on meadows, woodland margins, hedges and gardens, river floodplains, fields and weedy places, on deciduous trees and shrubs, also on fruit trees; larvae on roots of grasses, also cereals, and clover (Koch 1989b)

Taxon	2000.584 6063 MNI per Sample						Ecology
	4	6	7	10	12	16	
Hoplia philanthus (Fues.)	1			1			on sandy river floodplains and banks of rivers and lakes, heaths, part dry lawns, swarms in the morning; especially on small leaved *Salix* spp., but also on fruit trees, on twig ends of young *Pinus*, on cereals and flowers, Umbelliferae and Spiraea (Koch 1989b)
Gastrophysa viridula (Deg.)				1			in damp meadows; stream and river meadows; field and meadow margins; arable fields; woodland margins and wood pasture (Koch 1992); larvae and adults on *Rumex* sp. especially *R. obtusifolius* and *R. crispus* (Bentley and Whittaker 1979; Chuter 2000)
Prasocuris phellandrii (L.)						1	in swamps and bogs, swampy banks and meadows, copses (Koch 1992)
Galerucella sp.	1						N/A
Phyllotreta nemorum (L.)				2			on Cruciferae, often on disturbed or cultivated ground and a pest of cultivated turnip, *Brassica* sp. (Duff 1993)
Chaetocnema concinna (Marsham)			1				oligophagous on Polygonaceae, more rarely on *Beta*, *Fagopyrum* and *Rheum*; in winter, singly in leaves, twigs, moss, detritus, hay, straw, rotting vegetation and flood debris; larvae in the shoot leaf base region (Koch 1992)
Sitona lineatus (L.)				1			in fields, often Leguminosae fields, weedy places, causeways and embankments, stream and river meadows, dry and part dry lawns, gardens and city parks, more rarely swampy meadows

Taxon	2000.584 6063 MNI per Sample						Ecology
	4	6	7	10	12	16	
							and bogs. Oligophagous on very many Fabaceae, rarely also on *Robinia* sp., in winter singly in leaves, hay, straw, grass tussocks, litter, rotting vegetation, moss on trunks, also in flood debris (Koch 1992); a serious pest of peas (Jones and Jones 1974)
Magdalis carbonaria (L.)			1				on heaths and bogs; dry woodland margins, oligophagous on *Betula* sp. (Koch 1992)
Sitophilus granarius (L.)	3	1	1	5	2	4	lives and develops in grains of corn, rye, barley, maize, oats, buckwheat, millet, chickpeas, more rarely in chestnuts, acorns corn meal (Hoffmann 1954)
Mecinus pyraster (Hbst.)		1					on dry slopes, heaths, dry field margins, sunny stream and river meadows, sun-exposed woodland margins. Oligophagous on *Plantago* spp., especially *P. lanceolata*; occasionally in moss (Koch 1992)
Gymnetron pascuorum (Gyll.)		1					in degraded marshy grassland (Anderson 1998); on dry and warm slopes; dry swards; dry meadow edges. Monophagous on *Plantago lanceolata* (Koch 1992)

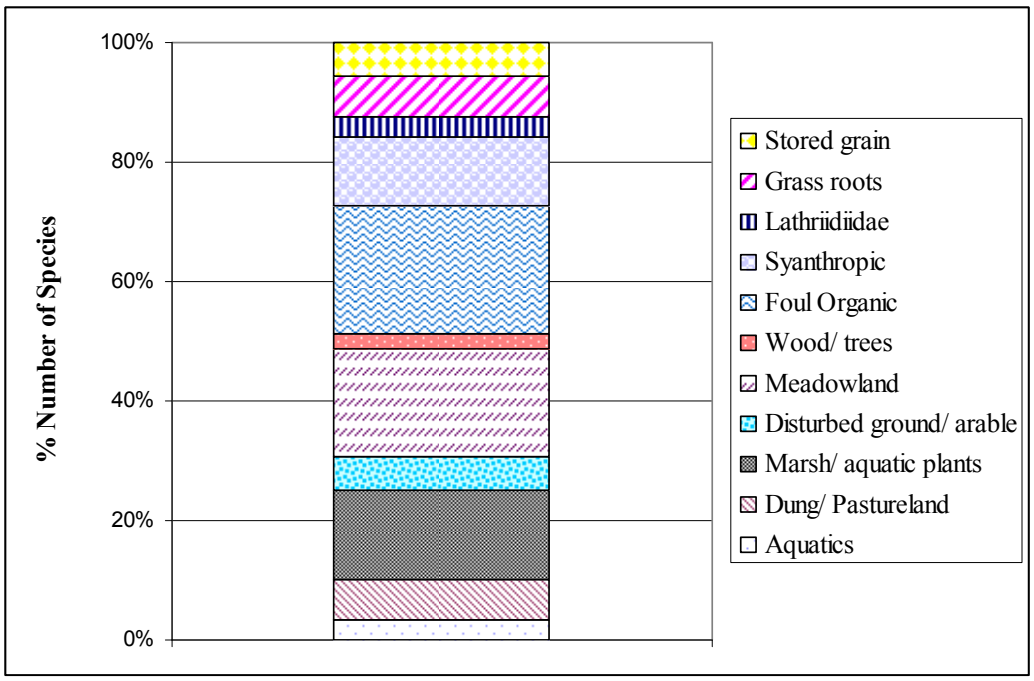
References for species' habitats and diets cited in Buckland and Buckland 2006

checklists for British Insects. A brief description of each species' modern habitat and diet is given along with the identifications.

Two taxonomic orders of insects, Diptera and Coleoptera, were recovered from the samples at Spurriergate. The dipteran remains were primarily represented by pupae and were not identified. However, the coleopteran remains were identified and

for the most part taken to the generic if not specific level. The Coleoptera were assigned to broad species groups based on ecology. In addition to the species ecological groups outlined by Robinson (1981; 1983), a twelfth group was utilised, species especially associated with stored grains. This group is comprised of strong synanthropes, e.g. *Sitophilus granarius*, which are associated with cereals and cereal products. The beetles are not known to infest cereals in the field and a typically considered to indicate stored products. Moreover, the 7-15 Spurriergate samples did

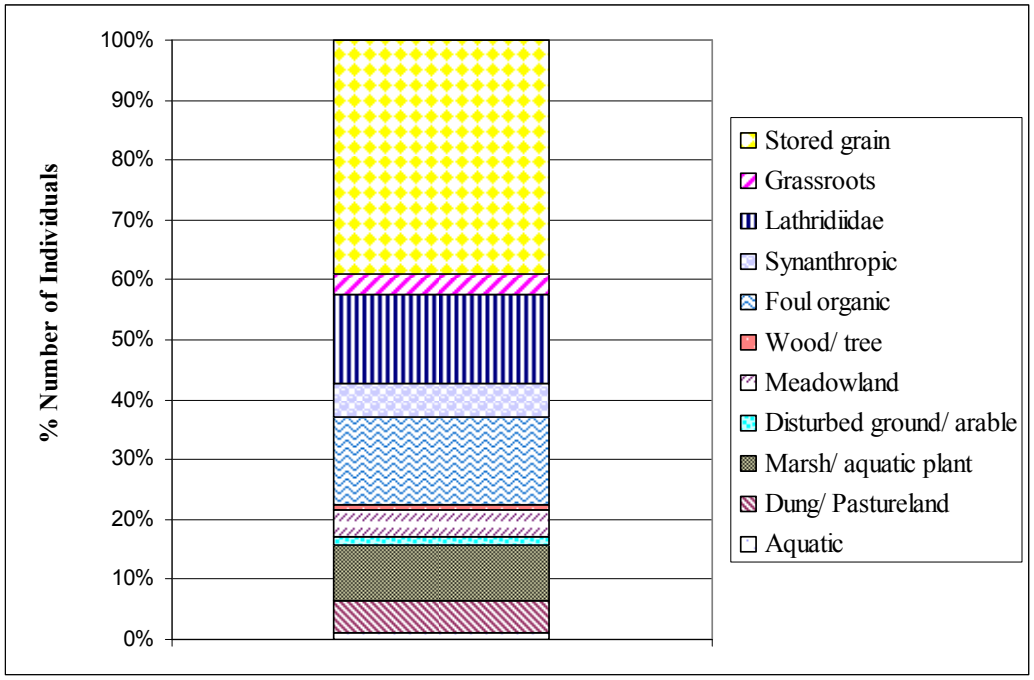
Figure 4.2 Number of species by ecological group



not contain any species associated with Species Group 10, species especially associated with structural timbers.

Approximately 95 % of the coleopteran remains have been classified into one of the ecological categories. The species groupings are presented in Figures 4.2- 4.3. Figure 4.2 shows the number of species recorded for each ecological group as a percentage of the assemblage. In Figure 4.3, the minimum number of individuals per ecological is displayed.

Figure 4.3 Minimum number of individuals by species group



4.2.4 Palaeoenvironmental Reconstruction of Roman Spurriergate

The aquatic and waterside environment

Water and marsh-related beetles comprised approximately 17 % of the coleopteran species from Spurriergate, York with the aquatic insect fauna only forming around 3.4 % of the entire assemblage. Although there was diversity in the species reported, the number of individuals constituted only 10 % of the assemblage. The aquatic beetles were largely associated with stagnant or muddy water. *Helophorus aquaticus*/*grandis* species, in particular, are common in stagnant pools of water. The species *Hydraena testacea* and *Cercyon tristis* are found in detritus on the muddy margins of well-vegetated ponds and sluggish drains (Friday 1988; Merritt 2006), and the beetles provide evidence towards the rich waterside fauna from the samples. Several Hydraenidae species readily leave water and have been recorded on the muddy banks of the watersides. The Spurriergate samples revealed several non-

aquatic species that frequent muddy environments. The staphylinids *Platystethus degener*, *P. cornutus*, and *P. nitens* are species that are found in environments comprised of highly organic mud and decaying litter such as near ponds and rivers (Hammond 1971; Duff 1993). Flood zone species of Carabidae were also noted in the assemblage. *Pterostichus melanarius* is a predaceous ground beetle that hunts in decaying vegetation and debris in wash zones (Koch 1989a).

The water and marsh- associated fauna paint a picture of a potentially fetid environment with stagnant pools of water. There appears to have been rich layer of vegetation, though perhaps decaying, overlaying or intermixed with a muddy or damp-disturbed matrix. Despite the site's proximity to the River Ouse (approximately 83 metres), there was no evidence of species associated with flowing water and little indication of species which are phytophagous on waterside vegetation. However, *Gastrophysa viridula* was present in small numbers and has been noted living on *Rumex* sp. near marshes, and *Prasocuris phellandrii* seems to be oligophagous on aquatic Umbelliferae such as: *Oenanthe phellandrium*, *O. aquatica*, *O. crocata*, *Cicuta virosa*, and *Sium latifolium* (Koch 1992; Bullock 1993). Although phytophagous taxa were scarce, the site did contain a number of species that would likely have been autochthonous to the muddy environments near the riverbanks.

The woodland and scrub

Wood and tree-related species made up less than 1 % of the Coleoptera from the first century AD Spurriergate contexts. This estimate is comprised of beetles associated with Group 4 of the species' ecological groupings discussed above. While other species in the assemblage may contribute to a woodland community, this category represents fauna associated with the bark, wood, leaves, etc. of trees and

shrubs rather than other forest elements such as litter or woodland herbs. The Group 4 fauna make up a minute portion of the assemblage. However, if *Cryptolestes ferrugineus* and *Palorus ratzeburgi*, which are considered primarily to be grain pests but have been recorded under tree bark, are added to Group 4, the number of individuals that are capable of being inhabiting trees increases to 23 % of the assemblage. The two of the species are fairly poor indicators of the presence of trees, and their abundance in the samples is more likely associated with stored cereals [see Chapter 5]. The scarabaeoid *Hoplia philanthus* has been recorded on *Salix* sp. (willow) and *Pinus* sp. (pine), especially on river banks, meadows, and heaths (Koch 1989a). However, the species has also been noted on cereals and flowers, and its larvae feed on grass roots. The curculionid *Magdalis carbonaria* is perhaps the only true representative of a Group 4 species in the samples. The weevil is fairly host-specific and may be a strong indicator for the presence of *Betula* sp. (birch). The larvae of *M. carbonaria* feed on the interior of dead branches and twigs of birch (Hyman 1992). As *Magdalis carbonaria* is only represented by a single specimen, MNI =1, from Sample 7, the presence of trees near or on the site is not strongly supported by the insect remains.

Grassland, arable, and the open environments

The Early Roman landscape around the Spurriergate site, or perhaps more accurately around York, was largely open. The region seemed to support grassland and/or pastureland. 18 % of the archaeologically recovered terrestrial Coleoptera and 4 % of the individuals fall in the Group 3 category, indicating the presence of meadowland. Moreover, there were a few species whose larvae feed on grassroots. The chafer *Phyllopertha horticola* as well as the *Hoplia philanthus* and other root

feeding scarabaeoids were present in the samples but not abundant. The phytophagous fauna of grassland species is representative of the presence of trefoils and flowery herbs.

A few of the more host-specific phytophagous beetles from the samples and their favoured plant foods include:

Gymnetron pascuorum	*Plantago lanceolata*
Mecinus pyraster	*P. lanceolata* and *P. media*.

While considered a pest of peas, the pea-leaf weevil *Sitona lineatus* has been recorded on *Fabaceae*, *Lathyrus* spp., *Pisum sativum*, *Pisum* spp., *Trifolium* spp., *Vicia faba*, and *Vicia* spp. (Bullock 1993; Morris 1997). Moreover, its larvae are oligophagous root feeders. The single specimen of *S. lineatus* from Spurriergate may hint at the presence of meadowland or agricultural land in the vicinity of the site.

Along with the pea-leaf weevil, 5 % of the Coleoptera species from the samples support the presence of disturbed or arable land. There were a few individuals of *Phyllotreta nemorum*, which is associated with various Cruciferae such as the turnip *Brassica* sp. An individual of *Chaetocnema concinna* was also recovered. While *C. concinna* feeds on various cultivated *Polygonum* sp. and *Rumex* sp. (see LeSage 1990 for a comprehensive list), it could also represent grassland or waterside environments (Richards 1926; Duff 1993). While primarily coprophilous, *Aphodius fimetarius* is also considered a pest of potatoes and cultivated mushrooms (Jessop 1986).

Several of the coleopteran species are representative of hay or straw. For example, Leclercq (1946) found numerous *Typhaea stercorea* in hay brought in from the meadow. However, the beetle is more commonly noted in mouldy or decaying hay refuse. Several other phytodetriticolous species, which are loosely associated

with decaying hay and dry vegetable matter, from Groups 7 and 9, were recovered from the Spurriergate samples. *Ephistemus globulus*, *Trechus quadristriatus*, *Omalium caesum*, and *Xylodromus concinnus* were prevalent in the samples. An individual specimen of *Acritus nigricornis* which is common in 'sweet' compost such as hay, straw, and cut grasses, was also found. The site also contained several other decomposer species, which while not particularly associated with hay does indicate the presence of vegetable refuse. Whereas these species are associated with vegetation, their association with decaying matter probably is a reflection of conditions on the site rather than the surrounding environment.

Along with the vegetation decomposer fauna, Group 7 was comprised of dung indicators. The foul organic-associated species constitute 21.5 % of the assemblage's species and 14.5 % of the individual specimens. However, most of Group 7 beetles will feed on decaying vegetation as well as herbivore dung, which is essentially another form of decaying vegetation. A better indication of the presence of dung is Species Group 2. 7 % of the recovered Coleoptera specimens are associated with dung and pastures. In general, Group 2 dung beetles are fairly strong indicators of the presence of dung as the species tend to burrow in or under patties. The recovery of Group 2 species at an MNI of 5 % suggests the presence of the herbivorous mammals at the site.

The dung-feeding beetles are not typically associated with the excrement of a single species. *Megasternum obscurum* was present in amble numbers and provides a more general indication of the presence of herbivore dung. *Aphodius granarius* and *Cercyon haemorrhoidalis* are common in cow patties but have also been found in the manure of other domesticated herbivores such as sheep and horses. *Cercyon atricapillus* is mainly associated with horse and cattle excrement. Hansen (1987)

proposed that *Cercyon terminatus* was mainly found in cattle and horse dung whereas Koch (1989a) put forth that the species was particularly associated with sheep and cattle manure. Most of the dung fauna are associated with domesticated species; however, Donisthorpe (1939) suggests that *Aphodius contaminatus* is more common in deer excrement. *A. contaminatus* was only evidenced by a single specimen at the site, and the beetle has also been recorded on old horse and cattle dung (Landin 1961).

The Spurriergate samples were comprised of a fair proportion of meadowland, arable, and foul organic species. Although the Coleoptera may suggest that agricultural land and grassland used for grazing were in the vicinity of first century AD Roman York, the MNI for the groups indicates that the fauna, while present, were not abundant. In comparison, the beetles, which were associated with decomposing vegetation and dung, were strongly represented. In an open environment, one would expect the presence of phytophagous and root-feeding fauna to be more pronounced in comparison to the rotting vegetation associates. The abundance of dung beetles in association with the synanthropic hay species such as *Typhaea stercorea* suggest the existence of a more confined environment that is suitable for maintaining domesticated herbivore mammals, i.e. a stable or barn, on the site.

Other habitats

There were several species associated with human habitation in the Spurriergate contexts. In addition to the synanthropic Coleoptera assigned to Group 9 (discussed above), 39 % of the individuals that were recovered from the samples were species which are strongly associated with the presence of stored cereals. *Cryptolestes ferrugineus* and *Oryzaephilus surinamensis* comprise part of the grain fauna and were abundant in all the samples. Additionally, an individual of *Tenebrio*

obscurus was also present. The species *Sitophilus granarius* has only been recorded from synanthropic environments in temperate regions; the granary weevil is strongly associated with stored cereals and does not appear to infest grains that are still in the field [see Chapter 5]. The recovery of significant numbers of *S. granarius* from the site is a good indicator of the presence of cereal grains. While *Palorus ratzeburgi* is also an indicator species for stored cereals, the species may also provide evidence of the condition of the grains. The small-eyed flour beetle is common on mouldy or damaged grains (Brendell 1975).

Group 8 associates were also prevalent in the samples. *Lathridius minutus* group, in particular, was abundant and constituted 10.5 % of the individuals from the Spurriergate assemblage. *Lathridius minutus* group species are typical but non-obligate synanthropes. The beetles are mycetophagous and are believed to feed on mould, spores, and hyphae (Larsson and Gigja 1959). Although the species have been noted in plant debris in birch forests (Böcher 1988) and in *Rumex* sp. in meadows (Bengtson 1981), *L. minutus* group is more frequently associated with hay barns, stables, and granaries (Horion 1961; Lindroth *et al*. 1973; Barker and Smith 1990).

4.2.5 Palaeoclimatic Reconstruction

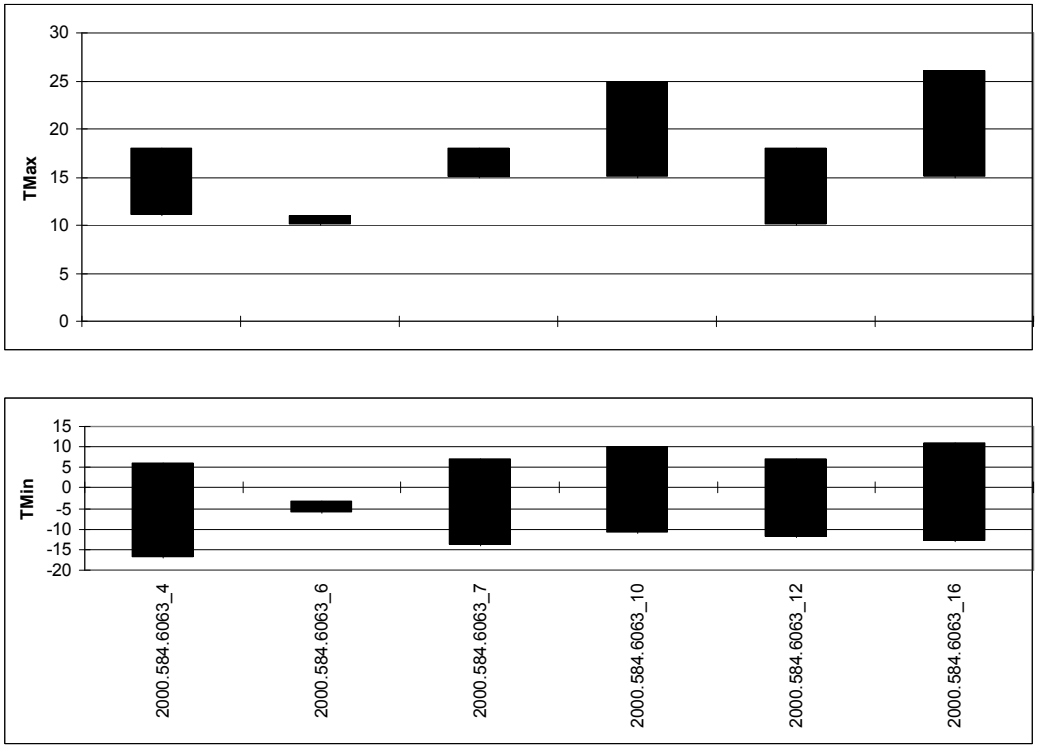
Table 4.2 Mutual Climatic Range method predictions for Roman 7-15 Spurriergate, York

Sample	TMaxLo	TMaxHi	TMinLo	TMinHi	TRange Lo	TRange Hi	N-SPECIES	Overlap
4	11	18	-17	6	11	30	7	100
6	10	11	-6	-3	14	16	6	100
7	15	18	-14	7	11	29	6	83.33
10	15	25	-11	10	9	28	6	83.33
12	10	18	-12	7	11	24	5	80
16	15	26	-13	11	9	32	4	100
Site	15	18	-9	6	11	24	15	93.33

(calculated using Buckland and Buckland 2006)

Table 4.2 and Figure 4.4 show the climate predictions calculated using the BugsMCR program (Buckland and Buckland 2006). Only carnivorous and scavenging species were analysed, as the ranges of herbivorous or phytophagous Coleoptera may only reflect the distribution of their food plants rather than provide a 'true' climatic signal. Fifteen species were evaluated [Appendix 1A], and predicted the temperature of the warmest month as ranging between 15 ˚C and 18 ˚C and the temperature for the coldest month between -9 ˚C and 6 ˚C. This range of temperatures is similar to the estimates evidenced by the beetles from other Romano-British sites such as Bedern Well, York, Alcester, Warwickshire, and Copthall Avenue, London [Appendix 1B].

Figure 4.4 7-15 Spurriergate, York MCR estimates by sample



(calculated using Buckland and Buckland 2006)

4.2.6 Discussion: The Environment and Climate of 7-15 Spurriergate and Implications for Culture Contact

The Early Roman insect assemblages from Spurriergate are interesting because they consist of strongly synathropic species as well as grassland and riverside fauna. Kenward and Hall (1997) have proposed that the presence of grain pests along with 'hay' fauna, house fauna, and decomposers is characteristic of stable manure. Although the Spurriergate samples evaluated here did not yield the characteristic spider beetles, *Ptinus fur* and *Tipnus unicolor*, which comprised part of Kenward and Hall's (1997) stable manure indicator group, the ecological association evidenced by the assemblage may infer a stable fauna.

The grains may have served directly as a part of the mammals' diet or, less possibly, the grain pests could have invaded residue grain in straw or chaff that was used for bedding. Moreover, Osborne (1983) demonstrated that insect remains can successfully pass through a human dietary tract without damage; it seems plausible that the same would hold true for large non-ruminant herbivores. The presence of meadowland fauna could have been ingested during grassland grazing and introduced to the urban site through the dung of the herbivores or may have been imported alongside vegetation used for floor litter. The site produced a range of fauna associated with plant debris, in various stages of decay. Furthermore, the samples yielded numerous dung beetles associated with large herbivores as well as coleopteran species reflecting the presence of hay. If viewed independently, the species in the assemblage could represent a number of habitats; however, collectively they strongly infer a stable or barn environment. The aquatic and waterside fauna, which perhaps do not categorise with the stable manure indicator group, were present in low

numbers, and may stand as a background fauna attracted to the muddy micro-habitat from the nearby River Ouse.

While most of the species are representative of a stable or barn environment, a few of the Coleoptera may also reflect local or foreign exchange. The grain fauna and the hay fauna, in particular, may provide evidence towards palaeoeconomic activities in Roman York as the species may reflect commodities which are transported and/or traded by man. Using of the palaeoecological approach, the potentially heterochthonous species will be identified by comparing the species' temperature requirements for completion of life cycle to the estimated MCR for the site at TMax 18 ˚C, which is three degrees lower than the average TMax for the warmest month in modern York (cf. WatkinsHire n.d.).

The grain fauna was comprised of species requiring a range of temperatures in order to carry out their developmental life cycle [see Figure 5.2 for a detailed comparison]. Based on temperature requirements, *Tenebrio obscurus* (14-30 ˚C) and *Sitophilus granarius* (15-35 ˚C) slightly overlap with the TMax of the assemblage, which implies that the species may have been capable of surviving and completing their development during the warmer months outside of human habitation in Roman Britain. However, both species have optimal temperature ranges that are significantly higher than the calculated maximum temperature for the warmest month. This suggests that the species are not indigenous to Britain and would have most likely been introduced at some point. The minimum temperature requirements for the other grain-associated species equal or exceed 18 ˚C. As such, the pests would not have been able to complete their development in the wild and are unlikely to have been native. However, the species would have likely been able to reproduce and develop in Roman Britain under synanthropic conditions. Granaries and fermenting vegetation

would have had higher temperatures than their surrounding environment, which would have enabled the species, once introduced, to become established. Solely on the basis of temperature requirements and palaeoclimatic reconstructions, the grain fauna, as a whole, suggest the importation of cereals from warmer regions by the Romans.

The hairy fungus beetle *Typhaea stercorea* is strongly associated with hay. While the species does not appear to damage the hay directly, as it is mycetophagous, it seems associated with the fungi and mould common to sweet compost. Laboratory assessments by Jacob (1988) have demonstrated that *T. stercorea* is capable of completing its development at 17.5 to 30 ˚C when held at 90 % relative humidity. At 15 ˚C, the eggs did not hatch and the pupa did not develop. Similar to the majority of the grain fauna, the hairy fungus beetle may have been able to endure and become established in synanthropic environments but would not have been capable of surviving in the wild during the first century of the Roman occupation of Britain. The presence of the species implies an original connection to a warmer climate.

4.2.7 Summary

The samples evaluated from 7-15 Spurriergate York yielded Coleoptera associated with a range of habitats. When the ecologies were viewed collectively, the fauna appeared to reflect a stable or barn environment used to keep herbivorous mammals. The presence of meadowland and cereal beetles may indicate that the domesticated animals had a diet that involved pastureland grazing and grain supplements. While the majority of the species were likely associated with the local and hinterland environments around Roman York, the temperature ranges for the grain beetles and *Typhaea stercorea* indicate warmer climate origins for those species

and suggest the potential introduction of those Coleoptera to the site, which would infer the importation of cereals and hay to York. However, the species would have most likely been able to survive in Britain under the increased temperatures presented by their synanthropic environments. As the present palaeoecological study does not consider other archaeoentomological evidence which is necessary to assess the spatial or temporal changes in species' distributions (that being considered with the biogeographical approach in Chapter 5), it is not possible to discern how early the grain beetles and hay associates arrived in York.

4.3 Case Study: 16-22 Coppergate, York Period 4b

4.3.1 Introduction

The archaeoentomological assessments regarding 16-22 Coppergate, York were carried out as part of a series of large-scale urban rescue excavations in York, which were conducted by the York Archaeological Trust during the 1970s and 1980s. The 16-22 Coppergate site is situated within York city centre approximately 200 m from the River Foss and 100 m from the River Ouse [Figure 4.4]. The site yielded contexts ranging in date from the mid-9th (cf. Hall and Kenward 1999a) to the early 11th century (cf. Hall and Kenward 1999c).

4.3.2 Background and Processing Methods

The insect remains were processed and identified following the procedures outlined in Kenward (1985; 1992). An account of the non-vertebrate biological remains, which were recovered from the site, has been published by Kenward and Hall (1995). During the original processing and identification period, the

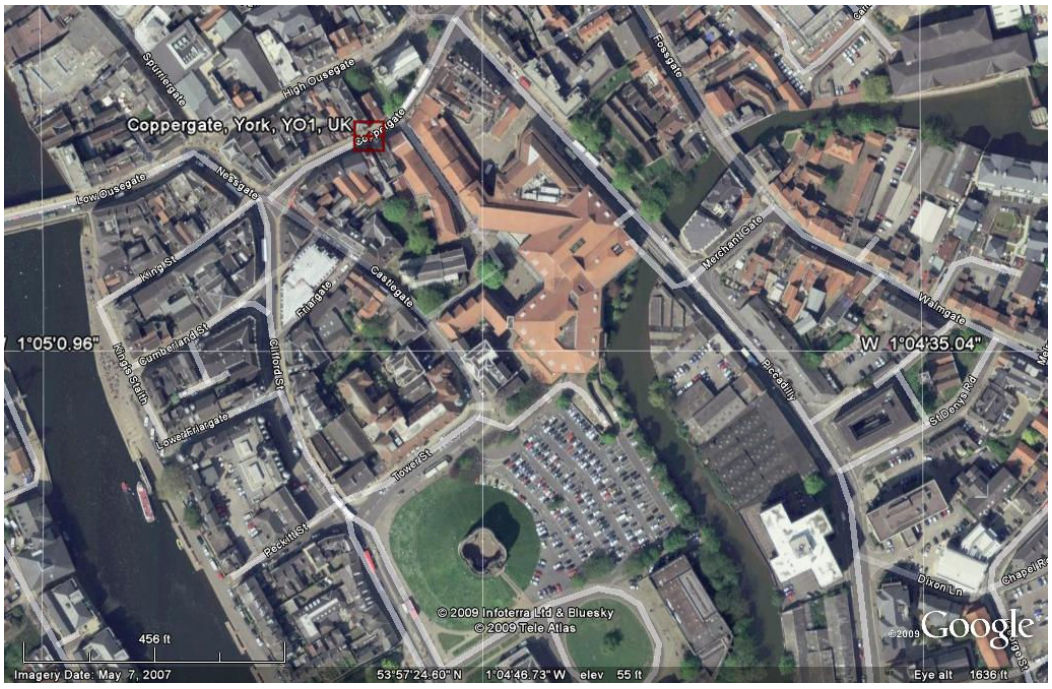


Figure 4.4 Location of 16-22 Coppergate site (near red icon). The site falls between the River Foss (right) and the River Ouse (left) near the Jorvik Viking Center. Clifford's Tower can be seen at the bottom middle of the photo (Goggle Earth 2009).

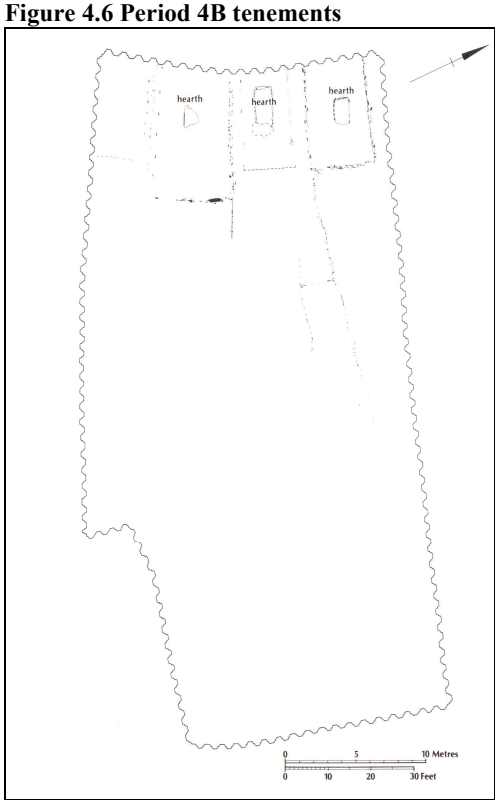
Figure 4.5 Post-and-wattle structures

(Richards 1991, 67)

investigators employed a range of recording methods: detail recording, scan recording, semi-quantitative scan recording, and non-qualitative rapid scan recording (Kenward and Hall 1995). In this study, insect fossils from five samples were selected for further evaluation. The materials relate to contexts 22574 and 22490, which were dated between 1020 to 975 BP (Period 4b; cf. Hall and Kenward 1999b). The contexts are believed to be associated with the Anglo-Scandinavian Period.

The remains of four tenements were found at the site, dated to Period 4b. The tenements, which are portrayed in Figures 4.5-4.7, were delineated by wattle fences comprised mainly of oak and hazel and were categorised as the single post-and-wattle style (O'Connor 1994). The five samples were retrieved from fills inside the 'west wicker building', Tenement C (Hall and Kenward 1999b). Context 22574 was comprised of very dark grey, silty-sandy clay, which contained lenses of brownish-yellow to olive-yellow compacted grass/straw and *circa* 10 % wood chips. Context 22490 was excavated from the uppermost fill; it was predominately a black, peaty, silty- clay loam, comprised of approximately 15 % wood chips (Hall and Kenward 1999b).

Figure 4.6 Period 4B tenements

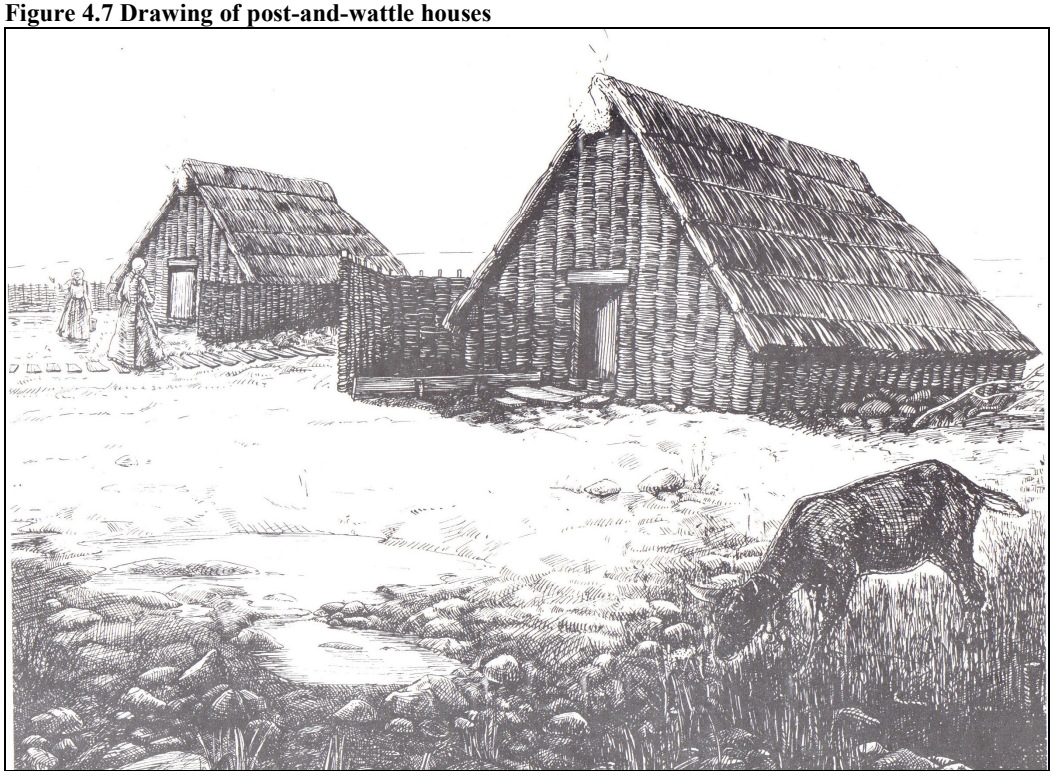


(Hall 1984, 50)

4.3.3 Results and Analysis of Data

Table 4.3 provides a detailed species list for contexts 22574 and 22490 and indicates the determined minimum number of individuals [MNI] of each species for each sample. Kloet and Hinck's (1964; 1976; 1977; 1978) revised checklists for British Insects was employed for species' nomenclature. Table 4.3 also provides a brief description of each species' modern habitat and diet.

Figure 4.7 Drawing of post-and-wattle houses



(Murray 1983, vi)

Six taxonomic orders of insects were recovered from contexts 22754 and 22490: Coleoptera, Diptera, Anoplura, Mallophaga, Siphonaptera (fleas), and Hymenoptera. The insect remains were identified to the generic if not specific level. The ecological coding system proposed by Robinson (1981; 1983) was utilised to assign the Coleoptera to broad species groups. An additional ecological group was added to denote species especially associated with carcasses. The species associated

Table 4.3 Species list for selected contexts from 16-22 Coppergate, York

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Coleoptera						
Carabidae indet.	1	1	1			N/A
Clivina fossor (L.)		2				a eurytopic species, usually in open country on rather humic ground with more or less dense vegetation of grasses; feeds on both vegetable and animal matter, including larvae and pupae of *Meligethes* sp. (Lindroth 1985)
Trechus micros (Clair.)		1				usually near water, but also in damp grassland, probably associated with runs of small mammals (Luff 1998); syn. *Trechoblemus micros* Hbst.
Trechus sp.		1				moist vegetation, usually near water
Bembidion gilvipes (Sturm)		1				in moist meadows, moist water meadows, woods, swampy woods, swampy banks. Under detritus and rotting vegetation, in flood debris, in grass (Koch 1989a)
Bembidion biguttatum (F.)		1				in eutrophic fens bordering lakes and rivers, usually among tall vegetation; moss and leaves at margins of ponds and pools (Lindroth 1985)

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Harpalus rubripes (Duft.)		1				dry arable fields with sparse vegetation; dry meadows, woodland margins and clearings; sandy river banks and coasts. Under grass tussocks, leaves and moss (Koch 1989a)
Pterostichus melanarius (Ill.)		1				prefers thick vegetation; loamy arable fields, flood plains, meadows, woodland margins; hedges and gardens. In decaying vegetation and flood debris; under loose bark (Koch 1989a)
Amara sp.	1					species in bare ground and arable on sandy soils (Robinson 1991)
Hydropor-inae indet.		1				aquatic
Ochthebius sp.		3			1	aquatic
Helophorus sp.		1			1	aquatic
Sphaeridium sp.		1				open-grazed land; dung
Cercyon haemorrh-oidalis (F.)	3	2			1	very eurytopic, in all kinds of decaying organic matter, mainly in cow, horse and sheep dung, but also frequently in rotting plant debris, especially compost

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
						heaps, also old mushrooms, flood debris on wetter habitats, carrion (Hansen 1987)
Cercyon unipunctatus (L.)		3			1	in all kinds of decaying organic matter, distinctly synanthropic, in various debris around farm buildings, e.g. compost heaps and barn manure (Hansen 1987)
Cercyon atricapillus (Marsham)		1				in fields, weedy places, cow pastures, river meadows, heaths, gardens and stables, especially in fermenting materials (compost, root heaps, stable manure, heaps of rotting vegetation), fresh dung and carrion (Koch 1989a)
Cercyon terminatus (Marsham)		1				in herbivore dung or decaying grass (Duff 1993)
Cercyon analis (Payk.)	6	4	1			in almost all rotting vegetation, in flood debris and litter (Koch 1971)
Megasternum obscurum (Marsham)	1	1				in decaying grass and herbivore dung (Duff 1993)
Cryptopl-eurum minutum (F.)	1					in all kinds of decaying organic matter, usually very abundant, mainly in compost heaps, rotting grass, in dung and at carrion, also among various plant debris near water (Hansen 1987)

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Hydrobius fuscipes (L.)		1				very eurytopic, mainly in stagnant water, but also in slower reaches of streams, both fresh and brackish water. Usually among vegetation in shallows near water's edge (Hansen 1987)
Histeridae indet.		1				dung and carrion
Acritus nigricornis (Hoff.)		1	1			in fields, meadows, gardens; especially in the lower layers of old stable dung heaps, in dung, rotting vegetation, compost and rootcrop heaps, tannery waste, wood debris and barn straw (Koch 1989a)
Orthoperus sp.	3	1				Moulds
Ptenidium sp.	1	1				rotting vegetation
Acrotrichis sp.	3	2				N/A
Dropephylla sp.	1					fungi under bark
Omalium rivulare (Payk.)		1				in grass tussocks including cereal crops, or in damp litter, fungi or carrion (Duff 1993)

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Xylodromus concinnus (Marsham)	2	9	1			in fields, river meadows, woodland margins and woods. In straw in barns and stalls in hay and compost heaps; occasionally in wood mould and in nests in hollow trees (Koch 1989a)
Omaliinae indet.					1	N/A
Carpelimus bilineatus (Steph.)	1	1	1			on sandy-muddy banks, fields, gardens, woodland margins. Littoral: wash zone. On mud, under detritus and flood debris, in wet compost, straw and stable manure heaps (Koch 1989a)
Carpelimus fuliginosus (Grav.)		1				in fields; gardens; weedy places. Subalpine pastures. In compost, stable and rotting hay heaps (Koch 1989a); associated with wetlands, in damp and marshy places under leaves, in moss, amongst herbage and in tussocks (Hyman 1994)
Carpelimus pusillus (Grav.)		1				in gardens, fields, weedy places, also on sandy and swampy banks. In stable manure and compost heaps, in dung beds; in rotting vegetation, in rotting straw and field barns and ricks, under grass tussocks and debris (Koch 1989a)

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Carpelimus sp.			1			fetid environments
Oxytelus sculptus (Grav.)		2			1	in fields; cattle pastures; weedy places; woodland margins; stables. In dung stable manure; in debris of *Phragmites* sp.; in rotting hay (Koch 1989a)
Anotylus rugosus (F.)			1		1	in rotting vegetation, also in fungi, in mouldering leaves, litter and flood debris, in compost, straw and stable manure, in dung of cattle and man, in bird nests and underground animal burrows, on mud and in *Sphagnum* sp. (Koch 1989a)
Anotylus sculpturatus (Grav.)		1				in more or less fresh dung; in carrion; in stable manure and compost heaps; in rotting vegetation (Koch 1989a)
Anotylus nitidulus (Grav.)	2	6	1			on damp soil, banks, swampy and wet meadows, river meadows. In rotting vegetation, also in fungi, in stable manure and compost heaps (Koch 1989a)
Anotylus complanatus (Er.)	1		1			in cut grass, fungi, damp straw, and moss (Donisthorpe 1939)
Anotylus tetracarinatus (Block)					1	in rotting vegetation, also fungi; in dung and carrion; in compost and stable manure heaps; in rotting straw in barns and ricks (Koch 1989a)

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Platystethus arenarius (Geoff.)		1	1			in herbivore dung and damp decaying vegetation (Duff 1993)
Platystethus nitens (Sahl.)		1				in mud and damp litter near water (Duff 1993)
Stenus sp.	2	2				N/A
Lithocharis ochracea (Grav.)	1					in meadows, woodland margins, woods, fields and gardens. In rotting vegetation, in straw debris, in straw and chaff in field barns and heaps (Koch 1989a)
Leptacinus pusillus (Steph.)	2					on field margins; weedy places; woodland edges. in old stable manure heaps, in compost and rotting vegetation; in rotting root crops; in rotting marginal straw in barns and heaps (Koch 1989a)
Gyrohypnus fracticornis (Müll.)	1					in rotting vegetation, also in fungi, in compost and stable manure heaps, in marginal straw in barns and heaps, in carrion, in detritus and flood debris (Koch 1989a)
Gyrohypnus sp.			1		1	fetid environments
Xantholinus linearis (Ol.)	1					in grass tufts, haystack refuse, dead leaves, at roots of heather (Buck 1955)

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Philonthus sp.		1	1		3	N/A
Staphylininae indet.		3				N/A
Tachyporus sp.		1	1			N/A
Tachinus rufipes (L.)	1					in decaying grass and grass tussocks or at plant roots, including arable crops, and in herbivore dung in woods and grassland (Duff 1993)
Cordalia obscura (Grav.)	1	5				in rotting vegetation, also fungi, in compost, stable manure, hay and straw heaps, also in dung and carrion, under stones and in grass tussocks, in detritus (Koch 1989)
Crataraea suturalis (Mann.)		3				in vicinity of dwellings, in mouldy straw in barns, sheep pens and cellars, also in nests (Harde 1984)

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Aleocharinae indet.	7	2			1	N/A
Pselaphidae indet.		1	1			N/A
Euplectini indet.	1					N/A
Melanotus sp.		1				rotting wood and bark
Cyphon sp.					1	near water
Dermestes sp.	1	1				animal carcasses
Brachypterus sp.		1				on *Urtica* sp. (nettles)

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Meligethes sp.	1	1			1	meadowland vegetation
Omosita sp.		2	1			carrion
Monotoma spinicollis (Aubé)	1					in rotting and mouldy vegetation, especially compost, hay and straw; also in old stable manure heaps (Koch 1989a)
Monotoma picipes (Hbst.)	1					on field and meadow edges; gardens; weedy places; rubbish dumps; in rotting and mouldy vegetation, compost, stable manure, hay, straw; occasionally on fungi, under dry cattle dung and with ants (Koch 1989a)
Monotoma bicolor (Villa)		3				in plant debris (Duff 1993); rotting vegetation, compost, hay (Koch 1989a)
Cryptophagus scutellatus (Newman)		1			1	in stables, barns and cellars, gardens, field and meadow edges, more rarely in stream and river meadows (Koch 1989b)
Cryptophagus sp.	1	9	1		1	N/A

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Atomaria sp.	13	9			1	N/A
Ephistemus globulus (Payk.)	8	1				in rotting hay and straw, as well as in stable manure and compost heaps, also in rotting vegetation, beet heaps, fresh grass cuttings, game food debris, dry dung and wild animal droppings, more rarely in woodland litter, detritus, grass tussocks and flood debris, as well as at sap flows on trees (Koch 1989b)
Lathridius minutus (grp.) (L.)	14	16	1		1	mycetophagous, in mould fungi; synanthropic, in barns, etc, in houses on damp walls, in granaries and warehouses, in rotting provisions, corn etc. In the wild, among mouldy leaves, vegetation, near fungi and tree fungi, *Polyporus* sp. (Horion 1961)
Enicmus sp.		1				mycetophagous
Corticaria sp.	1	5				mycetophagous

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Corticaria/ *Corticarina* sp.	2					mycetophagous
Aglenus brunneus (Gyll.)	4	10	6		1	mouldering wood, in fungi (Kenward 1975b); barns, stables, cellars and garden centres, also field margins and weedy places; under mouldy straw, hay, chaff, straw manure and mouldy chaff, under dry mouldy manure in chicken and dove cotes, in the ground under rotting boards in beet waste, single with Talpa sp. and Microtus sp. (Koch 1989a)
Lyctus linearis (Goeze)	1					ancient broad-leaved woodland, also in timber yards and in buildings, develops in dead wood, especially of oak, beech and ash, often in fresh oak palings (Hyman 1992); especially in dry dead wood of structural timbers (Robinson 1991)
Anobium punctatum (Deg.)	3	4	1		1	in furniture and tools; in joinery timbers and flooring and structural timbers of buildings. Attacks willow, alder and birch soon after the timber is dry, but softwoods require time to mature about 20 years and oak above 60 years before flight holes appear (Buck 1958)

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Ptilinus pectinicornis (L.)	2					in wood in debarked areas of dry standing and fallen trunks of hard deciduous wood, especially in *Fagus sylvatica,* but also *Quercus*, *Carpinus*, *Acer*, *Ulmus*, *Populus*, occasionally also in stumps and thick branches; sometimes in furniture (Koch 1989a)
Ptinus fur (L.)	2	2	1			common in mouldy straw and hay in barns and heaps, in cereal debris, in nests of *Passer domesticus*, in carrion and nesting materials in pigeon lofts, sometimes in old beehives, wasp nests and in damp walls in lavatories, in wild game food residues, in twig heaps and in wood mould of hollow trees. Very polyphagous (Koch 1989b).
Anthicus formicarius (Goeze)		1				in vegetable refuse, haystack bottoms, compost heaps, etc. (Buck 1954); syn. *Omonadus formicarius* Goeze

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Anthicus floralis/ *formicarius* (L.)/(Goeze)	1					*A. floralis*: in rotting and mouldy hay and straw in ricks, barns and stable manure heaps; in rotting vegetation, also fungi and compost; in wood shavings; occasionally on low plants as well as leaves and twigs (Koch 1989a), syn. *Omonadus floralis* L.; *A. formicarius*: in vegetable refuse, haystack bottoms, compost heaps, etc. (Buck 1954)
Anthicus (s.l.) sp.	1	1				decaying vegetation
Blaps sp.		1				non-obligate synanthrope; stored product pest
Tenebrio obscurus (F.)	1	1	1			in cellars, stalls, corn stores and mills, more rarely in deciduous woodland, parks and gardens. Above all in cereals and their products, also in pigeon lofts and nests of *Passer domesticus*, occasionally in hollow deciduous trees, mostly in association with old bird nests, under rotting bark, in mouldy stumps (Koch 1989b)
Trox scaber (L.)	1	1				in birds' nests, in hollow trees, mostly owl and other nests containing bones, and in detritus of animal origin (Jessop 1986).

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Aphodius prodromus (Brahm)			1			in all dung, especially horse and human faeces; more rarely in rotting vegetation, also fungi, compost, stable manure heaps, as well as in grape debris and rotting fruit (Koch 1989a)
Aphodius sp.	2	2				N/A
Melolonthinae indet.		1				N/A
Phymatodes alni (L.)	1					recently dead or decaying *Quercus* spp. (Alexander 1994); also found in *Alnus* sp. (Bullock 1993)
Chrysomelidae indet.					1	N/A
Phyllotreta nemorum (L.)		1	1			on Cruciferae, often on disturbed or cultivated ground and a pest of cultivated turnip, *Brassica* sp. (Duff 1993)
Phyllotreta sp.			1			found on vegetation in disturbed and arable ground
Longitarsus sp.		2				N/A
Altica sp.					1	N/A

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Scolytidae indet.		1				N/A
Curculionidae indet.		1				N/A
Apion (Exapion) difficile (Hbst.)	2					phytophagous associated with *Genista* spp., possibly only on dyer's greenweed, *G. tinctoria* (Hyman 1992)
Apion (s.l.) sp.		1				associated with vegetation in disturbed/arable land
Phyllobius sp.		1				N/A
Notaris acridulus (L.)		1				larvae on roots of aquatic grasses - *Glyceria* aquatica; adults on *Glyceria* ssp. and *Polygonum amphibium* (Hoffman 1958); tall, waterside vegetation (Duff 1993)
Hypera sp.	1					N/A

Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Micrelus ericae (Gyll.)	1					on heaths, especially closed *Calluna* heath, light pine plantations, bogs, also dry turf. Oligophagous on *Calluna vulgaris* and *Erica tetralix* (Koch 1992)
Ceutho-rhynchus contractus (Marsham)			1		1	polyphagous, especially on Brassicaceae, but also on Resedaceae and Papaveraceae, in winter occasionally in grass tussocks, hay, straw, leaves, twigs, moss on trunks and flood debris. Larvae in leaf mines (Koch 1992)
Ceutho-rhynchus (s.l.) sp.		2				N/A
Ceuthorhyn-chinae indet.		1				N/A
Anoplura						
Pediculus humanus (L.)					1	parasitic; the human louse
Mallophaga						
Damalinia ovis (L.)			1		1	parasitic; the sheep louse (Henriksen 1937)

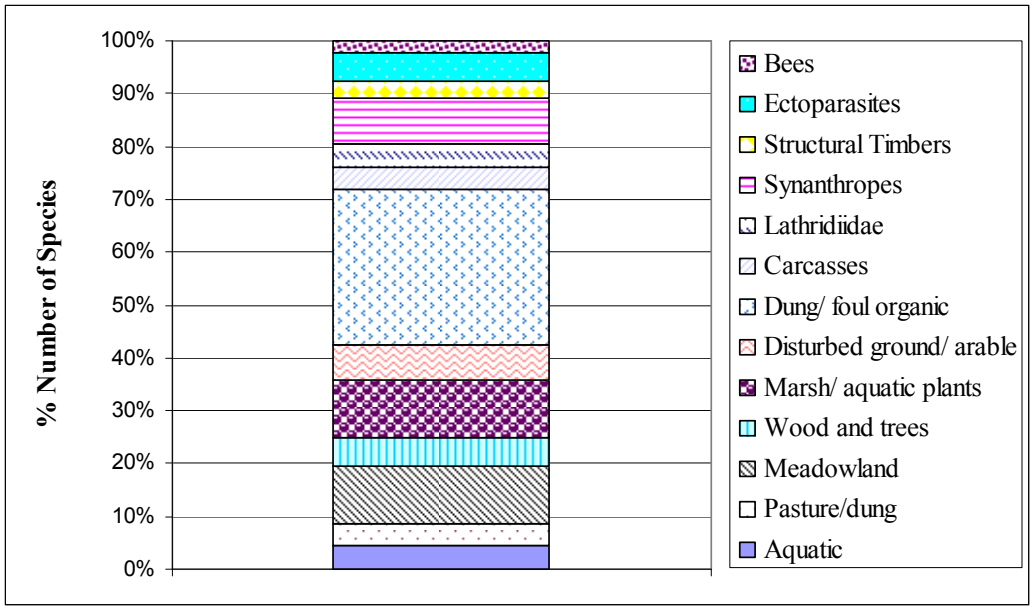
Taxon	22574 MNI per sample			22490 MNI per sample		Ecology
	1485/1	1486/1	1486/T	1469/1	1469/T	
Diptera						
Diptera indet.	16	1	18	15	6	
Melophagus ovinus (L.)		1	1			the sheep ked; lives in wool of sheep
Siphonaptera						
Siphonaptera indet.					1	Parasitic
Pulex irritans (L.)	1					the human flea; also found on goats, pigs, badgers, and foxes
Hymenoptera						
Apis mellifera (L.)	1000	50	50		20	anthophiles; the honey bee
Apoidea sp.					15	anthophiles

References for species' habitats and diets cited in Buckland and Buckland 2006

with the remaining orders were grouped as either ectoparasites or bees.

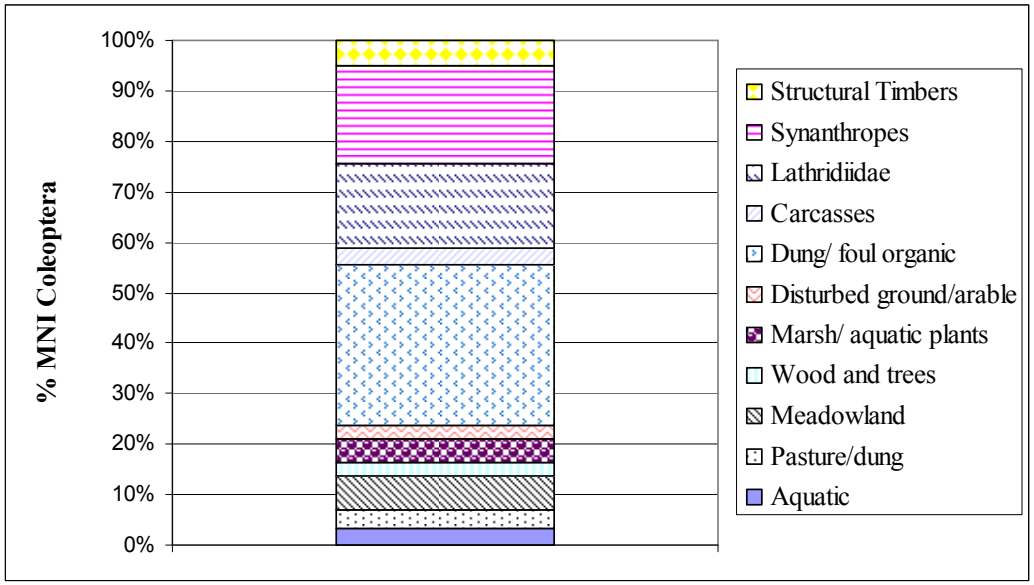
77 % of the coleopteran species have been categorised into one of the ecological categories. The species groupings are presented in Figures 4.8- 4.10. Figure 4.8 shows the number of species recorded for each ecological group as a percentage of the whole assemblage. Figure 4.9 expresses the results as the minimum number of individuals per species group, and Figure 4.10 displays the MNI values of the coleopteran fauna as a percentage of the beetle assemblage. Figure 4.11 does not

Figure 4.8 % Number of species per ecological group



include non-coleopterous species for clarification purposes as the hymenopteran individuals alone comprised 74.5 % of the whole assemblage, which rendered the other groups largely indiscernible in the chart. With the non-coleopterous individuals included, the MNI of only four of the species groups, in addition to the Bees, constituted greater than 1 % of the entire assemblage: Meadowland 1.1 %, Dung/foul organic material 5.1 %, Lathridiidae 2.7 %, and Synanthropes 3.1 %.

Figure 4.9 % Minimum number of individuals reported for each species group

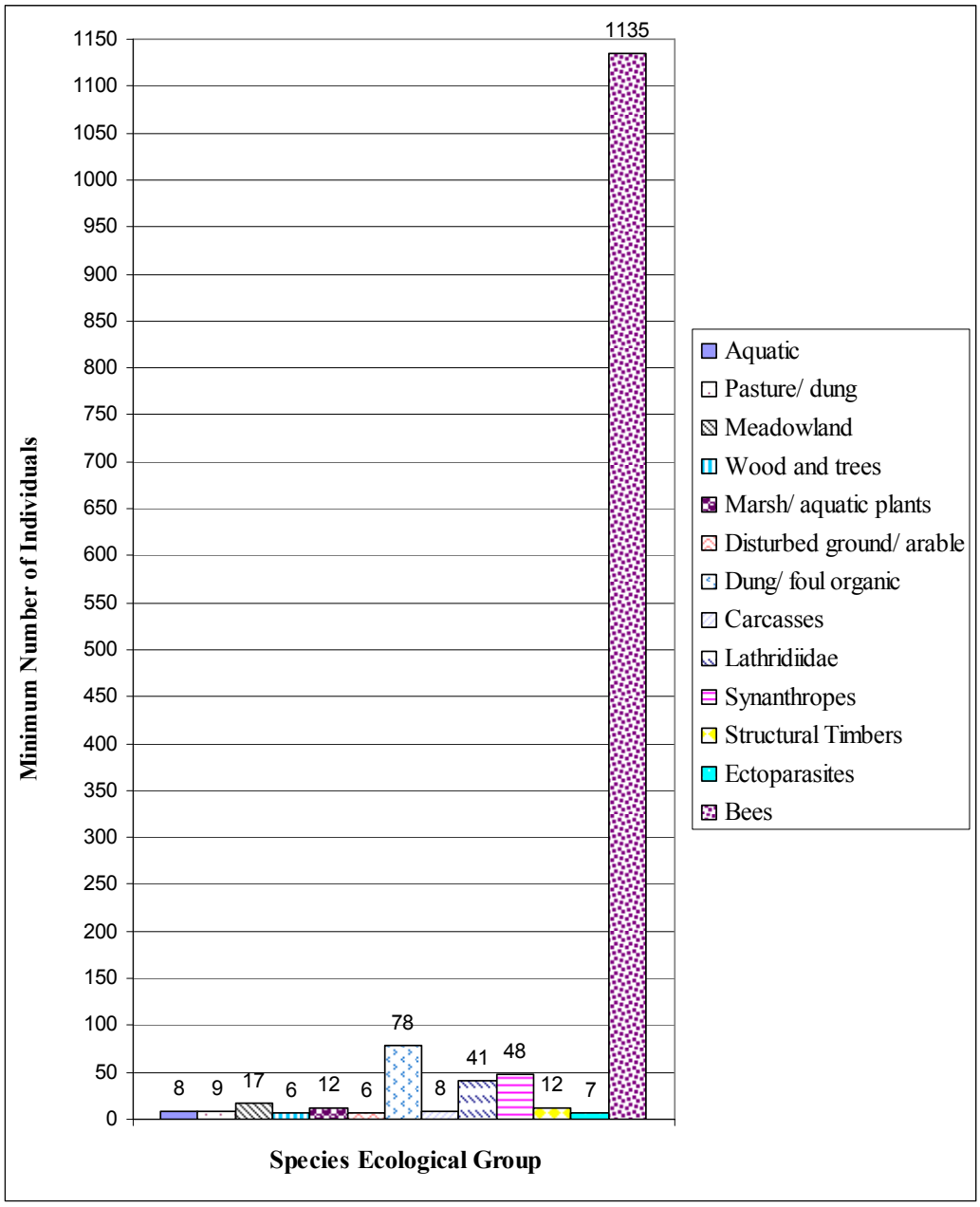


4.3.4 Palaeoenvironmental Reconstruction of Anglo-Scandinavian Coppergate

The aquatic and waterside environment

Coleoptera associated with aquatic (Group 1) and marshland (Group 5) habitats did not form a high proportion of the assemblage. Although combined the number of species from the two groups comprised 17 % of the total Coleoptera in the assemblage, the number of individuals recovered only represented about 8 % of the total beetles. Several of these species could have lived around the river. *Trechus micros*, in particular, is commonly recorded on the banks of running water (Lindroth 1974), and *Bembidion biguttatum* has been found on the banks of rivers and ponds (Lindroth 1985). *Pterostichus melanarius* and *Bembidion gilvipes* have been noted in flood debris and wash zones (Koch 1989a). Moreover, a number of the Staphylinidae (though not restrictively so) occur in muddy banks near water, e.g. *Carpelimus bilineatus* and *Platystethus nitens*. The majority of the waterside and aquatic species most likely entered the archaeological context through association with the nearby

Figure 4.10 MNI by ecological group for 16-22 Coppergate entomofauna



rivers. While the fauna may have occupied similar micro-habitats to their 'indigenous' waterside environment within Tenement C, i.e. puddles, mud, compost heaps, or damp decaying vegetation, the relatively low number of individuals recovered for each species is not unreasonable given the site's proximity to the rivers.

The beetles could have easily entered the structure through flight or, post-mortem, blown in by the wind.

The woodland and scrub

The samples analysed from contexts 22574 and 22490 yielded a limited number of beetles associated with wood and trees. 5.9 % of the coleopteran species and 2.4 % of the individuals from the assemblage are wood dependent. These figures do not include the data for *Anobium punctatum* as the species is almost entirely synanthropic. While *Lyctus linearis* is also strongly associated with structural timbers, the beetle has been recorded in ancient woodland where it develops in dead wood (Hyman 1992). The recovery of *Phymatodes alni* may indicate the presence of *Quercus* spp. (oak), and the species typically inhabits wood with the bark still intact. The beetle *Ptilinus pectinicornis* is especially associated with *Fagus sylvatica* (European beech); unlike *Phymatodes alni*, *Ptilinus pectinicornis* prefers to infest debarked wood. *Melanotus* sp. is indicative of rotting wood and bark. The wood entomofauna recorded from the samples is primarily suggestive of the presence of dead wood rather than living trees and shrubs. Moreover, the samples did not yield any phytophagous species, ground beetles, or staphylinids that are common in woodland communities. The absence of non-wood associated woodland species implies that the ancient environment surrounding the 16-22 Coppergate site was not heavily forested. The wood-related species were probably transported to the site with wood intended for use as timbers in structures, brushwood, and/or firewood.

Grassland, arable, and the open environments

Coleopteran species associated with open environments were fairly well represented in the Coppergate assemblages, though not abundant. Meadowland fauna comprised 11.7 % of the species and 6.9 % of the individuals recovered. The open environment-indicator species at the site were primarily phytophagous or phytodetriticolous. Species that are considered to be specifically grass-root feeders, i.e. assigned to Species Group 11, were not present. The samples yielded coleopterous species, such as *Tachinus rufipes*, which have been recorded at grass-roots (Duff 1993) but are more common in decaying grasses.

Some of the phytophagous Coleoptera recovered from the Coppergate samples are fairly host-specific, including:

Apion (Exapion) difficile	*Genista tinctoria*
Micrelus ericae	*Calluna vulgaris* and *Erica tetralix*
Brachypterus sp.	*Urtica* sp.

The weevil *Apion difficile* is highly indicative of the presence of the low-lying sub-shrub *Genista tinctoria,* dyer's greenweed. *G. tinctoria* performs poorly in wet soils and is believed to favour dry meadowland and heathland environments (Bown 1995). The plant is not likely to have been indigenous to the riverside environment near the Coppergate. The two individuals of *A. difficile* present in the samples were likely transported to the site along with the greenweed, which may have served as a dye source.

The weevil *Micrelus ericae* is supportive of a heathland connection. *M. ericae* feeds on *Calluna vulgaris* (common heather or ling heather) and *Erica tetralix* (the cross-leaved heath or bell heather). Both plant species inhabit wet heathland and bogs. Today, ling heather and to lesser extent bell heather are 'coveted' sources of

honey in Britain, and beekeepers will establish apiaries near heather stances (Weightman n.d.). Moreover, Beekman and Ratnieks (2000) found that honeybees would forage *Calluna vulgaris* stances located over 9.5 km from their hive. While the Anglo-Scandinavians may have also been exploiting heather for honey, especially given the large number of honeybees recovered from the site, the presence of *M. ericae* suggests the physical transportation of the plant to the site.

The British *Brachypterus* species are typically monophagous on nettles, e.g. *B. urticae* F. and *B. glaber* Steph. The nettles may have grown along the river bank. However, the disturbed ground of a grassland environment or woodland margin would also support the plants. The beetle was present but not abundant in the assemblage.

7 % of the Coleoptera species and 2.5 % of the minimum number of individuals were associated with arable or bare ground. Two individuals of *Phyllotreta nemorum* were recovered, which as mentioned above, is associated with Cruciferae. Many of the Ceuthorhynchinae species feed on weeds of the family Cruciferae. While common in flood plains and wash zones, the carabid *Pterostichus melanarius* also occurs in high numbers on the bare ground between ground level plant stems as well as in low numbers in grasslands (Robinson 1979).

There was little evidence of pastureland species recovered from the site. A large number of *Aphodius* species are associated with dung in the field. *A. prodromus* is most commonly recorded in horse dung but has been noted in decaying vegetation (Koch 1989a). *Cercyon atricapillus* is also an indicator of horse dung usually in pastures. Unfortunately the majority of the dung-related beetles, which were recovered from the site, are difficult to interpret because they are also known to inhabit decaying vegetation. Although the samples contained no purely dung related

fauna, which makes the presence of a pastureland-herbivore connection difficult to discern, the Coppergate contexts produced a number of insect species associated with decaying vegetation. Furthermore, the samples contained decomposer species like *Xantholinus linearis*, which appear to avoid faeces altogether (Buck 1955; Robinson 1979). If dung was present at the site, it was not abundant and may have been kept in low quantities to fuel fires.

Beetles associated with grassland, arable land, and pastureland environments suggest an imported component rather than local signal to the site. While *Brachypterus* sp. may be connected to the local riverside environment and *Phyllotreta nemorum* may have arguably inhabited the vegetation in the local gardens, *Apion (Exapion) difficile* and *Micrelus ericae* are representative of plants that may have been transported from the hinterland regions such as the heathland on Vale of York.

Other habitats

Several of the insect species recovered from the Coppergate samples are synanthropic. Beetles especially associated with structural timbers comprised 4.8 % of the coleopteran individuals. *Anobium punctatum* was present in four of the five samples. The species is strongly associated with worked wood and may infest furniture, structural timbers, and flooring as well as the wood in tools (Buck 1958). Although *Lyctus linearis* can occupy a similar habitat as *A. punctatum*, it was only present in one of the samples. The beetle *Ptilinus pectinicornis* was also present and has been known to infest furniture wood (Koch 1989a).

Many of the decomposer beetles are associated with decaying hay or straw and can be categorised as what Carrott and Kenward (2001; Kenward and Carrott 2006) called house fauna. Decomposers considered house fauna are typically associated

with dry, possibly mouldy habitats. *Ephistemus globulus*, *Xylodromus concinnus*, and *Acritus nigricornis* were ranked present to abundant in the samples and are common in decaying hay and straw. In sample 1487, Hall and Kenward (1999b) calculated the MNI of the dry decomposers as 35 %. *Crataraea suturalis* is also associated with mouldy straw and is strongly synanthropic (Harde 1984). Moreover, the mycetophagous Lathridiidae fauna from Species Group 8 and *Cryptophagus scutellatus* are frequently recorded in mouldy hay in barns. The hay indicator species suggest the presence of hay and straw at the site, which may have served as floor litter or thatch.

Ptinus fur is also representative of Carrott and Kenward's (2001) house fauna group. Although the beetle has been found living in mouldy hay and straw, it is rather polyphagous and has been noted in birds' nests and old beehives (Koch 1989b). While potentially associated with the material comprising the litter and/or thatch, the *P. fur* individuals may have also inhabited the hives of associated with the abundant remains of honeybees, MNI 1135, which constituted 74.5 % of the assemblage. While the bees may have been transported with the hives to the site and then killed off during the honey processing, the number of individuals suggests that the hives were most likely being kept on the site. This is further supported by the recovery of large numbers of bees from for of the five samples, which implies that *Apis mellifera* were fairly prevalent around the site as the mass death assemblage was not isolated to a single location.

The beetle *Ptinus fur* has also been considered a pest of stored cereal products (Mound 1989). *Tenebrio obscurus* and *Blaps* sp. are present in low numbers and support the presence of stored products, such as flour or cereals. However, *T. obscurus* has also been noted in rotting bark and bird's nests (Koch 1989a), and *Blaps*

sp. feed on a range of vegetable matter including straw waste (Horion 1956). While grains and cereal products may have been kept at the site, the recorded insect fauna is not conclusive as it neither proves nor disproves the presence of cereals in the contexts. The more indicative grain species, i.e. *Sitophilus granarius*, *Cryptolestes ferrugineus,* and *Palorus ratzeburgi*, were not present in the assemblage but also lack any convincing archaeoentomological record to support their presence in Britain between the end of the Roman occupation and the Norman Conquest.

Beetle species that are typically representative of animal carcasses and carrion comprised 4.7 % of the Coleoptera. *Omosita* species tend to infest carrion in the later stages of decay (Robinson 1991). Beetle species of the genus *Dermestes* have been known to feed on dead insects, animal carcasses, stored meats, skins, hides, furs and bones (cf. Hinton 1945). Two individuals of the beetle *Trox scaber* were also present in the contexts. The beetle has been noted in bird's nests, especially those containing bones and animal remains (Jessop 1986). However, Koch (1989a) noted *T. scaber* on horn cores, fleeces, animal skins, bird carcasses, wasp nests, and mouldy straw. The identified carrion/carcasses associated fauna recovered from the site tend to be more generalist feeders rather than being strongly indicative of a specific resource or material.

The remains of ectoparasites were found in the Coppergate samples. The sheep ked *Melophagus ovinus* and the louse *Damalinia ovis* are associated with sheep. Given the paucity of dung beetles in the contexts, the site was probably not used to keep sheep. However, both *M. ovinus* and *D. ovis* have been used by researchers as evidence of wool processing (Buckland and Perry 1989; Jaques *et al*. 2001; King 2006). The human flea *Pulex irritans* and the human louse *Pediculus humanus* were also present at the site.

4.3.5 Palaeoclimatic Reconstruction

Table 4.4 MCR estimates for fill contexts from Period 4b Tenement C

Sample	TMaxLo	TMaxHi	TMinLo	TMinHi	TRange Lo	TRange Hi	N-SPECIES	Overlap
22574.1485/1	15	26	-9	13	9	27	7	85.71429
22574.1486/1	15	18	-8	7	11	24	13	92.30769
22574.1486/T	15	18	-7	7	11	22	6	83.33334
22490.1469/1				0			0	0
22490.1469/T	11	28	-23	10	8	39	1	100
Site	15	18	-7	7	11	22	20	95

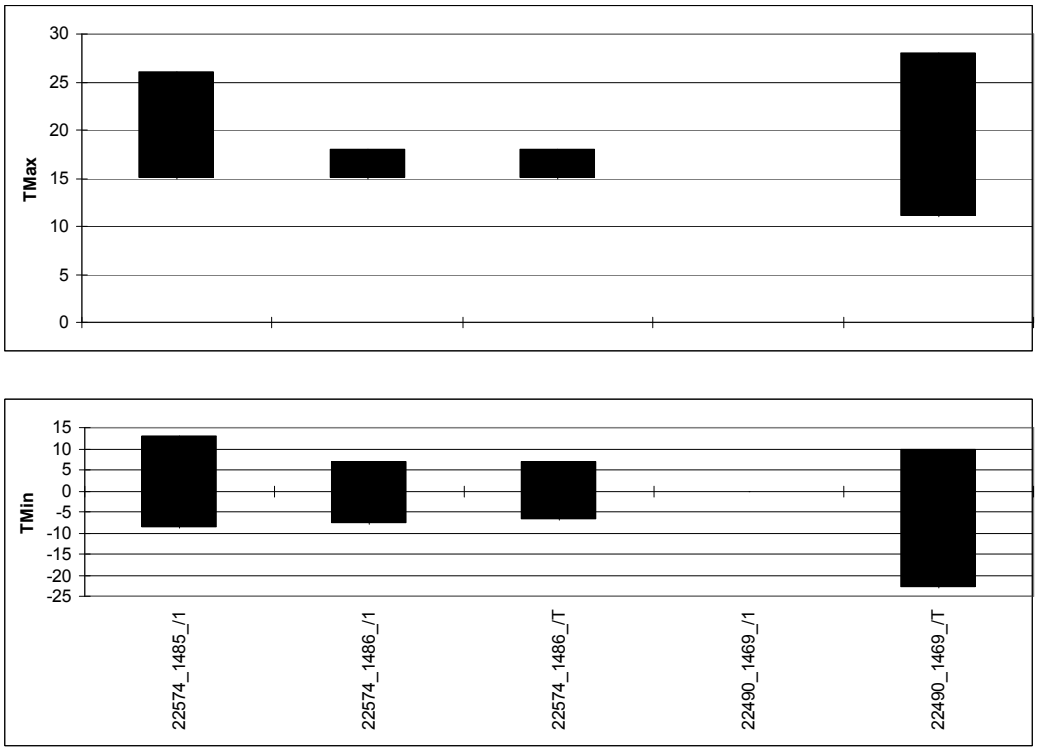
(calculated using Buckland and Buckland 2006)

The palaeoclimate predictions calculated using BugsMCR program (Buckland and Buckland 2006) are shown in Table 4.4 and Figure 4.11. As with the 7-15 Spurriergate samples, only the carnivorous and scavenging beetle species were assessed. Twenty species were analysed [Appendix 1C] and tabulated the temperature of the warmest month as ranging between 15 ˚C and 18 ˚C and the temperature for the coldest month between -7 ˚C and 7 ˚C. The MCR prediction for the Period 4b, 16-22 Coppergate Tenement C samples indicates slightly warmer temperatures during the coldest month relative to the 1st century AD York, but the insect remains from both periods suggest a similar range of temperatures during the warmest month. The range of temperatures estimated for Period 4b 16-22 Coppergate Tenement C samples approximates the range evidenced by beetles from other Anglo-Scandinavian sites in York [Table 4.5].

4.3.6 Discussion: The Environment and Climate of Period 4b 16-22 Coppergate and Implications for Culture Contact

Through the archaeological excavations conducted at 16-22 Coppergate, the insect remains recovered from contexts 22574 and 22490 were believed to be

Figure 11 16-22 Coppergate, York MCR estimates by sample



(calculated using Buckland and Buckland 2006)

associated with the inside of a structure, i.e. Tenement C. However, even without the aid of the archaeological interpretations, the ecological assessment of the insect remains suggests the presence of a structure [Figure 4.13]. *Anobium punctatum* and other Group 10 species implying the presence of worked wood. The samples yielded a number of dry decomposers and hay-associates which are typical of thatch and floor litter. Moreover, the contexts did not contain an abundance of outdoor fauna. While a few riverside and aquatic species were present in the samples, their presence was minimal and in the expected range given the proximity of the River Foss and River

Ouse. Kenward and Allison (1994b) include aquatics and waterside species as well as decomposers and wood associates [Figure 4.14] in their list the original habitats of urban sites. The majority of the other outdoor species, such as those associated with

Table 4.5 MCR estimates for Anglo-Scandinavian sites in York, UK

Sample	TMaxLo	TMaxHi	TMinLo	TMinHi	TRangeLo	TRangeHi	N-SPECIES	Overlap	Environmental Report
1-9 Micklegate	15	18	-7	2	16	22	26	100	Kenward and Hall 2000
6-8 Pavement	15	18	-7	6	12	22	48	100	Hall *et al.* 1983
5-7 Coppergate	15	18	-7	6	11	22	35	100	Hall *et al.* 1983
Period 3, 16-22 Coppergate	16	18	-6	6	11	22	48	100	Hall and Kenward 1999a
Period 4a, 16-22 Coppergate	15	18	-7	6	11	22	23	100	Hall and Kenward 1999b
Period 4b, 16-22 Coppergate; entire site	16	18	-6	6	11	22	40	100	Hall and Kenward 1999b

(calculated using Buckland and Buckland 2006)

meadowland, pastureland and heathland, are indicative of animal and plant materials, which are reflective of two potential industries: 1. honey and wax and 2. wool and dye.

The recovery of large quantities of honeybee remains suggests that the Anglo-Scandinavians were exploiting *Apis mellifera*. The physical presence of honeybee remains indicates that the Anglo-Scandinavians would have had access to 'local' honey and wax resources rather than needing to import the commodities. The number of individuals in the death assemblage suggests that the honeybees would have kept a

Figure 4.13 Likely sources of insect remains in building deposits (Kenward 1985, 105)

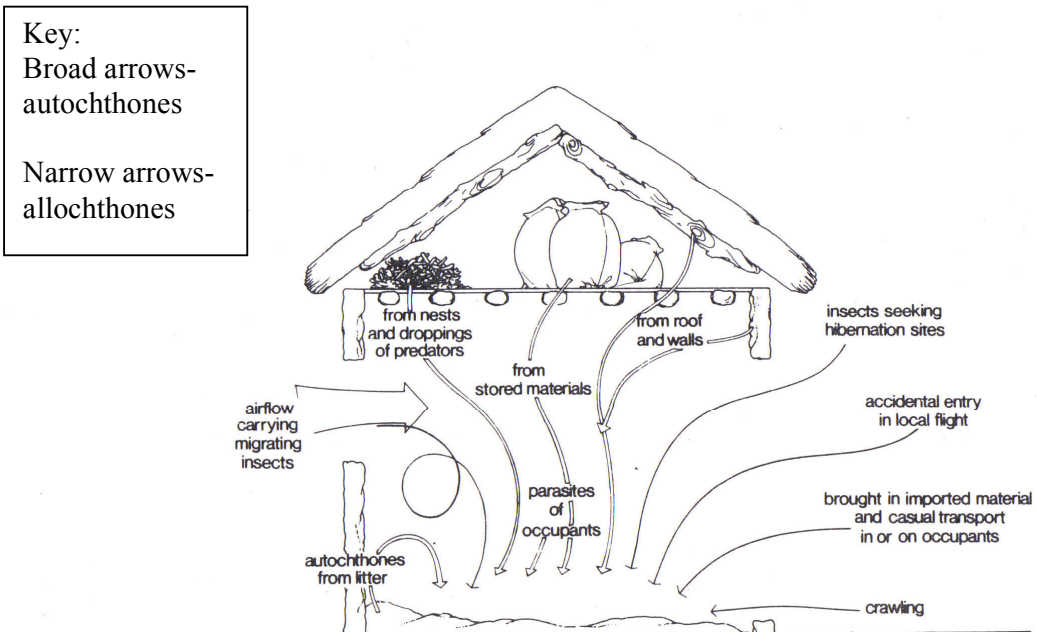
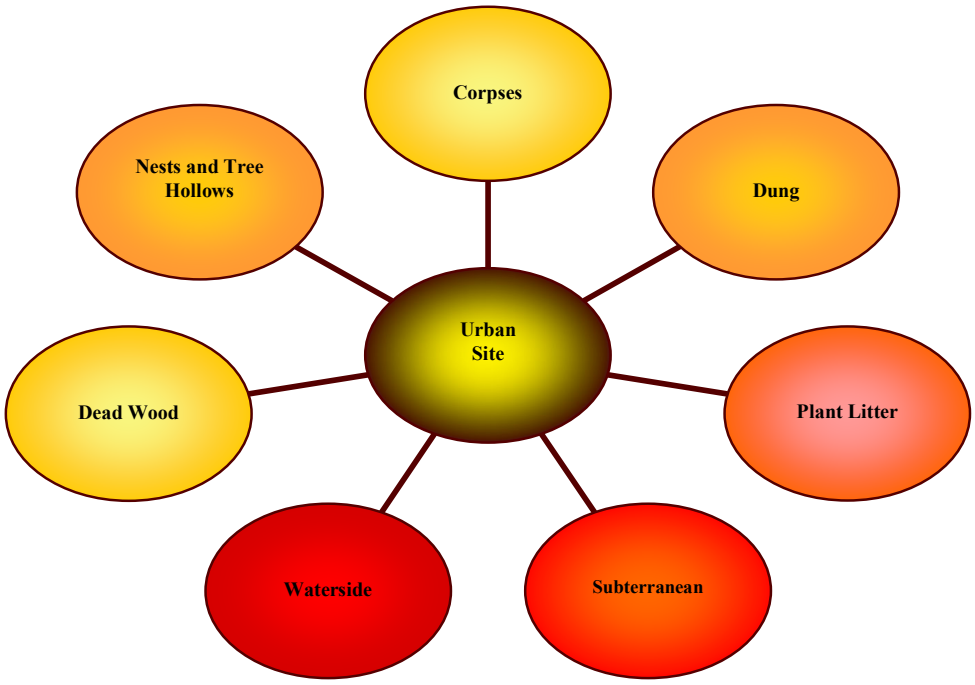


Figure 4.14 Probable starting habitats for urban insects



(King 2006, 79; Reconstructed from Kenward and Allison 1994b, 60-61)

hive near, if not within, the structure. Furthermore, although largely hypothetical and at risk of stretching the evidence, the presence of heather at the site, evidenced by *Micrelus ericae*, may have been gathered from the heathland, and potentially the turnip *Brassica* sp., suggested by *Phyllotreta nemorum*, from the meadowlands (see Columella's *RR IX* 1941) to encourage the pollination of sweet flowers and plants. The alternative is that the hive was located elsewhere and the bees and the hive were transported to the site for processing, but individuals would have likely been lost during transport resulting in a smaller death assemblage. However, if numerous hives were being transported and processed, a large death assemblage would also be expected under good preservational conditions. While the first possibility seems most likely, the interpretation is purely speculative and the possibility of hive transportation should not be dismissed. Given the documentary evidence describing the handling and relocation of beehives from the Roman era (cf. Columella's *RR IX* 1941), it is likely that Anglo-Scandinavians would have been familiar with methods of transporting active hives.

Did the Anglo-Scandinavians import the honeybee to Britain? There are several races of honeybees, and Kenward (pers. comm) has identified the Coppergate remains as *A. mellifera mellifera* L., the European Dark Bee, which is a cold-tolerant species. Today, natural distributions of the European Dark Bee are found as far north as 60˚ N latitude (Ruttner *et al*. 1990). Although the honeybee is capable of generating and regulating heat within clusters (Ruttner *et al.* 1990), Villa and Rinderer (1993) reported the death of whole colonies when temperatures were held at 0˚ C for 10 days. Considering the estimated coldest month temperature range of -7 ˚C and 7 ˚C in Anglo-Scandinavian York, colonies of *Apis mellifera mellifera* would have been

able to survive in the wild. As such, the palaeoecological assessment cannot provide insight into whether the Anglo-Scandinavians imported hives of honeybees from afar.

The insect remains recovered from the Tenement C contexts are also indicative of the processing of wool and dyeing. As mentioned above, there was little conclusive evidence to support the presence of dung and very little pastureland fauna at the site, which implies that the sheep-associated ectoparasites, i.e. *Melophagus ovinus* and *Damalinia ovis*, do not indicate the stabling of sheep but rather the processing of wool. Several other faunas support occurrence of the wool processing at the site. The carrion and carcass-associated species, especially *Trox scaber* and *Dermestes* sp., would have been attracted to the stored wool and skins. The foul organic species from Species Group 7 may have been attracted by storage and use of urine to bleach and delouse the wool (Stead 1982; Buckland and Perry 1989; King 2006). The recovery of *Apion (Exapion) difficile* evidences the presence of the plant dyer's greenweed, *Genista tinctoria*. *G. tinctoria* and quite possibly the heather species, *Calluna vulgaris* and *Erica tetralix*, could have been employed as dye plants (Kenward and Hall 1995; Hall and Kenward 1999b). The dye plants may have been brought to the site to aid in the dyeing of the wool or other fabrics.

In an effort to determine whether the wool was acquired from local or imported sheep, the thermal requirements of the ectoparasites were considered. Graham and Taylor (1941) reported no emergence of *Melophagus ovinus* from puparia at temperatures below 18 ˚C and the death of newly emerged keds within 24 days at 4 ˚C when the species was separated from its host. *Damalinia ovis* appears to be less cold tolerant. Murray (1957ab) demonstrated that temperatures between 32 and 40 ˚C were required for the sheep louse to lay eggs, and Murray (1960b) showed that morphogenesis of the eggs was only completed within the temperature range 30-

39 ˚C. However, when development was completed, the eggs hatched between 22 and 42.5 ˚C. It is important to note that temperatures near the skin of the sheep are warmer than the ambient temperatures. Murray (1960a) reported that temperatures near the skin, which was covered by five centimeters of wool, reached 39 ˚C when the atmospheric temperature was 28 ˚C.

The temperature requirements of the ectoparasites imply that neither species was likely to have evolved in Britain. However, *M. ovinus* would have been able to survive and reproduce in the wool microclimates once introduced to the region. As a wingless fly, the species is believed to spread only through direct contact (Small 2005). While the eggs of *Damalinia ovis* would have been able to hatch when kept in the wool, the thermal requirements necessary for ovipositioning to occur and the morphogenesis of the eggs would have barely been attainable during the warmest months in Anglo-Scandinavian York. Considering an 11˚ C temperature increase from the skin level microclimate to atmospheric temperature, a TMAX of 18˚ C would suggest a temperature under the wool approximating 29˚ C. If the sheep were kept in sheltered environments such as stables, the skin-level temperature would have been even higher. Moreover, if the Anglo-Scandinavians were keeping sheep species with longer hairs or thicker wools, the skin-level temperatures would have been warmer, which would have theoretically enabled the sheep louse to reproduce and survive in colder environments. Regardless, the presence of *D. ovis* implies a connection to warmer climates, which would have allowed the louse to enter Britain.

Unfortunately, temperature requirements and tolerances of the probable dye plant associates, *Apion (Exapion) difficile* or *Micrelus ericae*, are not known. According to modern distribution regards, both weevils appear to be fairly cold tolerant. *A. difficile* has been reported as far north as 54.1˚ N in the United Kingdom

(GBIF 2009a) and has been noted in Dorset, Sussex, Kent and Gloucester in England (Morris 1990). Morris (1990) also reports the distribution of the beetle extending north to Denmark. *M. ericae* is a subarctic to temperate species (Böcher 1995) and has been reported as far north as 64.7˚ N (GBIF 2009b) and is distributed throughout central Europe (Koch 1992) and the United Kingdom (Joy 1932; Duff 1993). The modern distribution of both species suggests that they may have been indigenous to Britain. However, neither species is likely to have been autochthonous to the Coppergate site given their habitat preferences (see above), and both were probably transported to the site from York's hinterlands.

4.3.7 Summary

The samples examined from Period 4b 16-22 Coppergate, York contained several indicator species associated with human commodities and industries. *Anobium punctatum* and *Lyctus linearis* indicated the presence of structural timbers, which were most likely associated with the post-and-wattle building. The recovery of *Apion (Exapion) difficile* suggested that dyer's greenweed was stored and/or used at the site. A similar interpretation was offered for the heathland species *Micrelus ericae* and its association with heather. The *Tenebrio obscurus* and *Blaps* sp. specimens may indicate the presence of stored cereals; however, as the species have also been associated with other habitats including nests, straw waste, and bark, which may have been present at the site, the findings were inconclusive. Wool processing was occurring at or near the site as evidenced by the sheep ked *Melophagus ovinus* and the sheep louse *Damalinia ovis*. *Trox scaber* may also support the processing and/or storing of animal materials such as wools, hides, and furs. The large number

of honeybees reported from the contexts evidences the availability of honey and wax to Anglo-Scandinavians.

The comparison of the species' thermal requirements and the site's MCR revealed that most of the indicator species would have been able to survive away from human habitation in Anglo-Scandinavian Britain. *D. ovis* was an exception as the species' preferred temperature range was indicative of warmer climates. However, the sheep louse may have been able to complete its life cycle once entering Britain if it infested sheep with thick or longhaired wool and/or sheep which were kept, at least part of the time, in indoor environments, e.g. stables.

Several of the indicator species are strongly associated with environments, e.g. heathland/moorland, which would not have likely been available in urban York. The species are more indicative of environments that, at least today, may be found in the York's hinterland regions, such as the Vale of York or Askham Bog. The presence of *Micrelus ericae* and *Apion (Exapion) difficile* suggest that the Anglo-Scandinavians were exploiting the hinterland environments and having *Genista tinctoria*, *Calluna vulgaris*, and/or *Erica tetralix* transported to the site. However, it is possible that both the plants and their associated beetles may have been imported from a greater distance, but such resolution is beyond the scope of a palaeoecological assessment.

4.4 Conclusion

The palaeoecological approach provides a very versatile tool for the assessment of archaeologically recovered insect remains. Insect subfossils have been effectively employed as bioindicators of palaeoecosystems and archaeological reconstructions as a result of their ecological diversity, their tendency to be often ignored or perceived as unimportant to humans, and their sensitivity and rapid

reaction to environmental change (see Coope 1977b; Elias 1994; Bain 1997; 1998; Kenward 1999; Whitehouse 2006). Insects, therefore, have huge potential to stand as evidence of past human activity, living conditions, diet, climate and ecology. While archaeological insects pose questions about the origin and development of regional faunas, palaeoentomological studies have revolutionized perceptions about rates of evolution and the morphological and ecological constancy of species, as well as climatic change. The fossil remains of insects buried deep in the earth are a crucial but often neglected part of investigations of the human, and wider ecological and climatic, past. In regards to the present evaluation, the analysis of archaeoentomological subfossils enables researchers to glean a better understanding of palaeoeconomic activities.

By superimposing the habitats and ecological requirements of modern insect species over the fossil record [Chapter 2], certain insect remains retrieved from the archaeological sites are invaluable as indicators of the presence of specific plant and animal materials, which may have been exploited by humans in the past. The insects may stand as primary, e.g. *Apis mellifera* indicating the availability of honey and beeswax, or secondary evidence, e.g. *Sitophilus granarius* suggesting the presence of stored grains, of exploitable commodities.

Although insect remains may be 'reliably' used as indicators of materials, they have limited effectiveness as a tool for discerning culture contact, human movement, and palaeoeconomics. By assigning species to broad ecological groups, the presence of certain environments is discernable, e.g. grassland, pastureland, heathland, woodland, etc. Moreover, quantitative assessment of the material may be employed to determine the autochthonous and allochthonous components (see Kenward 1978; Perry *et al.* 1985). Unfortunately, palaeoenvironmental tools do not provide a means

of assessing distance and researchers are forced to speculate as to the most likely source of the allochthonous species. For example, *Apion (Exapion) difficile* indicates a heathland or meadowland connection and the presence of *Genista tinctoria* in Anglo-Scandinavian York, but where did the dyer's greenweed originate? Today, *G. tinctoria* may be found in Vale of York (A. Hall pers. com); however, it is also has a continental European distribution ranging from Spain in the south to Norway in the north (see GRIN 2009). Were the Anglo-Scandinavians electing to import the dyer's greenweed, or were they harvesting it from the local hinterlands?

Another major limitation of single site palaeoecological assessments is that it does not provide a timeframe for the initial introduction of potential exploitable materials. For example, was *G. tinctoria* available in Northern England prior to the arrival of the Anglo-Scandinavians, or do the modern populations stem from individuals purposely introduced in the past? This is especially apparent in the palaeoclimatic aspect of the present analyses. While a comparison of the MCR data and species' temperature requirements may help identify probable ecological outlier taxa, it does not account for the possibility that the species may have been introduced during earlier periods.

A timeframe for the introduction of various insect species may be established through application of methods which consider the presence of individual species at multiple sites and assess changes in spatial and temporal changes in species' distribution, e.g. the biogeographical approach [see Chapter 5]. Furthermore, isotopic and genetic analyses may be of assistance in helping to overcome the problem of multi-region resource availability by identifying geographic and phylogenetic similarities and differences within and between assemblages [see Chapters 6, 7, and 8].

Chapter 5

Grain Pests: An Archaeobiogeographical Account of the History of their Dispersal

5.1 Introduction

Grain and other storage pests cause significant depletion of human food resources at the present day (e.g. Tyler and Boxall 1984; McFarlane 1989; Payne 2002), and the beetles are among the most economically important. Documentary records show that in the 19th and early 20th century they represented a very serious cause of food loss (cf. Munro 1966), and remains recovered from archaeological deposits indicate that grain beetles were often abundant at earlier dates as well. These beetles, which are strongly synanthropic in most of their range, are of substantial interest from the ecological point of view, as aliens which have invaded artificial habitats, often alongside native species. From a biogeographical angle they are significant as species spread by human activity, often well beyond their naturally viable distributions. Where did they originate, and when did they spread? They are also of considerable significance in studies of early agriculture: when did the first farmers encounter these pests, and how significant were they among the tribulations Neolithic people endured?

Biogeographers typically recognise three distinct types of dispersal pathway by which organisms may spread between areas through natural means: the corridor, the filter, and the sweepstakes route. In the corridor route, the pathway may include a wide variety of habitats with the areas at the two ends possessing an almost identical biota, e.g. pre-Ice Age Eurasia. The corridor pathway would enable the majority of organisms to transverse between the two end areas with little difficulty. The filter pathway consists of a more limited variety of habitats so that only organisms that can exist in those habitats can disperse between the interconnecting regions, e.g. the tropical lowlands of Central America. In the third type of dispersal pathway, the end regions are isolated as the result of the interconnecting regions consisting of

completely different environments, e.g. islands surrounded by sea (Cox and Moore 2000).

In *The Ecology of Invasions by Animals and Plants*, Elton (1958) introduced the concept of man as an impetus for the passive distribution of animals and plants beyond the prescribed boundaries of their 'original' geographic range. Building on that premise, Buckland (1981) reviewed the archaeoentomological records available at the time for stored product pests and attempted to trace their dispersal. While Buckland successfully demonstrated that pests were capable of being transported by man in the past, he was unable to conclusively deduce patterns of movement or origins for the evaluated species due to a paucity of fossil, particularly non-British, data. Buckland offered speculations and pleaded for the undertaking of more archaeoentomological evaluations in Eurasia. In this chapter, the currently available fossil and literary evidence is employed to attempt to take the story forwards and to ascertain the geographic origins of the stored cereal insect pests, their mode and route of dispersal in the past, and their likely impact on early societies from the Neolithic Period through the Roman Era.

5.2 The Grain Fauna

The beetle fauna associated with stored cereals consists of a group of species which have been ecologically classified in the northwest European archaeological context by Kenward (1978; 1997) as 'strong synanthropes', mostly thermophilic and wholly dependent on artificial habitats for survival in the region. This does not imply that the individual species are unable to survive beyond the boundaries of the human-created artificial environments in other regions, as the classification is climate-dependent, although in fact some of the species are virtually unknown in natural

habitats. A brief review of the biology of the typical grain pests is needed in order to set the archaeological records in an ecological context.

Stored grain insects are often grouped based on their capacity or ability to infest undamaged kernels as primary or secondary pests. Primary pests are

1.) "capable of successfully attacking, feeding and multiplying on previously undamaged grains;
2.) are adapted to feed on a narrow range of commodities;
3.) usually cause very distinctive damage;
4.) usually develop within the grains, and often complete their entire development within a single grain;
5.) are selective in their egg-laying behaviour;
6.) often infest the ripening crop before harvest; and
7.) usually cannot develop on the same food if the grains are ground (milled),

[and] secondary pests are

1.) not capable of attacking previously undamaged grains, but can only attack and breed in grains that have been damaged by primary pests, physical damage by bad handling, threshing, drying or intentional processing that removes or damages the seed coat;
2.) usually attack a very wide range of commodities;
3.) usually cause non-distinctive damage;
4.) sometimes develop within grains, but never complete their development within a single grain;
5.) do not usually have selective egg-laying behaviour;
6.) are very rarely found on the crop at harvest; and

7.) are usually capable of developing on the same food after it is ground" (Semple *et al.* 1992).

While a number of cereal pests have been recovered from non-synanthropic situations, mostly in tropical and subtropical areas, the granary weevil, *Sitophilus granarius* (L.), has yet to be found in a natural habitat and its origin is particularly uncertain. Hoffman (1954) has recorded the weevil from a wide range of stored products including wheat, rye, barley, maize, oats, buckwheat, millet, chickpeas, and even chestnuts, acorns and cornmeal; however, despite its catholic tastes, it is most common today as a primary pest in stored cereal crops. Buckland (1990) has observed that the caryopses of wild cereals may be too small for successful breeding as the larvae develop entirely inside the grain or seed, and on-going experiments at the laboratories at the University of York appear to confirm that *S. granarius* is unable to develop or unwilling to lay in grains smaller than millet. While both Zacher (1938) and Howe (1965) have proposed acorns as the original primary host of the weevil, the species seems unable to breech undamaged shells, and the micro-habitat similarities between rodent stores and the grain stores of man point to rodent stores as a more likely origin. The adult weevils are characterised by a forward, snout-like extension of the head, the rostrum, which bears the mouth parts. *S. granarius* has elongated oval punctures on the dorsal surface of the prothorax and has elytra that are longitudinally grooved with fine punctures. In contrast with its congeners *S. oryzae* and *S. zeamais,* which in the tropics may infest crops in the field (Krantz *et al.* 1978), the granary weevil is flightless, and it is capable of adjusting to unheated indoor habitats in the cooler climates of Northern Europe. As a poor disperser (cf. Mlambo 1980), its present cosmopolitan distribution can be attributed to accidental transportation by man.

The rice weevil, *Sitophilus oryzae* (L.), differs morphologically from the granary weevil in the deep round punctures on its prothorax and is almost identical to its sibling species the maize weevil, *Sitophilus zeamais* (Mots.). While mating incompatibility confirmed separate species (Floyd and Newsom 1959), only the aedeagal and eighth sternite of female characters appear consistent, as determined by DNA analysis (Hidayat *et al.* 1996), for morphological distinction between *S. oryzae* and *S. zeamais*. Both species are flighted and are believed to be of tropic origin. Despite their names, they attack a wide range of stored cereals: rice, rye, maize, wheat, barley, millet, etc (Harde 1984), as primary pests. The rice weevil has been known to infest crops in the field (Kranz *et al.* 1978; although this has been contested by some researchers, e.g. Mlambo 1980) and has been recorded under bark and on leaves in North America (Dillon and Dillon 1972). However, in Central Europe the species are not found in the open but only in artificial environments (Harde 1984). Because of the two species' tropic preferences, their presence in temperate regions can be viewed as invasive rather than native.

The bostrychid *Rhyzopertha dominica* (F.), the lesser grain borer, is a primary pest of stored grain as an adult and larvae. However, it has also been recorded on flour, dried tubers (Hill 1994a), and seeds. While the lesser grain borer was originally identified and described from South America, it is now completely pantropical (Munroe 1966) and appears to have had an Old World presence and origin (Kislev 1991). The pale to dark reddish-brown species is recognisable by the transverse row of teeth at the front of the pronotum (Kislev 1991). Like the *Sitophilus* weevils, *R. dominica* is capable of causing great damage to food supplies through extensive feeding.

The saw-toothed grain beetle, *Oryzaephilus surinamensis* (L.), is considered a secondary pest, typically feeding on grain previously attacked by primary pests such as *Sitophilus granarius*. The adults have been noted to be carnivorous, feeding on larvae, but they also feed on meal and other ground starchy foods as well as previously damaged or spoiled grains. Although the saw-toothed grain beetle has been recorded in warehouses, mills, granaries, and brewery silos (Zacher 1927), Hunter and others (1973) speculate that its primary habitat is under loose bark, and Horion (1960) additionally suggest fungoid timber. Buckland (1990) puts forth that the fungus may be a necessary intermediary between the natural and artificial environments however once established that the damp grain could mimic the micro-habitat conditions of the under bark pabulum resulting in a suitable environment for the species. *O. surinamensis* is recognisable by the six tooth-like projections along each side of the prothorax. While capable of flight, the worldwide distribution of *Oryzaephilus surinamensis* is most likely due to the transportation by man.

The flat grain beetle or rusty grain beetle, *Cryptolestes ferrugineus* (Steph.), is another secondary pest of stored product cereals and is largely associated with processed foods. It is found in wheat, ripe, maize, meal, and flour as well as dried fruits (Horion 1960). Like *Oryzaephilus surinamensis*, the original habitat of *C. ferrugineus* may have been under loose bark (Hunter *et al*. 1973) where it probably fed on fungi (Halsted 1993) and may have found a similar micro-habitat amongst the stored grains. *Cryptolestes ferrugineus* is a very small (1.5 mm) reddish-brown flattened beetle with long filiform antennae (Mound 1989). Although the flat grain beetle is cosmopolitan, Halsted (1993) suggests that it is being replaced by its congener the Mediterranean flat beetle, *C. turcicus* (Grouv.), in temperate regions. As

the two species have similar tastes, interspecific competition may have impacted survival and distribution in the past.

Palorus ratzeburgi (Wiss.), the small-eyed flour beetle, is found in stored cereal products, particularly mouldy grain residues previously attacked by grain weevils (Brendell 1975). The small-eyed flour beetle is known to be predacious on other pests as well as feed on the faeces of *Sitophilus granarius* (Pals and Hakbijl 1992). Having been recorded living under bark in Germany (Reitter 1911 cited in Solomon and Adamson 1955), *P. ratzeburgi* possesses a similar ecology to *C. ferrugineus* and *O. surinamensis* and mostly likely adapted to stored product environment in a similar fashion. *Palorus ratzeburgi* is noted as a small (2-3 mm), oblong, flattened reddish-brown beetle. The sides of its head are not strongly flexed upwards and the eyes are small and round (Brendell 1975). *P. ratzeburgi* occupies a similar habitat to its congener *P. subdepressus* (Woll.), but while both are found in the Mediterranean region, *P. subdepressus* is not established in Britain (Brendell 1975) and is particularly widespread in the tropics (Rees 2007).

Tribolium castaneum (Hbst.), the rust-red flour beetle, is a secondary pest of stored grain and an important pest of cereal products, flour and bran (Brendell 1975). It is characterised by its parallel sides and, in adults, the eye partly divided by a side margin of the head (Kislev 1991). Although it is now cosmopolitan, Hinton (1948) believes it to have originated in India where it has been recorded in the wild. Outside of the tropics, it is largely restricted to heated buildings (Brendell 1975) and occasionally under bark (Whitehead 1999). It appears unable to survive cold temperatures (Solomon and Adamson 1955).

The tenebrionid *Tribolium confusum* (Duval), the confused flour beetle, is more cold tolerant than its congener *T. castaneum* and has been regarded as a

temperate species (Solomon and Adamson 1955). Kislev (1991) states that it differs morphologically from the rust-red flour beetle by possessing a wider separation between the eyes underneath the head. The confused flour beetle has been recorded infesting stored grains and cereal derivations where it is believed to be a secondary pest (Brendell 1975). Although *Tribolium confusum* may be regarded as a temperate species, Panagiotakopulu (2001) notes that, like *T. madens* (Charp.), it is thought to be of African origin.

While the species described above have an established, if not extensive, fossil record, the archaeological presence for some of the other beetle grain pest fauna is more sporadic, but noteworthy. The thermophilic khapra beetle, *Trogoderma granarium* (Everts), is a small (1.5-3.0 mm), oblong oval insects with unicolorous elytra and evenly rounded eyes (Mound 1989). While the adults do not normally feed, the khapra beetle larvae feed almost exclusively on grain and cereal products (Munro 1966). *Tenebroides mauritanicus* (L.), the cadelle, is a large (5-11 mm) shining-black oblong beetle with a prothoraxic base distinctly separated from the base of the elytra (Mound 1989). As both adults and larvae, the cadelle attack cereals, cereal products, nuts, and dried fruit and have been known to be partly predacious (Dillon and Dillon 1972). The cadelle is larger than most stored product pests other than the *Blaps* and *Tenebrio* species, which have a preference for grain but are largely omnivorous scavengers. Similarly, the lesser mealworm beetle, *Alphitobius diaperinus* (Panz.), attacks a wide range of stored products including grain but is primarily an omnivorous feeder (Brendell 1975). *Alphitophagus bifasciatus* (Say), the two-banded fungus beetle, is commonly recovered from mouldy and decaying grain and vegetable products in stables, granaries, and warehouses where both the adults and larvae feed on mould (Brendell 1975). Some of the species usually listed among

'pests' in the stored products literature are in fact quite eurytopic, able to exploit material such as birds' nests and debris under bark in nature, and thatch and litter in settlements. One such beetle is the biscuit beetle (or drugstore beetle), *Stegobium paniceum* (L.), a pest of a range of farinaceous foods (Buck 1958). It tolerates quite low temperatures.

5.3 Records of the Fauna

5.3.1 Pre-Roman Middle East

At the present, the Har-ra==Hubullu Tablets XI-XV contain the earliest written zoological record supporting the human acknowledgement of the presence of stored product pests, listing 33 names of crop and stored product pests (Landsberger 1934). During the nineteenth century, these cuneiform texts were recovered from the royal library of the Assyrian king Ashurbanipal (2618-2577 BP) at the ruins of Nineveh in Mesopotamia. While it was compiled during the ninth century B.C. in bilingual Sumero-Akkadian script, the tablets are believed to be based upon Hammurabian period (3678-3636 BP) lists which in turn developed from even older ones (Harpaz 1973).

On Tablet 14, the Sumerian *uh* (Akkadian *kal-ma-tum*) denotes the group containing insect vermin. According to Landsberger's (1934, 20-21) translation, the Sumerian *uh.*še*, uh.*še*.kú* and *uh.zí(d).da* (Akkadian *kal-mat* še*-im, ri-a-*šu and *kal-mat qé-mi*) pertain to insect pests of grain and flour, specifically barley. While Landsberger attempts to draw parallels between the *uh.*še*.kú* and *uh.zí(d).da* and the *Kornwurm* and *Melhwurm*, respectfully (1934, 177), retranslation of the Sumero-Akkadian text using Briggs *et al*. (2006) demonstrates that the transliteration is only capable of referring to insect pests infesting stored grain (barely) and flour, making

species level identification a bit ambitious. The Sumerian determinative *uh* is often interpreted as louse. However, it is often used in conjunction with the words for grain, fields, forest, etc. and, as such, should more accurately be defined as vermin or pest (Tawil 1977). *Uh* combined with the word š*e*, meaning barley or cereal, denotes a pest of barley but does not specify the location/condition of the barley. The addition of the *kú*, meaning fodder, in *uh*.š*e.kú* versus its absence in *uh*.š*e* in the Har-ra==Hubullu likely serves to separate the pest of stored product barley, *uh*.š*e.kú*, from the pest of field barley, *uh*.š*e*. The position of *uh*.š*e* in the tablet following shortly after *uh.a.šà(g).ga*, rendered as a pest of the fields, further supports its position as a pre-harvest pest rather than stored product. The tablet also lists a pest of processed grain, i.e. flour—*uh.zí(d).da*, literally the insect pest with or in flour. The Sumero-Akkadians appear to have recognised three separate insect pests of cereals with preference to different conditions of the cereal; pre-harvest, *uh*.š*e*; post-harvest, unprocessed, *uh*.š*e.kú*; and post-harvest, processed, *uh.zí(d).da*. While the Har-ra==Hubullu provides insight into the habitat preference of cereal pests, it does not provide the physical description necessary for identification of the insects. The grain pests are also referred to in other literature of the period. For example, Brodenheimer (1947) presents "A piece of linen is spread for a flea, a tissue for a moth, a granary for grain pests" as a proverb with Sumero-Akkadian origins.

The earliest archaeological evidence [Table 5.1] for the presence of cereal pests in the region can be dated to the Pre-Pottery Neolithic C period (PPNC), 8000-7500 BP. One of the earliest accounts of grain pests comes from layer VI at Hacilar, SW Anatolia, dated to 7700-7550 BP (Helbaek 1970). From structures Q.VI.1 and Q.VI.5, Helbaek describes the fragments of several adult *Sitophilus* sp. in small heaps of charred wheat and barley. Additionally, one of the grains contained an adult

weevil and some kernels showed evidence of length-wise tunnelling. As evidence of its congeners *S. oryzae* and *S. zeamais* has yet to be recovered in the region at that date, the unidentified *Sitophilus* sp. remains are likely to have been *S. granarius*. More conclusive evidence for the presence of the granary weevil in the region at the time comes from a near contemporaneous well at Atlit-Yam (circa 7500 BP) where Kislev *et al*. (2004) records 27 specimens of *Sitophilus granarius*.

Moving substantially forward in time, indirect evidence for the presence of *S. granarius* in Assyrian and Hellenistic barley from Nimrud was referred to briefly by Helbaek (1970) as weevil ravaged grain. Hopf and Zachariae (1921) found the grain weevil in 10th century BCE grain deposits from Tel Arad in Northern Negev, and Kislev and Melamed (2000) reported insect remains, dating to the 9th-10th century BCE, from charred grain and pulses found in store rooms near or in broken jars at an Iron Age storage fort and village at Horbat Rosh Zayit, Israel. Around 350 individuals of *Sitophilus granarius* were recovered with or in wheat, *Triticum parvicoccum*, charred grain. Other grain pests were noted: *Alphitophagus bifasciatus*, *Oryzaephilus surinamensis* (adult and pupa), and an adult and whole larva of *Tenebroides maritanicus*.

5.3.2 Prehistoric Europe

The earliest evidence [Table 5.1] of cereal pests in Europe comes from a bandkeramic well in Eythra village in Leipzig region of Germany. Well 2 (radiocarbon dated 7269-7180 BP) contained 204 individuals of *Sitophilus granarius* (Schmidt 2005). Schmidt has also recorded the granary weevil from bandkeramic wells at Plaußig, dendrochonologically dated 7219 BP (2010a), from two wells at Erkelenz-Kückhoven dated 7040 BP and 7007±5 BP (Schmidt 1998; 2010b), Eythra

Well 1 dated 7034 BP (2005), and Köln approximately 6200 BP (1998). Büchner and Wolf (1997) have also found *Sitophilus granarius* at Göttengen, Germany, 6030 BP.

While the granary weevil was clearly well established in northwestern Europe less than 500 years after its earliest fossil appearance to date in the Middle East, its path is unclear. It is obvious that archaeological record is incomplete as the only other Neolithic account for *Sitophilus granarius* comes from a cast in a piece of pottery from Servia (6700 BP), south Macedonia, Greece (Hubbard 1979). While the archaeoentomological record for the granary weevil in Neolithic Europe is scarce, it is practically non-existent for the other stored cereal pests. Valamoti and Buckland (1995) provide a record of a Neolithic grain pest in Europe from Mandalo in western Macedonia, Greece, dating 5490 ± 55 BP (Kotsakis *et al.* 1989). A single charred head of *Oryzaephilus surinamensis* was recovered from a large cache of emmer wheat during study of plant remains from the site. Additionally, *Tenebroides mauritanicus* has been recovered from Erkelenz-Kückhoven (Schmidt 1998, 2010b) and Plaußig (Schmidt 2010a) in Germany. *T. mauritanicus* has also been recorded from the German site of Singen Offwiese (Schmidt 2007), which is associated with the Groß Gartach culture and dated 6950 BP (Dieckmann *et al.* 1997).

The paucity of archaeoentomological accounts for grain pests continues throughout the Bronze and Iron Age. Fasani (1976) mentions the recovery of *Sitophilus granarius* from a Middle Bronze Age site in Northern Italy, and the granary weevil was also present in Late Bronze Age France at the site of Lake Bourget (Pecreaux 2008). Moreover, *Rhyzopertha dominica* has been recorded in Middle Bronze Age contexts at Cova Punta Farisa in Fraga Huesca, Spain (Alonso and Buco 1993), and *Stegobium paniceum*, has been found in Late Bronze Age Britain: Runnymede Bridge, Staines, Surrey (Robinson 1991) and Wilsford, Wiltshire

(Osborne 1989). The biscuit beetle has also been recovered from an Iron Age site in Britain (Tattershall Thorpe, Lincolnshire, Chowne *et al.* 1986). Smith and associates (2006) have found *Sitophilus granarius* in Iron Age contexts at Okruglo, Croatia, and Compte and Perales (1984) have recovered the granary weevil, *Rhyzopertha dominica*, and *Tribolium* sp. from Siriguarch, Alcañiz, Teruel, Spain.

5.3.3 Ancient Egypt

Like the Sumero-Akkadians, the ancient Egyptians left a scarce but usable documentary record for the presence of grain pests. While Egyptian inscriptions have revealed images of invertebrates which can be morphologically identified to genus (cf. Harpaz 1973; Levinson and Levinson 1998) the ancient Egyptian language, like biblical Hebrew, lacked the generic term for 'insect'. Depictions of kheper beetles, scarabs, wasps, and locusts are clearly recognisable in glyphs and jewellery, but very little distinction was made between worms, slugs, certain snakes, and holometabolic insect larvae. In fact the Egyptian term *h f a t* (*tola'ath* in Hebrew) was indiscriminately used to denote all of the aforementioned groups.

The *Ebers Papyrus* is an Egyptian medical document (c. 3552 BP) describing magical formulas and remedies and is one of the earliest written records containing methods for deterring pests. The *Ebers Papyrus* XCVIII provides instructions for controlling *kkt*-animals using burnt gazelle dung diluted in water. Although Panagiotakopulu and others (1995) suggested that the use of *kkt*-animals was a reference to grain weevils, it merely transliterates as 'small animal' and the species identification is purely speculation based on context.

While species recognition through transliteration of hieroglyphs is tentative, the recovery of palaeoentomological remains allows for more definite identification

[Table 5.1]. Moreover, the integration of archaeological material in addition to documentary evidence provides greater insight into the presence and significance of grain pests in the region. The earliest archaeological records come from Helbaek (cited in Solomon 1965), who notes *Sitophilus granarius* from the *circa* 4900 BP Tomb in Saqqarah, and Solomon (1965), who mentions *S. granarius* having been recovered from the tomb beneath the Step Pyramid of Saqqarah *circa* 4300 BP. The granary weevil and *Stegobium paniceum* were recovered at the tomb of Queen Ichetis at Saqqarah, c. 4334-4150 BP (Chaddick and Leek 1972).

A wheat deposit from a Middle Kingdom tomb at el-Gebelein (4181-4055 BP) yielded *Stegobium paniceum* as well as the earliest fossil evidence for *Trogoderma granarium* (Panagiotakopulu 2003). Panagiotakopulu recognised five individuals of the khapra beetle and seventeen individuals of the biscuit beetle. *Tribolium* sp. was recovered from a mid-3rd millennium BC (5000-4000 BP) Egyptian tomb by Alfieri (in Andres 1931). *Tribolium confusum* was identified from an offering pot from c. 3000 BP (Alfieri 1976), and Zacher (1937) recorded *T. castaneum* from Egypt *circa* 3500 BP. Seifert (1987) reports the earliest record of *Alphitobius diaperinus* in an unnamed New Kingdom Period site in Egypt.

Fossil evidence for *Rhyzopertha dominica* and *Stegobium paniceum* was available from Liverpool Museum collections from Twelfth Dynasty Kahun, 3990-3800 BP (Panagiotakopulu 1998). The *R. dominica* was recovered from a small sample of barley and is the earliest on record. The lesser grain borer was also recovered in botanical remains from a vessel in Tutankhamun's tomb, c. 3345 BP (Alfieri 1931), and Zacher (1937) recorded *T. castaneum, S. paniceum, Oryzaephilus surinamensis, and Rhyzopertha dominica* from another vessel from the tomb.

Material from the Workmen's Village at Tell el-Amarna (thought to be dated between 3350-3323 BP based on pottery remains) contained grain pests from pigsty deposits. Panagiotakopulu (1999) discusses the remains of *S. granarius* and *Palorus ratzeburgi* from coprolites at the site. Additionally, Panagiotakopulu (2001) refers to *Tribolium confusum*, *T. castaneum*, *Palorus subdepressus* and *Cryptolestes turcicus* as all having been recovered from Pharoanic Amarna. Zacher (1934ab) notes *Oryzaephilus surinamensis* from a Minoan period vessel, 3350 BP.

Table 5.1 Archaeological sites presenting grain pests from Neolithic through Roman date contexts[1]

Location	Time, period	Species	Reference
Hacilar, SW Anatolia	Pre-Pottery Neolithic C, 7700-7550 BP	*Sitophilus granarius*	Helbaek 1970
Atlit-Yam, Israel	Pre-Pottery Neolithic C, *circa* 7500 BP	*Sitophilus granarius*	Kislev *et al*. 2004
Eythra village in Leipzig region of Germany; Well 2	LBK, 7269-7180 BP	*Sitophilus granarius*	Schmidt 2005
Plaußig, Germany	LBK, 7219 BP	*Sitophilus granarius, Tenebroides mauritanicus*	Schmidt 2010a
Erkelenz-Kückhoven, Germany, two wells	LBK, 7040 BP and 7007±5 BP	*Sitophilus granarius, Tenebroides mauritanicus*	Schmidt 1998, 2010b
Eythra, Germany Well 1	LBK, 7034 BP	*Sitophilus granarius*	Schmidt 2005
Singen Offwiese, Germany	Neolithic, 6950 BP	*Tenebroides mauritanicus*	Dieckmann 1997; Schmidt 2007
Servia, south Macedonia, Greece	Neolithic, 6700 BP	*Sitophilus granarius*	Hubbard 1979
Köln, Germany	LBK, 6200 BP	*Sitophilus granarius*	Schmidt 1998
Göttengen, Germany	LBK, 6030 BP	*Sitophilus granarius*	Büchner and Wolf 1997
Mandalo in western Macedonia, Greece	Neolithic, 5490 ± 55 BP	*Oryzaephilus surinamensis*	Valamoti and Buckland 1995
Tomb in Saqqarah, Egypt	Early Dynastic Period, *circa* 4900 BP	*Sitophilus granarius*	Helbaek cited in Solomon 1965

Egyptian tomb	Early Dynastic Period- Middle Kingdom, 5000-4000 BP	*Tribolium* sp	Alfieri cited in Andres 1931
Step Pyramid of Saqqarah, Egypt	Old Kingdom, *circa* 4300 BP	*Sitophilus granarius*	Solomon 1965
Tomb of Queen Ichetis at Saqqarah, Egypt	Old Kingdom, 4334-4150 BP	*Sitophilus granarius, Stegobium paniceum*	Chaddick and Leek 1972
Tomb at el-Gebelein, Egypt	Middle Kingdom, 4181-4055 BP	*Stegobium paniceum, Trogoderma granarium*	Panagiotakopulu 2003
Kahun, Egypt	Middle Kingdom, Twelfth Dynasty, 3990-3800 BP	*Rhyzopertha dominica*, *Stegobium paniceum*	Panagiotakopulu 1998
Egypt	New Kingdom, 3520- 3020 BP	*Alphitobius diaperinus*	Seifert 1987
Egypt	New Kingdom, *circa* 3500 BP	*Tribolium castaneum*	Zacher 1937
West House, Akrotiri Santorini, Thera	Late Minoan, *circa* 3500 BP	*Sitophilus granarius*, *Rhyzopertha dominica*, *Stegobium paniceum*, *Oryzaephilus sp*.	Panagiotakopulu and Buckland 1991
Knossos, Greece	Late Minoan, c. 3425 BP	*Sitophilus granarius*	Jones 1984
Kommos, Greece	Late Minoan, c. 3425 BP	*Sitophilus granarius, Tribolium confusum*	Shaw and Shaw 1995
Northern Italy	Middle Bronze Age, 3450-3250 BP	*Sitophilus granarius*	Fasani 1976
Cova Punta Farisa in Fraga Huesca, Spain	Middle Bronze Age, 3450-3250 BP	*Rhyzopertha dominica*	Alonso and Buxo 1993
Workmen's Village at Tell el-Amarna, Egypt	New Kingdom, 3350-3323 BP	*Sitophilus granarius*, *Palorus ratzeburgi*	Panagiotakopulu 1999
Egypt	New Kingdom, 3350 BP	*Oryzaephilus surinamensis*	Zacher 1934ab
Tutankhamun's tomb, Egypt	New Kingdom, c. 3345 BP	*Rhyzopertha dominica, Tribolium castaneum, Stegobium paniceum, Oryzaephilus surinamensis*	Alfieri 1931; Zacher 1937
Wilsford, Wiltshire, UK	Late Bronze Age, 3330 ± 90 BP	*Stegobium paniceum*	Osborne 1989

Lake Bourget, Savoie, France	Late Bronze Age, 3250-2750 BP (Gauthier and Richard 2009)	*Sitophilus granarius*	Pecreaux 2008
Amarna, Egypt	Pharaonic	*Tribolium confusum*, *T. castaneum*, *Palorus subdepressus*, *Cryptolestes turcicus*	Panagiotakopulu 2001
Egypt	Third Intermediate, Twenty-first Dynasty, 3000 BP	*Tribolium confusum*	Alfieri 1976
Nimrud	Assyrian and Hellenstic Periods, 3900-2273 BP	*Sitophilus granarius*	Helbaek 1970
Runnymede Bridge, Staines, Surrey, UK	Late Bronze Age, 2950-2800 BP	*Stegobium paniceum*	Robinson 1991
Tel Arad in Northern Negev	Iron Age, 2950-2851 BP	*Sitophilus granarius*	Hopf and Zachariae 1921
Horbat Rosh Zayit, Israel	Iron Age, 2950-2751 BP	*Sitophilus granarius, Alphitophagus bifasciatus*, *Oryzaephilus surinamensis, Tenebroides mauritanicus*.	Kislev and Melamed 2000
Okruglo, Croatia	Iron Age, 2760-2640 BP	*Sitophilus granarius Laemophloeus* (=?*Cryptolestes*) *spp*.	Smith *et al*. 2006
Siriguarach, Alcañiz, Teruel, Spain	Iron Age, 2650-2551 BP	*Sitophilus granarius, Rhyzopertha dominica, Tribolium sp.*	Compte and Perales 1984
Tomb from Hunan Province in China	2100 BP	*Trogoderma persicum, Sitophilus oryzae*	Chu and Wang 1975
Tattershall Thorpe, Lincolnshire, UK	Iron Age, 2350 ± 90 BP	*Stegobium paniceum*	Chowne *et al.* 1986
Santa Pola, Spain	Roman, 1950-1851 BP (1^{st} c. AD)	*Sitophilus granarius*	Moret and Martin Cantarino 1996
Alphen aan den Rijn, Netherlands	Roman, 1950-1851 BP (1^{st} c. AD)	*Sitophilus granarius*	Kuijper and Turner 1992
Neuss (Novaesium IV), Germany	Roman, 1950-1900 BP (early 1^{st} c. AD)	*Sitophilus oryzae*	Knörzer 1970

Neuss (Novaesium), Germany	Roman, 1920 BP (30 AD)	*Oryzaephilus surinamensis*, *Sitophilus granarius*	Cymorek and Koch 1969; Koch 1970
1 Poultry, Central London, UK	Roman, 1903-1890 BP (47-60 AD)	*Sitophilus granarius*, *Oryzaephilus surinamensis*, *Cryptolestes ferrugineus*, *Palorus ratzeburgi*	Rowsome 2000; Smith in press
21 Saint Peters Street, Colchester, UK	Roman, 1888-1870 BP (62-80 AD)	*Sitophilus granarius*, *Oryzaephilus surinamensis*, *Cryptolestes ferrugineus*, *Palorus ratzeburgi*	King and Hall 2008
Coney Street, York, UK	Roman, 1879-1876 BP (71-74 AD)	*Tenebroides mauritanicus, Cryptolestes ferrugineus, Oryzaephilus surinamensis, Palorus ratzeburgi, Tenebrio obscurus, Sitophilus granarius*	Hall and Kenward 1976; Kenward and Williams 1979
Touffréville Calvados, France	Roman, *circa* 1875 BP (c. 75 AD)	*S. granarius*, *Stegobium paniceum*, *Tenebrio obscurus*, *Oryzaephilus* sp.	Ponel *et al.* 2000
Herculaneum, Naples, Italy	Roman, *circa* 1871 BP (c. 79 AD)	*Sitophilus granarius*, *Oryzaephilus* sp.	Dal Monte 1956
Papcastle, Cumbria, UK	Roman, approximately 1875- 1800 BP (late 1st to mid-2nd c. AD)	*Cryptolestes ferrugineus, Oryzaephilus surinamensis, Palorus ratzeburgi, Alphitobius diaperinus, Sitophilus granarius*	Kenward and Allison 1995
Amiens, France	Roman, c. 1849-1750 BP (2nd c. AD)	*Stegobium paniceum*, *Cryptolestes ferrugineus*, *Oryzaephilus surinamensis*, *Tenebrio* sp., *Palorus ratzeburgi*, *Sitophilus granarius*	Matterne *et al.* 1998; Yvinec 1997
Mons Claudianus, Egypt	Roman, c. 1849-1750 BP (2nd c. AD)	*Oryzaephilus sp.* and *Cryptolestes turcicus*	Panagiotakopulu and van der Veen 1997

Woerden, Zuid-Holland	Roman, c. 1775-1750 BP (late 2nd c. AD)	*Sitophilus granarius*, *Oryzaephilus surinamensis*, *Cryptolestes ferrugineus*, *Palorus ratzeburgi*, *Tenebrio molitor*, *Alphitophagus bifasciatus*	Pals and Hakbijl 1992
Skeldergate Well, York, UK	Roman, 1750 ± 80 BP (c. 200 AD)	*Sitophilus granarius, Cryptolestes ferrugineus, Palorus ratzeburgi, Tribolium castaneum, Tenebrio obscurus, Oryzaephilus surinamensis, Stegobium paniceum*	Hall *et al.* 1980
Alcester, Warwickshire, UK	Roman, 1750-1651 BP (3rd c. AD)	*Sitophilus granarius, Palorus subdepressus, Tenebrio obscurus, Oryzaephilus surinamensis, Stegobium paniceum*	Osborne 1971
Hambacher Forest near Köln, Germany	Roman, 1712 ± 5 BP (c. 238 AD)	*Sitophilus granarius*	Schmidt 2006b
Towcester, Northamptonshire, UK	Roman, 1620-1585 BP (330-365 AD)	*Oryzaephilus surinamensis, Cryptolestes turcicus, Cryptolestes ferrugineus, Tribolium castaneum, Tribolium confusum, Sitophilus granarius*	Girling 1983

[1]**Table does not contain a comprehensive list of Romano-British sites containing grain pests**

5.3.4 Ancient Greece and Aegean

The Greek names *κίς, κορίς, φθείρ, σής, ἴψ, σκνίψ,* and *θρίψ* refer to small insect pests (Beavis 1988). *Κίς*, in particular, is normally restricted to insects infesting grains or pulses. Although *κίς* is often read as weevil by modern scholars, inferring *Sitophilus granarius*, the term, like the Sumero-Akkadian *uh.*še*.kú*,

comprised a number of modern grain species, and in Suidas' lexicon is simply defined as *vermis*, or vermin. The Greeks, like the earlier writers, do not offer a description of the insect pests, and as such, the terms could refer to any number of stored product insects. For example, Theophrastus (2321-2236 BP) *CP* IV.15.6 has been translated as "Each kind of seed-crop when put under a roof produces from its proper fluidity certain animals of a form peculiar to itself: so wheat and barley produce their weevils…" (1990, 355); whereas it may be more accurate if the term 'weevils' was replaced by 'grain pests'.

The fossil record for pre-Roman Greece and Aegean Islands is remarkably slight [Table 5.1]. A carbonised *Sitophilus granarius* was found in a sample of barley from a destruction deposit at the 'unexplored' mansion complex at Knossos, with a Late Minoan date, around 3425 BP (Jones 1984), and Shaw and Shaw (1995) report *S. granarius* and *Tribolium confusum* from a contemporaneous site at Kommos. The remains of *Sitophilus granarius*, *Rhyzopertha dominica*, *Stegobium paniceum*, and *Oryzaephilus sp*. were identified in samples from the West House, Akrotiri Santorini, Thera *circa* 3500 BP (Panagiotakopulu and Buckland 1991).

5.3.5 China

The palaeoentomological record for the Orient is very limited [Table 5.1]. In regards to stored product pests, Chu and Wang (1975) reported *Trogoderma persicum* (Pic.) (i.e. *T. variabile* Ball.) and *Sitophilus oryzae* from a tomb dated about 2100 BP in Hunan Province in China. Archaeological excavation accompanied by bioarchaeological analysis will surely produce many ancient records of pests and other insects in Asia and the Indian subcontinent in due course.

5.3.6 The Roman Period

In comparison to earlier periods, the Roman authors wrote prolifically about grain pests starting with Marcus Porcius Cato's 2185 BP *De Re Rustica* (*Ag*. XCII), and seemed particularly concerned with a grain pest known as *curculio*. In his poem, Virgil exclaims "populatque ingentem farris acervum curculio" (*G.* I.CLXXXVI)—a huge grain (spelt)-heap *curculio* ravages, and Plautus' play *Curculio* features a character named Curculio Parastus (parasite), who is portrayed as a greedy, gluttonous, and unscrupulous character. In his opening lines, Curculio utters:

> "Make way for me, friends, strangers, while I do my duty here! Scatter, clear out, get off the street, everybody, so that I may not career into anyone and lay him out with my head, or elbow, or chest, or knee! I tell you what, it's a sudden, pressing, urgent job I'm charged with now, and there's no man rich enough to block my path—neither general, nor despot, any of 'em, nor market inspector, no mayor, nor burgomaster, I don't care how grand he is—down he'll go, down he'll drop from the sidewalk and stand on his head in the street!" (*PC,* 219-221).

It appears that *curculio* was perceived as an insect that was capable of ravaging enormous piles of grain and infesting the cereals of people regardless of societal position.

Moreover, the Roman writers seem to differentiate between curculio and other grain-associated insects, as indicated in Vitruvius's commentary on architecture "granaria sublimata et ad septentrionem aut aquilonem spectantia disponantur, ita enim frumenta non poterunt cito concalescere, sed ab flatu refrigerata diu servantur.

namque ceterae regiones procreant curculionem et reliquas bestiolas quae frumentis solent nocere," (*Arch* VI.VI.IV)—the granaries are raised, and must be towards the north or east, so that the grain may not heat, but be preserved by the coolness of the air; if towards other aspects, curculio, and other insects that harm grain, will be generated. Although the Romans recognized different species of grain pests, only *curculio* was named, and as in previous periods, the species, unfortunately, lacks a physical description making species level identification difficult.

The majority of the references to *curculio* concern agriculture or natural history, in which the authors discuss methods for preventing the contamination of cereals and purging an infestation. A brief investigation of a few these works is worthwhile as the authors provide insight into the behaviour of *curculio* as well as a few locations in which it was found. Approximately 1986 BP, Varro (as translated by Hooper and Ash 1935) writes:

> "Wheat should be stored in granaries, above ground, open to the draught on the east and north, and not exposed to damp air rising in the vicinity. The walls and floor are to be coated with marble cement, or at least with clay mixed with grain-chaff and amurca, as this both keeps out mice and worms and makes the grain more solid and firm. Some farmers sprinkle the wheat, too, with amurca, using a quadrantal to about a thousand modii. Different farmers use different powders or sprays, such as Chalcidian or Carian chalk, or wormwood, and other things of this kind. Some use underground caves as granaries, the so called sirus, such as occur in Cappadocia and Thrace; and still others use wells, as in the Carthaginian and Oscensian districts in Hither Spain. They cover the bottom of these

with straw, and are careful not to let moisture or air touch them, except when the grain is removed for use; for **[*curculio*]** does not breed where air does not reach. Wheat stored in this way keeps as long as fifty years, and millet more than a hundred. Some people, as in Hither Spain and in Apulia, build granaries in the field, above ground, so constructed that the wind can cool them not only from the sides, through windows, but also beneath from the ground. […] Grain which **[*curculio*]** has begun to infest should be brought out for protection. When it is brought out, bowls of water should be placed around in the sun; **[*curculio*]** will congregate at these and drown themselves. Those who keep their grain under ground in the pits which they call sirus should remove the grain some time after the pits are opened, as it is dangerous to enter them immediately, some people having been suffocated while doing so. Spelt which you have stored in the ear at harvest-time and wish to prepare for food should be brought out in winter, so that it may be ground in the mill and parched." (*RR* I.LVII 1935).

Around 1900 BP, Columella (as translated by Ash1941) writes:

"And I am not unaware that some consider the best place for storing grain to be a granary with a vaulted ceiling, its earthen floor, before it is covered over, dug up and soaked with fresh and unsalted lees of oil and packed down with rammers as is Signian work. Then, after this has dried thoroughly, it is overlaid in the same way with a pavement of tiles consisting of lime and sand mixed with oil lees instead of water, and these are beaten down with great force by

rammers and are smoothed off; and all joints of walls and floor are bound together with a bolstering of tile, for usually when buildings develop cracks in such places they afford holes and hiding-places for underground animals. But granaries are also divided into bins to permit the storage of every kind of legume by itself. The walls are coated with a plastering of clay and oil lees, to which are added, in place of chaff, the dried leaves of the wild olive or, if these are wanting, of the olive. Then, when the aforesaid plastering has dried, it is again sprinkled over with oil lees: and when this has dried the grain is brought in. This seems to be the most advantageous method of protecting stored produce from damage by **[*curculio*]** and like vermin, and if it is not carefully laid away they quickly destroy it. But the type of granary just described, unless it be in a dry section of the steading, causes even the hardest grain to spoil with mustiness; and if it were not for this, it would be possible to keep grain even buried underground, as in certain districts across the sea where the earth, dug out in the manner of pits, which they call siri, takes back to itself the fruits which it has produced. But we, living in regions which abound in moisture, approve rather the granary that stands on supports above the ground and the attention to pavements and walls as just mentioned, because, as I have said, the floors and sides of storerooms so protected keep out **[*curculio*]**. Many think that when this kind of pest appears it can be checked if the damaged grain is winnowed in the bin and cooled off, as it were. But this is a most mistaken notion; for the insects are not driven off by so doing, but

> are mixed through the whole mass. If left undisturbed, only the upper surface would be attacked, as **[*curculio*]** breeds no more than a palm's breadth below; and it is far better to endanger only the part already infested than to subject the whole amount to risk. For it is easy, when occasion demands it, to remove the damaged portion and use the sound grain underneath. But these latter remarks, though brought in extraneously, I nevertheless seem to have introduced not unseasonably at this point." (*RR* I.VI.XV-XII 1941).

The commentaries of Varro and Columella seem to depict *curculio* as a primary pest by insinuating that the species was responsible for infesting undamaged grains. Based on archaeoentomological accounts, the Mediterranean region was infested by two primary pests of grains, *Sitophilus granarius* and *Rhyzopertha dominica*. As *R. dominica* does not appear to have had a widespread distribution in the past (though this may be a reflection of a poor fossil record), the Roman authors may have been referring to *Sitophilus granarius*, which is the species most commonly associated with the term *curculio* by modern scholars in translating it as weevil. However, the possibility cannot be completely discounted of *curculio* having been used in reference to both species.

Varro specifies several regions—Cappadocia, Thrace, Carthaginian and Oscensian districts in Hither Spain, and Apulia—that sought to establish a means of pest control against infestations of *curculio*. As there is not presently an established fossil record for 1986 BP, Varro's *De Re Rustica* provides the best evidence for the distribution of *curculio* at that time. Strabo's description of Cappadocia places the region in modern-day central Anatolia where it extended northwards to the Black Sea from Mount Taurus, east to the Euphrates and west to Lake Tuz. Thrace refers to the

region north of Thessaly extending northwards to the Hæmus Mons (Balkan Mountains), west to the Nestos (Mesta) River, and east to the Black Sea (Carr 1838). Hither Spain, most likely, refers to Hispania Citerior, which included the northeastern coast and Ebro valley of modern Spain, and Strabo's description of Apulia places the area in southeastern Italy (in the heel-region of the boot), bordering the Adriatic and Ionian Seas (S*G* VI.III). Varro's reference implies that *curculio* was established along most of the Mediterranean coast of southern Europe during the Roman Republic.

First Century AD

Records of insect assemblages from Continental Europe in the Roman period are rare and there is a dearth of observations of grain pests [Table 5.1]. The earliest remains of Roman age grain pests are dated to 30 AD, *Oryzaephilus surinamensis* and *Sitophilus granarius* from Neuss (Novaesium) in Germany (Cymorek and Koch 1969; Koch 1970), and early first century AD contexts from Neus-Novaesium IV, Germany have provided *Sitophilus oryzae* in association with charred rice (Knörzer 1970). In France, Ponel and associates (2000) noted *S. granarius*, *Stegobium paniceum*, *Tenebrio obscurus*, and *Oryzaephilus* sp. from Touffréville Calvados, dated circa 75 AD, and Dal Monte (1956) recorded larval, pupal and adult *Sitophilus granarius* as well as a single *Oryzaephilus* sp. in infested charred wheat from beneath the AD 79 tephra at Herculaneum, Naples, Italy. *S. granarius* was also recovered from contexts at Alphen aan den Rijn, Netherlands dating to the first century AD (Kuijper and Turner 1992) as well as Valkenburg fort (Hakbijl 1988).

The archaeoentomological evidence suggests that the grain pests entered Britain immediately following the arrival of the Roman legions; there are no records

to indicate the presence of grain pests in Britain prior to the arrival of the Roman military forces. Buildings, workshops, yards and pits at Poultry, Central London, were dated from just after 47 AD, the start of the occupation of Roman London (Rowsome 2000; Smith in press), and the deposits were all sealed by the 60 AD 'fire horizon' interpreted as the burning of London during the Boudiccan revolt (Rowsome 2000). From the Poultry site samples, Smith (loc. cit.) identified myriad insect remains including *Sitophilus granarius*, *Oryzaephilus surinamensis*, *Cryptolestes ferrugineus*, and *Palorus ratzeburgi*. The same range of species was present in the timber drain at 21 Saint Peters Street, Colchester, constructed immediately following the Boudiccan revolt (King and Hall 2008).

In northern England, grain pests have been noted in the Roman Fort at the Millennium site at Carlisle Castle 72/3 AD (Smith unpublished), at other sites in and near the Roman fortress at Carlisle (Kenward *et al.* 2000; Kenward and Carrott 2006), and the fort at Ribchester, Lancashire 71-4 AD (Large *et al*. 1994; Buxton and Howard-Davis 2000). The humic silts from in and around the beam slots of a late first century wooden building at Coney Street, York produced immense numbers of grain pests associated with spoilt grain. The humic silt layer 2105 yielded a range of grain fauna—*Tenebroides mauretanicus, Cryptolestes ferrigineus, Oryzaephilus surinamensis, Palorus ratzeburgi, Tenebrio obscurus,* and *Sitophilus granarius*—representing a massive infestation (Hall and Kenward 1976; Kenward and Williams 1979).

Second, Third, and Fourth Centuries AD

While there is a dearth of information concerning the Italian sites, the grain pests continue to be represented in France, Germany, and England beyond the first

century [Table 5.1]. In France, a Gallo-Roman granary burned during the second century in Amiens provided a fauna which included *Stegobium paniceum*, *Cryptolestes ferrugineus*, *Oryzaephilus surinamensis*, *Tenebrio* sp., *Palorus ratzeburgi*, and *Sitophilus granarius* (Yvinec 1997; Matterne *et al.* 1998), and Schmidt (2006) demonstrates the presence of *S. granarius* in the second century of Hambacher Forest near Köln in Germany. In Britain, grain associated insect faunas have been recorded from numerous sites throughout England (e.g. Buckland 1982; Kenward and Carrott 2006) and as far north as Invereskgate in West Lothian, Scotland (Smith 2001) until the end of the 4th century AD. The second century provides evidence for the arrival of *Alphitobius diaperinus* (Kenward *et al*. 1986; Hall and Kenward 1990; Kenward and Allison 1995; Kenward *et al*. 2000), *Stegobium paniceum* (Hall and Kenward 1990), and *Tribolium castaneum* (Hall *et al.* 1980; Hall and Kenward 1990) in Northern England. Moreover, the third and fourth centuries AD indicate the introduction of *Palorus subdepressus* (Osborne 1971*)* as well as *Cryptolestes turcicus* and *Tribolium confusum* (Girling 1983), respectively, to England. On the other side of the Mediterranean, *Oryzaephilus sp.* and *Cryptolestes turcicus* have been recovered from a second century quarry site at Mons Claudianus in Egypt (Panagiotakopulu and van der Veen 1997).

Additionally, the Roman period provides the earliest archaeological evidence for the movement of grain pests via ships. Pals and Hakbijl (1992) report *Sitophilus granarius*, *Oryzaephilus surinamensis*, *Cryptolestes ferrugineus*, *Palorus ratzeburgi*, *Tenebrio molitor*, *Alphitophagus bifasciatus,* and the parastoid wasp *Lariophagus distinguendus* (Förster) from the remains of a late second century ship near the presumed Roman fort of Laurium in Woerden, Zuid-Holland. Similarly, Rule and Monaghan (1993) have reported *Sitophilus sp.* (likely *S. granarius*) from the third

century ship wreck near Guernsey. At minimum, the present of pests in these vessels reveals that grain was still a traded commodity in the Roman Empire during the second and third centuries.

5.4 Discussion: The Origins and Diffusion of the Species

While a few early writers acknowledged the depredations of the various grain fauna dating back to the Hammurabian period, the literature does not allow conclusive reconstruction of species' distributions, as pointed out by Buckland (1981), even when species level identification is discernable from the texts. Thus the early literary accounts are not viable alternatives to archaeological and palaeoecological data when assessing dispersal patterns of the cereal pests. In this section, the diffusion of the grain-associated entomofauna will be assessed through an evaluation of spatial and temporal changes in the various species, i.e. biogeography.

5.4.1 Neolithic

At present, the earliest archaeological evidence of farming communities and founder crops associated with Neolithic agriculture dates to c. 12000 BP in southwestern Asia (Colledge *et al.* 2004), c. 8350 BP in southern Greece (Perlès 2001), and c. 7450 BP in Germany (Stäuble 1995). As early as the 7th millennium BP, the archaeoentomological evidence, predominantly from *Sitophilus granarius*, indicates the presence of pests in three regions: Germany, Macedonia, and the Middle East. In the Middle East, there is approximately a 4,000 year gap between the earliest archaeological evidence for the emergence of farming communities and the first indication of grain-associated insects. Moreover, while a difference of *circa* 1700 years exists in the Greco-Macedonian region, the grain pests are seemingly present

almost immediately (c. 7269 BP) following the agriculturalisation of Germany. Did the grain pests make the transition to synanthropy independently in separate locations or in a single region and disperse via anthropic transportation?

Currently, the earliest fossil record of grain pests, i.e. *S. granarius*, dates to 7700-7550 BP in southwest Anatolia (Helbaek 1970). As this early record pre-dates the emergence of agriculture in northwest Europe by approximately 300 years and the earliest German specimens by *circa* 500 years, it likely signifies the region of origin in which the species became associated with human-stored cereals. There has been an unfortunate paucity of archaeoentomological investigations undertaken in the Middle East, particularly in regards to the early Neolithic, and even the earliest grain pest accounts, i.e. Helbaek 1970 and Kislev *et al.* 2004, were stumbled upon haphazardly during archaeobotanically aimed investigations of charred material. Whereas the majority of archaeobotanical studies may have overlooked or not been concerned with the recovery of insect remains, even the few archaeoentomologically aimed assessments, e.g. G. A. King's (unpublished) sampling of Pre-Pottery Neolithic A and B contexts at Catalhöyük, have not recovered evidence of grain fauna prior to the Pre-Pottery Neolithic C (PPNC). Despite this, it would be premature to completely dismiss an earlier Middle Eastern presence as future investigations may reveal earlier evidence for grain pests in the region.

The initial introduction of the grain fauna and their subsequent dispersal in the Middle East would have been inhibited by factors during the early Neolithic. The granary weevil is the sole fossil evidence for cereal pests in the Pre-Pottery Neolithic C Middle East, and, as stated above, the species is flightless and regarded as a poor disperser (Mlambo 1980). Because of its hypothesised commensal relationship with pre-Neolithic rodents, *S. granarius* would have likely been introduced into the man-

made grain stores via their associated rodents. When the rodents began constructing their dens in anthropic environments (zooarchaeological accounts suggest this move towards commensalism occurs as early as the PPNA (11500-10500 BP) with the house mouse, *Mus musculus*, Bar-Yosef *et al.* 1991; Tchernov 1994; Jenkins 2003), the granary weevils would have been able to make the transition from the rodent stores to the similar microhabitat found in the grain stores of man. This would suggest that the *S. granarius* may be present in archaeological contexts dating to the PPNA. Additionally, excavations at Dhra', near the Dead Sea in Jordan, have revealed evidence of 3 X 3m circular structures interpreted as extramural (located between buildings) granaries, dated to 11300-11200 BP (Kuijt and Finlayson 2009). These granaries suggest that cereals may have initially been owned communally, but by 10500 BP, there is a shift to small-scale, house-hold level storage (Kuijt and Finlayson 2009). If the grain fauna were present in the region during the early PPNA, there may be evidence of infestations in the extramural granaries; however, the later adoption of small-scale storage of grain would have reduced the chances of pest infestation and the archaeological presence of the grain pests. Moreover, dispersed settlement patterns and lack of settlement continuity would have limited or contained the diffusion of early pest infestations (Buckland 1990).

Alternatively, ecological constraints may not have presented the opportunity for the initial introduction of the granary weevil until the Late PPNB- Early PPNC. At this date, the large agricultural villages along the Mediterranean zone of the Jordan Valley shifted to the eastern side of the valley into Mediterranean and desert areas; many of these new settlements are larger than previous villages and are founded in locations with no evidence of earlier PPNB occupation (Rowan and Golden 2009). Following this shift, there is an apparent contraction in population (Rowan and

Golden 2009). Around 8200 BP, paleoclimate studies (e.g. Berger and Guilaine 2009; Magney *et al.* 2003; Figure 5.1) indicate a drastic change in the region's climate towards a more temperate zone in Anatolia and northern Israel, which is favoured by the granary weevil (Kislev *et al*. 2004). If the grain pests had not made the transition to man-made grain stores by the mid-PPNB, the combination of elements present during the Late PPNB-PPNC would have favoured its infestation.

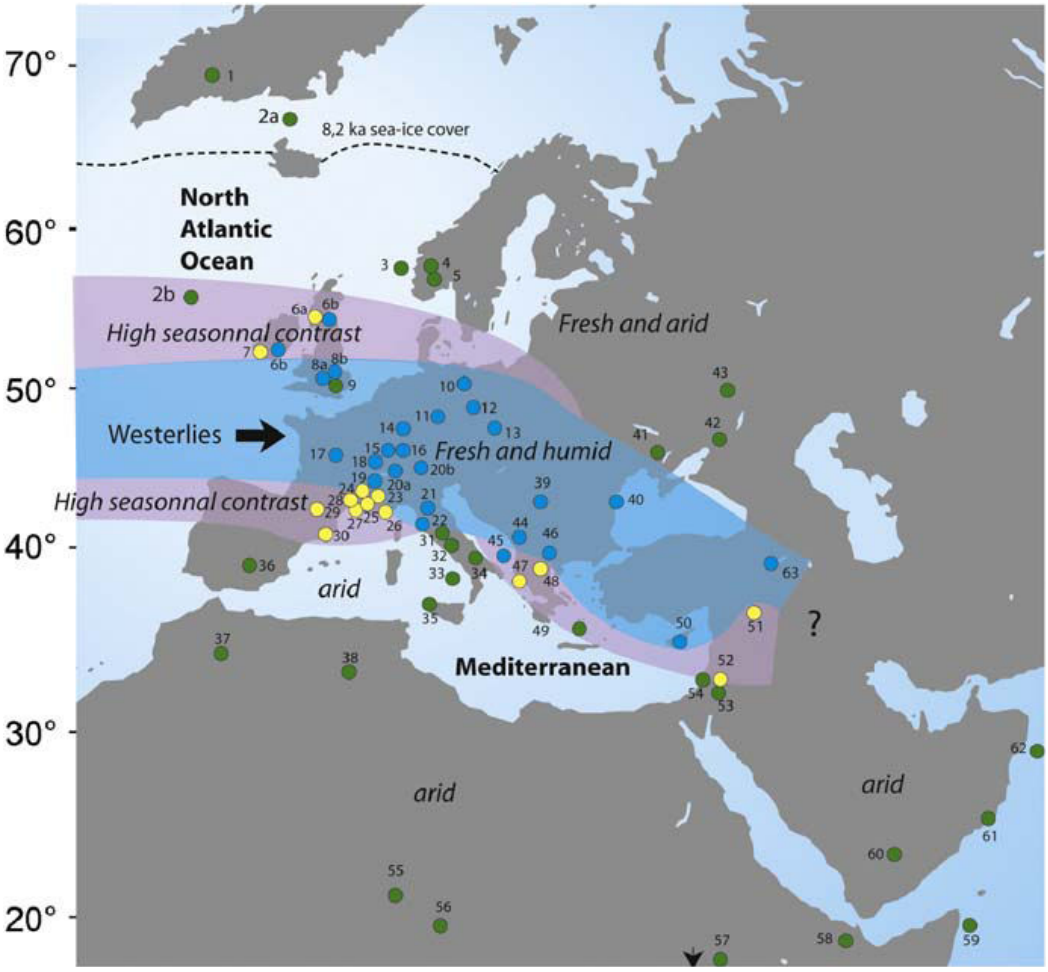


Figure 5.1 Climate zones across Eurasia and North Africa around 8200 BP (Berger and Guilaine 2009; Magney *et al.* 2003); the green circles represent arid climate and fresh for northern Europa; yellow circles indicate a very contrasted climate; and blue circles denote a wet and fresh climate

Unlike the Middle East, there have been a number of archaeoentomological investigations carried out on Neolithic, early Linearbandkeramik (LBK), sites in

northwestern Europe, particularly Germany. These investigations have demonstrated the presence of grain pests in some of the earliest sites with evidence of neolithization. The recovery of *Sitophilus granarius* from sites dating to 7269 BP at Eythra (Schmidt 2005) in Neolithic Germany comprehends a demic expansion of agriculture, i.e. through the immigration of people (cf. Childe 1925), resulting from the anthropic transportation of pest infested cereals during population movement or grain trade rather than through cultural transmission, i.e. the adoption of cultural traits not necessarily associated with the long-distance movement of individuals (cf. Whittle 1996), and the multi-regional synanthropic transition of the granary weevil. The hypothesis of *Sitophilus granarius* as an introduced species is supported by archaeological, ecological and geographical factors:

1) The myriad ecological and geographical barriers between the Middle East and northwestern Continental Europe, e.g. the Black Sea, the Carpathian Mountains, and the Mátra Mountains, would not have provided a corridor pathway by which the flightless weevil could have freely dispersed and populated the European regions naturally;
2) The Near East fossils are morphologically similar to the remains recovered in the German contexts. If the *Sitophilus* populations had evolved independently through geographic isolation, vicariance would be expected; as theoretically the subdivision of the geographic area would have contributed to the splitting of the taxon. However, genetic analysis should be adopted to explore this possibility;
3) According to the present zooarchaeological record, commensal rodents do not arrive in the region until 6450 BP (Auffray *et al*. 1990; Sommerville 1999) with the recovery *Mus musculus* from Place St-Lambert, Liège Belgium

(Cordy and Stassart 1982). Without the presence of commensal rodents to provide a stepping stone towards synanthropy, the weevils would have had to have been introduced via another route; in the absence of indigenous cereal progenitor species, perhaps through the initial collection and storage of infested acorns or seeds. However, a population adapted to the long-term infestation of acorns or seeds would be morphologically larger than a population adapted to small cereal grains.

In addition to the recovery of *Sitophilus granarius*, another grain pest, *Tenebroides mauritanicus*, has been recovered in the region as early as 7219 BP at Plaußig (Schmidt 2010a) and slightly later at Erkelenz-Kückhoven (Schmidt 1998, 2010b). While *T. mauritanicus* may have been imported into Germany alongside the granary weevil, the absence of earlier fossil evidence supports the idea that it is likely endemic to Europe. Unlike *Sitophilus granarius*, which develops entirely within the confines of the cereal kernels and thus can be unwittingly transported by man, the cadelle is one of the largest stored product beetles. As an adult it can grow to a length of 11 mm, and its larvae can reach up to 20 mm (Mound 1989). During the small-scale transportation of cereals, it would have been a visible contaminant (though perhaps not a concern to Neolithic people). Although largely synanthropic today, Palm (1959) has recorded the cadelle under beech bark in southern Europe. The transition from under bark pabulum to grain storage has been discussed above for *Oryzaephilus*, *Cryptolestes*, and *Palorus*. *Tenebroides mauritanicus*, as a scavenger and predator, would have been well adapted for the micro-habitat of the grain storage environment.

Alternatively, as the species has been recovered from Iron Age sites in the Near East, e.g. Horbat Rosh Zayit, Israel (Kislev and Melamed 2000), it may have

been indigenous to that region and dispersed alongside *Sitophilus granarius*. The temperature requirements required for the completion of the cadelle's life cycle closely resemble that of *Sitophilus granarius* [Figure 5.2], with both species requiring temperatures above 15 °C. Palaeoecological studies on the 8200 BP climate event suggest that the summertime temperatures in northwestern Europe were only around 1 °C (Berger and Guilaine 2009), which would not have met the needs of the species prior to their synanthropic transition. Additionally, Klitgaard-Kristensen *et al.* (1998) observed a reduction in the tree-ring growth of oaks from Bamberg Germany *circa* 8200 BP, which may be attributed to lower summer time temperatures. Despite the absence of fossil evidence, the cadelle's temperature requirements suggest that the climate in Germany around 8200 BP would not have been conducive to supporting viable populations of the cadelle. As such, it was most likely anthropically transported into the region from the Middle East alongside the granary weevil. However, the tree-ring studies by Klitgaard-Kristensen *et al*. (1998) as well as oxygen-isotope ratios from deep-sea ostracods from the Amersee in southern Germany (von Grafenstein *et al*. 1998) propose that the low temperatures may have been the result of rapid climatic change. In the absence of a fossil record, the possibility that *T. mauritanicus* occupied the region prior to the decrease in temperatures, survived in refugia, and reoccupied afterwards must be considered. The MCR data calculated using insect remains recovered archaeologically from well contexts in Germany, which were contemporaneous to the cadelle's Neolithic presence, support the possibility of non-synanthropic populations by 7200 BP. The MCRs indicate that the temperatures during the warmest month were above 15 °C, which falls within the thermal range for the species to complete its life cycle [Appendix 1D]. The lack of fossil record could be attributed to 1) the few

archaeoentomological surveys conducted on Neolithic sites in the Middle East and 2) the large size of the beetle resulting in the increased fragmentation of remains and problematic preservation (Kenward pers. comm).

The Neolithic presence of grain fauna in Macedonia is late in comparison to the arrival of agriculture in the region. Moreover, the evidence is meager, consisting of an imprint of *Sitophilus granarius* from a piece of pottery in Servia (Hubbard 1979) and a single charred head of *Oryzaephilus surinamensis* from an emmer cache in Mandalo (Valamoti and Buckland 1995). If we assume that the cast represents the presence of granary weevil populations in the region, the Greek *Sitophilus granarius* could present a similar scenario to the German specimens and infer the importation of cereals into the area from the Near East. Otherwise the populations would have been geographically separated by mountains and waterways, which would have restricted the diffusion of the species naturally, and vicariance would be present. However, because of the paucity of archaeoentomological and contextual evidence, it would be ill-advised to discount the possibility that the granary weevil was native to the region.

Alternatively, as the evidence is based solely on a cast, the presence of the granary weevil in Macedonia cannot be irrefutably confirmed as the pottery may even have been imported into the region. The absence of *S. granarius* in Greece would be significant as it could indicate that agriculture was initially introduced into the region through cultural transmission. This would explain the absence of *S. granarius* from the large emmer cache at Mandalo, which contained the saw-toothed grain beetle; a concern noted by Valamoti and Buckland (1995). The *Oryzaephilus* specimen most likely represents an autochthonous component, introduced from the local environment as a mould-feeder.

The archaeoentomological evidence for the Neolithic is limited. However, a biogeographical interpretation of the remains permits speculation in regards to the spread of agriculture. The recovery of the granary weevil from the Near East and northwest Europe supports the argument for a demic expansion of agriculture with a direct connection between the regions; whereas the Greek material could infer the introduction of agriculture from the Near East largely through cultural transmission, but the evidence is fairly inconclusive.

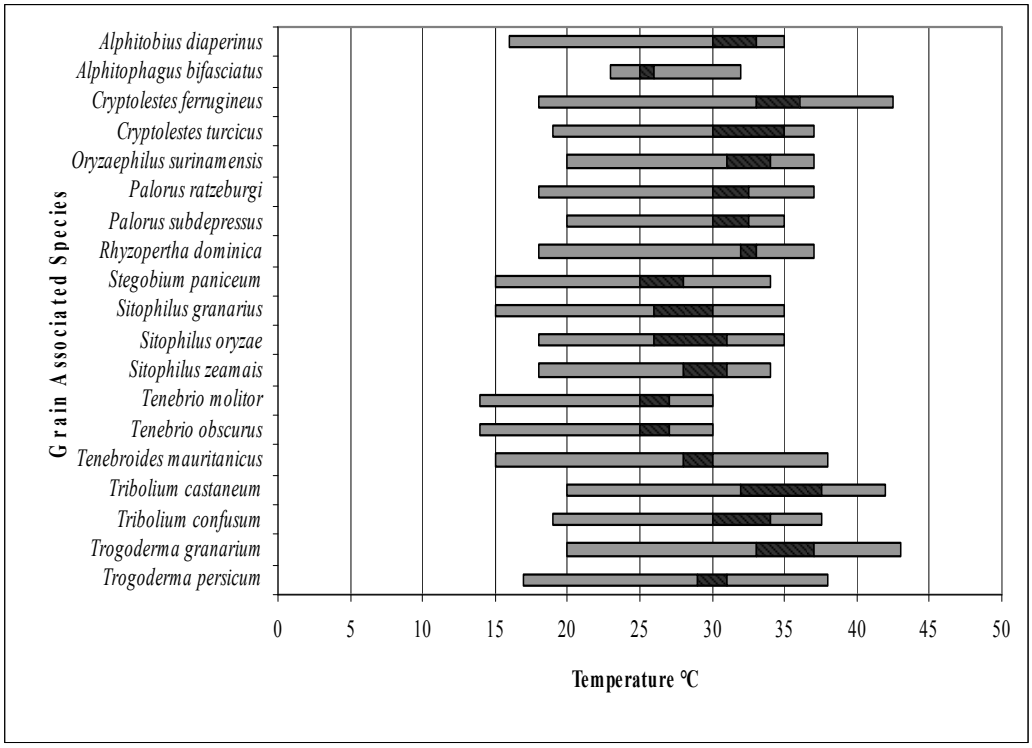
5.4.2 The Bronze Age

While the Neolithic heralded the emergence and diffusion of agriculture, the Bronze Age, noted archaeologically for metalworking involving the use of bronze alloy, witnessed the rise of trade-networks. Archaeoentomologically, the Bronze Age provides evidence towards the emergence of grain-associated faunas initially in Egypt and later in the Aegean and southern Europe. Although archaeological evidence shows that crops had been domesticated ubiquitously around the Mediterranean by this date, the archaeoentomological evidence suggests that cereals were being transported, if not exchanged, during the Bronze Age.

The earliest Bronze Age account of grain pests, i.e. *Sitophilus granarius*, dates to an Early Dynastic Period tomb in Saqqarah, Egypt *circa* 4900 BP (Helbaek cited in Solomon 1965). The granary weevil remains present in Saqqarah throughout the Early Dynastic Period and Old Kingdom then becomes absent from archaeological contexts in the region for around 1000 years. Saqqarah is believed to have been the necropolis for the *ancient* city of Memphis, which was constructed after the unification of Upper and Lower Egypt. Traditionally, the unification is credited to Menes (Herodotus *HH* II.XCIX 1791; Manetho 1940) as early as 5050 BP (Kitchen

1991; Savage 1998). Because of the cultural link between the tombs at Saqqarah and Memphis and the alleged transportation of the cereals to the tombs from the city as part of the funeral procession, the grain pests most likely infested the cereal stores at the capital rather than having entered the context at the necropolis. The archaeological disappearance of the granary weevil from Egypt also coincides with the relocation of the Egyptian capital to Thebes at the start of the Middle Kingdom.

Figure 5.2 Range (light) and optimal (dark cross-hatching) ranges of temperature °C, which are required for the completion of developmental life cycle, for grain fauna



Sources consulted: Sinha and Watters 1985; Sinha 1991; Semple *et al.* 1992; Rees 2007

Sitophilus granarius may have entered the Egyptian contexts as a result of early trade with Mesopotamia. Although the species has been recorded from Neolithic contexts in Israel (Kislev *et al.* 2004), the Sinai Peninsula would have presented a multitude of geographical obstacles (deserts, river valleys, mountains, etc.) that would have inhibited, if not prevented, the granary weevil's dispersal into Egypt by the Bronze Age, without human assistance. Meanwhile, the recovery of

Sumerian Late Uruk and Jemdet Nasr Period (c. 5050- 4850 BP) pottery in Egyptian contexts (Roaf and Postgate 1991) supports the existence of a trade link between the regions. However, the resulting diffusion of the granary weevil into Egypt only infers the transport of infested unprocessed grains from Mesopotamia, not that the cereals were intended as a traded commodity. The grains could have alternatively been used as a food source for the Mesopotamian merchants and/or their animals during their journey to Egypt and have been deposited upon arrival in exchange for fresh cereals. Archaeobotanical studies should be referred to in order to determine whether Mesopotamian cereals were being imported into Egypt during the Early Dynastic Period.

The recovery of *Stegobium paniceum*, the biscuit beetle, from the Old Kingdom tomb of Queen Ichetis at Saqqarah (Chaddick and Leek 1972) represents the earliest archaeological evidence of the species. While the beetle is known to feed on a range of stored products (Buck 1958), it was found in context with *Sitophilus granarius* suggesting a synanthropic association with cereals at this point. It is unlikely that the biscuit beetle was endemic to Egypt as it has a preference for temperate environments and a life cycle range similar to *S. granarius* [Figure 5.2]. If *Stegobium paniceum* was indigenous to the Middle East, it could have been introduced into Egypt through a filter pathway across the Sinai or anthropogenically via culture contact. Whereas the Sinai presented an obstacle for the unflighted granary weevil, the biscuit beetle, capable of flight during its adult stage, may have been able to cross the peninsula by dispersing between food sources (dried animal or vegetable material, Rees 2007). As with *Sitophilus granarius*, *Stegobium paniceum* may have been introduced from the Middle East as a result of trade and/or culture contact between the regions. Once introduced into Egypt, the biscuit beetle maintains

an archaeological presence through the New Kingdom Period. The species would have been better adapted for survival than *Sitophilus granarius* after the Old Kingdom Period society collapsed because it is:

- a more generalist feeder, capable of surviving in the absence of cereals;
- a better disperser, permitting movement between settlements with or without human transportation; and
- more tolerant of arid conditions (cf. Evans 1983; Rees 2007).

During the Middle Kingdom and New Kingdom Periods, the Egyptian contexts indicate the introduction of insect species tolerant of warm temperate and tropical regions: *Alphitobius diaperinus, Palorus ratzeburgi, Rhyzopertha dominica*, *Tribolium castaneum*, and *Trogoderma granarium*,. These are species which have an optimal range for their cycle above 30 °C [Figure 5.2], and in the case of *T. granarium,* require a minimum temperature of 24 °C for breeding (Hunter *et al.* 1973). The continued presence of *Stegobium paniceum*, which places the maximum temperature around 34 °C, as well as the lack of earlier fossil records suggests that new introductions are for the most part heterochthonous and probably the result of the expanding Egyptian trade networks.

The particularly warm temperature requirements of *Tribolium castaneum* and *Trogoderma granarium* pose an interesting problem by suggesting a more tropic region of origin, perhaps India, despite earlier fossils of the species having not been found outside of Egypt. The granaries excavated at Harappa and Mohendojaro (Wheeler 1966) would have been ideal habitats for the two species (Buckland 1981), and Caspers (1972) provides an argument for coastal trade activity around the Arabian Sea at the time. While step-wise trade could have occurred between Egypt and the Indus Valley via the Fertile Crescent, the absence of the *Tribolium castaneum* and

Trogoderma granarium in the Middle Eastern sites would suggest a more direct form of trade between the two regions.

The life cycle requirements and optimal ranges (30-33 °C) of *Alphitobius diaperinus* and *Palorus ratzeburgi* infer a warm temperate origin similar to modern-day Mediterranean Europe. The species could have been introduced through culture contact with the Aegean kingdoms; however, the species have not been recovered archaeoentomologically from contemporaneous sites in those regions. Another option is the North African coast between Tunisia and Morocco. As archaeoentomological investigations have not been conducted in the region, the Bronze Age insect fauna remains a mystery.

The lesser grain borer *Rhyzopertha dominica* is tolerant of both warm temperate and tropic climates. Given the archaeoentomological evidence for potential Middle Kingdom connections with India, it is possible that the species was introduced alongside the khapra beetle or Alfieri's *Tribolium* sp., if perceived as *T. castaneum* (cited in Andres 1931). However, the lesser grain borer does not appear as thermophilic as either *Trogoderma granarium* or *Tribolium castaneum*, having an optimal range around 33 °C inferring another origin. It is also probable that *R. dominica* was of African origin from either the temperate North African coastline or tropical sub-Sahara. As stated above, there is not a fossil record for the North African coastline; however, the lesser grain borer has been recorded in a Middle Bronze Age site in Spain (Alonso and Buxo 1993). If Marinval's (1992) proposal for a North African agricultural diffusion into Spain is considered, it could tentatively stand as evidence of *R. dominica*'s presence in North Africa. The recovery of *Cryptolestes turcicus* (a species which has optimal requirements similar to *P. ratzeburgi* and *Alphitobius diaperinus*) at Pharaonic Amarna (Panagiotakopulu 2003) could reinforce

the North African connection. The possibility of a sub-Saharan tropic origin for the species, and thus evidence of a trade connection for the Egyptians, is largely speculative based upon the lesser grain borer's life cycle requirements. However, the Pharaonic Amarnan presence of *Tribolium confusum* and *Palorus subdepressus* could also imply the movement of cereals between sub-Saharan Africa and Egypt. Both species possess a life cycle similar to *Rhyzopertha dominica* and are not as thermophilic as *Trogoderma granarium* and *T. castaneum*. Moreover, *P. subdepressus* is widely distributed in the tropics in modern times (Rees 2007).

The archaeoentomological evidence supports the existence of a trade network between the Egyptians and the Minoans. While the presence of *koulouras* suggests that the Minoans were capable of storing large quantities of grain and may have been largely self-sufficient (Kieser 2005), the insect evidence supports the importation of commodities from southern Europe (Greece), Anatolia, and Egypt. Prior to the Late Minoan Period sites, *Oryzaephilus* sp. (likely *O. surinamensis* based on context and species associations) had only been archaeologically visible from the Neolithic Mandalo context in Macedonia; its recovery from Akrotiri (Panagiotakopulu and Buckland 1991) implies maritime trade connection between the regions. Similiarly, the presence of *S. granarius* at Akrotiri (Panagiotakopulu and Buckland 1991), Knossos (Jones 1984), and Kommos (Shaw and Shaw 1995) suggests a link to the Near East, and the *Rhyzopertha dominica*, *Stegobium paniceum*, and *Tribolium confusum* specimens imply a trade connection to Egypt. Additionally, the introduction of *O. surinamensis* (Alfieri 1931; Zacher 1934ab; Zacher 1937) to and the reappearance of *Sitophilus granarius* (Panagiotakopulu 1999) in Egypt during this period, suggests that cereals were being imported and exported from the Minoan

settlements. This could mean that cereals were being used as a form of currency in the Eastern Mediterranean into the Middle and Late Bronze Age.

Were the Aegean and Egyptian traders content with their Eastern Mediterranean connections, or did they expand westwards in search of new cultures and commodities? The Late Bronze Age records of the granary weevil from Italy and France cannot be viewed as confirmation of westward exploration on the basis of biogeographical evidence alone. While *Sitophilus granarius* may have been introduced to those regions through contact with the Eastern Mediterranean cultures during the Bronze Age, sufficient archaeoentomological analysis has not been conducted on Neolithic sites to discard the possibility of an earlier presence, particularly when the species was so well established in Germany. However, the species has not been noted on Bronze Age sites in Germany, which suggests that a Bronze Age introduction of the species from the north was unlikely. The Middle Bronze Age evidence of *Rhyzopertha dominica* in Spain (Alonso and Buxo 1993) could stand as evidence of culture contact with the Eastern Mediterranean, but as stated above, it is likely to represent a connection with the North African coast settlements.

The most conclusive archaeoentomological support for a westward movement during the Bronze Age comes from the recovery of *Stegobium paniceum* in Britain (Osborne 1989; Robinson 1991), the earliest accounts of the species in the region. Despite numerous archaeoentomological assessments having been undertaken in the United Kingdom, the biscuit beetle has only been noted on two Bronze Age sites and in both cases as a single specimen, which suggests that the species was not indigenous. The additional absence of species from Continental Europe during this era is interesting as it seemingly denotes a direct connection with the Egyptian (the

term used here is inclusive of the North African settlements in Tunisia, Algeria, and Morocco) and Eastern Mediterranean kingdoms. Due to the absence of other grain associated insects in the Bronze Age British contexts, *Stegobium paniceum* was unlikely to have been introduced during the transportation of cereals, but anthropically imported in association with another stored product.

The Bronze Age archaeoentomological accounts are indicative of the appearance and diffusion of most of the major stored cereal pests of antiquity. Egypt, in particular, seemed to serve as a hub for the movement of grains as made evident through appearance of a number of heterochthonous species of varying temperature preferences. The influence of the Eastern Mediterranean trade networks appears to have been far reaching with the insect evidence suggesting direct contact spanning from India in the east to Britain in the west.

5.4.3 The Iron Age

The Pre-Roman Iron Age was a time of socio-economic turmoil. The Egyptian power that had dominated the Bronze Age collapsed, conquered first by the Assyrians during the Third Intermediate, and whose fate seemed to be largely dictated by whichever empire controlled the Near East—the Assyrians, the Persians, the Macedonians, etc. The Pre-Roman Iron Age also witnessed the emergence of the Phoenicians as a Mediterranean maritime power. Unfortunately, the archaeoentomological record is meager for the period.

In the Near East, the granary weevil maintains a presence at Tel Arad (Hopf and Zachariae 1921) and Horbat Rosh Zayit (Kislev and Melamed 2000). Despite the absence of grain pest records (due to the lack of archaeoentomological assessments in general) from the region during the Bronze Age, the species most likely indicates a

continuation of the Neolithic populations, and the *Sitophilus granarius* specimens, noted in the Minoan and New Kingdom contexts, can be perceived as a reflection of the species presence in the area between the Neolithic and the Iron Age. Additionally, *Alphitophagus bifasciatus* and *Tenebroides mauritanicus* may also be representative of Neolithic remnants as opposed to later introductions. All three species have an optimal temperature for the completion of their developmental cycle falling between 25 and 30 °C, possibly reflecting a similar region of origin. While the cadelle and the granary weevil have been recorded together in Neolithic contexts, *A. bifasciatus* has a very limited fossil record. However, the two-banded fungus beetle has been recorded living in the wild in Israel (Chikatunov *et al.* 1997) suggesting an adaptation to an arid climate. It is possible that the Near East hosted environments meeting the temperate preferences of the cadelle and granary weevil as well as the arid conditions for *A. bifasciatus* [Figure 5.1]. Although the Iron Age sites may have contained some indigenous pests, the presence of *Oryzaephilus surinamensis* is indicative of an introduced species. As with the Bronze Age Egyptian records, the Israeli specimen likely denotes an original introduction that dates to the Minoan Period connection to Aegean and mainland Greece. Having adapted to a warm temperate climate, the species is tolerant of warm temperatures [Figure 5.2] and would have flourished in an environment suited for *S. granarius* and *T. mauritanicus*.

Similarly, the account of *Sitophilus granarius* in Okruglo, Croatia (Smith *et al.* 2006) does not necessarily signify an Iron Age introduction. As with the Bronze Age record from Italy (Fasani 1976), it could represent a population that was established during the Minoan Period or possibly from the Neolithic, if the pottery impression from Servia is considered.

During this period, the earliest accounts of *Trogoderma persicum* and *Sitophilus oryzae* have been documented by Chu and Wang (1975). Though it is worth noting their early presence outside of the Mediterranean arena, neither species appears to have become widely dispersed until the Post-medieval period (e.g. Carrott *et al*. 1995b). However, a single record of *S. oryzae* has been reported for the Roman era (Knörzer 1970) supporting the occurrence of exchange of commodities between the Orient and the Mediterranean cultures.

The Iron Age stored product pest records from Spain and Britain are likely the result of culture contact established by the Phoenicians. In Spain, Perales (1984) records two new species, *S. granarius* and *Tribolium* sp., in a context with *R. dominica*. The Phoenicians were a major seapower from 3150 to 2750 BP, and its North African city-state Carthage flourished into the Roman Period (Markoe 2000). Whereas *R. dominica* has been recovered from a Bronze Age context, the presence of *S. granarius* and *Tribolium* sp. reflects a connection with the Eastern Mediterranean cities, possibly Phoenicia. However, although *Tribolium* has not been recovered from Phoenicia, *T. confusum* and *T. castaneum* could have been introduced there from Egypt during the Bronze Age. Alternatively, all three species have been found in archaeological contexts from Bronze Age settlements in the Aegean and in Egypt, which may have served as ports for their diffusion into Spain.

A Mediterranean maritime connection with the British Isles is also reflected by the insect remains. As with the Bronze Age, *Stegobium paniceum* has been recovered an from Iron Age site in England. While the biscuit beetle's presence could be attributed to a residual population from the Bronze Age, neither the earlier (Osborne 1989; Robinson 1991) nor the Iron Age (Chowne *et al*. 1986) records suggest the existence of the well-established populations evident in the later Roman

period. However, though unlikely, a derivative of the Bronze Age populations cannot be discarded solely on the basis of a biogeographical survey and phylogenetic methods should be pursued (cf. King *et al.* 2009). As with the Bronze Age sites, the Iron Age *Stegobium paniceum* is unaccompanied by more discernibly grain associated species implying that contact between the regions did not involve the transport of large quantities of unprocessed cereals, which is supported by the Roman geographer Strabo's (S*G*) remarks on the tin trade between the Phoenicians and the inhabitants of the British Isles.

Leading up to the Late Iron Age, there is little archaeoentomological evidence regarding the Roman Republic. The best evidence for the presence of grain-associated insects is indirectly derived from Varro's *De Re Rustica*, where it is possible to ascertain a few locations that had infestations of *curculio* [see 5.3]. Although species level identification is problematic, Varro's sites roughly correspond with the archaeobiogeographical distribution of *S. granarius* from the earlier Iron Age contexts.

5.4.4 The Roman Empire

The later Mediterranean Iron Age played host to the rise of the *Imperium Romanum* and the furthest expansion of Roman control. It also affected a radical shift in the distribution of cereals around the Mediterranean. During the Roman Republic, until the annexation of the North African provinces, grains were produced on a small-scale by farmers, with their surplus transported to Rome as taxation. After the annexation, the grain trade remained largely centralized, but immense quantities of cereals were imported to Italian ports, such as Ostia, from Egypt and Africa for redistribution to citizens; a socio-economic change which Yeo (1946) proposed would

have severely undercut cereals grown in Italy itself, resulting in a redirection of the local agricultural efforts towards other commodities. The movement of cereals was also influenced by the Roman military. The Roman Republic did not maintain a standing army, and therefore the legions were supplied only during campaigns, and act, in the Middle and Late Republic, which involved the maintenance of lengthy supply lines distributed from the centralized source with supplements in times of crisis directly from allied regions (cf. Roth 1999). During the *Imperium*, Augustus restructured the Roman military to create a widely dispersed standing army. The garrisons were fed through local resources and supplemented by supply lines. However, whereas during the Republic the provisions needed to be transported first to a central location then redistributed, the Empire saw the movement of cereals to the garrisons directly from the grain-producing provinces (Roth 1999). As a result of these changes, the Roman Empire provided an outlet for the wide-spread dispersal of the grain-associated insect fauna.

In Central Europe, the first half of the first century AD was a period of conquest transitioning into military occupation for the Roman legions (Bakels and Jacomet 2003). The archaeoentomological remains provide evidence for the importation of cereals. The reappearance of *Sitophilus granarius* in the region, the first post-Neolithic record of the species, indicates that the imported grains were unprocessed as the weevil does not typically infest milled materials. The presence of the granary weevil in contexts with *Oryzaephilus surinamensis* (cf. Cymorek and Koch 1969; Koch 1970) is a commonly seen association around the coastal Mediterranean region as early the Bronze Age (see above), and *Oryzaephilus* sp. and *S. granarius* have established populations in France and Italy during the first century AD, e.g. Ponel *et al*. 2000; Dal Monte 1956, respectively. However, the absence of

other grain fauna at the German and Netherland sites (specifically those species common to North Africa and the Middle East during the Bronze and Iron Ages) infers an introduction of the pests, and thus the grains, from southern Europe. Moreover, as *Oryzaephilus surinamensis* has not been recovered from Spain at this date, France and Italy seem promising hubs for the dispersal. Knörzer's (1970) record of *S. oryzae* is notable as the species is previously unknown from the Mediterranean region and represents the earliest European record prior to the Post-Medieval Period. The presence of the rice weevil, during the first century AD, signifies the importation of exotic (luxury) cereal commodities to Neus-Novaesium, Germany that originated in the Far East (considering Chu and Wang's 1975 record from the Iron Age).

The Roman invasion and subsequent occupation of southern Britain in 43 AD are made evident by the additional arrival of grain pests to the region. The Romano-British sites, 1 Poultry (Rowsome 2000) and 21 Saint Peters Street (King and Hall 2008; Appendix 2), provide evidence towards a military introduction of the fauna as the sites are closely dated to the onset of the Roman occupation; in particular, the 1 Poultry specimens, which pre-date the Boudican Revolt of 60 AD's burning of the twenty-year-old Roman commercial settlement of Londinium, present-day London (Rowsome 2000). Mason (2003) estimates that 3,500 tonnes of grain would have been needed to supply the invading troops during the first three months, not including the supplies needed to support the animals. Although Britain had been exporting cereals to Roman provinces since Julius Caesar, the burden of supporting the legionaries in addition to the local populations would have required imported supplements until the garrisons were established. A single legion would have required over 2,800 tonnes of grain per year to support the troops (Mason 2003).

Based on the species present at these early sites, can the fauna be used to delineate the port of origin for the military supply lines? Because of their proximity to Britain, the European hubs seem the most likely suppliers of cereals during the invasion. The possibility of a European grain source is supported by the recovery of *Sitophilus granarius* and *Oryzaephilus surinamensis,* which have a first century AD, and earlier, presence in the grain-producing regions of Europe (modern-day Germany, France, and Spain). However, *Palorus ratzeburgi* and *Cryptolestes ferrugineus* have not yet been recovered from contemporaneous sites in those regions. If *P. ratzeburgi* and *C. ferrugineus* were absent from Europe during this time, the two species would signify the existence of a longer supply line. Moreover, as the species are secondary pests of stored products, they would not have been able to infest undamaged cereals at their source of origin, which would suggest the presence and likewise simultaneous introduction of a primary pest such as *S. granarius*. As *Palorus ratzeburgi*'s only pre-Romano-British record comes from Egypt (and *Oryzaephilus surinamensis* and *Sitophilus granarius* have also been recorded there in similarly dated contexts), cereals may have been shipped from the Egyptian and/or North African markets, but as these accounts date to the Bronze Age, the argument is tenuous.

The absence of a pre-Roman fossil record for *Cryptolestes ferrugineus* does not help clarify the problem. While modern populations of *C. ferrugineus* are capable of breeding in a range of climates (cf. Howe and Lefkovitch 1957), the species developmental optimal range for completion of its life cycle is around 35 °C with a relative humidity of 90 % (Rees 2004). Given its temperature specifications, *Cryptolestes ferrugineus* likely entered the Roman Empire from two regions:

1.) the Mediterranean warm temperate zone, or

2.) a tropic zone, and its tolerance of warm temperatures and high humidity is similar in range to *Trogoderma granarium* and *Tribolium castaneum*, both presumably from the Indian subcontinent.

However, considering the extensive movement of cereals that occurred around the Mediterranean and the exchange networks between the Mediterranean cultures, sub-Saharan Africa and India that date back to the early Bronze Age, the lack of an earlier record for *Cryptolestes ferrugineus* is suspicious if the species was endemic to those regions. Another possibility may be a late introduction from the island of *Trapobane* (Sri Lanka). Pliny the Elder *NH* VI.XXII portrays the first encounter between Rome and *Trapobane* in a meeting between the Emperor Claudius (41-54 AD) and four ambassadors from the island, and discusses the size, fierceness, and ferocity of Sri Lankan elephants in comparison to the Indian species as depicted in earlier accounts by Onesicratus, an admiral of Alexander the Great. The establishment of a first century AD trade market with Sri Lanka would have provided a pathway for the introduction of new stored product insects, such as *Cryptolestes ferrugineus*. Egyptian Red Sea trade, at the time, seemed concerned with the establishment of elephant hunting stations (S*G* XVI.IV.VII, 1877; NH VI.XXXIV.CLXX-CLXXV, 1635). Hypothetically, if the Romans imported live Sri Lankan elephants into the Empire for performances or warfare, the grain species may have been introduced into the Mediterranean region at the Egyptian ports along the east coast of Africa, in association with the fodder needed to sustain the elephants on the journey across the Indian Ocean and the Red Sea. The port of call in Egypt would have limited and controlled *C. ferrugineus*' initial infestation and dispersal. A major port, like Alexandria, would have enabled the species to disperse into Italy and throughout the Empire from the Italian distribution centers. However, a minor port

along the East African coast would not have necessarily affected a mass diffusion of the species. As the species does not appear to have become widely established in Egypt by the second century (it is absent from Mons Claudianus, Panagiotakopulu and van der Veen 1997, though this could be attributed to unsuccessful competition with its congener *C. turcicus*, see Grain Fauna above) or first century Herculaneum, Italy (Dal Monte 1956), the species may never have reached the Alexandrian or Italian ports in sufficient numbers. Instead, it may have diffused across land via the trade caravans into the North African provinces and then into Britain. A North African pathway would also explain the introduction of *Palorus ratzeburgi* (another species absent from the Mons Claudianus site, Pangiotakopulu and van der Veen 1997). While the Romano-British records of *C. ferrugineus* and *P. ratzeburgi* infer a non-European military supply line, the presence of *O. surinamensis* and *S. granarius* allows for archaeoentomological evidence of additional supply lines extending from European grain-producers. Moreover, it is possible that multiple populations (denoting different ports of origin) of the saw-toothed grain beetle and the granary weevil were introduced into Britain, but genetic analysis would need to be conducted (cf. King *et al.* 2009).

As the Roman legions extended their conquest into northern England, the grain associated insects were transported to the northern forts, e.g. Carlisle (Kenward *et al.* 2000; Kenward and Carrott 2006), Ribchester (Large *et al*. 1994; Buxton and Howard-Davis 2000), and York (Hall and Kenward 1976; Kenward and Williams 1979). The diffusion of *Sitophilus granarius*, *Oryzaephilus surinamensis*, *Palorus ratzeburgi*, and *Cryptolestes ferrugineus* following the military advancement indicates that supply lines were maintained, to some extent, overland from southern Britain.

However, the introduction of *Tenebrio obscurus*, the dark mealworm, and *Tenebroides mauritanicus* implies that supply lines were established and/or maintained through maritime sources as well. Although its congener *Tenebrio molitor*, the yellow mealworm (a potential endemic to Britain inferred from its early presence; cf. Howard *et al.* 1999; Smith and Howard 2004, and cold-temperate adaptation [Figure 5.2]) has an early British presence, *T. obscurus* does not have a previous British record. However, the contemporaneous presence of the species in France (Ponel *et al.* 2000) may imply a supply line extending from France to the British frontier forts. The Roman introduction of *T. obscurus* to England appears to have negatively impacted its congener *T. molitor* in Britain with the invasive dark mealworm seemingly replacing the endemic species in the area by the end of the Roman Period (Kenward in press). The ecological and thermal similarities between the two species suggest that they may have experienced allopatric, or even peripatric, speciation as a result geographic isolation. Furthermore, the two species are fairly morphologically distinct (see Mound 1989), which implies a long period of separation, possibily in the range of millions of year (Kenward pers. com). Both species seem adapted to the maritime temperate zone of Western Europe and occupy similar niches, which would result in competition [Chapter 2]. As such, populations of the yellow mealworm were probably initially limited to Britain and *T. obscurus* to the western coastal regions of Europe. However, the dark mealworm, as an introduced species, would have had the advantage in Roman Britain. The landscape alterations and changes in grain storage practices brought about by the Romans would have initially, potentially, displaced the indigenous *T. molitor* from anthropic contexts and into the natural environment, e.g. birds nests (Mound 1989). Moreover, if the introduction of *T. obscurus* from France and Western Europe was in cereals, the dark

mealworm would have been directly imported into anthropic contexts and presenting as more archaeologically prevalent than its congener. In areas with established populations of *T. obscurus*, the yellow mealworm would have difficulty competing in order to establish itself in grain contexts. However, in the absence of, or the existence of limited, populations of the dark mealworm, *T. molitor* may have been able to re-invade the anthropic contexts, explaining its sporadic archaeological record.

Although *Tenebroides mauritanicus* could survive in temperate environs of France and may have been imported to Britain alongside *Tenebrio obscurus*, the species lacks a Roman fossil record in the region. Biogeographically, this suggests a supply line extending to the Eastern Mediterranean where the cadelle was last archaeologically visible in the Iron Age contexts of Israel (Kislev and Melamed 2000). A connection to the Eastern Mediterranean is also supported by the introduction of *Alphitobius diaperinus* to Papcastle, Cumbria (Kenward and Allison 1995) as well as *Tribolium castaneum* to second century York (Hall *et al.* 1980).

The importation of cereals appears to have continued throughout the Roman occupation of the island. The third century AD account of *Palorus subdepressus* from Alcester, Warwickshire (Osborne 1971) implies a connection to the Egyptian provinces, as does the fourth century record of *Tribolium confusum* and *Cryptolestes turcicus* at Towcester, Northamptonshire (Girling 1983).

However, during the second century AD, there is evidence to suggest that the Britain was exporting cereals. *Cryptolestes ferrugineus* and *Palorus ratzeburgi* are present at the site of Amiens, France in context with *Sitophilus granarius* and *Oryzaephilus surinamensis* (Yvinec 1997; Matterne *et al.* 1998). *C. ferrugineus* and *P. ratzeburgi* archaeobiogeographically represent new species in the region, and in addition to the presence of *S. granarius* and *O. surinamensis* may be indicative of an

exported Romano-British "fauna package"; a combination of ecologically interrelated stowaways that flourished in Britain and accompanied the movement of cereals beyond its shores.

Moreover, Pals and Hakbijl's (1992) assessment of the palaeoecological remains from a late second century sunken ship in the Netherlands confirms that the grain fauna were transported with the movement of cereals during the Roman Empire. While the authors suggest the loess region of Belgium as the potential source for the grain (Pals and Hakbijl 1992, 298), the distinctive arthropod fauna provides evidence towards another origin. While the presence of *Cryptolestes ferrugineus*, *Oryzaephilus surinamensis*, *Palorus ratzeburgi*, and *Sitophilus granarius* hints at a Romano-British origin, as mentioned above, the fauna had also been introduced to France by the second century. However, the identification of *Tenebrio molitor* from the ship substantiates a British connection. The Woerden specimen represents the earliest record of the yellow mealworm outside of Britain. Pals and Hakbijl (1992) also report *Mycetophagus quadriguttatus*, a fungal feeder associated with foods. While not necessarily indicative of the presence of cereals, the beetle supports an argument for a British origin. As with *T. molitor*, prior to this account, the species appears to have been to the limited to the British Isles (e.g. Robinson 1979; Smith *et al*. 1999; Smith and Howard 2004). The recovery of *Alphitophagus bifasciatus* is interesting as the species does not have an earlier connection to Britain. However, the two-banded fungus beetle does not have an extensive fossil record and may have easily been imported to England along with the other Romano-British Period introduced species, i.e. the cadelle, the lesser mealworm beetle, or the rust-coloured flour beetle, with Eastern Mediterranean ties. On the basis of biogeographical accounts, the fossil insect assemblage from Woerden appears strongly indicative of a British origin for the

cereals. Furthermore, the true benefit of the Woerden site and its insect assemblage is that it demonstrates that grain-associated insects were transported long-distances in cereals during the Roman Era.

5.5 Conclusion

Biogeography provides a tool enabling the examination of a range of human activities. By investigating the archaeoentomological evidence for changes in the distribution of the grain species over time, hypotheses may be formulated in regards to the past occurrence of human migration, cultural contact, and trade. While biogeography is capable of providing a time frame for the introduction and diffusion of grain-associates, the approach suffers from limitations, and the resolution of its results is ultimately dependant on the quality of the fossil record. When provided with a well-established fossil record, such as that in Britain, a biogeographical approach clearly provides evidence for the introduction of cereal pests with the arrival of the Roman garrisons. However, when confronted with meagre evidence, similar to the present Neolithic record, the method can only offer some insight into human activities and largely limits inferences to the realm of speculation.

The paucity of the archaeoentomological assessments outside of the United Kingdom, an issue addressed by Buckland 1981, continues to pose problems for the completion of successful biogeographical assessments, particularly in attempting to ascertain accurate shifts in species' distributional ranges. For example, *Sitophilus granarius* has been recovered from Neolithic sites in northwestern Europe. The next record of the species in the region comes from 8,000 years later during the Roman occupation. Was the granary weevil truly absent from the northwest during the Bronze and Iron Ages? Was the northwest a potential source for the diffusion of the

species into Bronze and Iron Age sites in southern Europe? When applied in isolation, biogeography is unable to address the problem without a more refined fossil record, and it is only when material archaeological accounts are consulted (the trade and cultural contact between Britain and northwestern Europe during the Bronze and Iron Age, cf. Childe 1957, would have provide opportunity for the introduction any extant populations of the granary weevil to Britain prior to the Roman Era) that the species' absence from the region between the Neolithic and Roman Periods can be inferred.

The major limitation of the biogeographical approach is that it is unable to discern multiple introductions of a species as it does not distinguish between different populations of the same species. During the early Roman conquest and occupation of Britain, the Roman garrisons appeared to have been receiving cereal supplies from several provinces. As populations of *Sitophilus granarius* appear around the Mediterranean, the species was likely transported to Britain from multiple regions on several occasions. However, in the absence of other pests, a biogeographical investigation of *S. granarius* would be blind to these introductions and, as such potential trade connections to regions with early Roman settlements would be obscured. This is evidenced in areas like Spain (Moret and Martin Cantarino 1996) and the Netherlands (Kuijper and Turner 1992) where *S. granarius* has been the only grain pest recovered from sites dating to the early Roman period, which renders the species' potential to delineate culture contact largely ineffective. However, the presence of other grain pest species would provide additional clues towards discerning any potential trade connections, which would enhance the efficacy of the biogeographical approach.

Regardless, the application of the biogeographical method towards grain-associated beetles has an advantage over the strictly palaeoecological assessments [Chapter 4]. It moves beyond a site based investigation of product-associations and autochthonous-allochthonous components in an effort to holistically map species' distributions in a spatial and temporal context. This allows for the consideration of a human-historic, rather than solely ecological, component in the investigations. The limitations of the approach may be curbed by the incorporation of isotopic [Chapters 6 and 7] and/or phylogenetic analyses [Chapter 8].

Chapter 6

Stable Isotopes ($\delta^{2}H$, $\delta^{13}C$, and $\delta^{15}N$) from Beetles are Geographic Indicators of the Origins of Cereals

6.1 Introduction

It has been demonstrated that the stable isotope composition of animal body tissues closely corresponds to that of their diets (cf. Gannes *et al.* 1998), and in recent years, this concept has been applied to the study of animal migrations (e.g. Hesslein *et al.* 1991; Best and Schell 1996; Hobson 1999; Hobson *et al*. 1999; Rubenstein and Hobson 2004). Stable isotopes of carbon and nitrogen have been employed to delineate geographically distinct populations of animals on the premise that stable isotope ratios in foodwebs differ regionally, providing naturally occurring signatures in organisms that can be traced to origin (e.g. van der Merwe *et al.* 1990; Vogel *et al.* 1990; Alisauskas and Hobson 1993). Moreover, stable-hydrogen isotope measurements (δ^2H) in several species of Neotropical migratory songbirds (Hobson and Wassenaar 1997) and monarch butterflies *Danaus plexippus* (Hobson *et al.* 1999) exhibited a geographic fingerprint permitting the deduction of the North American origins of individuals of the respective species. These studies make use of the fact that deuterium in rainfall is reflected in plants (Yapp and Epstein 1982), and subsequently, the stable-hydrogen and carbon isotopic ratios are transferred through the foodweb by trophic-level consumers.

The present evaluation seeks to apply stable isotope methods towards discerning the origins of modern cereals as made evident through chitin analysis of their associated beetle fauna. In archaeological investigations, grain beetles commonly serve as evidence for the presence of cereals at sites, and in the absence of charred plant material, may stand as the sole indicators that cereals had been present. Although stable isotopes measurements of chitin have been used to address palaeoecological issues (e.g. Miller *et al*. 1988; Motz 2000; Gröcke *et al*. 2006), the applications have not been employed towards disentangling palaeoeconomic

questions such as the origins of traded perishable products in the past. By determining the applicability of stable isotopes towards unravelling the issue using modern materials, this study will hopefully serve as a platform to launch future investigations involving insect fossils.

6.2 Materials and Methods

6.2.1 Laboratory Rearing Experiment

Adult populations of the granary weevil *Sitophilus granarius*, which were initially provided by Central Science Laboratories in Yorkshire, UK, served as Generation 1 (G1) in the experiment. The egg, larva, and pupa stages of each individual of *Sitophilus granarius* occur within a single cereal kernel, and at 30 °C fully formed adults emerge 3-5 weeks after hatching and live 7 to 8 months (Knopf 1980; Rees 2007). The adult weevils do not moult, and thus their chitin should provide a material that is metabolically inert following the adults emergence from the grain. This is tested during the experiment using weevils bred on British barley that were subsequently allowed to feed on cereals from other geographic regions. Because the granary weevils mature in the interior of the cereal kernels, the isotopic signature of their chitin should more closely correspond to the value of the starchy layer (endosperm) of cereals than their exterior seed coat (brancoat). This was briefly examined during the present experiment.

The barley (*Hordeum vulgare*) and wheat (*Triticum sp*.) were locally-grown and purchased in York, UK, and the oats (*Avena sativa*) were gathered from Macon, Mississippi. These cereals provided a control with a stable-isotope measurement from a known geographic region to which both the δ^2H of the growing season precipitation and the chitin isotopic values could be aligned. Buckwheat (*Fagopyrum esculentum*),

purchased in York but with an unknown geographic origin, were used in blind tests to assess whether stable-hydrogen and carbon isotope measurements of beetle chitin can be used to determine the geographic origins of the plants. Additionally, groups of granary weevils were bred in tubes containing all four cereals to serve as a second blind test.

Groups of 15 weevils from G1 were placed in 50 x 25 mm tubes half-filled with individual species of grains. A proportion of the remaining G1 weevils were frozen for isotopic analysis. The tubes were held at 28 °C for 30 days to promote the oviposition of the granary weevils. Generation 2 adult weevils emerged in the tubes 30 days after the removal of G1. Fifty percent of the second generation specimens (G2a) were immediately frozen for the isotope experiments, and the remainder (G2b) were each transferred to separate tubes containing a second cereal type and kept at 28 °C for 30 days. G2b was then frozen for analysis.

6.2.2 Preparation of Chitin

The elytra were separated from the thorax and placed in 5 ml glass tubes. The samples were rinsed in a solution of 2:1 dichloromethane: methanol in order to remove waxes. To eliminate proteinaceous material, the elytra were then fully immersed in 2 ml 10 % NaOH, vortexed gently, and incubated for 72 hours at 110 °C with gentle agitation (Tsao and Richards 1952; Miller *et al*. 1988). The NaOH solution was formed using distilled water of known isotopic value. After incubation, the resulting products were added to a spin column, spun through a filter at 10000 g for 1 minute, and the collection tubes emptied. The products were re-suspended in the distilled water and spun at 6000 g for 1 minute. The collection tubes were emptied

and the step repeated three times. The product was then transferred to 2 ml Eppendorf Biopur tubes then dried overnight at 60 °C.

6.2.3 Removing Exchangeable Hydrogen

Because natural chitin contains some strongly absorbed water (Muzzarelli 1977) that can isotopically exchange its hydrogen with ambient H_2O, resulting in isotopic noise, Schimmelmann and Miller (2002) investigated various strategies to eliminate or isotopically control the exchangeable hydrogen from chitin. The most economical approach discussed in the study involved the equilibration of exchangeable hydrogen in chitin in H_2O of known δ^2H, succeeded by drying and high-temperature pyrolitic liberation of H_2 from the chitin in the presence of excess carbon (cf. Schimmelmann 1991; Schimmelmann *et al*. 1993). A similar procedure was adopted in the present investigation, but was modified to include the use of a standard (whale baleen) to further account for the presence of exchangeable hydrogen in the chitin (see below). In an effort to limit exposure to multiple sources of exchangeable hydrogen, the water (-47.43 ‰ Vienna Standard Mean Ocean Water standard, VSMOW; Appendix 3F) employed for the NaOH solution and rinsing stages of the chitin preparation was used for equilibration.

6.2.4 Stable Isotope Analysis

Hydrogen

The equilibrated chitin (1 mg) was weighed into silver capsules (5 x 8 mm). Additionally, the starch-layers at the centres of the grain kernels were separated from the caryopses using a scalpel and weighed into capsules. The filled capsules were left open for a period of 4 days to allow the exchangeable hydrogen in the samples to fully

equilibrate with the moisture in the laboratory air. The stable-hydrogen isotope assays were performed at Iso-Analytical Limited Laboratories in Cheshire, UK. The sample capsules were sealed just prior to analysis.

EA-IRMS (Elemental Analyser - Isotope Ratio Mass Spectrometry) was used for analysis with the samples and references placed in silver capsules, sealed, and loaded into an auto-sampler. The sealed capsules were then placed in a furnace at 1080 °C and thermally decomposed to H_2 and CO. Any trace water produced was removed by magnesium perchlorate, while, any trace CO_2 was removed using a Carbosorb™ trap. The H_2 was resolved by a packed column gas chromatograph held at 45 °C. The resultant chromatographic peak entered the ion source of the IRMS where it was ionised and accelerated. Gas species of different mass were separated in a magnetic field then simultaneously measured on a Faraday cup universal collector array. Masses 2 and 3 were monitored for H_2.

The reference material used for δ^2H analysis was IA-R002 (mineral oil, $\delta^2H_{V\text{-}SMOW}$ = -111.2 ‰). IA-R002 has been calibrated against NBS-22 (mineral oil, $\delta^2H_{V\text{-}SMOW}$ = -118.5 ‰), an inter-laboratory comparison standard distributed by the International Atomic Energy Agency [Appendix 3G].

Test samples of IA-R002 and IAEA-CH-7 (polyethylene foil, $\delta^2H_{V\text{-}SMOW}$ = +100.3 ‰) were analysed along with the samples as quality control checks. Moreover, BWB-II (whale baleen) with a known non-exchangeable $\delta^2H_{V\text{-}SMOW}$ value of -108 ± 4 ‰ was assayed within each batch of samples. The capsules containing BWB II were treated identically to those containing samples during weighing and equilibration with laboratory air. By using the measured $\delta^2H_{V\text{-}SMOW}$ value for BWB-II in each batch, a simple correction for exchangeable hydrogen to the $\delta^2H_{V\text{-}SMOW}$ data

was able to be applied. The results for δ^2H [Appendices 3D-3E] are expressed in per mil relative to VSMOW in Formula 6.1:

$$\delta^2H_{V\text{-}SMOW}\,‰ = [(R_{Sample} - R_{VSMOW}) / (R_{VSMOW})] \times 1000\,‰.$$

Replicates of samples and inter-comparison material yielded an external reproducibility of better than ± 1.90 ‰ for δ^2H measurements.

Carbon and Nitrogen

EA-IRMS was likewise employed for stable-carbon analyses. The samples and reference materials were weighed into tin capsules (0.5 mg), sealed, and then loaded into an automatic sampler on a Europa Scientific Roboprep-CN sample preparation module. The materials were placed into a furnace held at 1000 °C and combusted in the presence of oxygen. Moreover, the tin capsules flash combusted, which raises the temperature around the sample to ~ 1700 °C. The combusted gases were then rinsed in a helium stream over a combustion catalyst (Cr_2O_3), copper oxide wires (to oxidize hydrocarbons), and silver wool to remove sulphur and halides. The resultant gases (N_2, NO_x, H_2O, O_2, and CO_2) were swept through a reduction stage of pure copper wires held at 600 °C, in order to remove any oxygen and converted NO_x species to N_2. A magnesium perchlorate chemical trap was utilized to remove water, and a Carbosorb trap removed CO_2 during nitrogen-15 analysis. Nitrogen and carbon dioxide were resolved with a packed column gas chromatograph held at an isothermal temperature of 100 °C. The resultant chromatographic peak entered the ion source of the Europa Scientific 20-20 IRMS, was ionised and accelerated. Gas species of different mass were separated in a magnetic field then simultaneously measured on a Faraday cup universal collector array. For N_2, masses 28, 29, and 30 were monitored, and for CO_2, masses 44, 45, and 46 were assessed.

The reference material [Appendix 3C] employed for $\delta^{13}C$ and $\delta^{15}N$ analysis was IA-R042 (powdered bovine liver, $\delta^{13}C_{V\text{-}PDB}$ = -21.60 ‰, $\delta^{15}N_{Air}$ = 7.65 ‰). IA-R042, a mixture of IA-R005 (beet sugar, $\delta^{13}C_{V\text{-}PDB}$ = -26.03 ‰) and IA-R045 (ammonium sulfate, $\delta^{15}N_{Air}$ = -4.71 ‰) and a mixture of IA-R006 (cane sugar, $\delta^{13}C_{V\text{-}PDB}$ = -11.64 ‰) and IA-R046 (ammonium sulphate, $\delta^{15}N_{Air}$ = 22.04 ‰) were run as quality control check samples during the sample analysis. IA-R042 was calibrated against and traceable to IAEA-CH-6 (sucrose, $\delta^{13}C_{V\text{-}PDB}$ = -10.43 ‰) and IAEA-N-1 (ammonium sulfate, $\delta^{15}N_{Air}$ = 0.40 ‰). IA-R005 and IA-R006 were calibrated against and traceable to IAEA-CH-6. IA-R045 and IA-R046 were calibrated against and traceable to IAEA-N-1. IAEA-CH-6 and IAEA-N-1 are inter-laboratory comparison standards distributed by the International Atomic Energy Agency (IAEA), Vienna. The results for $\delta^{13}C$ were reported relative to the PDB standard, and the $\delta^{15}N$ was calibrated to atmospheric N_2 [Appendices 3A, 3B, 3I]. Formula 6.2 shows the expression of stable C and N isotope ratios as:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \text{ X } 1000,$$

where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$ for $\delta^{13}C$ or $\delta^{15}N$, respectively. Replicates of samples and inter-comparison material yielded an external reproducibility of better than ±0.10 ‰ for $\delta^{13}C$ and ±0.23 ‰ for $\delta^{15}N$ measurements.

6.3 Results

Table 6.1 δ^2H (‰) VSMOW of G2a weevils and associated cereals

δ^2H (‰) VSMOW Chitin (N)	Associated Cereal	δ^2H (‰) VSMOW Starch	Body-diet Fractionation	δ^2H (‰) VSMOW Seed coat
-90.81± 7 (6)	Barley	-96.21± 6	+5.40	-59.60
-114.61± 9 (6)	Buckwheat	-127.69± 7	+13.08	-81.60
-101.39± 9 (4)	Oats	-103.16± 7	+1.77	-51.00
-84.7 (1)	Wheat	-88.94± 3	+4.24	-70.00

6.3.1 δ^2H and $\delta^{13}C$ Measurements from the Control Component

The data presented in Table 6.1 illustrate the intraspecific variation of δ^2H exhibited by granary weevils bred in the same host cereal as well as in host cereals grown in different geographic regions. Within the test groups of the same host cereal, there was evidence of intraspecific variation approximating ± 9‰ in the oats- and buckwheat-associated weevils. This exceeds the levels of ± 6‰ that have been recorded in previous control experiments (Miller 1984; Miller *et al.* 1988) and may indicate the remaining presence of exchangeable hydrogen.

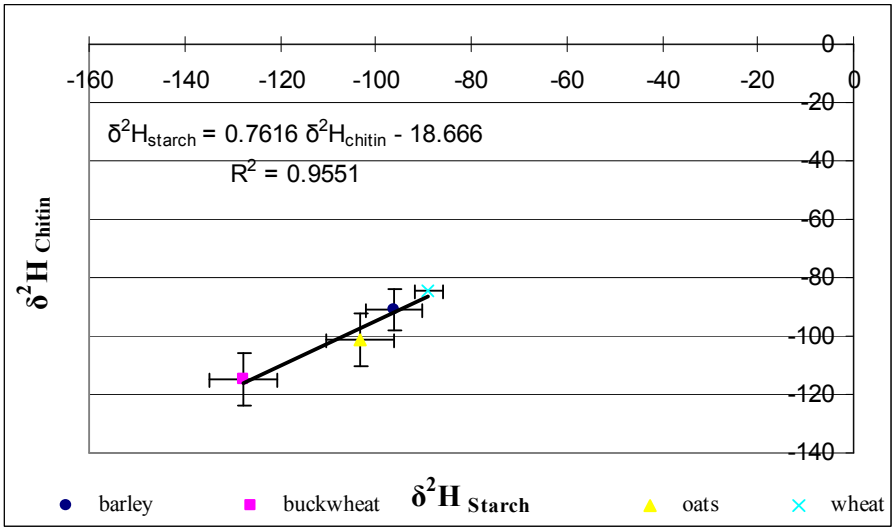
Table 6.2 $\delta^{13}C$ (‰)$_{V\text{-}PDB}$ and $\delta^{15}N$ (‰)$_{Air}$ of G2a Weevils and Associated Cereals

$\delta^{13}C$ (‰) Chitin (N)	Associated Cereal	$\delta^{13}C$ (‰) Starch	Body-diet fractionation	$\delta^{15}N$ (‰) Chitin	$\delta^{15}N$(‰) Starch
-27.64± 0.45 (5)	Barley	-28.26± 0.59	+0.62	1.50± 0.36	2.89±0.22
-25.38± 0.90 (4)	Buckwheat	-24.71± 0.20	-0.67	0.46± 2.39	2.27±0.17
-25.55± 0.98 (6)	Oats	-26.31± 0.18	+0.76	2.08± 0.67	2.46±0.14
-20.45± 0.36 (4)	Wheat	-22.23± 0.40	+1.78	2.19± 0.61	3.23±0.22

The elytra were strongly correlated with the isotopic signal of the endospermal starch layers of their host plants [Figure 6.1; Figure 6.2]. The chitin was slightly enriched, averaging +6.1 ‰, in deuterium compared to the starch, and the analyses indicated an approximate correlation of 0.90 for the stable-carbon [Table 6.2] isotope measurements. The body-diet fractionation in the $\delta^{13}C$ is similar to the range (± 0.5-1.1 ‰) reported in other investigations for trophic level variation (e.g. DeNiro and Epstein 1978; Wada *et al.* 1987; Ostrom and Fry 1993; Michener and Schell 1994; Ostrom *et al.* 1997; Bocherens and Drucker 2003). The enrichment of the deuterium in the chitin is indicative of a typical trophic level increase (e.g. Birchall *et al.* 2005). However, this was not supported by the stable-nitrogen [Table 6.2]. The chitin

contained heavier nitrogen than the starch (with an average body-diet fractionation of -1.16 ‰) and exhibited little correlation (R^2= 0.42) with the isotopic nitrogen from

Figure 6.1 Correlation of δ^2H in weevil chitin and starch of host cereal



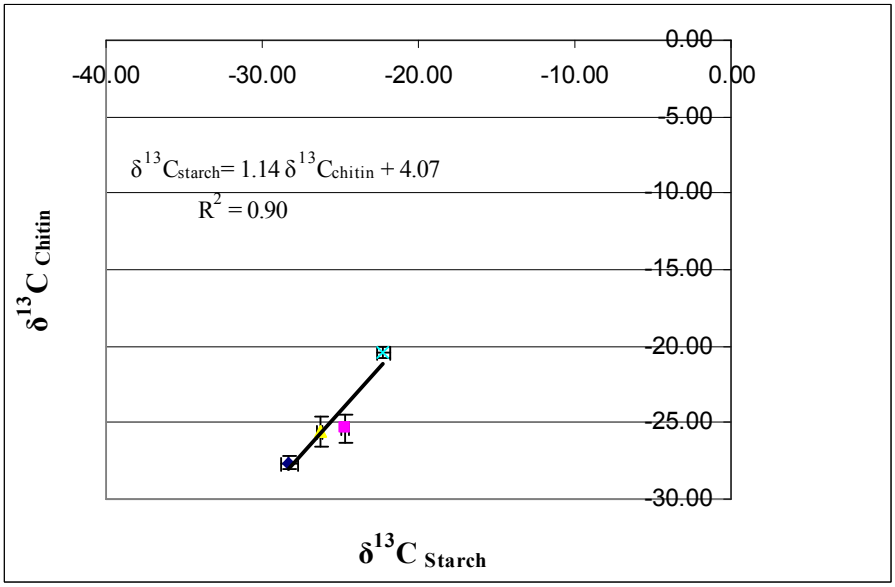


Figure 6.2 Relationship between the $\delta^{13}C$ in *Sitophilus granarius* and host cereals

the starch [Figure 6.3]. This may imply that the chitin nitrogen was acquired from a source other than the endospermal nitrogen. The absence of trophic level increase was also found elsewhere in the laboratory samples of aphids bred on sorghum (body-diet difference of 0:0; Ostrom *et al.* 1997). However, the nitrogen signal may reflect the use of dietary nitrogen in cuticular formation, with the depleted $\delta^{15}N_{chitin}$ being

attributed to the process used during the removal of the wax layer. When the analyses were replicated at the University of Bradford with the wax-layer preserved [Appendix 3E], a trophic level change was made evident through the stable-nitrogen results. While sufficient material was not available to re-test ^{15}N-wheat, the barley provided a $\delta^{15}N_{chitin+wax}$ value of 6.64± 0.54, the buckwheat indicated a $\delta^{15}N_{chitin+wax}$ of 6.40± 0.18, and the oats expressed a $\delta^{15}N_{chitin+wax}$ of 6.56± 0.06. The deuterium from both the chitin and the starch were depleted in comparison to the seed coats, exhibiting an average difference of -31.33 ‰ and -37.45 ‰, respectively. This result confirms the granary weevil's developmental association with the interior of the grains.

Figure 6.3 $\delta^{15}N$ of chitin versus $\delta^{15}N$ of starch

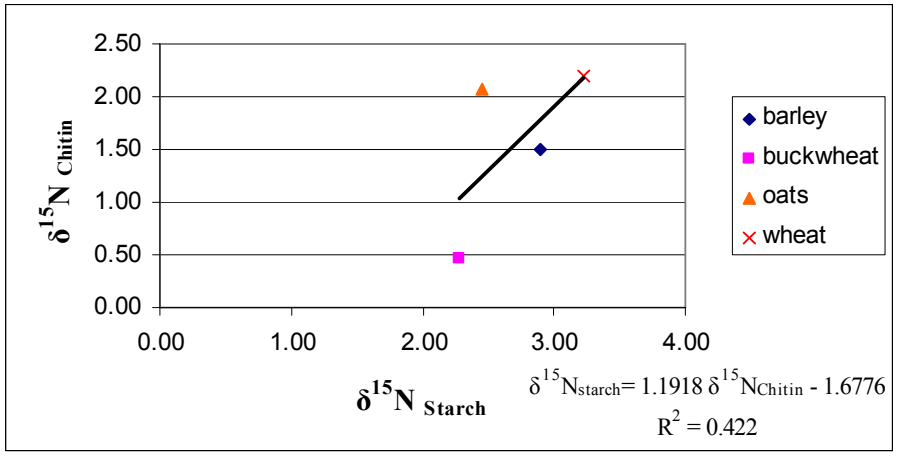


Table 6.3 presents the results of the barley-bred (G2b) weevils that were transferred to additional cereals in order to assess the metabolic stability of chitin in non-moulting beetles. *Sitophilus granarius* specimens were allowed to mature in barley before being transferred to containers with individual species of oats, buckwheat, and wheat. The G2b weevils exhibited

Table 6.3 $\delta^{2}H$ (‰) VSMOW of G2b that were bred in barley then transferred to a second cereal

$\delta^{2}H$ (‰) VSMOW Chitin (N)	**Associated Cereal**
-91.35± 5.35 (3)	Barley → Oats
-87.09± 3.65 (2)	Barley→ Buckwheat
-91.30± 2.98 (3)	Barley → Wheat

a D/H ratio within the range of the barley-bred G1 beetles, -90.81± 7. In comparison to the $G2a_{barley}$ specimens, the $G2b_{oats}$ presented a standard deviation of 0.38, the $G2b_{buckwheat}$ 2.63, and the $G2b_{wheat}$ 0.34. This suggests that the chitinous hydrogen remains relatively inert in adult forms of non-moulting beetles and reflects the hydrogen signal incorporated during development rather than the dietary habits after emerging from the grains.

OIPC (The Online Isotopes in Precipitation Calculator) was consulted to predict the isotopic value for the average meteoric precipitation of the host plant's total growing season (δ^2H_p) and the predicted period of maximum tissue growth for the cereal kernels (δ^2H_g) based upon geographic perimeters (e.g. latitude; Bowen 2007) [Table 6.4]. In each case, both the δ^2H_p and δ^2H_g were enriched in comparison to the δ^2H_{chitin}, δ^2H_{starch}, or $\delta^2H_{seedcoat}$ of materials from the corresponding sites [Fig. 6.4]. Both δ^2H_p and $\delta^2H_{seedcoat}$ followed the geographic trend suggested by the Raleigh distillation model with light hydrogen presenting as more abundant in higher latitudinal regions. However, δ^2H_{chitin} and δ^2H_{starch} were inversely proportionate to the predicted meteoric precipitation for the host plant's growing season, and showed the availability of relatively high levels of light hydrogen at low latitudes. This may be a reflection of continentality as there is a notable difference in the deuterium ratios of longitude 88.34˚ W (-100 ‰ $\delta^2H_{annualprecipitation}$) and 1.04˚ W (-56 ‰ $\delta^2H_{annualprecipitation}$) when tabulated for a constant latitude 53.57° N and altitude 11.9 m. Moreover, depleted deuterium values were reported by Hobson and colleagues (1999) for butterfly keratin retrieved from Metairie, LA (-96 ‰ δ^2H, latitude 29.58° N; longitude 90.09˚ W).

Between the intra-regional Yorkshire cereals, barley and wheat, there was isotopic discrepancy in both the stable-carbon and hydrogen analyses. These may

most likely be attributed to differences in altitude where the plants were grown, relative humidity, and seasonality (winter wheat versus spring barley). Previous studies have shown that ^{13}C (e.g. Körner *et al.* 1988; Körner *et al*. 1991) and ^{15}N (Körner and Diemer 1987; Körner *et al.* 1988) increase in plants in respect to altitude and relative humidity. As the cereals were purchased commercially, the location in Yorkshire where the grains were cultivated is unknown. However, the relative humidity can be calculated based on the local growing season of the cereals. The winter wheat would have been subjected to an approximate RH of 80.6, and the spring barley an RH of 74.5, which may partially explain the enriched stable-carbon and nitrogen values of the wheat. However, relative humidity is not the sole factor influencing the stable-nitrogen and carbon. The Mississippian oats were cultivated during a period of relative humidity approximating 88 but exhibit a lower isotopic composition than the wheat, which implies the effect of additional factors such as altitude. Yorkshire displays a very complex series of altitudinal variations, which would have had a significant impact on the isotopic composition of the cereals. For

Table 6.4 Precipitation values based on geographic perimeters

Location (Associated Cereal)	**Geographic data[1]**		**Growing Season**	**Period of Max Tissue Growth for Kernel**	**δ^2H_p[2,3]**	**δ^2H_g[2,4]**
	Latitude	**Longitude**				
Yorkshire, UK (Barley)	53.57° N	1.04° W	Feb-Sept	May-July	-52.85	-55.33
Macon, MS, USA (Oats)	33.06° N	88.34° W	Sept-April	Jan-March	-36.5	-43.33
Yorkshire, UK (Wheat)	53.57° N	1.04° W	Sept- July	March-May	-62.78	-64.66

[1] Coordinates retrieved from Google Earth (Google Inc 2009)
[2] Average δ^2H values predicted through OIPC (Bowen 2007)
[3] δ^2H_p = Average meteoric precipitation for total growing season of host plant
[4] δ^2H_g = Average meteoric precipitation for period of max tissue growth for host plant kernel

Figure 6.4 Relationship of average growing season precipitation (δ^2H_p) with $\delta^2H_{seedcoat}$, δ^2H_{starch}, and δ^2H_{chitin}

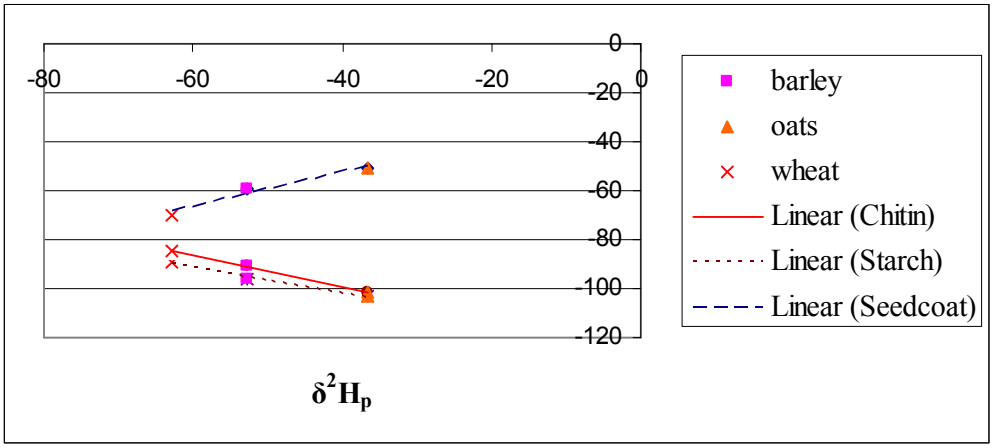
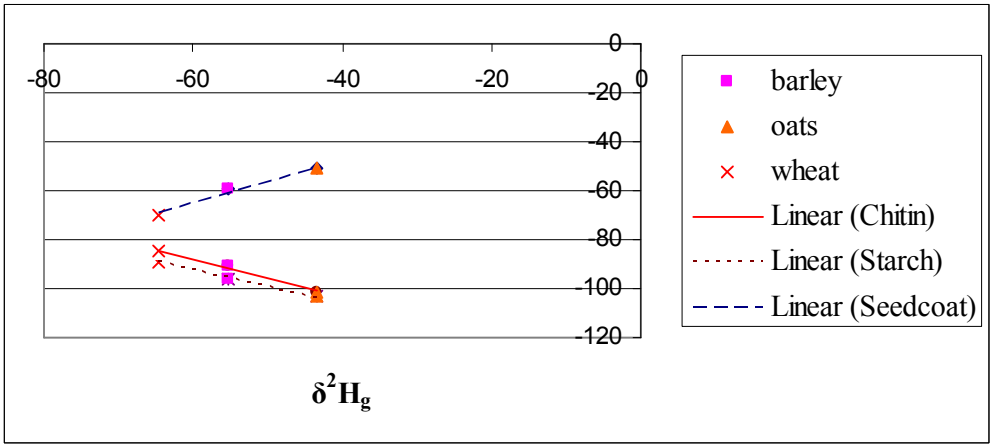


Figure 6.5 Relationship of average precipitation for period of maximum tissue growth (δ^2H_g) with $\delta^2H_{seedcoat}$, δ^2H_{starch}, and δ^2H_{chitin}



example, the Vale of Pickering, for the most part, lies less than 30.5 m above sea-level whereas the North Yorkshire Moors are almost entirely above 243.8 m, and in parts above 426.7 m, above sea level (Darby and Maxwell 1978).

The deuterium results indicated that the barley crops were raised at warmer temperatures than the wheat. As the grains were cultivated within the same region, the inferred temperature difference conveys seasonality. δ^2H has been shown to vary up to 70 ‰ seasonally at a single site (White and Gedzelman 1984). An increase in temperature affects the rate of evapo-transpiration that occurs within the environment.

In studies conducted on the affects of evapo-transpiration and temperature upon the deuterium signal from leaves of high rooted plants (e.g. Roden and Ehleringer 1991), an enrichment of the deuterium was observed as the light isotopes in water vapour escape the surface more readily than the heavy isotopes (Craig and Gordon 1965). In the present experiment, this was apparent to some degree in the seed coats, which would explain their enrichment over the starches. However, the deuterium values in all the samples were more depleted than their respective predicted meteoric precipitation. The presence of higher levels of light hydrogen may suggest that the seed coats and interior starches were not influenced as strongly by the temperature and evapo-transpiration factors that affected the rainwater deuterium. Regardless, the enrichment of the seed coats in comparison to the starches may be indicative of evapo-transpiratory impact. Furthermore, the $\delta^2H_{starch\text{-}seedcoat}$ fractionation may provide evidence of exposure levels to high temperatures, which result in an increase in evapo-transpiratory processes. The fractionation increases with respect to temperature and decreases with latitude, which is the inverse of the effect predicted by the Raleigh distillation model, and similarly the stable-hydrogen composition of the endosperm reveals retention of light hydrogen rather than the expected enrichment of deuterium, which is also reflected in the deuterium of the chitin.

6.3.2 Mixed Cereal Blind Tests δ^2H

Table 6.5 presents the δ^2H results from the blind tests conducted on *Sitophilus granarius* bred in mixed cereal samples. The isotope values mirror the range of measurements expressed by the four component cereals when standard deviation was taken into consideration, and the results could be roughly divided into four categories relative to the cereals [Table 6.6]. Because of the breadth of standard deviation, there

Table 6.5 Blind Test: δ^2H (‰) VSMOW of G2a weevils bred in mixed cereals

G2a *Sitophilus granarius*	δ^2H (‰) VSMOW Chitin
GK1	-88.71
GK2	-91.53
GK3	-84.66
GK4	-89.55
GK5	-96.09
GK6	-108.54
GK7	-108.30
GK8	-101.41
GK9	-90.52

Table 6.6 Categorisation of blind test results Based on δ^2H_{Chitin} range in control experiments

Barley (-90.81± 7 δ^2H_{Chitin})	GK1; GK2; GK4; GK5; GK9
Buckwheat (-114.61± 9 δ^2H_{Chitin})	GK6; GK7; GK8
Oats (-101.39± 9 δ^2H_{Chitin})	GK5; GK6; GK7; GK8
Wheat (-84.7 δ^2H_{Chitin})	GK3

were overlaps in the ranges of the control values, particularly between buckwheat and oats, resulting in the cross-categorising of specimens. During the laboratory-rearing stage, the weevils demonstrated a preference towards the unprotected kernels of buckwheat and barley over the hull-concealed oat grains, and as such, it is probable that the cross-listed specimens in the oats category should be attributed to the other cereals. However, based solely on the δ^2H values presented by the examination, further distinction cannot be inferred.

6.3.3 Buckwheat Blind Tests

The isotopic measurements for the weevils from the buckwheat samples [Table 6.1; Table 6.2] expressed a strong correlation between the chitin and the starch-layers of the grains. The stable-carbon and nitrogen suggest a geographic origin with a low relative humidity and low altitude. The depleted deuterium composition, while typically indicative of high latitudinal regions, was similar in

range to the low latitude oats. Following the trend presented by the other cereals, a high light isotopic-hydrogen value in the buckwheat starch and chitin may reflect exposure to high temperatures and/or a low latitude origin.

6.4 Discussion

A strong positive correlation was observed between the δ^2H value of chitin and the δ^2H value of the starch of the host plant (R^2= 0.96). This indicated that the grain weevil δ^2H reflected the deuterium signal of its diet prior to metamorphosing to its adult stage. A slight trophic-level increase was noted in the positive body-diet fractionation ranging from +1.77 ‰ in oats to +13.08 ‰ in buckwheat. The trophic level enrichment was also exhibited in the $\delta^{15}N$ assays conducted at the University of Bradford ranging from +3.75 ‰ in barley to +4.48 ‰ in oats. The amount of hydrogen fractionation reported here is similar to other laboratory controlled experiments. Miller (1984) noted a +10 ‰ enrichment in wheat flour-fed *Tribolium molitor* and *Periplaneta americana* fed on sucrose-supplemented Purina while Hobson *et al*.'s (1999) milkweed-bred *Danaus plexippus* only exhibited a body-diet fractionation of + 1.5 ‰. In the present experiment, the body-diet fractionation for $\delta^{13}C$ was negligible. Additionally, the G2b trial demonstrated that the hydrogen composition in *Sitophilus granarius* chitin remained metabolically inert following synthesis. Both the carbon and non-exchangeable hydrogen in chitin were primarily representative of dietary C-H. However, can they be used as geographic indicators?

A myriad of investigations concerning plant stable-hydrogen have found a strong relationship between δ^2H signal of the source water and the δ^2H of the plant (cf. White 1988; Zeigler 1988; Flanagan and Ehleringer 1991; Hobson *et al*. 1999). Although the deuterium ratio of the source water was unknown in the present

analysis, the deuterium results recovered for the seed coats (R^2= 0.9844) and the starchy-layer (R^2= 0.9928) when correlated against average growing season precipitation for the period of maximum tissue growth (δ^2H_g) [Figure 6.5] indicate a primarily rainwater-based water source during the cultivation period. However, the starch displayed a non-unity slope of -0.6626 compared to the 0.8826 value of the seed coats for the regression with the water δ^2H. These results differ in comparison to the deuterium results for the seed coats (R^2= 0.9625) and the starchy-layer (R^2= 0.9767) with a non-unity slope of 0.7034 and -0.5396 respectively, which were calculated for the average meteoric precipitation for the total growing season (δ^2H_p) [Figure 6.4]. The subtle discrepancies between δ^2H_p and δ^2H_g in the seed coat and starchy-layer most likely reflect temporal variations for the primary period of stable-hydrogen acquisition is the respective tissue layers. The stronger correlation present in δ^2H_g graph suggests the majority of deuterium in the cereal kernels was assimilated during the period of maximum tissue growth rather than gradually over the entire growing season of the plant.

In general, plant tissues have been found to be depleted in deuterium relative to source water (Estep 1980; Hayes 2001), and the milkweed results presented in Hobson and associates' (1999) laboratory rearing experiment suggest that this discrepancy increases in respect to an increased presence of heavy deuterium in the source water. Moreover, Flanagan *et al.* (1991) have shown a difference between stem water isotopic composition and leaf water isotopic composition ranging from -39 ‰ to -51 ‰ within plants from a single locale, and have proposed that the variation corresponded to water-length pathway. Between the endospermal starch and the seed coat, the discrepancy ranged from -18.94 ‰ in wheat to -46.09 ‰ in the barley from Yorkshire. Within the plant species, the starch-seed coat deuterium fractionation

theoretically reflects a difference in water usage. The seed coats may have been supplied water from a source, which was on average, more enriched in deuterium than the endosperm (perhaps leaf water that was enriched through transpiration; see White 1988, Ziegler 1988, Flanagan and Ehleringer 1991).

While water-length and water-use pathways may have been a factor within the individual plant species, the starch-seed coat variation, as mentioned above, also corresponded with differences in the average temperature of the growing season between the wheat and barley. With a growing season of September to July, winter wheat would have been exposed to an average temperature of 12.82 °C, whereas spring barley (growing season March through September) would have been subjected to an average temperature around 16.67 °C. This inference is further supported by the starch-seed coat fractionation displayed by the oats of -52.16 during an average growing season temperature of 19.88 °C. Moreover, studies on bone collagen have suggested that relative humidity could account for regional variation (Cormie *et al*. 1994), but as indicated by the depleted nitrogen and carbon in the oats compared the wheat, the effects of relative humidity are not apparent through a 1:1 correlation. Unfortunately, the full impact of physiological and environmental factors on plant deuterium still requires further investigation.

Nevertheless, the strong linear relationship noted between meteoric precipitation for the period of maximum tissue growth and both starch and seed coats was also present in chitin demonstrating that the deuterium value of the water source controlled the isotopic composition of the cereals and the grain pests [Figure 6.5]. A linear regression of the data yields the expression:

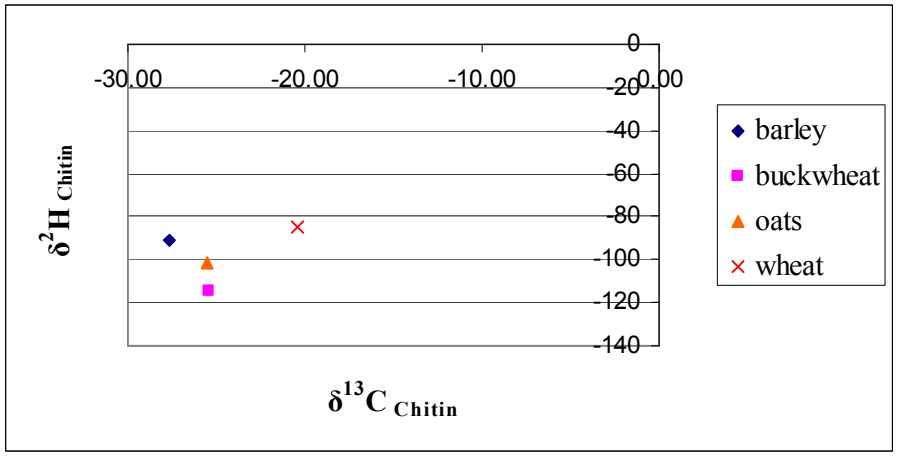
$$\delta^2H_{chitin} = -0.7871\ \delta^2H_g - 135.15$$ **[Formula 6.3]**

with a correlation of 0.9934. When this linear regression was utilised to predict the isotopic signal for the origin of the buckwheat samples, the average meteoric precipitation for the period of maxium tissue growth was approximated to have a $\delta^2H_{g\text{-buckwheat}}$ of -26.10 ‰. If the average meteoric precipitation for the total growing season is considered using Formula 6.4:

$$\delta^2H_{chitin} = -0.6363\ \delta^2H_p - 124.57 \quad \textbf{[Formula 6.4]},$$

the buckwheat seeds can be hypothesised to have originated from a region with an $\delta^2H_{p\text{-buckwheat}}$ of -15.65 ‰. According to the Raleigh distillation model, both predictions would back-trace the buckwheat to a low-latitude region.

Figure 6.6 Relationship between δ^2H and $\delta^{13}C$ values of chitin from *Sitophilus granarius*



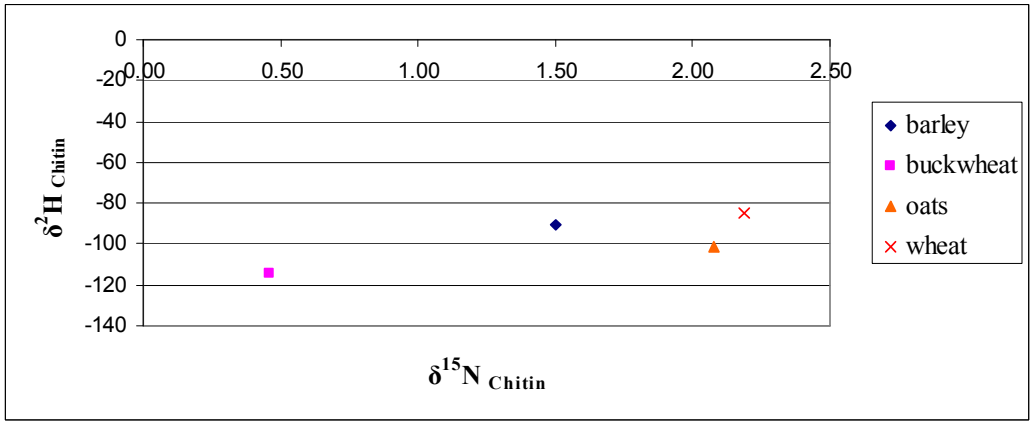
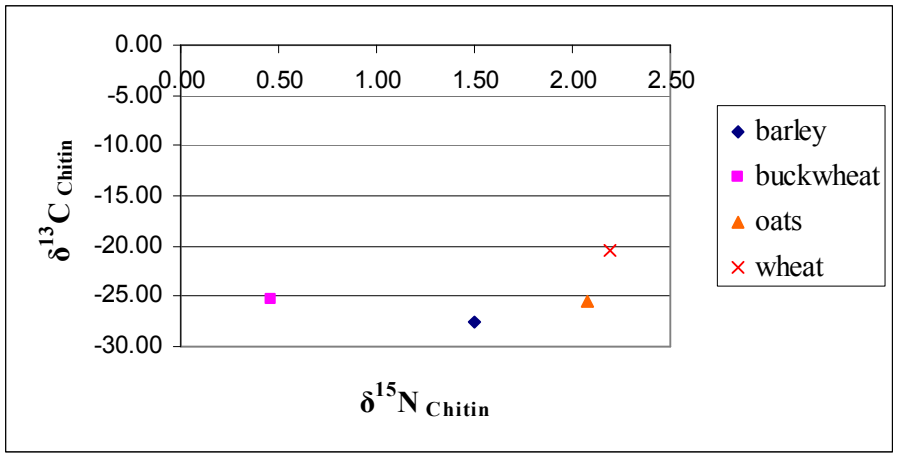


Figure 6.7 Relationship between δ^2H and $\delta^{15}N$ values of chitin from *Sitophilus granarius*

However, examination of the results indicates that the deuterium of chitin becomes more enriched in deuterium relative to meteoric water in higher latitudes compared to lower latitudes and in colder months in respect to warmer months; a trend that is consistent with the deuterium of the starch but in contradiction to the seed coat values. This implies that the chitin-water relationship may be more complex than the straight line approximation indicates. The physiological and ecological factors resulting in the internal discrepancies of the individual species of host plants also affect the δ^2H of the chitin. In order to effectively back-trace the geographic origins from chitin and account for multiple influences, Rubenstein and Hobson (2004) and Bowen *et al*. (2005) have offered a non-linear approach that has had success in tracing origins of wildlife. However, because of the parameters set forth in this experiment, there is insufficient geographic and species data to successfully pursue a non-linear interpolation approach.

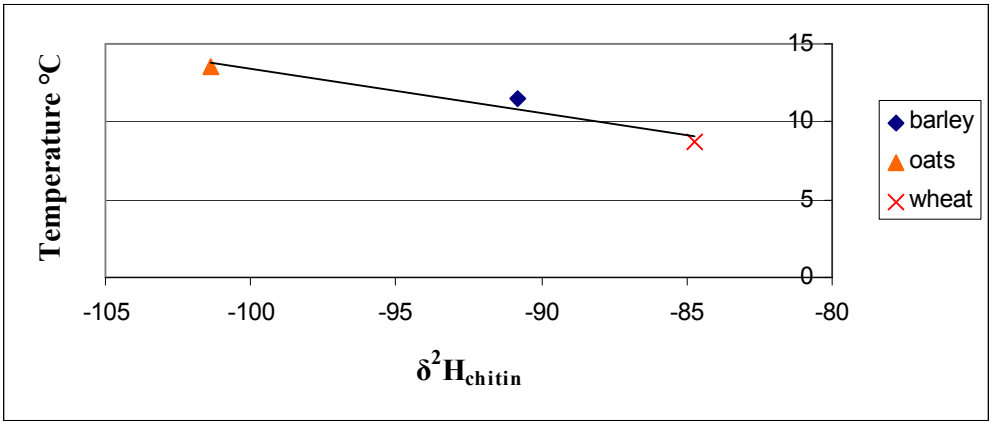
Regardless, through comparison of the data collated from isotopic ($\delta^{13}C$, δ^2H, and $\delta^{15}N$) analyses of the chitin, it was possible to glean insight concerning the geographic details of the blind-tested buckwheat's region of origin. The similarities

Figure 6.8 Relationship between $\delta^{13}C$ and $\delta^{15}N$ values of chitin



between the oats and the buckwheat apparent in Figure 6.6 demonstrate that the buckwheat was more closely aligned with isotopic signal of the Mississippian oats than either the Yorkshire barley or wheat. Its close orientation to the oats signal (δ^2H-$\delta^{13}C$) may be indicative of a low latitude origin. Furthermore, the $\delta^{13}C$- $\delta^{15}N$ and δ^2H - $\delta^{15}N$ [Figures 6.7 and 6.8] buckwheat values were severely depleted in relation to the other cereals, which primarily reflects differences in altitude and relative humidity. The results predict a region of origin for buckwheat of low altitude and high aridity.

Figure 6.9 Relationship between average temperature (°C) for season of cereal tissue growth and δ^2H values of grain weevil chitin



Further information may be ascertained in Figure 6.9, which suggests a strong linear model (R^2= 0.9375) for predicting temperature (T) in relation to δ^2H_{chitin}:

$$T= -0.2785\ \delta^2H_{chitin} - 14.48$$ **[Formula 6.5]**.

If other potentially influential factors (proximity to ocean, day-length, elevation, relative humidity, etc.) are ignored, the regression approximation predicts an average growing season temperature of 17.43 °C for buckwheat based on an isotopic deuterium value of -114.61 ‰ for chitin. This places the buckwheat in a region with much higher growing season temperatures than the other three cereals.

6.5 Summary

This experiment has shown that the stable hydrogen and carbon isotopic compositions in granary weevils (*Sitophilus granarius*) are closely correlated with those of the endospermal starch-layer of their host cereals. While the isotopic signature of the host cereals is in turn controlled by the local hydrology and climate, the isotopic composition of seed coat and starch within each host plant indicates discrepancy in water-usage and water-pathways that deplete the deuterium of the source water. Through the analysis of stable-carbon, hydrogen, and nitrogen from associated chitin, certain details can be ascertained concerning the geographic origins of the buckwheat samples, suggesting a region of low-latitude, low altitude, high aridity, and high temperature. The combined application of multiple isotopes increases the resolution of isotopes as geographic indicators, and may prove effective as a palaeoeconomic tool for discerning trade patterns.

Chapter 7

The Application of Isotopic Analyses towards Insect Remains: Modern and Neolithic Case Studies

7.1 Introduction

Chapter 6 introduced the concept of insect fossils as palaeoeconomic indicators and, through laboratory experiments, explored the isotopic relationship between geographically distinct cereals and their respective granary pests. It was found that the stable-isotope signal of the dietary source is locked into the chitin, presumably during chitin synthesis, which occurs when the exoskeleton is formed during metamorphosis into the adult stage. In Chapter 7, carbon-13, deuterium, and nitrogen-15 ratios are employed towards insect remains recovered from a modern reconstructed Anglo-Saxon village and three German archaeological sites dated to the Linearbandkeramic Neolithic period. In the present study, the stable-isotope signatures acquired from the chitin are assessed both independently and collectively in order to attempt recognition of insect species which are associated with host materials that are indigenous to the location of the site, foreign to the site but endemic to the nearby hinterland regions, and foreign to the region.

7.2 Methods

The elytra were selected for isotopic analysis of the modern and archaeological insect specimens. To isolate the chitin, the insect remains were rinsed in 2:1 dichloromethane: methanol then immersed in 1 M NaOH for 24 hours at 110 °C. The stable-isotope analyses were conducted at Iso-Analytical Limited Laboratories in Cheshire, UK using EA-IRMS.

All δ^2H results are expressed in typical delta notation, in units per mil (‰), and normalised to the VSMOW-VSLAP standard scale. The reference material used for hydrogen isotope analysis was IA-R002 (mineral oil, $\delta^2H_{V\text{-}SMOW} = -111.2$), which was calibrated against NBS-22 (mineral oil, $\delta^2H_{V\text{-}SMOW} = -118.5$ ‰) distributed as an

isotope reference standard by the IAEA. Samples of IAEA-CH-7 (polyethylene foil, $\delta^2H_{V\text{-}SMOW}$ = -100.3 ‰) were analysed along with the samples as quality control checks [Appendix 4C]. In order to account for exchangeable hydrogen, whale baleen (BWII) was analysed alongside the chitin. The exchangeable hydrogen was then accounted for using the Formula 7.1:

$$\delta^2H_{chitin\text{-}corrected} = \text{measured } \delta^2H_{chitin} \text{ (-108/BWBII measured value).}$$

Carbon-13 results are calibrated to the Chicago Peedee Belemnite (PDB), and the Nitrogen-15 values were normalised to the standard atmospheric N_2. The reference material employed for $\delta^{13}C$ and $\delta^{15}N$ analysis was IA-R042 (powdered bovine liver, $\delta^{13}C_{V\text{-}PDB}$ = -21.60 ‰, $\delta^{15}N_{Air}$ = 7.65 ‰). IA-R042, a mixture of IA-R005 (beet sugar, $\delta^{13}C_{V\text{-}PDB}$ = -26.03 ‰) and IA-R045 (ammonium sulfate, $\delta^{15}N_{Air}$ = -4.71 ‰) and a mixture of IA-R006 (cane sugar, $\delta^{13}C_{V\text{-}PDB}$ = -11.64 ‰) and IA-R046 (ammonium sulfate, $\delta^{15}N_{Air}$ = 22.04 ‰) were run as quality controls during the analyses. The IA-R042 was calibrated against and traceable to IAEA-CH-6 (sucrose, $\delta^{13}C_{V\text{-}PDB}$ = -10.43 ‰) and IAEA-N-1 (ammonium sulfate, $\delta^{15}N_{Air}$ = 0.40 ‰). IA-R005 and IA-R006 were calibrated against and traceable to IAEA-CH-6. IA-R045 and IA-R046 were calibrated against and traceable to IAEA-N-1 [Appendix 3C].

7.3 Case Study 1: West Stow, Sussex

7.3.1 Site Information

While notably an archaeological site of international significance West Stow presently hosts a program for the experimental reconstruction of Anglo-Saxon buildings, initiated in 1973 (West 1985). Six buildings have been constructed on the site using the traditional tools, materials, and techniques thought to have been employed during the Anglo-Saxon period. In particular, West Stow tests West's re-

interpretation of the *Grubenhaus*, or Sunken-Feature Building (SFB), featuring ground level planked floors covering a 'pit,' which served as a storage area (West 1969, 1985; Tipper 2004). The reconstruction is located at latitude 52.18° N; longitude 0.4° E, and is at an approximate altitude of 26 m above sea level.

7.3.2 Collecting Methods

The beetles were collected from the reconstructed buildings using pitfall traps placed on 6th June 2008 and recovered 3rd April 2009. The traps consisted of cat food tins, 70 mm in diameter, half-filled with sodium chloride solution with one drop of detergent, which served as a wetting agent so that the insects were not trapped on the surface film. The traps were placed so that the neck of the tin was level with the surrounding soil surface, and covered with a 15 cm square of expanded aluminium mesh of approximately 1 cm aperture (cf. Kenward and Tipper 2008). Traps W7 and W19 were placed under the floor at the base of the sunken feature of the Old House, a reconstruction of a two-post SFB (SFB 21) with a suspended floor above the sunken feature. The insect remains were recorded using a low-power binocular microscope and the initial identifications were performed with the assistance of H. Kenward.

7.3.3 The Fauna

Of the coleopteran fauna recovered from the pitfall traps, a limited range of species was selected for isotopic analysis. The specimens were chosen based on:

- species biomass in pitfall traps,
- ecological associations,
- assumed trophic level, and
- prevalence in archaeoentomological contexts.

Anobium punctatum (Deg.), the furniture beetle or woodworm, is a serious pest of worked wood, e.g. structural timbers and furniture (Palm 1959). The furniture beetle is primarily synanthropic in Britain but has been recorded in the wild in dead trees (Duff 1993), particularly in association with parts of the trees where branches and bark had been removed (Hickin 1968). *Anobium punctatum* is commonly believed to infest only old dead wood—oak sapwood of at least 60 years and twenty years for softwoods (Hakbijl 1989; Kenward and Hall 1995).

The carabid *Carabus problematicus* (Hbst.) is a predominantly predacious ground beetle, which is commonly recovered in woodland, grassland, heathland, and moorland (Lindroth 1974; Harde 1984; Duff 1993). Eyre (2000) includes members of Lumbricidae (earthworms), Enchytracidae (e.g. potworms), Nematoda (roundworms), Diplopoda (millipedes), Acari (mites and ticks), Collembola (springtails), Diptera (true flies), and Coleoptera (beetles) amongst *C. problematicus*' prey. While primarily carnivorous, *C. problematicus* has been known to feed on fungi (Eyre 2000).

Catops nigricans (Spence) is a saprophagous species that benefits from dead and decaying insects (Topp 1990). It has been recorded in wood pastures, woodland margins, mammal dens and nests (Koch 1989a), as well as under leaf litter (Topp 1990; Duff 1993) and faggots (Donisthorpe 1939). Topp (1993) and Grist and Gurney (1997) have found that *C. nigricans*' life cycle is seasonally synchronized through photo-period, with it entering diapause during the summer, reproducing in the autumn, and being most active during the winter.

Cryptophagus scutellatus (Newman) is the smallest European *Cryptophagus* species. The beetle is believed to be mycetophagous, feeding on fungi, and has been noted in haystack and vegetable refuse (Hinton 1945; Lindroth *et al*. 1973; Koch

1989b). It has also been recorded in association with ants, *Formica* sp. (Palm 1959; Koch 1989b).

Ptinus fur (L.), the white-marked spider beetle, is a typical but non-obligate synanthrope. The beetle is remarkably polyphagous and will infest a wide-range of animal and plant products (Zacher 1927; Dillon and Dillon 1972; Koch 1989a). The white-marked spider beetle is very common in cereal stores (Mound 1989), and has also been recorded in birds' nests, hives, and hay and straw waste (Horion 1953).

The granary weevil, *Sitophilus granarius* (L.), is considered an obligate synanthrope. Unlike the spider beetle, *S. granarius* is oligophagous, known to feed on a restricting range of food substances, i.e. cereals. The granary weevil is discussed in more detail in Chapters 5 and 6. While grains were not stored on site for consumption, *Sitophilus granarius* is assumed to have been associated with the cereals present in the wheat thatch, indicating that the thatch material was stored prior to its use.

7.3.4 Carbon Isotope Results

The application of ^{13}C ratios is a well-established technique in the study of past dietary patterns and subsistence strategies (Katzenberg and Pfeiffer 2000). These isotopic signatures can vary spatially based on differences in biogeochemical processes, which in turn are passed through the foodweb and evidenced in the consumers (DeNiro and Epstein 1978). Table 7.1 presents the stable-carbon isotope ratios of chitin from the six species of Coleoptera from West Stow. The predicted results range from -24.76 ‰ to -27.88 ‰.

The stable carbon isotopic fractionation provides information regarding the types of plants in the foodweb, in terms of C_3 or C_4 plants. C_3 are typically temperate

Table 7.1 Carbon isotope ratios from West Stow

Species	$\delta^{13}C$ ‰ PDB
Sitophilus granarius	-25.16
Cryptophagus scutellatus	-24.76
Ptinus fur	-27.29
Catops nigricans	-27.39
Anobium punctatum	-27.88
Carabus problematicus	-26.09

plants, grasses, shrubs and trees, and include economically important crops such as wheat, barley, and oats. C_4 plants, such as sorghum and millet, tend to be arid adapted plants and grasses. C_3 and C_4 plants are isotopically distinguishable through assessment of the related stable carbon fractionation, which is associated with metabolic pathway for carbon fixation during plant photosynthesis (Peterson and Fry 1987; Tieszen and Boutton 1988). C_3 plants tend to have stable carbon isotope ratios are -26 ‰, and C_4 plants have more enriched $\delta^{13}C$ values approximating -12 ‰ (Schoeninger 1995).

All of the West Stow specimens fell within the C_3 category. The woodworm beetle exhibited the most depleted stable-carbon isotopic values, and *Cryptophagus scutellatus* was the most enriched in $\delta^{13}C$. *Ptinus fur* and *Catops nigricans* produced $\delta^{13}C$ values close to *Anobium punctatum*. However, *Sitophilus granarius* and *Carabus problematicu*s were slightly more enriched in $\delta^{13}C$ than the woodworm.

In terms of diet, the herbivorous and mycetophagous insects had stable-carbon isotope signatures that were, in general, more enriched than the omnivorous and carnivorous species. *Anobium punctatum* was an exception as the beetle had a $\delta^{13}C$ approximating the carnivores and omnivores. Table 7.2 shows the adjustment of stable-carbon isotopes to predict the isotopic signature of the primary photosynthetic source. In order to calculate the approximate carbon signature for the primary photosynthetic organism from the chitin, the herbivores were adjusted by one trophic

level, carnivores by two, and the omnivorous *Ptinus fur* was modified by one and a half trophic levels. The following formulas were employed to calculate the isotopic signature for the primary photosynthetic ($\Delta^{13}C_t$):

Formula 7.2: $\Delta^{13}C_t = \delta^{13}C_h - 0.62$;

Formula 7.3: $\Delta^{13}C_t = \delta^{13}C_c - (\delta^{13}C_c - \delta^{13}C_x) - 0.62$;

Formula 7.4: $\Delta^{13}C_t = \delta^{13}C_o - [(\delta^{13}C_o - \delta^{13}C_x + 0.62)/2] - 0.62$,

where $\delta^{13}C_h$ is the measured value for the chitin of the herbivorous beetles, $\delta^{13}C_c$ is the determined ratio for the chitin of the carnivorous beetles, $\delta^{13}C_x$ is the approximated average of stable-carbon isotope measurements in the assemblage, $\delta^{13}C_o$ is the observed ratio for omnivorous beetles, and 0.62 is the average fractionation tabulated from $\delta^{13}C_{body\text{-}diet}$ of grain-associated weevils in Chapter 6. The $\Delta^{13}C_t$ for the carnivorous and omnivorous species is only an approximate value based on available data; it must be noted that an unmeasured $\delta^{13}C$ element inevitably comprises a proportion of their actual diet. Thus the $\Delta^{13}C_t$ formulated here simulates an artificial rather than a real trophic step adjustment; however, it is used to clarify the results through limiting trophic level distortion.

Cryptophagus scutellatus proposes an interesting problem as a fungal-feeder. Fungi are typically enriched in $\delta^{13}C$ relative to their associated substrate, and the level of enrichment is dependent upon the type of fungi. Ectomycorrhizal species are known to be 1- 5 ‰ enriched compared to their host foliage (Hobbie *et al*. 1999; Högberg *et al*. 1999; Kohzu *et al.* 1999); whereas other species exhibit a 0- 2 ‰ enrichment of $\delta^{13}C$ over associated carbohydrates (Gleixner *et al.* 1993; Hobbie *et al.* 2003). Will *et al*. (1986) have recorded the enrichment as high as 7 ‰. Henn and Chapela (2001) have found a fractionation effect that differentiates the ecological groups of ectomycorrhizal and saprotrophic fungi. Ectomycorrhizal species exhibit a

mean $\delta^{13}C$ of -25.29 ‰, and saprotrophic fungi have a mean of -22.14 ‰. Overlap exists between the ecological groups in the -25.19 to -23.98 ‰ range. The stable-carbon isotopic value measured for the beetle *Cryptophagus scutellatus* would have been affected by the isotopic signature of its diet. The $\delta^{13}C_{chitin}$ falls in the range of overlap for the two ecological groupings of fungi. As such, the dietary source cannot be determined solely through the assessment of the carbon enrichment, and the stable-nitrogen signature needs to be consulted. If an average stable carbon isotope enrichment is taken (2.25 ‰), the calculated $\Delta^{13}C_t$ for *Cryptophagus scutellatus* becomes -27.63 ‰.

Table 7.2 Predicted carbon isotopic values of primary photosynthetics

Species	**Trophic level**	**$\Delta^{13}C_t$**
Sitophilus granarius	Herbivore	-25.78
Cryptophagus scutellatus	Herbivore[1]	-27.63
Ptinus fur	Omnivore	-27.81
Catops nigricans	Carnivore	-27.08
Anobium punctatum	Herbivore	-28.5
Carabus problematicus	Carnivore	-27.08

[1] A fungal-feeding species

Through comparison of the $\Delta^{13}C_t$ predictions, it was apparent that the West Stow site contained materials from three different stable-carbon isotopic sources. The thatch-cereal material is represented by the enriched signature from the *Sitophilus granarius*. The structural beams and worked wood are likely signified by the depleted values from *Anobium punctatum*. The $\Delta^{13}C_t$ from the remaining beetle species may be an indication of isotopic values from plants in the local environment. Under that assumption, the thatch would have originated in a geographic region with a higher

altitude and the structural material from a location with a slightly lower altitude than the West Stow site.

7.3.5 Nitrogen Isotope Results

Stable-nitrogen isotopes are often employed towards discerning trophic level (e.g. DeNiro and Epstein 1981; Hobson 1990; Gu *et al*. 1996; O'Connell and Hedges 1999; Kelly 2000). However, as mentioned in Chapter 6, nitrogen can be used as indicator of altitude and relative humidity. Table 7.3 shows the nitrogen-15 results for the West Stow Coleoptera. The $\delta^{15}N_{chitin}$ values range from -1.25 ‰ to 21.10 ‰.

Table 7.3 Nitrogen isotope ratios from West Stow

Species	**δ^{15}N ‰ Air**
Sitophilus granarius	4.02
Cryptophagus scutellatus	21.10
Ptinus fur	6.86
Catops nigricans	3.91
Anobium punctatum	-1.86
Carabus problematicus	-1.25

While trophic level is evidenced by nitrogen-15 in beetle chitin, it is not as clearly defined as in studies involving terrestrial vertebrates (e.g. Craig *et al*. 2009). The mycetophage *Cryptophagus scutellatus* was the most enriched in $\delta^{15}N$, and the woodworm beetle *Anobium punctatum* exhibited the most depleted nitrogen-15 values. The predatory ground beetle *Carabus problematicus* was also fairly depleted in $\delta^{15}N$, but the other species fell in a range between 3.91 ‰ to 6.87 ‰. In general, the carnivores showed lower nitrogen-15 signatures than the herbivores.

While shown to be slightly variable (~1- 6 ‰) in dietary experiments (Hilderbrand *et al*. 1996; Hobson *et al*. 1996; Ambrose 2000; Bocherens and Drucker 2003), most models assume a 3 ‰ trophic enrichment of ^{15}N. For simplicity, the 3 ‰ trophic enrichment was adopted here, and the modified values to primary

photosynthetic ($\Delta^{15}N_t$) presented in Table 7.4. Additionally, the enriched isotopic nitrogen-15 value for *Cryptophagus scutellatus* is evidence of a diet consisting of primarily ectomycorrhizal fungus (cf. Henn and Chapela 2001). Unfortunately, the range of $\delta^{15}N$ values in ectomycorrhizal fungi is variable and the nitrogen signature could not be sufficiently adjusted beyond $^{15}N_{chitin\text{-}diet}$ fractionation. However, a tentative range is offered.

The $\Delta^{15}N_t$ ranges from -4.86 ‰ to 2.36 ‰ (excluding *C. scutellatus*). The depleted values evidenced by *Carabus problematicus*, *Anobium punctatum*, and *Catops nigricans* (cf. Hebert and Wassannar 2001) may be indicative of primary photosynthetics originating in nitrogen poor soils. The depleted $\Delta^{15}N_t$ may indicate a separate geographic source from the more enriched nitrogen-15 value of the cereals represented by *Sitophilus granarius*. Moreover, the enriched ratios evidenced by *Catops nigricans* in relation to *Carabus problematicus* and *Anobium punctatum* may reflect seasonality. As indicated by the *Sitophilus granarius* bred in winter wheat [see Chapter 6], the ^{15}N values are more enriched in the colder season, and as *Catops nigricans* has been noted to reproduce in the autumn and be most active during the winter, a comparatively enriched nitrogen-15 ratio is expected in respect to the warmer season species. However, because of the number of geographic and environmental factors influencing stable-nitrogen isotopic values,

Table 7.4 Predicted nitrogen isotope signatures of the primary photosynthetics

Species	**$\Delta^{15}N_t$**
Sitophilus granarius	1.02
Cryptophagus scutellatus	$18.10 \geq {}^{15}N_t \leq -2.9$
Ptinus fur	2.36
Catops nigricans	-2.09
Anobium punctatum	-4.86
Carabus problematicus	-4.25

even at the primary photosynthetic level, insight into the geographic origins of materials remains obscured when ^{15}N values are considered independently of other isotopic assessments.

7.3.6 Hydrogen Isotope Results

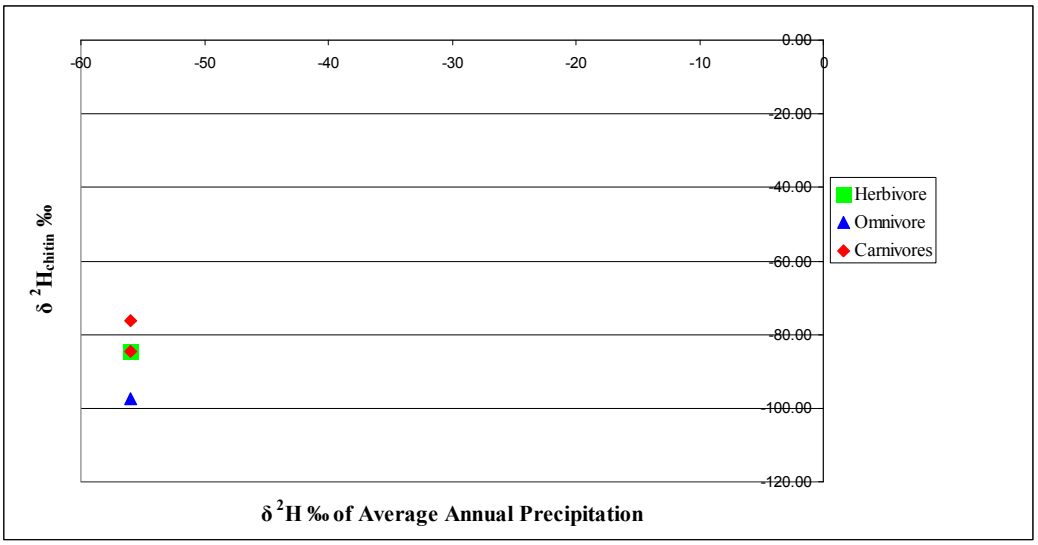
Stable-hydrogen isotopic ratios are indicative of both trophic level (e.g. Birchall *et al*. 2005; Reynard and Hedges 2007) and latitude (e.g. Meehan *et al*. 2004; Bowen *et al.* 2005). Of the six coleopteran specimens from West Stow, sufficient chitin material for deuterium analysis was only available from four beetle species, and the results are presented in Table 7.5. The predicted stable-carbon isotopic ratios ranged from -97.58 ‰ to -76.17 ‰. The annual meteoric precipitation (δ^2H_p= -56 ‰) for West Stow was calculated using OPIC (Bowen 2007).

Table 7.5 Deuterium ratios from West Stow

Species	**δ^2H ‰ VSMOW**
Sitophilus granarius	-84.68
Cryptophagus scutellatus	---
Ptinus fur	-97.58
Catops nigricans	-84.69
Anobium punctatum	---
Carabus problematicus	-76.17

In vertebrates, Birchall *et al.* (2005) recorded an average stable-hydrogen isotope difference of 46 ‰ between carnivores and the combined herbivore and omnivore group. Similar findings were reported by Reynard and Hedges (2007), who noted a 40 ‰ to 50 ‰ difference between the herbivore and human groups. A 30 ‰ to 50 ‰ step was observed between the herbivore and the omnivore groups, and from omnivores to humans, a 10 ‰ to 20 ‰ difference (Reynard and Hedges 2007). In the West Stow specimens [Figure 7.1], the carnivore, *Carabus problematicus*, exhibited the most enriched deuterium values. However, the herbivorous granary weevil

Figure 7.1 Deuterium-chitin results versus the average deuterium ratio for annual precipitation at West Stow

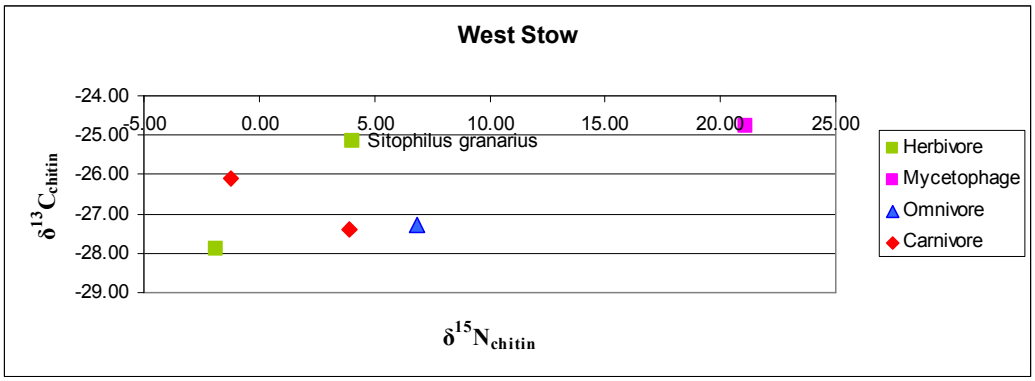


predicted a more enriched stable-hydrogen isotopic ratio than the omnivorous white-marked spider beetle. Moreover, the deuterium signature determined for *Sitophilus granarius* (-84.68 ‰) approximated the δ^2H_{chitin} for carnivorous *Catops nigricans* (-84.69 ‰), and only an 8.51 ‰ variation separated the granary weevil from the ground beetle. As the polyphagous *Ptinus fur* expressed a trophic level omnivore-carnivore step between 12.89 ‰ and 21.47 ‰ (similar in range to the omnivore-human step found by Reynard and Hedges 2007) to *Catops nigricans* and *Carabus problematicus*, respectively, the deuterium value for *Sitophilus granarius* does not follow the expected trend for a herbivore indigenous to the same micro-population as the other beetles. The δ^2H of an endemic herbivore, or herbivore bred on a locally cultivated plant source, would be predicted to be at least a full trophic step below the carnivores and a half step below the omnivores. Therefore, the granary weevil is likely representative of an imported component to West Stow.

7.3.7 Comparison of Isotopic Assays

The application of isotopic analyses to the insect specimens recovered from West Stow revealed the presence of autochthonous and allochthonous materials on the site. In all three assessments, the isotopic signatures procured from *Sitophilus granarius* did not follow the trend of the other species in the assemblage and were generally more enriched than expected. Additionally, the stable-carbon isotopic ratio from *Anobium punctatum* was slightly more depleted than the other beetles; however, the nitrogen-15 values were similar to the predictions of *Carabus problematicus* and *Catops nigricans*. In this section, the isotope results will be plotted together in an effort to glean further information concerning the geographic origin of the material components represented by the chitin [Figures 7.2- 7.5].

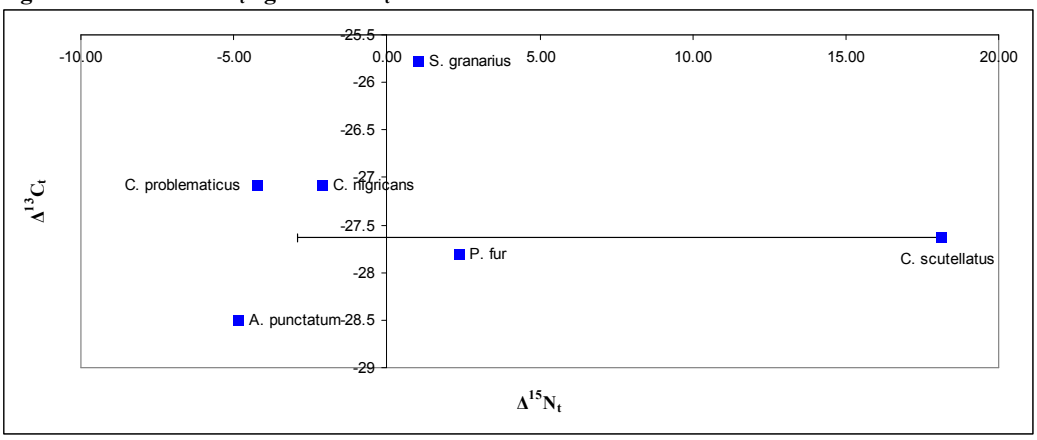
Figure 7.2 Carbon-13 and Nitrogen-15 plot of the insect remains from the Old House, West Stow. The herbivorous (green) and mycetophagous (pink) species are indicated by squares. The omnivorous species is denoted by a yellow triangle, and the carnivores are indicated by red diamonds



The ground beetle *Carabus problematicus* is viewed here as representative of the local isotopic signal at West Stow. This is based on the assumption that its diet consists of earthworms, slugs, etc. (Eyre 2000) which are organisms that would have inhabited the local soil and vegetation. Similarly, *Catops nigricans*, as a carrion-feeder, is assumed to be an indicator of the local signal. As carnivores, the beetles are predicted to exhibit trophic level-enriched isotopic signatures relative to the local

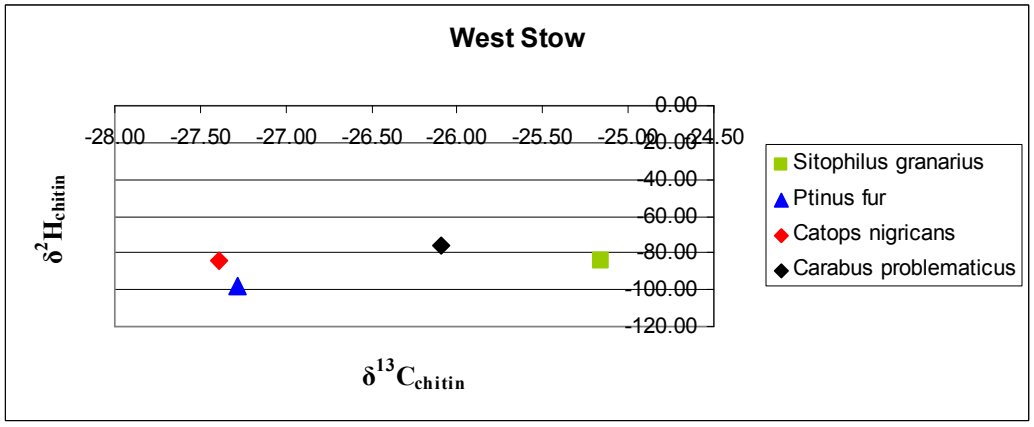
herbivores and omnivores. The isotopic differences between the species likely reflect seasonality and variation in diet.

Figure 7.3 Plot of $\Delta^{13}C_t$ against $\Delta^{15}N_t$



The isotopic results of *Ptinus fur* are enigmatic. The deuterium and carbon-13 ratios exhibited by the species are indicative of the pattern established by the carnivores, but the nitrogen-15 signature was comparatively enriched. As the deuterium result was a trophic step below the local carnivores, the enriched stable-nitrogen does not support the adjustment expected for a trophic level change. As a

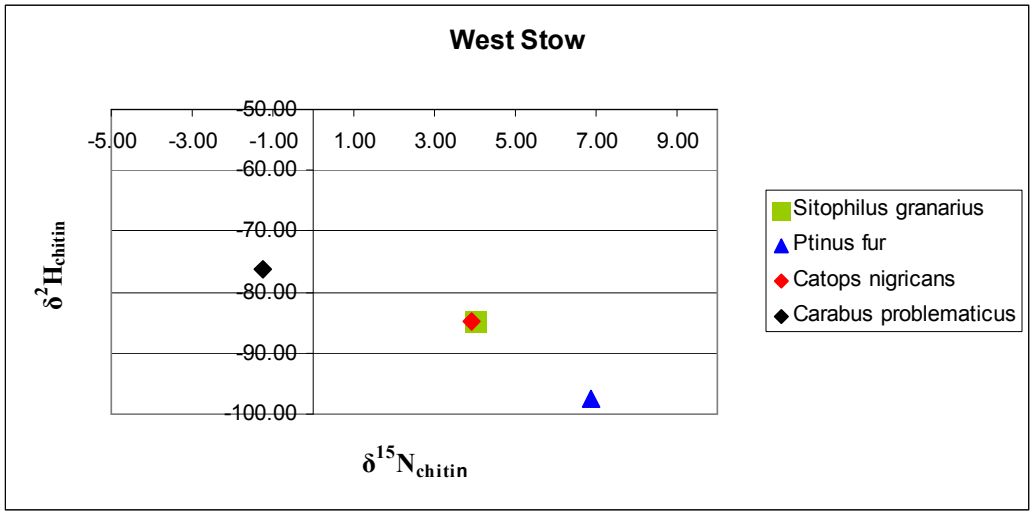
Figure 7.4 Carbon-13 and deuterium plot of the insect remains from the Old House, West Stow. *Sitophilus granarius* is represented by a green square. *Ptinus fur* is denoted by a yellow triangle, and *Catops nigricans* and *Carabus problematicus* are indicated by diamonds, red and black respectively



polyphagous beetle, the enrichment may be evidence of a diet supplemented by nitrogen-rich materials such as fungi or moulds. However, as indicated by

Cryptophagus scutellatus, a fungi-based diet enriches the isotopic values of both the carbon and nitrogen.

Figure 7.5 Deuterium and Nitrogen-15 plot of the insect remains from the Old House, West Stow. *Sitophilus granarius* is represented by a green square. *Ptinus fur* is denoted by a blue triangle, and *Catops nigricans* and *Carabus problematicus* are indicated by diamonds, red and black respectively



The data from Figure 7.2 suggests that the carbon and nitrogen isotopic ratios for *Anobium punctatum* reflect the local signal because the woodworm appears a trophic step below the carnivorous *Catops nigricans*. However, the beetle presented a nitrogen-15 value similar to *Carabus problematicus* and was more depleted in $\delta^{13}C$ than the other species. This suggests that the woodworms' associated dietary source (the structural timbers and floorboards in the houses) may not have been indigenous to West Stow. When the isotopic ratio for the primary photosynthetic [Figure 7.3] is considered, the signature for *Anobium punctatum* is independent of the local feeders. This suggests that some of the worked wood used in the reconstruction of the Old House was imported to West Stow.

Like the single isotope comparisons, the multi-isotopic assessment for *Sitophilus granarius* implies that the weevil fed on a diet, originating from a different geographic region than the other species. *S. granarius* is a highly synanthropic species and has not been recorded in the wild in Britain. Given the weevil's strong

association with stored cereals, the species' isotopic signature is most likely representative of the wheat cereals used in the roof thatch. The isotopic enrichment evidenced by the granary weevil chitin is suggestive of a geographic region of higher altitude than West Stow.

7.3.8 Synopsis

For the West Stow site, the insect evidence permitted calculation of the local isotopic signal for carbon, deuterium, and nitrogen. When trophic level effect was assumed, unusual patterns were noted in *Anobium punctatum*, *Cryptophagus scutellatus*, and *Sitophilus granarius*. The isotopic enrichments presented by *C. scutellatus* were attributed to its fungi-based diet. However, the variations present in the woodworm and granary weevil are believed to signify the importation of materials to the site.

7.4 Case Study 2: Neolithic Germany

7.4.1 Site Information

The three archaeological sites date to the Neolithic Linearbandkeramic Period. Eythra is located at latitude 51.13˚ N, longitude 12.18˚ E, and 67.9 m above sea level. The material selected for isotopic analysis is associated with Well 2, c. 7269 BP. Insect remains were also retrieved from the contemporaneous site of Plaußig, c. 7219 BP. Plaußig is located near Leipzig at latitude 51.23˚ N, longitude 12.27˚ E, and altitude 115.5 m. The LBK site of Erkelenz-Kückhoven dates slightly later than Eythra or Plaußig, *circa* 7040 BP. Erkelenz-Kückhoven is located near Colon at latitude 51.03˚ N, longitude 6.2˚ E, and 92 m above sea level.

7.4.2 Collection Methods

Environmental samples were selected from well contexts during the respective archaeological excavations. The processing and the identification of the insect remains were conducted by E. Schmidt at the Zoological Institute of the University of Freiburg using a binocular microscope and reference collection. Official reports were generated for the sites: Erkelenz-Kückhoven (Schmidt 1998, 2010b); Eythra (Schmidt 2005); and Plaußig (Schmidt 2010a).

7.4.3 The Fauna

From the identified faunal assemblages, Schmidt selected and donated beetle and fly specimens for isotopic analysis. The criteria established during selection of the West Stow entomofauna were also used for the Neolithic Germany specimens.

The beetle *Aphodius granarius* (L.) is saprophagous, feeding on decaying matter, and coprophilous, associated with excrement. The species appears to have a fairly polyphagous diet (Landin 1961). Koch (1989b) has recorded the scarab in pastures, fields, and stables, especially in rotting vegetation and herbivore dung. The larvae are believed to be predominantly saprophagous but have been noted feeding on the roots of grasses (Hanski 1991).

The carabid *Calathus fuscipes* (Goeze) has been recorded in open habitats, particularly cultivated fields and meadows (Lindroth 1974; Bengtson 1981; Luff 1988; Duff 1993), and under hay and straw heaps (Koch 1989a). The species is purely carnivorous (Koch 1989a).

Carabus irregularis (F.) is a predatory ground beetle. Its head is disproportionate to the other parts of its body and its mandibles are short and powerful (Casale *et al.* 1998). While little is known about the prey of this species, the mandibles resemble those of *Licinus* specimens (species adapted to opening shells), which suggests that *C. irregularis* may be a specialised snail hunter (Assmann *et al*. 2000).

Copris lunaris (L.) is a dung beetle that has been noted under herbivore excrement in unploughed pastures with sandy soils (Jessop 1986; Koch 1989). The adults excavate a 10- 20 cm tunnel under the dung leading to a brood chamber that usually contains 4 to 7 balls of dung holding one egg each (Shirt 1987). The species is more commonly associated with cattle dung, but has been found under sheep and horse manure (Koch 1989a).

The lesser stag beetle *Dorcus parallelopipedus* (L.) inhabits the rotten wood of broad-leaf trees, especially the stumps (Donisthorpe 1939; Bullock 1993). The adults have been recorded under the bark while the larvae develop within the trunk, branches, and roots (Palm 1959; Telnov n.d.).

Geotrupes vernalis (L.) is another beetle associated with dung. The species has been reported in carnivore and herbivore excrement (Jessop 1986; Kuhne 1995) and has been recovered from bird corpses (Jessop 1986). It burrows under the dung and lays one egg in each burrow (Jessop 1986).

Biström *et al.* (1991) have documented *Hister (Atholus) corvinus* (Germar) in dung and decaying vegetation. It has also been noted in ant nests and the dens of foxes and sand martins (Biström *et al.* 1991). The beetle is primarily predacious on maggots and other insects.

The dipteran *Musca domestica* (L.) is commonly known as the house fly. The larvae are often present in nutrient-rich substrates such as faeces or decaying vegetation (Hewitt 1914; Amano 1985; Hogsette 1996). Adults require a high protein diet in order to breed, and longevity is increased with access to sugar (Lyske 1991, 1993).

Onthophagus ovatus (L.) (syn. *O. joannae* Goljan), like other scarabaeoid beetles, is primarily coprophilous, and has been recorded beneath the dung of domesticated and wild animals (Koch 1989a; Duff 1993), where it creates a pupal chamber in the earth (Whitehead 2006). The species may have a rather polyphagous diet as Horion (1957) has described the species in carrion and rotting vegetation.

The chrysomelid *Oreina caerulea* (Olivier) is a leaf beetle associated with Cardueae (Asteraceae) plant species (Pasteels *et al*. 1995). The beetle is purely phytophagous.

The Alfalfa snout beetle, *Otiorhynchus ligustici* (L.), is an occasional agricultural pest of legume crops. The species is polyphagous but is often associated with the kidney vetch, *Anthyllis vulneraria* (Shirt 1987; Bullock 1993; Morris 1997), and alfalfa, *Medicago sativa* (Vasilev 1914). The larvae are root feeders (Shirt 1987).

Otiorhynchus raucus (F.) is a ground living weevil, which prefers chalky and sandy soils in gardens and woodland (Hyman 1992; Morris 1997). The commonly named root weevil is phytophagous but feeds on a variety of plants. The larvae are root feeders while the adults frequent the base of the plants and surrounding litter.

Pterostichus (Poecilus) cupreus (L.) is a thermophilic ground beetle commonly recorded on arable land (Anderson *et al.* 2000). The species is predatory of cereal aphids and springtails (Kielty *et al*. 1999; Mundy *et al.* 2000).

The pea leaf weevil *Sitona lineatus* (L.) is a capable of seriously damaging peas (especially *Pisum sativum*), vetch (particularly *Vicia faba*), lentils, and fodder-beans (Jones and Jones 1974; Bullock 1993; Morris 1997). Both the larvae and adults feed on the leaves and roots of leguminous plants (Koch 1992). The weevil has been noted in gardens, meadows, and agricultural land (Morris 1997).

Sitophilus granarius (L.) and *Tenebroides mauritanicus* (L.) are synanthropic in cereals. As detailed in Chapter 5, the cadelle is predacious (particularly on the larvae of *Sitophilus* and *Stegobium*; Reitter 1911) but also attacks grains and cereal products (Koch 1989a). *T. mauritanicus* has been recorded in the wild under tree bark of oak in Italy (Crowson 1958) and of beech and firs in Calabria and Slavonia (Palm 1959).

7.4.4 Carbon Isotope Results

Table 7.6 presents the stable-carbon isotopic results for the three Neolithic archaeological sites. At the site of Eythra, the $\delta^{13}C_{chitin}$ values ranged from -24.62 ‰ to -18.28 ‰; the ground beetle *Pterostitus (Poecilus) cupreus* gave the most depleted signature and the dung beetle *Aphodius granarius* exhibited the most enriched stable-isotopic carbon. At Plaußig, the stable-carbon isotopic values varied from -27.54 ‰ to -21.89 ‰. The root weevil *Otiorhynchus raucus* had the most depleted results and *Sitophilus granarius* had the most enriched. From the site of Erkelenz-Kückhoven, $\delta^{13}C_{chitin}$ produced values extending from -29.38 ‰ to -23.30 ‰. The dung beetle *Copris lunaris* had the most depleted isotopic value and *Sitophilus granarius* had the most enriched signature. All of the isotopic predictions for the LBK sites were within the accepted range for C_3 plants. Each of the sites exhibited an isotopic fractionation of approximately 6 ‰. In order to clarify the results and account for trophic level

variability, Formulas 7.2- 7.4 were employed to calculate $\Delta^{13}C_t$ [Table 7.7]. For Plaußig assessments, the isotopic ratio for *Sitophilus granarius* was excluded from the tabulation of $\delta^{13}C_x$ as the herbivore species was enriched compared to the rest of the

Table 7.6 Predicted stable-carbon ratios from Neolithic Germany

Species	**Site**	**$\delta^{13}C$ ‰ PDB**
Calathus fuscipes	Plaußig	-23.39
Onthophagus ovatus	Plaußig	-25.87
Aphodius granarius	Plaußig	-24.74
Hister (Atholus) corvinus	Plaußig	-26.88
Otiorhynchus raucus	Plaußig	-27.54
Sitophilus granarius	Plaußig	-21.89
Aphodius granarius	Eythra	-18.28
Pterostichus (Poecilus) cupreus	Eythra	-24.62
Sitophilus granarius	Eythra	-22.96
Musca domestica	Erkelenz-Kückhoven	-25.23
Otiorhynchus ligustici	Erkelenz-Kückhoven	-26.25
Geotrupes vernalis	Erkelenz-Kückhoven	-28.20
Sitona lineatus	Erkelenz-Kückhoven	-25.42
Copris lunaris	Erkelenz-Kückhoven	-29.38
Dorcus parallelopipedus.	Erkelenz-Kückhoven	-25.91
Oreina caerulea	Erkelenz-Kückhoven	-29.37
Tenebroides mauritanicus	Erkelenz-Kückhoven	-26.21
Sitophilus granarius	Erkelenz-Kückhoven	-23.30
Carabus irregularius	Erkelenz-Kückhoven	-25.65

Table 7.7 Calculated carbon isotopic values of primary photosynthetics

Species	Trophic level	$\Delta^{13}C_t$
Calathus fuscipes	Carnivore	-28.16
Onthophagus ovatus	Omnivore/ Herbivore[1]	-27.64/ -26.49
Aphodius granarius	Omnivore/ Herbivore[1]	-27.07/ -25.36
Hister (Atholus) corvinus	Carnivore	-28.16
Otiorhynchus raucus	Herbivore	-28.16
Sitophilus granarius	Herbivore	-22.51
Aphodius granarius	Omnivore/ Herbivore[1]	--
Pterostichus (Poecilus) cupreus	Carnivore	$\leq$ -25.24
Sitophilus granarius	Herbivore	-23.58
Musca domestica	Omnivore/ Herbivore[1]	-26.79/ -25.85
Otiorhynchus ligustici	Herbivore	-26.87
Geotrupes vernalis	Omnivore/ Herbivore[1]	-28.28/ -28.82
Sitona lineatus	Herbivore	-26.04
Copris lunaris	Omnivore/ Herbivore[1]	-28.87/ -30.00
Dorcus parallelopipedus.	Herbivore	-26.53
Oreina caerulea	Herbivore	-29.99
Tenebroides mauritanicus	Carnivore/ Omnivore	-27.11/ -27.28
Sitophilus granarius	Herbivore	-23.92
Carabus irregularius	Carnivore	-27.11

[1] **Associated with dung**

assemblage which would enrich the overall average. Additionally, because of the limited availability of materials, $\Delta^{13}C_t$ could not be formulated for the dung beetle from Eythra, and only a maximum value was predicted for the ground beetle substituting $\delta^{13}C_c$ for $\delta^{13}C_h$ in Formula 7.2 as the carbon-13 signature of the *Pterostichus (Poecilus) cupreus* was an unknown variable.

Table 7.8 Nitrogen-15 results for three LBK sites in Germany

Species	**Site**	**$\delta^{15}N$ ‰ AIR**
Calathus fuscipes	Plaußig	5.85
Onthophagus ovatus	Plaußig	1.06
Aphodius granarius	Plaußig	4.66
Sitophilus granarius	Plaußig	2.73
Sitophilus granarius	Eythra	6.89
Musca domestica	Erkelenz-Kückhoven	-6.02
Otiorhynchus ligustici	Erkelenz-Kückhoven	-2.16
Geotrupes vernalis	Erkelenz-Kückhoven	-5.99
Sitona lineatus	Erkelenz-Kückhoven	-1.60
Copris lunaris	Erkelenz-Kückhoven	2.28
Dorcus parallelopipedus.	Erkelenz-Kückhoven	10.10
Oreina caerulea	Erkelenz-Kückhoven	3.09
Sitophilus granarius	Erkelenz-Kückhoven	0.80
Carabus irregularius	Erkelenz-Kückhoven	-1.66

7.4.5 Nitrogen Isotope Results

Whereas it was possible to retrieve stable-carbon isotopic results from all the specimens, nitrogen-15 assays could only be conducted on 15 of the 19 species, and

Table 7.8 displays the results. $\delta^{15}N_{chitin}$ was only predicted for *Sitophilus granarius* from Eythra, and the granary weevil had an stable-nitrogen isotopic signature of 6.89 ‰. From the Plaußig site, the four assessed species had a range of 1.06 ‰ to 5.65 ‰. *Onthophagus ovatus* had the most depleted nitrogen-15 values and *Calathus fuscipes* predicted the most enriched $\delta^{15}N_{chitin}$ results. $\delta^{15}N_{chitin}$ results were procured for nine of the insect species from Erkelenz-Kückhoven, with a range of -6.02 ‰ to 10.10 ‰. The house fly *Musca domestica* had the most depleted signature and the lesser stag

Table 7.9 Tabulated nitrogen isotopic values of primary photosynthetics

Species	**Trophic Level**	**$\Delta^{15}N_t$**
Calathus fuscipes	Carnivore	-0.15
Onthophagus ovatus	Omnivore/ Herbivore	-3.44
Aphodius granarius	Omnivore/ Herbivore	0.16
Sitophilus granarius	Herbivore	-0.27
Sitophilus granarius	Herbivore	3.89
Musca domestica	Omnivore/ Herbivore[1]	-9.02
Otiorhynchus ligustici	Herbivore	-5.16
Geotrupes vernalis	Omnivore/ Herbivore[1]	-8.99
Sitona lineatus	Herbivore	-4.60
Copris lunaris	Omnivore/ Herbivore[1]	-2.22
Dorcus parallelopipedus.	Herbivore	7.10
Oreina caerulea	Herbivore	0.09
Sitophilus granarius	Herbivore	-2.20
Carabus irregularius	Carnivore	-7.66

beetle *Dorcus parallelopipedus* had the most enriched values. In an effort to account for the trophic level variability within the nitrogen isotopic results, $\Delta^{15}N_t$ was predicted [Table 7.9].

7.4.6 Hydrogen Isotopic Results

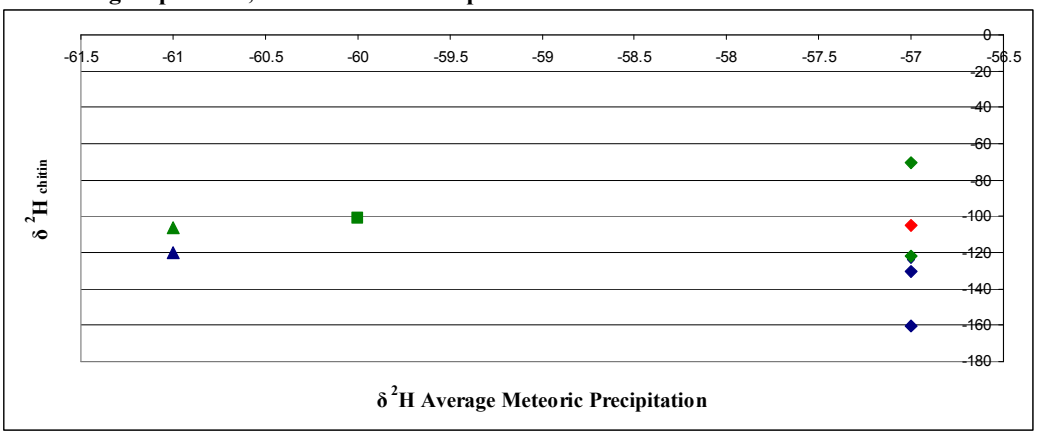
Table 7.10 Deuterium ratios for Neolithic Germany

Species	**Site**	**δ^2H ‰ VSMOW**
Onthophagus ovatus	Plaußig	-119.98
Sitophilus granarius	Plaußig	-106.45
Sitophilus granarius	Eythra	-100.99
Musca domestica	Erkelenz-Kückhoven	-123.81
Otiorhynchus ligustici	Erkelenz-Kückhoven	-121.78
Geotrupes vernalis	Erkelenz-Kückhoven	-160.31
Copris lunaris	Erkelenz-Kückhoven	-130.46
Dorcus parallelopipedus.	Erkelenz-Kückhoven	-70.71
Carabus irregularius	Erkelenz-Kückhoven	-104.74

Sufficient archaeoentomological material to conduct stable-isotopic hydrogen assays was only available from nine of the LBK specimens. Intra-site comparison was available to some extent; however, because of the paucity of material, the values from three sites were consolidated to mimic a bigger assemblage. The results were presented together in Table 7.10. For the three sites, the deuterium values varied over a range of -160.31 ‰ to -70.71 ‰. *Geotrupes vernalis* recovered from Erkelenz-Kückhoven predicted the most depleted δ^2H_{chitin} whereas the *Dorcus parallelopipedus* from Erkelenz-Kückhoven exhibited the most enriched stable-hydrogen isotopic

signature. The modern annual meteoric precipitation for each of the three sites was calculated using OPIC (Bowen 2007): $\delta^2H_{p\text{- Eythra}}$= -60 ‰, $\delta^2H_{p\text{- Plaußig}}$ = -61 ‰, and $\delta^2H_{p\text{- Erkelenz-Kückhoven}}$ = -57 ‰ [Figure 7.6].

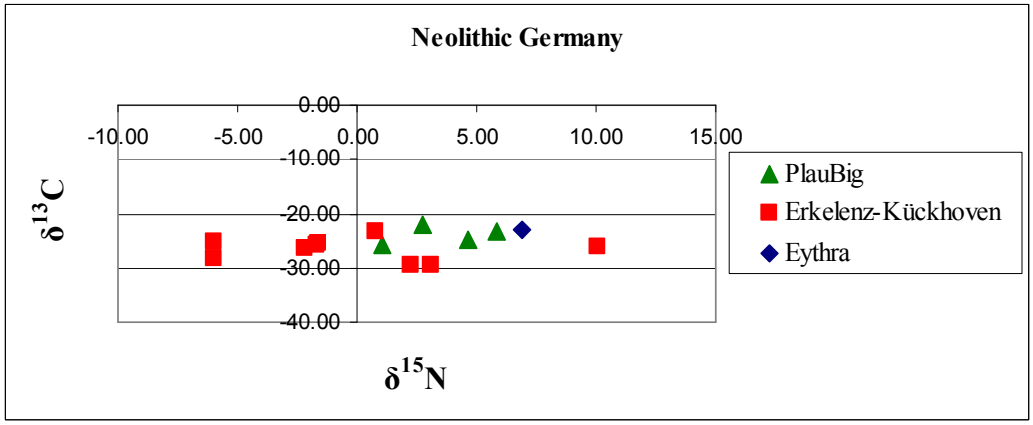
Figure 7.6 Plot of δ^2H_{chitin} against δ^2H_p. Erkelenz-Kückhoven is represented by diamonds; Plaußig is indicated by triangles; Eythra is denoted by a square. Herbivores are green, omnivore/ herbivore group is blue, and the carnivore species is red.



7.4.7 Comparison of Isotopic Analyses and Discussion

The isotopic values were variable within and between the sites [Figures 7.7-7.10]. The herbivorous species, in particular, evidenced a large range of variation, which suggests an allochthonous element for their associated plant species. This was especially apparent in $\delta^{13}C$, δ^2H, and $\delta^{15}N$ results from Erkelenz-Kückhoven.

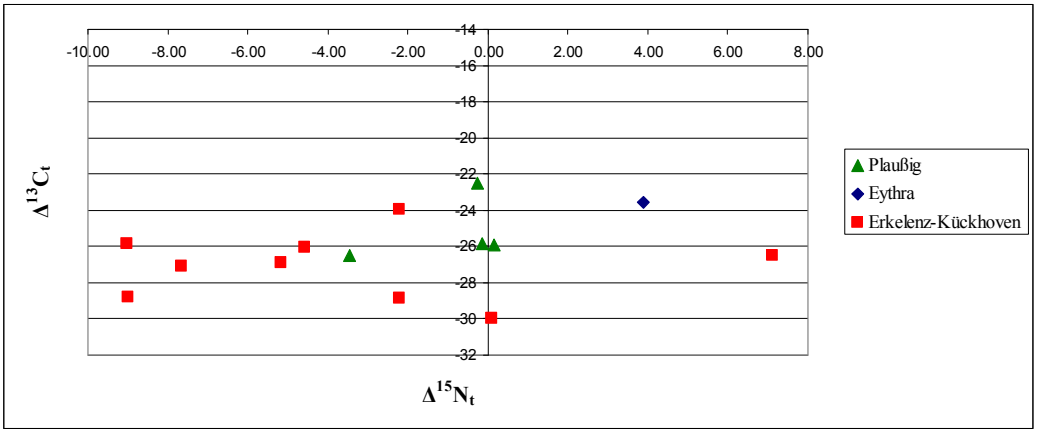
Figure 7.7 Carbon-13 and Nitrogen-15 plot of the insect remains from LBK Germany



The dung fauna

The dung-associated species recovered from the Linearbandkeramic sites most likely reflect the diet of the inhabitants, human and animal, living at the sites. The species, including the house fly, lay their eggs directly in the manure or in dung balls manufactured from the excrement. When the larvae emerge, they subsist on the nutrients and proteins available in the manure, which in turn are used to help form the chitin after the species pupate.

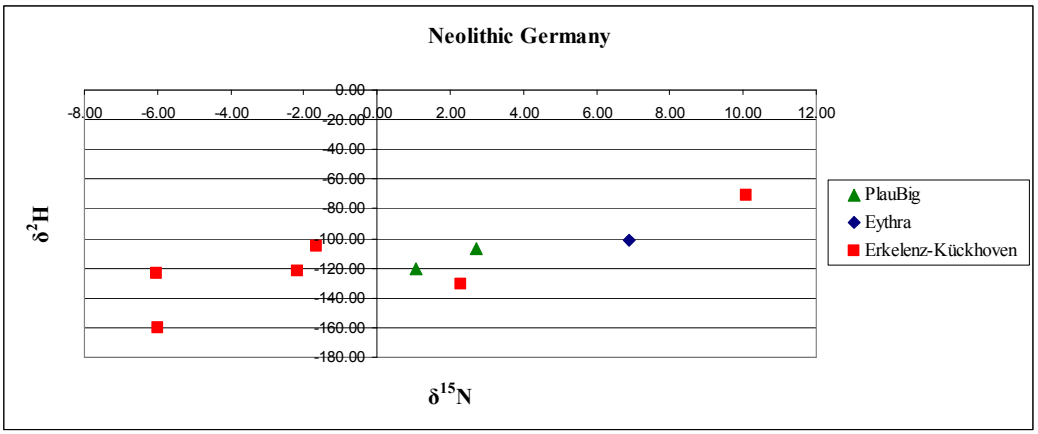
Figure 7.8 Plot of $\Delta^{13}C_t$ against $\Delta^{15}N_t$



At Eythra, *Aphodius granarius* exhibited an enriched $\delta^{13}C$ value compared to the other species from the assemblage that were analysed. The -18.28 ‰ ratio approaches the range expected for C_4 plants (Schoeninger 1995). However, because of the period and location, the isotopic signature is probably connected to an omnivorous animal or humans as the carbon-13 value from *A. granarius* is 4.68 ‰ more enriched than the signature from the granary weevil, approximating a trophic level step. An herbivorous vertebrate such as a cow or a sheep would be expected to give an isotopic ratio similar to *Sitophilus granarius*, if bred on a diet consisting entirely of cereals. An herbivore bred on a mixed diet of cereals and local grasses would have an isotopic signature that is a blend of the two dietary values. For example, if the $\Delta^{13}C_t$ from the *Pterostichus (Poecilus) cupreus* is a reflection of the

carbon-13 ratio from the primary photosynthetic in the local environment (≤ -25.24), the herbivore would be expected to predict an isotopic value in the range of -22.96 ‰ ≥ herbivore ≤ -25.24 ‰. Alternatively, if the *Aphodius granarius* is considered to reflect the isotopic ratio transferred through the dung of an indigenous herbivore, the local carbon-13 value would approximate -18.28 ‰, and the granary weevil and ground beetle would reflect allochthonous materials. Unfortunately, more specimens were not available for analysis, and an association with omnivorous or higher trophic level species is inferred for the dung beetle.

Figure 7.9 Plot of Deuterium and Nitrogen-15 from Neolithic Germany

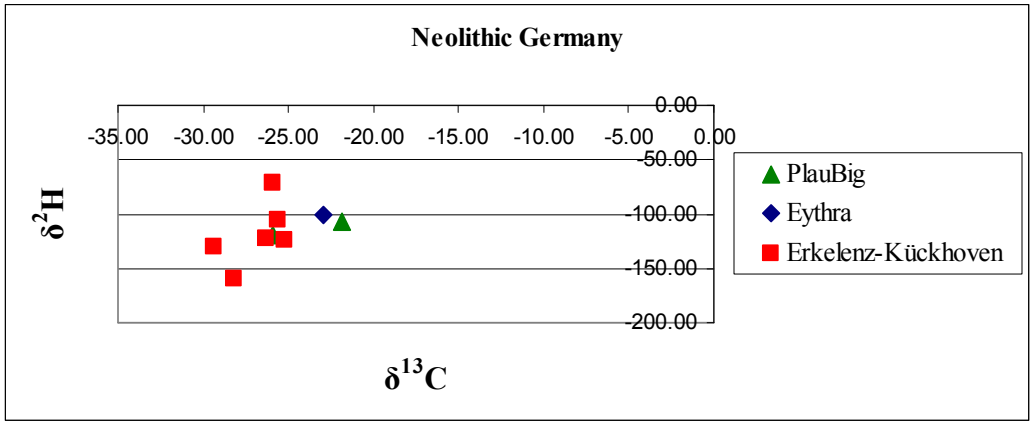


The dung beetles from Plaußig may reflect an herbivore which had a diet consisting of the local flora and cereals. The $\delta^{13}C$ ratios for *Onthophagus ovatus* and *Aphodius granarius* fall close to the carbon-13 signature for the root weevil *Otiorhynchus raucus* but below the $\delta^{13}C$ ratio for *Sitophilus granarius*. However, both the $\delta^{13}C$ and the $\Delta^{13}C_t$ values for the granary weevil fall outside the average predicted isotopic range of the rest of the assemblage ($\Delta^{13}C_{t\text{-average}}$ = -27.76) suggesting that the species may in itself be associated with allochthonous plants; whereas the $\Delta^{13}C_t$ of the dung beetles approximates the average for the assemblage. The addition of the deuterium and nitrogen-15 isotopes did not help to further elucidate the dung beetle's association due the availability of relatively few samples.

The 1.13 ‰ difference in $\delta^{13}C$ ratio between *Onthophagus ovatus* and *Aphodius granarius* presents as a 3.5 ‰ variation in $\delta^{15}N$ values. The variability evidenced by the isotopic ratios of the dung beetles could signify differences in altitude of the associated herbivores' grazing ground or seasonality in the beetle's chitin formation.

Copris lunaris, *Geotrupes vernalis*, and *Musca domestica* represent the dung fauna from Erkelenz-Kückhoven. The isotopic ratios were highly variable. *G.*

Figure 7.10 Plot of Deuterium and Carbon-13 from the German palaeoentomological specimens



vernalis and *M. domestica* exhibited depleted nitrogen-15 ratios while *C. lunaris* had a relatively high value for the assemblage. *Geotrupes vernalis* was approximately 30 ‰ more depleted in deuterium than *Copris lunaris* and 37 ‰ more depleted than *Musca domestica*. *Copris lunaris* exhibited the most depleted carbon-13 signature with *Geotrupes vernalis* approximately 1 ‰ more enriched and *Musca domestica* about 4 ‰. The discrepancy among the dung fauna can probably be attributed to differences in grazing areas and seasonality. The trophic level of the manure source may have been a factor, but the isotopic assays gave conflicting results. For example, the $\delta^{15}N$ ratio of the house fly was more nitrogen poor (implying a lower trophic level position) than expected relative to its deuterium signature. Despite the interspecific variation, the three dung-associates appear to be representative of herbivorous dung sources. The deuterium and carbon-13 values of the house fly are similar to those

predicted for the Alfalfa snout beetle *Otiorhynchus ligustici* [Figure 7.10] and the carbon-13 and nitrogen-15 values of *Copris lunaris* are grouped close to the chrysomelid [Figure 7.7]. The stable-carbon isotope value for *Geotrupes vernalis* is also similar to *Oreina caerulea* but the dung beetle's nitrogen-15 prediction is more depleted. The depleted stable-carbon and deuterium values (relative to *Musca domestica*, *Carabus irregularis*, *Sitona lineatus*, and *Otiorhynchus ligustici*) of *Copris lunaris* and *Geotrupes vernalis* suggest the exploitation of a lower altitude areas for the grazing of herbivores.

While previous studies have shown that manure increases the ^{15}N content of soils and plants (e.g. Choi *et al.* 2003; Bogaard *et al.* 2007), the chitin of the dung fauna did not appear to exhibit any nitrogen-15 enrichment. In comparison to the other species in the assemblages, the dung-associates, in general, were more nitrogen deprived. This suggests that the majority of the dung associated insects were not feeding directly on the nitrogen-enriched aspects of the dung. However, *Copris lunaris* may be an exception as it was slightly enriched relative to the majority of the invertebrate assemblage from Erkelenz-Kückhoven.

The plant-associated insect species

The invertebrate remains from the Neolithic German sites may give evidence concerning the exploitation of natural resources, agricultural practices, and possibly trade. As discussed in Chapter 4, insects are very important indicators of plant resources (e.g. wood, hay, cereals, dyeplants, moss, turf and brushwood). While the traditional archaeoentomological evaluations permit inferences concerning the probable origins of the plant resources, the application of isotopic analyses may be

utilised to substantiate the otherwise largely hypothetical palaeoecological suggestions.

Only a limited range of plant-associated species were available for isotopic analyses from the Early Linearbandkeramic sites of Eythra and Plaußig. The granary weevil represents the Eythra assemblage and *Sitophilus granarius* and *Otiorhynchus raucus* were selected for isotopic evaluation from Plaußig. At Eythra, the granary weevil was more enriched in carbon-13 than the predatory *Pterostichus (Poecilus) cupreus* but more depleted than the dung beetle. Based on the assumption that $\delta^{13}C$ ratios are more enriched in carnivores than herbivores within the same foodweb, *P. cupreus* was not feeding on *S. granarius*, and the two species likely reflect the isotopic values of separate areas. The granary weevil would likely represent cereal cultivated at a higher altitude or lower latitude than occupied by the ground beetle's prey.

While both Eythra and Plaußig were discovered in the Leipzig region of modern Germany, the granary weevil specimens from the two sites predicted different isotopic values. The *Sitophilus granarius* recovered from Eythra had more enriched stable-nitrogen and deuterium isotopic ratios but more depleted stable-carbon values than the Plaußig specimen. As Plaußig is located at a higher altitude than Eythra but approximately the same latitude, the isotopic signatures of the local flora and fauna should be more enriched in the Plaußig specimens. The intraspecific variation may reflect differences in seasonality, nitrogen-content in the soil, or cereal species.

When the root weevil *Otiorhynchus raucus* is considered, the stable-carbon isotope values for the plant-associated fauna at Plaußig vary by approximately 6 ‰. As the stable-carbon isotopic value for the root weevil approximates the average $\Delta^{13}C_t$ of the rest of the assemblage, the species is most likely autochthonous, which would

imply that the $\delta^{13}C$ ratio for the local environment around Plaußig is probably close to -27 ‰. Based on difference in elevation, the local environment signature for Eythra would be ≤ -27 ‰, which supports the prediction of ≤ -25.24 ‰ tabulated from *Pterostichus (Poecilus) cupreus*. This would suggest that the granary weevil specimens from Eythra and Plaußig reflect allochthonous cereals. While the enriched isotopic values of the granary weevils may signify the importation of cereals to the sites from slightly lower latitude regions, the enrichment most likely supports a local cultivation of the crops in the higher altitude hinterlands (see Körner *et al.* 1991). Both sites are at a lower elevation than their surrounding hinterlands. In comparison to Eythra and Plaußig, more plant-associated invertebrates were available for analysis from the later Linearbandkeramic site of Erkelenz-Kückhoven: *Dorcus parallelopipedus, Oriena caerulea*, *Otiorhynchus ligustici, Sitona lineatus, Sitophilus granarius,* and *Tenebroides mauritanicus*.

As mentioned above, the recorded isotopic values for *Oriena caerulea*, *Otiorhynchus ligustici*, and *Sitona lineatus*, though variable amongst themselves, are similar to the dung fauna. The species may have been transported to the site as the Neolithic people exploited their local and hinterland plant resources. *O. ligustici* and *S. lineatus*, in particular, are associated today with edible plant species. Both the pea leaf weevil and the Alfalfa snout beetle exhibited similar isotopic predictions to the ground beetle *Carabus irregularis*. It is likely that the beetles represent the isotopic signature for the local vegetation. Given the isotopic correlation with *Musca domestica*, the house fly was probably breeding in dung and waste materials on the site.

The depleted stable-carbon ratio of *Oriena caerulea* may reflect the use of a lower altitude region compared the pea leaf weevil and the Alfalfa snout beetle. As

the hinterland decreases in elevation to the east of Erkelenz-Kückhoven, this may be a likely origin for the species. The nitrogen-enrichment evidenced by *O. caerulea* in addition to its stable-carbon ratio similarity to *Copris lunaris* and *Geotrupes vernalis* may imply that the chrysomelid originated from the region set aside for the grazing of the domesticated vertebrate herbivores. As Choi *et al.* (2003) and Bogaard *et al.* (2007) have shown, manure causes nitrogen enrichment in plants. While probably not intentionally fertilized by the Neolithic people, the Cardueae (Asteraceae) plants would have indirectly benefited from the presence of herbivore dung. The enriched nitrogen values would have then been transferred to the phytophagous *Oriena caerulea*.

The isotopic values predicted for *Dorcus parallelopipedus* are interesting. The lesser stag beetle exhibited a stable-carbon isotopic ratio similar to the perceived autochthonous insect species; however, had much more enriched $\delta^{2}H$ and $\delta^{15}N$ values. The deuterium signature of the stag beetle is approximately 51 ‰ more enriched relative to *Otiorhynchus ligustici* and the nitrogen-15 fractionation around 12 ‰. As both beetles are herbivorous, the discrepancy suggests the introduction of *D. parallelopipedus* to Erkelenz-Kückhoven. The lesser stag beetle is often associated with rotten or old wood, and in a village, its habitat would most likely be mimicked by the presence of wood piles intended for firewood. While *Dorcus parallelopipedus* may have been transported to the site along with the wood, the isotopic discrepancy presented by its chitin suggests that the wood would have had to have been transported a fair distance from a warmer region. As the beetle is flighted, it is more likely that the species originated in a warmer environment and arrived at the site through natural means rather than anthropic.

Both *Sitophilus granarius* and *Tenebroides mauritanicus* are associated with cereals today. However, the two beetles suggest different stable-carbon isotopic values for the cereals at Erkelenz-Kückhoven. While the isotopic ratios may reflect trophic level differences, *T. mauritanicus*, as a carnivore and an omnivore, should exhibit a more enriched carbon-13 ratio than the herbivorous *S. granarius*. However, this was not the case in the present study. Unfortunately, $\delta^{2}H$ and $\delta^{15}N$ values could not be procured for the cadelle specimen, due to limited fossil material, so interpretation is limited. The $\delta^{13}C$ ratio for *Sitophilus granarius* implies a higher altitude origin for the cereals (the hinterlands to the north and west of the site are higher in elevation than Erkelenz-Kückhoven) whereas the signature for *Tenebroides mauritanicus* is closely correlated with the species assumed to be from the local environment. The discrepancy between the two grain associates has been interpreted in three ways:

1) cereals were being cultivated near the village and in the higher altitudinal hinterlands;
2) cereal was being cultivated locally and being imported from a location higher in altitude or lower in latitude;
3) cereal was being cultivated only in the hinterlands and represented by the granary weevil, whereas the cadelle was not associated with the cereals.

The cereals were most likely being cultivated in different areas around the village; perhaps different grains were grown at different altitudes. However, because of the variation between the two grain associates, the possibility of cereal importation cannot be dismissed. The third suggestion regarding *Tenebroides mauritanicus* not being regarded as a cereal associate is remote. While the cadelle has been documented living beneath the bark in trees, those records are from warmer climates

(Crowson 1958; Palm 1959), and even though the species is considered cold hardy, it has not been found in non-synanthropic habitats in the cold temperate regions (cf. Hunter *et al*. 1973) and exhibited life cycle requirements inferring warmer climate origins [see Chapter 5].

7.4.8 Synopsis

This case study provides evidence of isotopic differences in insect species both within and between sites in Linearbandkeramic Germany. The isotopic predictions indicated a highly variable arthropod population, which was interpreted as evidence of the exploitation of the natural and cultivated resources in the local environment and the surrounding hinterlands. Both the dung fauna and plant-associates suggested that the domesticated vertebrate herbivores and agricultural plants were tended away from the site. At Eythra, Plaußig, and Erkelenz-Kückhoven, the isotopic ratios associated with cereals suggested that the agricultural crops were cultivated at higher altitudes than their corresponding sites. Moreover, at Erkelenz-Kückhoven, the stable-isotope signatures of dung beetles implied that the lower altitude regions may have served as grazing areas for the vertebrate herbivores. While the isotopic discrepancies between the perceived local vegetation entomofauna and the grain associates were interpreted as local versus hinterland exploitation, the enriched ratios evidenced by the grain fauna may be indicative of the importation of cereals from lower latitude regions. The carbon-13 variation reflected by grain-associates *Sitophilus granarius* and *Tenebroides mauritanicus* at Erkelenz-Kückhoven may represent the importation of cereals in addition to the local 'subsistence' agriculture.

7.5 Conclusion

The stable-isotope analysis of insect remains has potential as a method for discerning human activity in the past. Because the geographically distinct isotopic signatures of a region are assimilated into insect chitin through diet and become locked into the chitin following adult metamorphosis, recovered archaeological insect fossils are excellent isotopic indicators.

However, interpretation of the isotopic values requires an understanding of the ecology of the insects. The trophic level variability of isotopes presented by vertebrate herbivores, omnivores, and carnivores appears to be more convoluted in insects with the additional inclusion of mycetophagous and, potentially, coprophilous species, which may further distort the isotopic signal, especially in regards to carbon-13 and nitrogen-15 ratios. As interpretation of isotopic results is limited by an understanding of species' ecology, it is crucial to select species for analysis, which have habitats and dietary habits that have been well documented.

The application of stable-isotopic carbon, hydrogen, and nitrogen on insects recovered from West Stow and Neolithic Germany showed potential as a means of assessing local versus non-local signatures. In the present study, low levels of isotopic fractionation were interpreted as differences in seasonality or altitude, for which latter was construed as indicating a hinterland connection. In regards to long-distance introductions, the *Dorcus parallelopipedus* specimen provided the only clear evidence of a species of non-local origin although the Erkelenz-Kückhoven grain pests may be indicative of a second case. While the lesser stag beetle most likely represents a natural invasive rather than a human introduction, the species' isotopic signature was distinct from the other species in the assemblage clearly identifying it

as non-indigenous. This suggests that isotopic analyses may be of use in recognising species associated with long-distance exchangeable commodities in the past.

Unfortunately at this stage, the stable-isotopes recovered from archaeological insect remains are unable to serve as a means of identifying the origins of foreign goods. While well-correlated, the isotopic fractionation between the meteoric precipitation and the chitin is not back traceable to geographic origins through linear models. Although Rubenstein and Hobson (2004) and Bowen *et al*. (2005) offer non-linear interpolation methods which have proven successful in modern studies, the models require an isotopic-geographic patterning correlated with the data set. Because insect remains have not been as frequently analysed as vertebrates, the isotopic data necessary to back-trace or map the species do not yet exist.

While the application of isotopic analysis towards insect remains is still in its infancy, it has its advantages as a palaeoeconomic tool. Although the method operates on a similar premise as the palaeoecological method discussed in Chapter 4, it advances beyond inferential assumptions of foreign and local product-associates and provides tangible evidence towards the isotopic signal of the geographic origin of the species' (primary level) dietary source. The isotopic approach is also an improvement to the biogeographical method as it by-passes the inherent limitations of a spatial-temporal approach [see Chapter 5]. Isotopic analysis offers inferences based upon the individual specimens analysed and is not contingent upon the documented archaeological presence of the species beyond the site.

Chapter 8

Recovery of DNA from Archaeological Insect Remains: First Results, Problems and Potential

Modified from the Journal of Archaeological Science publication

Recovery of DNA from archaeological insect remains: First results, problems and potential.

Journal of Archaeological Science 36, 1179-1186 (2009)

Gary A. King [a], M. Thomas P. Gilbert [b], Eske Willerslev [b], Matthew J. Collins [c, d] and Harry Kenward [a]

[a] Department of Archaeology, University of York, The Kings Manor, York YO1 7EP, UK

[b] Biological Institute, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark

[c] BioArch, Department of Archaeology, University of York, UK

[d] BioArch, Department of Biology, University of York, UK

Abstract

We report the recovery of short fragments of PCR amplifiable ancient DNA from exoskeletal fragments of the grain weevil *Sitophilus granarius* (L.) extracted from Roman and medieval deposits in Northern England. If DNA preservation in archaeological insect remains is widespread then many applications in the spheres of evolutionary studies and archaeology can be conceived, some of which are outlined.

Key words: ancient DNA, thermal age, beetles, Roman, medieval, *Sitophilus granarius*

8.1 Introduction

The disarticulated remains of insects have long been successfully employed as bioindicators of natural palaeoecosystems and in archaeological reconstructions (e.g. Coope *et al.* 1998; Buckland 2000; Coope 2000; Robinson 2001). The huge potential of archaeological insects as evidence of past human activity and palaeoecology arises from their ecological diversity, their tendency to be ignored or perceived as unimportant to humans, and their sensitivity and rapid reaction to environmental change. The discipline of archaeoentomology works from the premise that in most temperate and arctic environments of the northern hemisphere, all or most insects have maintained morphological and physiological stability during the Quaternary (Coope 2004). On this basis, palaeoecological information can be extracted by superimposing the climatic range and ecological role of modern insects over the fossil record.

Here we report a preliminary investigation of the preservation of DNA in insect remains from archaeological sites in Northern England. There are numerous

reasons why analysis of DNA from such fossils should be carried out, but three are perhaps the most significant. The first is to test the hypothesis that morphological constancy can be equated with genetic, and thus presumably physiological and behavioral, constancy. The second is to refine characterization and identification of species, 'races', or other populations. While they are normally disarticulated, the preservation of insect fossils is such that they typically retain morphological characteristics, including microsculpture, and can be identified by comparison with modern reference material. However, the morphological similarity of many closely related taxa limits identification to species group, genus, or even subfamily. This is evident from inspection of most published species lists. In order to overcome the difficulties associated with the classical methods, other means for identification must be investigated. Some mainstream entomologists have been researching the benefits of genetic (DNA-based) identification methods with a large degree of success; the method permits rapid and accurate determination, regardless of developmental stage or specimen damage, and has even been proposed as a solution to the problem of the shortage of skilled taxonomists (Tautz *et al.* 2003).

The third reason for analysing DNA from fossil insects is the possibility of recognising intraspecific variations which may provide clues as to the past demography and history of dispersal, whether natural or by humans, of species. Where insects (and other organisms) have been investigated, local populations have been found to have subtly different genetic characteristics. In Europe, for example, these have been used to track postglacial recolonisation from glacial refugia (Hewitt 1999, 2000, 2004). While problems have been signaled (Reiss 2006), recovery of DNA from Pleistocene and archaeological insect fossils might thus open up significant new lines of research.

For the present investigation we have chosen the granary weevil, *Sitophilus granarius*. This is an economically important beetle which is not a native of Britain, but whose remains are commonly recovered from waterlogged archaeological deposits and have yielded amino acids in tests conducted on Roman Age subfossils [Appendix 5]. A non-destructive method for ancient DNA (aDNA) extraction (Gilbert *et al.* 2007) has been employed to demonstrate the presence of ancient DNA in weevils from Roman and medieval deposits in Northern England.

8.2 Materials and Methods

Subsamples of raw sediment from 62-8 Low Petergate, York (excavated in 2004; Hall *et al.* 2007) and Park View School, Chester-le-Street, County Durham (excavated in 2006; Schmidl *et al*. 2006) were processed in 2007 using methods outlined by Kenward *et al.* (1980). Paraffin flotation was employed for the extraction of insect remains, and the resulting 'flots' were stored in alcohol until they were sorted using a low-power binocular microscope. Selected fossils were temporarily stored on damp filter paper in closed dishes together with a few thymol (*i.e.* 6-isopropyl-m-cresol) crystals to prevent mould, then placed in small glass vials containing industrial methylated spirit (an approximately 90/10 mixture of ethanol/methanol). Fragments of *S. granarius* from six archaeological samples were selected for DNA analysis, and modern specimens from a laboratory culture were used as controls (Table 8.1). Precautions were followed to avoid contamination of the material with previously amplified DNA (following Cooper and Poinar 2000, as modified by Gilbert *et al.* 2005). Prior to Polymerase Chain Reaction (PCR) amplification, the DNA extractions and subsequent manipulation were performed in a laboratory designated for research on samples containing low concentrations of DNA,

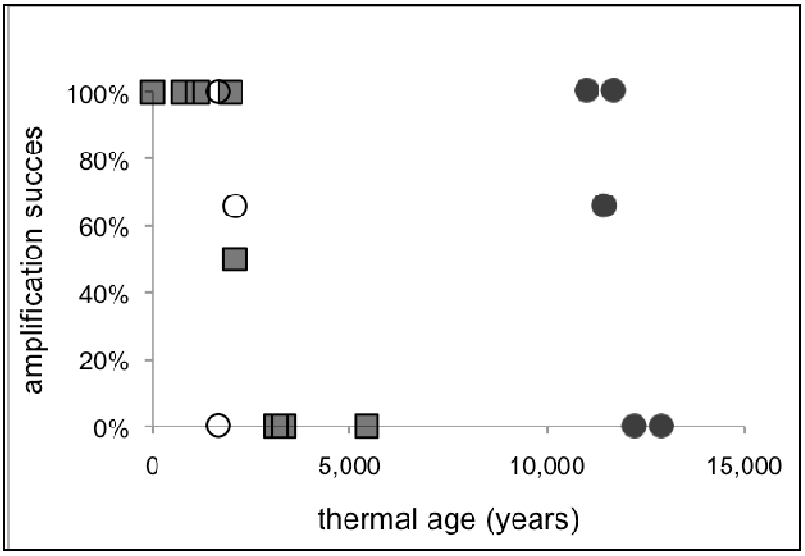
Table 8.1 Details of specimens of *Sitophilus granarius* examined

Specimen	Fragments	Sample	Date	Amplifiable mtDNA		Amplifiable nuDNA	
GK1	Whole specimen	Yorkshire	Modern	98bp	Y	57bp	Y
				148bp	Y	88bp	Y
				256bp	Y		
GK5	3 heads; 5 elytra; 1 leg	62-8 Low Petergate, York 4977 76/t2	14th c.	98bp	Y	57bp	Y
				148bp	Y		
				256	Y	88bp	Y
GK6	8 elytra	62-8 Low Petergate, York 4977 76/t1	14th c.	98bp	Y	57bp	Y
				148bp	Y	88bp	Y
				256bp	Y		
GK7	2 elytra	Park View School, Durham 113	Roman	98bp	Y	57bp	N
				148bp	N	88bp	N
				156bp	N		
GK8	5 elytra	Park View School, Durham 144	Roman	98bp	Y	57bp	N
				148bp	N	88bp	N
				256bp	N		
GK10	1 head; 1 probiscus; 4 legs	Park View School, Durham 152	Roman	98bp	N	57bp	N
				148bp	N	88bp	N
				256bp	N		

including aDNA. This laboratory is physically isolated from the laboratory where post-PCR work is conducted. Furthermore, the PCR amplified DNA was both cloned and sequenced from multiple overlapping PCR amplifications from each sample to ensure sequence accuracy.

DNA is expected to degrade rapidly following cell death, limiting the potential PCR amplifiable size of extracted DNA template molecules (Lindahl 1993a). Therefore to investigate the relative preservation of mitochondrial DNA (mtDNA) and nuclear DNA (nuDNA) in the archaeological samples, the PCR assays were designed to screen for DNA survival at a range of fragment sizes in order to assess thermal age [see Figure 8.1]. For detailed methods and arguments for data authenticity see Appendix 6A.

Figure 8.1 Comparison of amplification success of different amplicons when converted to thermal age. Results are shown for mtDNA (■), and for nuDNA where the ratio of target numbers to mtDNA is either 1:100 (●) or 1:2 (○)



8.2.1 Thermal age: Accounting for Target Length and Copy Number

Thermal age (Smith *et al.* 2003) attempts to normalise different samples for the effects of burial temperature and time. Thermal age was estimated assuming an activation energy of (127.8 kJ mol^{-1}) giving an approximate rate for DNA depurination at 10 °C of 4 x 10^{-6} yr^{-1}.

Thermal age is a useful way of contrasting the relative likelihood of amplification success of different initial copy number (sample type, target) and

different amplicon lengths. The number of sites of potential depurination, which increases with amplicon length, increases the probability of chain scission (Deagle *et al*. 2006). By normalising to an amplicon length of 100 bp (including primers), samples from the same site and of the same age will have different thermal ages that reflect target size (and hence probability of depurination).

The number of targets surviving is also a function of starting copy number. If one tissue type has more target copies than another (e.g. muscle *versus* bone), or if mitochondrial and nuclear targets are analysed from the same sample, these targets will have different thermal ages (assuming that rates of chain scission do not differ). For example nuDNA of equal length to mtDNA will have a higher thermal age, because the lower initial starting copy number implies fewer targets will be present in the sample for any given time interval. In the absence of estimates of absolute concentration in recently buried insect cuticle, the differing relative concentration of targets such as mtDNA and nuDNA can be explored. Equivalent thermal ages imply equal probabilities of successful amplification.

8.3 Results

Mitochondrial DNA was successfully extracted, PCR amplified, cloned and sequenced from five of the six specimens. While the modern and medieval samples yielded mtDNA at all the fragment lengths investigated, only the shorter 98 bp mtDNA fragments could be amplified from two of the three Roman specimens, with the last yielding no amplicon. Similarly, while short nuDNA fragments were successfully extracted and sequenced from the medieval and modern samples, nuDNA preservation was not identified in the Roman fossils. No PCR or extraction blanks exhibited evidence of contamination. The identity of the sequenced DNA as

Sitophilus granarius was confirmed both through the modern control sample sequences, and through positive identification against the NCBI GenBank database. Thermal age estimates were very similar for samples from York and Durham. The former could be compared with a direct measurement from measured soil temperature (at 4 m depth, 10.9 °C; Chang 1958**)** giving an estimate of 1.17 times the rate at 10 °C.

Normalising for fragment length, data from mtDNA amplifications suggests that the thermal limit (the point at which no amplification is successful) for mtDNA is an order of magnitude lower than estimated for bone. The small sample size will reduce the errors on this estimate, but would not account for such a large difference in thermal limit. Assuming a very conservative estimate of the ratio of mitochondrial to nuclear DNA (1:100), thermal age estimates for nuDNA are an order of magnitude higher than mtDNA. It is necessary to reduce the ratio to 1:2 in order that the thermal limits overlap. If we discount the possibility that this ratio is an inaccurate estimate of starting copy number, then the result indicates that the respective success rates of mtDNA and nuDNA does not correspond to an equivalent chemical (i.e. temperature/time dependent) process. The two most probable explanations for this are (i) differential rates of depurination due to differences in the packing of the two types of DNA within insect remains or (ii) additional biological (nuclease activity) which has preferentially targeted nuDNA. The results do suggest that nuDNA is preferentially preserved relative to mtDNA in these samples.

8.4 Discussion

We have shown that PCR amplifiable levels of mtDNA and multicopy nuDNA survive in the exoskeletons of fossil beetles. Preserved insect DNA has been

reported from amber-encased fossils dating to the Ogliocene (25-35 mya), e.g. stingless bees (Cano *et al*. 1992a, 1992b), termites (DeSalle *et al*. 1992, 1993), and wood gnats (DeSalle and Grimaldi 1994), and the Cretaceous (120-135 mya), e.g. Lebanese weevils (Cano *et al*. 1993). However, as few recent studies have succeeded in amplifying DNA from remains older than several hundred thousand years, it is suggested that the results of amber studies should be regarded carefully. Investigations of sub-glacial deposits in Greenland (Willerslev *et al.* 2007) and insect carapaces from museum collection samples (less than one hundred years old, e.g. Zakharov *et al.* 2000; Junquiera *et al.* 2002; Gilbert *et al.* 2007) have yielded DNA fragments with no indication of contamination. While previous analyses have been conducted with varying degrees of success, the recovery from terrestrial fossils in archaeological deposits opens up many new possibilities, providing preservation is fairly common and occurs in a range of other taxa.

Intraspecific variation of DNA between modern local populations and races has been demonstrated for a number of insect taxa, including honey bees (e.g. Garnery *et al.* 1995; Arias and Sheppard 1996; Lee and Hall 1996), ground beetles (e.g. Ashworth 1996; Reiss *et al.* 1999; Cardoso and Vogler 2005), some other groups of beetles (e.g. Schrey *et al.* 2005; Smith and Farrell 2005), human lice (Leo *et al.* 2002; Yong *et al.* 2003), and butterflies (e.g. Nice *et al.* 2005). All of these studies of modern genomes have been relevant to palaeoecological questions, but all lack an essential element: information about the genetic constitution of ancient populations. Given the success of genetic analysis of modern insects, its application to subfossil insect remains clearly deserves exploration.

In the present study, ancient DNA was successfully extracted from one species of beetle from Roman and medieval contexts. The failure to amplify nuDNA and

longer strands of mtDNA from the Roman material is consistent with what would be expected as a result of postmortem fragmentation of the DNA (Lindahl 1993a; Deagle *et al.* 2006). However thermal age analysis suggests that the thermal age limit at which no amplification success is possible (for a nominal 100 base pairs at a constant 10 °C) is at least an order of magnitude less for DNA in these insect remains (2-3 ka) than in bone (Smith *et al.* 2003). This analysis also reveals that nuDNA is relatively more resistant to hydrolysis than mtDNA. The reasons for these two observations are as yet unknown, but together they do imply a significantly greater role of biological processes (nuclease) activity in the destruction of DNA in these remains when contrasted with available data from bone (e.g. Poinar *et al.* 2006). The reason that specimen GK10 did not yield mtDNA of 98 bp lengths while other material of similar age gave good recovery is unknown, but given probable role played by nuclease activity in polymer scission, this may reflect early taphonomic processes. However, the GK10 fossils did not demonstrate any visible signs of morphological degradation which differed from specimens GK7 and GK8.

If DNA can be recovered from *S. granarius*, it is likely to be preserved in many other insects, at least in those with similarly substantial exoskeletons. A priority is therefore to test a wider range of robust fossils, and to investigate the possibility that DNA may survive in more delicate fossils as well. For the mtDNA analysis used here, we targeted a conserved portion of the cytochrome oxidase I gene for two predominant reasons. Firstly, it has previously been sequenced in modern samples, so that a reference sequence was available against which to design primers and compare the data (O'Meara and Farrell unpublished; Genbank ID: AY131101); and, secondly, its relatively conserved state within species suggested that the ancient sequences were unlikely to be sufficiently different from the modern sequences such

as to lead to PCR amplification problems. However, the conserved nature of that gene segment also means that its use for characterizing populations or tracing micro-evolutionary change is likely to be limited. Therefore, for future studies the analysis of more variable genes or at least a more variable portion of the cytochrome oxidase I gene (see Juan *et al.* 1998) will need to be employed. One potential candidate is the mtDNA cytochrome oxidase II gene, which has recently been used by Moya *et al.* (2004) in phylogenetic investigation of, and discrimination between, ground beetles of the genus *Eutrichopus*. Additionally, Juan and collaborators (1998) have had success utilizing the 255 base pair fragment of the cytochrome oxidase I gene that coincides with the 5' end positions of the 2410 and 2665 in the *Drosophila yakuba* mitochondrial genome to formulate the phylogeography of the darkling beetle *Hegeter politus* in the Canary islands.

How might we use DNA from ancient insects? Numerous taxonomic, evolutionary and archaeological applications spring to mind. It may prove useful for crucial identifications, although there are probably few cases where the effort would be justifiable; one exception might be the differentiation of races of human lice (see below). The possibility of detecting minor genetic change through time (microevolution), whether gradual, or perhaps in sudden steps, such as when new selection pressures were applied when populations were translocated geographically or into artificial environments, would open up the opportunity to make comparisons with genetic changes seen following invasions at the present day (e.g. Huey *et al.* 2000). The morphological constancy of insects through the Quaternary is ascribed to remixing of genetically divergent populations by climate change. Although some PCR amplifiable insect DNA may be expected to survive in deep frozen (*i.e.* permafrost environments), routine recovery of Pleistocene insect DNA is perhaps too

much to hope for. However if it were achieved, for example using fossils from tundra deposits, we should be able to trace this process of differentiation and rehomogenization through time.

Do modern natural and synanthropic (human-associated) insect populations differ genetically, can this be seen in ancient populations, and if so, does this indicate adaptation or founder effect in isolated populations (cf. Frankham *et al.* 1999)? More fundamentally, do the genomes of fossils differ substantially from modern examples, and if so can we reasonably continue to assume that past populations exploited similar habitats to present ones and can thus be used in reconstructing past ecology? Specific problems might be soluble: for example, the ground beetle *Pterostichus madidus* (Fabricius) is very common today, but rather rarely found as a fossil: why did it become more common? Was there a genetic change (*i.e.* adaptation) associated with increasing synanthropy? There are some 'sibling species' among insects which appear to have identical habitats and which often occur together. A case is provided by *Anthicus floralis* (Linnaeus) and *Anthicus formicarius* (Goeze), found in materials such as stored hay and both with a substantial fossil record. Might the origin of such pairs be traced, and the cause (adaptation or isolation?) be determined? A third case worthy of note is the head and body races of human lice, whose origin seems on the basis of studies of the modern genomes to be complex, the races perhaps having arisen twice independently (Leo *et al.* 2002; Yong *et al.* 2003); might fossils clarify the relationship between them? Perhaps one of the most valuable uses of genetic analysis of fossils in archaeology might be in characterizing past local populations and tracing patterns of natural or human distribution. The sources of imported materials such as dye plants might conceivably be traced through recognition of geographically localized genotypes of insects associated with natural-habitats. The

history of synanthropic pests such as *S. granarius*, itself, might be traceable: for example, were British populations derived from a small number of Roman introductions, or established and maintained by continued trade? Did the population present following the Norman Conquest arise from British survivors of the 'Dark Ages', or from a new introduction from Continental Europe?

Single or multiple introductions to a settlement might stand as evidence of intensity of trade (a parallel to work on synanthropic insects, Kenward 1997). To cite a specific case, an Early Christian site in Country Antrim, Northern Ireland, seems to have had far more synanthropes than would be predicted from its apparent isolation (Kenward 1997; Kenward *et al.* 2000). Was this a result of intense exchange over a period of time (multiple genotypes being predicted), or of one large-scale introduction of small numbers of a range of synanthropes, in hay for example (restricted range of genotypes predicted)? As with studies of DNA generally, it is suspected that, providing preservation is widespread, many new uses will arise.

8.5 Conclusion

In this study the investigation of mtDNA and multicopy 18s nuDNA survival from the anoxic waterlogged remains was conducted on the granary weevil *Sitophilus granarius* as part of a pilot study for on-going research. The genes were selected based on the existence of GenBank records and their genetic sustainability. As previously noted, the portion of the CO1 gene was selected for analysis because of its conservative nature and consequentially reduced chance of variability due to population and specific mutations overtime. 18s was selected because it is found in multiple copies, not to the extent of mtDNA, but more than the single copy of other nuDNA genes. It is likely that future studies will to some extent benefit from also

testing whether single copy nuDNA survives in similar samples, although this is likely to be sample dependent, as indicated by the variation in the medieval and Roman material recorded here. We believe that the results conveyed in the present study are authentic and that the successful recovery of ancient DNA from waterlogged insect remains indicates significant potential.

8.6 Acknowledgements

We are grateful to Terry O'Connor and Ellie Jones for their comments on a draft. A special thanks to PCA North and Palaeoecological Research Services for supplying Roman samples from the Park View School site. GAK's research was supported by the Short-term Marie Curie PALAEO Fellowship and the kind contributions from the Department of Ancient DNA and Evolution at University of Copenhagen. HK was co funded by English Heritage and the University of York.

Chapter 9

Conclusions and Future Directions

9.1 Thesis Summary

The field of palaeoentomology is rich in unfulfilled potential and promise. The study of insect remains retrieved from archaeological contexts has been particularly effective in reconstructing past ecologies and living conditions. Furthermore, it presents the opportunity to investigate an exciting range of previously unaddressed or un-approachable questions concerning past social and economic activities; an endeavour which was explored in the present thesis.

The effectiveness of palaeoentomology as an interpretative tool relies on an understanding of insect species' morphology and physiology. Chapter 2 provides a brief survey on the role of morphological features in species identification and behavioural interpretations. Additionally, an understanding of cuticular composition and formation is invaluable in the successful design and performance of biochemical and biomolecular extractions [Chapters 6, 7, and 8]. In order to discern information regarding past human activity, it is essential to understand how an organism interacts with its environment, its trophic position, and ecological constraints [Chapter 2].

In an effort to explore the potential of palaeoentomology as a palaeoeconomic tool, three analytical approaches were tested—palaeoecology, biogeography, and isotopic analyses—and a fourth a method was proposed, i.e. phylogeography. Each of the tools had distinct advantages and limitations.

9.1.1 The Palaeoecological Approach

Through analysis of species' morphology and ecological preferences, palaeoecological reconstructions may be formulated and potential socio-economic indicator species pinpointed [Chapter 4]. The palaeoecological approach to discerning past trade and human movement involved:

1.) The processing of environmental samples and the identification of insect remains from a single archaeological site;

2.) The interpretation of the retrieved arthropod fossils to discern the habitat preferences and diet of individual species. The information was employed to compile palaeoenvironmental reconstructions, which aided in interpreting the environment at and near the site. The abundance of insect remains and species ecological groups served to identify autochthonous and allochthonous components;

3.) The evaluation of the preferred habitats and diets of modern species to draw parallels with the archaeological fauna. The ecological preferences of the modern taxa were viewed as analogous and thus were superimposed over the archaeological specimens in order to identify insect species associated with human exploitable commodities;

4.) The application of the Mutual Climatic Range model to calculate the temperature range at the site for the warmest and coldest months. The results of the model were based on the temperate requirements and geographic range of carnivorous and scavenging beetles. It is important to note that in the present study, the insect species used as indicators of human activity were primarily stenotopic herbivores and/or ectoparasites. Thus the selected indicator fauna was independent of the fauna used in the MCR model, which means the temperature predictions of the model were not influenced by potentially foreign species; and,

5.) The comparison of the determined palaeoenvironmental and palaeoclimatic signature of the site with the geographic and thermal requirements of the proposed indicator species. These evaluations were used to hypothesise as to

whether the species could have inhabited and survived in the ambient environment.

The palaeoecological approach provides a comparatively quick and non-destructive means of identifying insect species that may stand as direct or indirect evidence of human-driven socio-economic activities, including probable evidence towards the exploitation of local versus foreign commodities. The method suffers in that it is highly speculative and can be unconvincing in its conclusions. While it can effectively target taxa associated with exploitable commodities, e.g. honeybees implying the availability of honey and beeswax, a single site palaeoecological assessment lacks the ability to provide a timeframe for the introduction of the species. For example, the *Damalinia ovis* recovered from 16-22 Coppergate was taken as a strong indication of the presence of wool in Anglo-Scandinavian York. Based on its thermal requirements, it was identified as a species that was not indigenous to the United Kingdom and which was adapted to a warmer climate. However, does this imply that the Vikings were importing sheep and/or wool from warmer geographic regions, or was the species introduced to Britain during an earlier period and able to endure in micro-climates? The palaeoecological approach cannot account for the latter possibility. Furthermore, how would palaeoecological approach rationalise the predominantly northern fossil record of the sheep louse (e.g. Perry *et al*. 1985; Buckland *et al.* 1992; Kenward and Allison 1994a; Schelvis and Koot 1995; Buckland *et al*. 1998)?

The other major limitation of the palaeoecological method, as utilised here, is its difficulty in ascertaining the origin of the exchangeable resources. Species, such as *Apion (Exapion) difficile*, which were capable of surviving in Britain and have a modern British presence, are assumed to be representative of the local exploitation of

resources. However, the Anglo-Scandinavians, in the case of *A. difficile*, may have introduced the weevil with imported dye plants from Continental Europe, where it may have been much more abundant. Fortunately, the trade signal is not always completely ambiguous when using this approach. For example, in the case of the *Hesperophanes fasciculatus* recovered from Roman Alcester (Osborne 1971), the species, which is associated with structural timbers and furniture and believed unable to survive in Britain, has a modern distribution extending through southern Europe and the Middle East, and is particular common in Greece. The thirteen individuals of *H. fasciculatus* in Roman Britain are indicative of maritime connections with the Mediterranean.

Despite the method's limitations, the palaeoecological assessment has two key advantages as tool for indicating trade and cultural contact.

1.) It is relatively cost-effective. The approach does not burden the researcher with excessive laboratory fees. It requires access to a water source, a bucket, sieve, and paraffin, and some costs may be incurred if travel is necessary for specimen identification or document retrieval; and
2.) It also produces fairly timely results. Single sample processing can usually be achieved over the course of a few hours, but can vary depending on soil matrix and weight. The time involved in specimen identification and palaeoecological reconstruction is relative to the experience of the analyst and the number of fragments present in the flot.

The outcome of both factors may vary between sites and samples. However, they constitute the core aspects of the palaeoecological approach. Furthermore, the other analytical methods must also account for these factors, especially the processing and identification costs, as they comprise part of each of the methodological

approachs. Thus, the palaeoecological approach provides the quickest and most affordable results.

9.1.2 The Biogeographical Approach

Through employment of the biogeographical method, a few of the limitations of the palaeoecological approach may be addressed. Palaeobiogeographical investigations rely on archaeological, ecological, and historical accounts to map changes in a species' distribution through time and space [Chapter 5]. This enables the researcher to discern a timeframe for the initial introduction of species to a region. The biogeographical approach involved the following steps:

1.) The selection of indicator species. In the present study, grain-associates were used;
2.) The compilation of historic and archaeological data on the species. These were used to evaluate the location of each beetle at different points in time;
3.) The examination of the temperature specifications of each species. Because most members of the grain fauna have a cosmopolitan distribution today, the thermal conditions necessary for a species to complete the development of its life cycle were viewed as an indication of the probable temperature range of its native region, i.e. the area where it evolved and was adapted to survive in the wild; and,
4.) The archaeological, ecological, and historical information was correlated to determine when a grain species first entered a particular geographic region and whether the species may have been endemic to that area.

By applying the biogeographical method to the grain pest fauna, it was possible to glean an understanding of human activity in the past. Though there are

exceptions, the grain beetles, in general, tend to be both strongly synathropic and poor dispersers. For example, *Sitophilus granarius* only infests cereals that have been harvested and stored. Additionally, *S. granarius* does not fly, which would impede its effectiveness as a disperser, especially across geographic barriers, e.g. bodies of water, deserts, mountains, etc. Although the weevil may have been able to self-disperse between habitats via corridor pathways, filter and sweepstake routes would have presented obstacles. Thus the species wide-spread distribution, even as early as the Neolithic, is likely to have been attributed to anthropogenic methods, i.e. the species would have hitchhiked to various locations in cereals carried by man. Because of this anthropogenic connection, the biogeographical interpretation of the distribution of the grain-associated insect fauna may effectively stand as evidence of human movement through trade, culture contact, or migration.

As mentioned in Chapter 5, the major limitations of the biogeographical approach are:

1.) It is unable to distinguish between multiple introductions of the same species to a region and, as such, is only able to imply contact between cultures or regions that involved the 'initial' introduction of the pest; and,

2.) Its effectiveness is restricted to the accessibility and availability of reliable archaeological and historical accounts.

Although the method has some limitations, it is a proficient means of discerning human movement in the past. By examining the geographic distribution of an indicator species at a set period of time, it is possible to propose likely points of origin for trade or culture contact. For example, the hypothesis that the grain from the late second century ship, which was excavated in the Netherlands (Pals and Hakbijl 1992), originated in Britain based upon the grain fauna 'community' that was present

in the assemblage [Chapter 5]. This is a distinct improvement over the palaeoecological method which would only have been able to recognise the grain pests as potential allochthonous species and suggest a connection to warmer climates on the basis of their thermal requirements.

The biogeographical approach is also fairly cost effective. Although it may involve the processing of environmental samples, the method is primarily dependent upon the review of available literature. While this may be time consuming depending on the species being assessed, it is a relatively low cost means of exploring potential trade connections and culture contact as made evident through insect subfossils.

9.1.3 The Isotopic Approach

The isotopic analysis of insect remains is not a well-established field of research. Although isotopic studies (e.g. Miller *et al.* 1988; Gröcke *et al.* 2006) have proposed the application of insect fossils to palaeoclimatological research, few attempts have been made (e.g. Wooller *et al*. 2004; Hardenbroek 2006; Hardenbroek *et al.* 2007). Despite this, isotopes extracted from modern insects appear to be well-correlated to the meteoric precipitation of their environment, especially stable carbon and hydrogen (cf. Miller 1984; Hobson *et al.* 1999), which suggests their potential as palaeoenvironmental indicators. Furthermore, Chapter 6 demonstrated the ability of insects, under laboratory conditions, to assimilate and retain the isotopic signature of their host plant's (comprising both foreign and locally grown cereal crops) region of origin, which implies the ability of insect remains to stand as evidence of past trade. In Chapter 7, stable-isotopic carbon, hydrogen, and nitrogen were examined to pioneer the application of isotopes from archaeologically recovered insect remains toward discerning palaeoeconomic activities. The isotopic approach involved:

1.) The recovery of insect remains from modern and Neolithic sites;

2.) The isolation of the chitin to avoid the potential of assaying conflicting isotopic signatures from proteins and lipids (see Miller 1984). This is significant as it involves the destruction of the insect fossil, which needs to be taken into consideration when applying the method to specimens, rare or otherwise;

3.) The extraction of stable isotopes from the insect chitin. Carbon-13, deuterium, and nitrogen-15 were assayed; and,

4.) The comparison of the isotopic signatures of species within and between sites; accounting for trophic level variation.

The isotopic method proved an effective means of assessing past socio-economic activities. The analyses denoted isotopic variation within the modern and Neolithic sites. In most cases, the isotopic signature procured from the cereal-associated species differed from the ratios of the entomofauna that were presumably feeding on materials endemic to the site. The discrepancy was low and was interpreted as expressing exploitation of resources from the local hinterland. The isotopic variation was most likely attributed to differences in altitude or seasonality. Although the present study did not recover an indication of a long-distance economic connection from the archaeological sites, the stable-isotopes extracted from *Dorcus parallelopipedus*, which based on the isotopic results was assumed to be a natural invasive to the Neolithic site, evidenced the ability of the method to distinguish between local and potentially foreign signatures. From the modern site of West Stow, the isotopic ratios from *Anobium punctatum* and *Sitophilus granarius* may imply importation of building materials to the site, i.e. wood for structural timbers and cereal for thatch, respectively. However, the discrepancy between the autochthonous and

allochthonous species from West Stow was not sufficient to assume the foreign importation of the products, rather it merely suggested that the structural timbers and thatch materials originated beyond the site.

Because of the paucity of previous isotopic analyses on archaeoentomological materials, the isotopic method suffers from an inability to back trace the origins of potentially foreign materials. Thus while the approach can provide convincing, if not conclusive, evidence as to whether a commodity was local or imported, which is an improvement over the speculations of the palaeoecological approach, it is unable to identify a port of origin. If more archaeoentomological evidence was assayed in the future, non-linear interpolation methods based on geographic-patterning (e.g. Rubenstein and Hobson 2004; Bowen *et al*. 2005) may be employed to back trace the materials.

The other major disadvantage of the isotopic method over the palaeoecological and biogeographical approaches is cost. In addition to the minor expenditure involved in the processing of the environmental samples, the isotopic assays incur costs (sometimes in the range of thousands or tens of thousands of pounds sterling) from the purchase of chemicals and tin and silver capsules as well as the fees required for the use of the laboratory equipment necessary for analysis and computation. Depending on where the analyses are conducted, the isotopic method may require the assistance of grants or other sources of funding. Although potentially costly, the isotopic approach has potential as tool for discerning the localised exploitation of resources, trade, migration, and culture contact in the past.

9.1.4 The Phylogeographic Approach

Chapter 8 presents the seminal discovery of ancient DNA from insect fossils recovered from waterlogged archaeological contexts and outlines myriad lines of research that would benefit from its application. Unfortunately, a full phylogeographic analysis of archaeologically retrieved insect specimens was not within the scope of this thesis. However, previous studies have shown the applicability of modern insect remains towards discerning phylogeographic relationships (e.g. Juan *et al.* 1998).

As a tool for discerning the introduction of indicator species in the past and thus culture contact, it is hypothesised that species derived from different populations will yield variation within their genetic code. In the modern darkling beetle, Juan and associates (1998) determined a variation to be present with in the CO1 gene. Moya *et al.* (2004) observed mitochondrial variation within the CO2 gene of the ground beetle genus *Eutrichopus*. If genetic discrepancy is evidenced in species recovered from the same archaeological context or sample, it may indicate the introduction of the species to the site, and thus may arguably stand as evidence of trade or culture contact, especially if the species is associated with a resource which is exploitable by man.

In order to effectively back trace the origins of a species, phylogeographic methods need to be employed. This requires knowledge of the region of genetic variability from populations of the same species that are established in different locations. Ideally, this information would be derived from contemporaneous populations.

For example, a project wishing to determine the origin of the *Sitophilus granarius* specimens from 21 St. Peters Street Colchester, UK (King and Hall 2008), would attempt to compare the genetic code from the Roman Colchester samples to the Roman Age specimens recovered from 1 Poultry, London, UK (Rowsome 2000),

Santa Pola, Spain (Moret and Martin Cantarino 1996), Alphen aan den Rijn, Netherlands (Kuijper and Turner 1992), Neuss, Germany (Cymorek and Koch 1969), Touffréville Calvados, France (Ponel *et al.* 2000), Herculaneum, Naples, Italy (Dal Monte 1956), and potentially the Iron Age specimens from Okruglo, Croatia (Smith *et al*. 2006) and Horbat Rosh Zayit, Israel (Kislev and Melamed 2000). By comparing the *S. granarius* recovered from the different sites, the distinct genetic signature of each population could be ascertained. If the Colchester and London populations were identical, then it could be assumed that *S. granarius* was, at least originally, probably introduced with cereals derived from a single geographic point. However, if the populations differed, it may imply that Romans were importing cereals from different locations. By analysing the European and Mediterranean populations, it may be possible to infer the source population and thus the origin of both the Roman Colchester *S. granarius* and likely the cereals with which it was introduced. However, caution would need to be exercised in interpreting data as the *Sitophilus granarius* from the other regions may also have been imported [see Chapter 5].

While untested, the phylogeographic approach has potential as tool for assessing social and economic activities in the past. As with the isotopic analyses, the method can be relatively expensive, particularly in comparison to the biogeographical and palaeoecological methods. However, it is non-destructive method which may be capable of providing 'definitive' answers to otherwise un-approachable questions.

9.2 Future Directions

Various improvements to the methods and research approaches would enable significant progress to be made as to effectiveness of palaeoentomology as research tool for assessing past trade, migration, and culture contact. Underpinning the success

of future endeavours is the need for increased palaeoentomological research in geographic areas which have received little or no prior attention. For example, the present study was severely impeded by the absence of archaeoentomological material from regions such as North Africa and India, and suffered due to the paucity of materials from continental Europe, the Middle East, and the Far East. The lack of subfossil insect studies results in gaps in the palaeoentomological record, which in turn, limits the effectiveness of the methods in being able to discern geographic and ecological patterns.

The application of ancient genetics and isotopes towards the study of archaeological insect remains are nascent fields of research. As it has now been proven possible to extract uncontaminated aDNA from waterlogged preserved insect fossils, concerted efforts need to be made to test the applicability of a phylogeographic method towards addressing palaeoeconomic issues. Modern taxa should be analysed to determine regions of intraspecific genetic variation, and further ancient DNA should be extracted from archaeological specimens to determine geographic patterning within species. Can ancient DNA be recovered from pre-Roman waterlogged specimens? In addition, there is a need to evaluate the survival of aDNA in charred and desiccated insect remains as they comprise a fair proportion of the archaeoentomological remains from some regions. Moreover, the isotopic method would be greatly advantaged by investigation of archaeoentomological remains from additional archaeological sites. The procurement of further isotopic data would enhance the approaches ability to back trace the origins of allochthonous species.

It may also be a worthwhile endeavour to apply holistically the methods addressed in this thesis to more recent archaeological sites. Such an assessment would

likely foster a clearer understanding of migration, distribution, and origins of production through the multifaceted establishment of spatial and chronological patterning. Consequently, contextual patterning may be evident through the incorporation of evidence from associated historical and archaeological arenas. The Colonial Period settlements in the Americas have recently proven rich in archaeoentomological remains (e.g. Bain 1997, 1998; Bain *et al.* 2009; King *et al*. 2010). In assessments of the modern fauna, Sailer (1983) estimated the presence of 1683 immigrant arthropod species in the continental United States, of which 66 % are believed to have originated in the Palaearctic eco-zone, and Lindroth (1957) claimed that 14 % of the Newfoundland ground beetles were European. As the archaeoentomological remains from Colonial Era sites are more recent than those evaluated in King *et al.* (2009), there is the potential for both mitochondrial and nuclear DNA survival as the basepair sequences would be expected to have undergone comparatively less decay than in the Roman and 14th century specimens. The presence of longer, less fragmented DNA sequences would enhance the likelihood of finding key regions of intraspecific variability which would be invaluable to phylogeographic analyses. While individually each approach has proven informative in its own right, a holistic assessment integrating the detailed results and analyses of all the methods should be considered.

9.3 Conclusion

The methods reviewed in this thesis explored the potential of insect remains to stand as evidence of past human interaction as well as to discern the origins of potentially foreign commodities. It is suggested that through scrutiny of their ecological preferences, archaeologically retrieved insect species may be relied upon to

represent the presence of human exploitable resources. Three methodologies were tested to back trace the origins of the indicator species. The approaches differed in the degree of confidence with which they could identify autochthonous and allochthonous species and propose potential origins. Additionally, a fourth approach was suggested but not applied. Although the methods have limitations, it is proposed that palaeoentomological remains can be used as a means of assessing culture contact. Furthermore, their effectiveness will be improved as future studies expand the availability of applicable data sets, which will enhance the resolution of the methods by enabling comparative geographic patterning.

Bibliography

Ag. Catos' De Re Rustica: Hooper, W. D. and Ash, H. B. (trans.) (1935). *Marcus Porcius Cato On Agriculture; Marcus Terentius Varro On Agriculture*. London: William Heinemann Ltd.

Alden, J. R. (1982). Marketplace exchange as indirect distribution: An Iranian example. In J. E. Ericson and T. K. Earle (eds.), *Contexts for prehistoric exchange*. New York and London: Academic Press, 83-101.

Alexander, K. N. A. (1994). *An annotated checklist of British lignicolous and saproxylic invertebrates*. Cirencester: National Trust Estates Advisors' Office.

Alfieri, A. (1931). Les insects de la tombe de Toutankhamon. *Bulletin de la Société Royale Entomologique d'Égypt* 3(4), 188-189.

Alfieri, A. (1976). *The Coleoptera of Egypt*. Cairo: Atlas Press.

Alisauskas, R. T. and Hobson K. A. (1993). Determination of lesser snow goose diets and winter distribution using stable isotope analysis. *Journal of Wildlife Management* 57, 49-54.

Allison, E. P. and Kenward, H. K. (1987). Insect remains from Copthall Avenue, London. *Ancient Monuments Laboratory Report* 194/87.

Alonso Martinez, N. and Buxo Capdevilla, R. (1993). Resultados iniciales del studio arqubotánico de semillas y frutos del yacimiento de Cova Punta Farisa (Fraga). *Estudioes de la Antigűedad, Universidad Autònoma de Barcelona 6-7 (1989-1990*), 49-56.

Amano, K. (1985). Breeding of the house fly, *Musca domestica*, (Diptera; Muscidae) in fresh dung of cattle fed on pasture grass. *Applied Entomological Zoology* 20, 143-150.

Ambrose, S. H. (2000). Controlled diet and climate experiments on nitrogen isotope ratios in rats. In S. H. Ambrose and M. A. Katzenberg (eds.), *Biogeochemical approaches to paleodietary analysis*. New York: Kluwer Academic/Plenum Publishers, 243–259.

An, C-C., Li, Y., and Zhu, Y-X. (1995). Molecular cloning and sequencing of the 18S rDNA from specialized dinosaur egg fossil found in Xixia Henan, China. *Acta Scientiarum Naturalium Universitatis Penkinensis 31***,** 140-147.

Anderson, R., McFerran, D., and Cameron, A. (2000). *Ground beetles of Northern Ireland (Coleoptera: Carabidae).* Belfast: Ulster Museum.

Andres, A. (1931). Catalogue of the Egyptian Tenebrioidae. *Bulletin de la Société Entomologique d'Égypt* 1, 29-36.

Anthony, D. W. (1990). Migration in archaeology: The baby and the bathwater. *American Anthropologist* 92, 895-914.

Arch. Vitruvius' De Architectura: Ross, V. (ed.) (1899). *Marcus Vitruvius Pollio: De Architerctura*. Leipzig: Teubner

Arias, M. C. and Sheppard, W. S. (1996). Molecular phylogenetics of honey bee subspecies (*Apis mellifera* L.) inferred from mitochondrial DNA sequence. *Molecular Phylogenetics and Evolution* 5, 557-566.

Ashby, S. P. (2001). *The inference of the movement of animals and animal products using archaeological data: a methodological review*. Unpublished MSc dissertation, University of York.

Ashby, S. P. (2004). Understanding human movement and interaction through the movement of animals and animal products. In M. Mondini, S. Muñoz, and S. Wickler (eds.), *Colonisation, migration and marginal areas: A zooarchaeological approach*. Oxford: Oxbow Books, 4-9.

Ashby, S. P. (2006). *Time, trade, and identity: Bone and antler combs in Northern Britain c. AD 700-1400*. Unpublished PhD thesis, University of York.

Ashworth, A. C. (1996). The response of arctic Carabidae (Coleoptera) to climate change based on the fossil record of the Quaternary period. *Annales Zoologici Fennici* 33, 125-131.

Assmann, T., Schröder, E., and Terlutter, H. (2000). Morphometric differentiation in a specialised snail predator: *Carabus pyrenaeus* (Coleoptera: Carabidae). In P. Brandmayr, G. Lövei, T. Zetto Brandmayr, A. Casale, and A. Vigna Taglianti (eds.), *Natural history and applied ecology of carabid beetles: Proceedings of the IX European Carabidologists' meeting (26-31 July 1998, Camigliatello, Cosenza, Italy).* Sofia-Moscow: Pensoft, 171-178.

Atkinson, T. C., Briffa, K. R., Coope, G. R., Joachim, J. M. and Perry, D. W. (1986). Climatic calibration of coleopteran data. In B. E. Berglund (ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology*. Chichester: J. Wiley and Son, 851-858.

Auffray, J-C., Vanlerberghe, F., and Britton-Davidian, J. (1990). The housemouse progression in Eurasia: A palaeontological and archaeozoological approach. *Biological Journal of the Linnean Society* 41, 13-25.

Bain, A. L. (1997). *Archaeoentomological analysis at the Ferryland site, Newfoundland*. Memorial University of Newfoundland Archaeology Unit, St. Johns.

Bain, A. L. (1998). A seventeenth century beetle fauna from colonial Boston. *Historical Archaeology* 32, 38-48.

Bain, A. L., Bouchard-Perron, J-A., Auger, R., and Simoneau, D. (2009). Insectes, graines et mauvaises herbes sur le site du Palais de l'intendant: Étude d'un paysage en evolution. *Post-Medieval Archaeology* 43(1) / *Archéologiques* 22.

Bakels, C. and Jacomet, S. (2003). Access to luxury foods in Central Europe during the Roman period: the archaeobotanical evidence. *World Archaeology* 34 (3), 542-557.

Bar-Yosef, O., Gopher, A., Tchernov, E., and Kislev, M. E. (1991). Netiv Hagdud: An early Neolithic village site in the Jordan Valley. *Journal of Field Archaeology* 18 (4), 405-424.

Barker, P. S. and Smith, L. B. (1990). Influence of granary type and farm practices on the relative abundance of insects in granary residues. *Canadian Entomologist* 122, 393-400.

Barrett, J. H. (1997). Fish trade in Norse Orkney and Caithness: A zooarchaeological approach. *Antiquity* 71, 616-638.

Barrett, J. H., Beukens, R. P., and Nicholson, R. A. (2001). Diet and ethnicity during the Viking colonization of Northern Scotland: evidence from fish bones and stable carbon isotopes. *Antiquity* 75, 145-154.

Bauch, H. A. and Erlenkeuser, H. (2003). Interpreting glacial-interglacial changes in ice volume and climate from subarctic deep water foraminiferal d18O. *Geophysical Monograph* 137, 87–102.

Bayford, E. G. (1903). Beetles in peat. *Naturalist*, 407-408.

Beekman, M. and Ratnieks, F. L. W. (2000). Long-range foraging by the honey-bee, *Apis mellifera* L. *Functional Ecology* 14, 490-496.

Begon, M. Harper, J. L., and Townsend, C. R. (1990). *Ecology—individuals, populations, and communities*. Oxford: Blackwell Scientific Publications.

Bengtson, S. A. (1981). Terrestrial invertebrates of the Faroe Islands: III. Beetles (Coleoptera): Checklist, distribution, and habitats. *Fauna Norvegica* B28, 52-82.

Bentley, S. and Whittaker, J. B. (1979). Effects of grazing by a Chrysomelid beetle, *Gastrophysa viridula* on competition between *Rumex obtusifolius* and *R. crispus*. *Journal of Ecology* 67, 79-90.

Berger, J-F. and Guilaine, J. (2009). The 8200 cal BP abrupt environmental change and the Neolithic transition: A Mediterranean perspective. *Quaternary International* 200, 31-49.

Best, P. B. and Schell, D. M. (1996). Stable isotopes in southern right whale (*Eubalaena australis*) baleen as indicators of seasonal movements, feeding and growth. *Marine Biology* 124, 483–494.

Birchall, J., O-Connell, T. C., Heaton, T. H. E., and Hedges, R. E. M. (2005). Hydrogen isotope ratios in animal body protein reflect trophic level. *Journal of Animal Ecology* 74, 877-881.

Biström, O., Silfverberg, H., and Rutanen, I. (1991). Abundance and distribution of coprophilous Histerini (Histeridae) and *Onthophagus* and *Aphodius* (Scarabaeidae) in Finland (Coleoptera). *Entomologica Fennica* 2, 53-66.

Böcher, J. (1988). The Coleoptera of Greenland. *Meddelelser om Grønland Bioscience,* 26.

Böcher, J. (1995). Palaeoentomology of the Kap Kobenhavn Formation, a Plio-Pleistocene sequence in Peary Land, North Greenland. *Meddelelser om Grønland, Geoscience* 33.

Bocherens, H. and Drucker, D. (2003). Trophic level isotopic enrichment of carbon and nitrogen in bone collagen: Case studies from recent and ancient terrestrial ecosystems. *International Journal of Osteoarchaeology* 13, 46-53.

Bodenheimer, F. S. (1947). A survey on the zoology of the ancient Sumerians and Assyrians. In *Actes du Ve Congres Internationales d'Histoire des Sciences: Lausanne, 20 Septembre-6 Octobre 1947*. Paris: Academie Internationale d'Histoire des Sciences.

Bogaard, A., Heaton, T., Poulton, P., and Merbach, I. (2007). The impact of manuring on nitrogen isotope ratios in cereals: Archaeological implications for reconstruction of diet and crop management practices. *Journal of Archaeological Science* 34, 335-343.

Boom, R., Sol, C. J., Salimans, M. M., Jansen, C. L., Wertheim-van Dillen, P. M., and van der Noordaa, J. (1990). Rapid and simple method for purification of nucleic acids. *Journal of Clinical Microbiology* 28, 495-503.

Boore, J. L. and Brown, W. M. (1998). Big trees from little genomes: Mitochondrial gene order as a phylogenetic tool. *Current Opinion in Genetics and Development* 8, 668-674.

Borror, D. J. and White, R. E. (1970). A field guide to insects: America north of Mexico. In R. T. Peterson (ed.), *The Peterson field guide series*. New York: Houghton Mifflin Company.

Boswijk, G. and Whitehouse, N. J. (2002). *Pinus* and *Prostomis*: A dendrochronological and palaeoentomological study of a mid-Holocene woodland in eastern England. *The Holocene* 12, 585-596.

Bowen, G. (2007). *Waterisotopes.org OIPC: The Online Isotopes in Precipitation Calculator*. Page Consulted on 9th March 2009. http://wateriso.eas.purdue.edu/waterisotopes/pages/data_access/oipc.html

Bowen, G. J., Wassenaar, L. I., and Hobson, K. A. (2005). Global applications of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia* 143, 337-348.

Bown, D. (1995). *Encyclopaedia of herbs and their uses.* London: Dorling Kindersley.

Brendell, M. J. D. (1975). *Coleoptera: Tenebrionidae. Handbooks for the identification of British Insects* 10. Royal Entomological Society of London.

Briggs, R. D., Brinkman, J. A., Civil, M., Farber, W., Gelb, I. J., Oppenheim, A. L., Reiner, E., Roth, M. T., and Stolper, M. W. (2006). *The Assyrian dictionary of the Oriental Institute of the University of Chicago*. Chicago: The Oriental Institute.

Brothwell, D. R. and Jones, R. (1978). The relevance of small mammal studies to archaeology. In D. R. Brothwell, K. D. Thomas, and J. Clutton-Brock (eds.), *Research problems in zooarchaeology*. London: Institute of Archaeology, 47-57.

Büchner, S. and Wolf, G. (1997). Der Kornkäfer—*Sitophilus granarius* (Linné)—aus einer bandkeramischen Grube bei Göttingen. *Archäologisches Korrespondenzblatt* 27, 211-220.

Buck, F. D. (1955). A provisional list of the coleoptera of Epping Forest. *Entomologist's Monthly Magazine* 91, 174-192.

Buck, F. D. (1958). The British Anobiidae. *Proceedings of the South London Entomological and Natural History Society 1958*, 51-64.

Buckland, P. C. (1976). The environmental evidence from the Church St. Roman sewer system. *The Archaeology of York* 14 (1). Council for British Archaeology, London

Buckland, P. C. (1978). Cereal production, storage and population: A caveat. In S. Limbrey and J. G. Evans (eds.), The effect of man on the landscape: The lowland zone. *Council for British Archaeology Research Report* 21. London: Council for British Archaeology, 43-45.

Buckland, P. C. (1981). The early dispersal of insect pests of stored products as indicated by archaeological records. *Journal of stored Product Research* 17, 1-12.

Buckland, P. C. (1982). The Malton burnt grain: A cautionary tale. *Yorkshire Archaeological Journal* 54, 53-61.

Buckland, P. C. (1988). North Atlantic faunal connections: Introductions or endemics?. *Entomologica Scandinavica, Supplement* 32, 7-29

Buckland, P. C. (1990). Granaries stores and insects: The archaeology of insect synanthropy. In D. Fournier and F. Sigaut (eds.), *La préparation alimentaire des cereals*. Rapports présentés à la Table ronde, Ravello au Centre Universitaire pour les Biens culturels, avril 1988. Rixensart, Belgium: PACT 26, 69-81.

Buckland, P. C. and Perry, D. W. (1989). Ectoparasites of sheep from Stóraborg, Iceland and their interpretation. Piss, parasites, and people: A palaeoecological perspective. *Hikuin* 15, 37-46.

Buckland, P. C. and Sadler, J. (1989). A biogeography of the human flea, *Pulex irritans* L. (Siphonaptera: Pulicidae). *Journal of Biogeography* 16, 115-120.

Buckland, P. C., Ashworth, A. C., and Schwert, D. W. (1995). By-passing Ellis Island: Insect immigration to North America. In R. Butlin and N. Roberts (eds.), *Ecological Change in Historical Time*. London: Blackwell, 226-244.

Buckland, P. C., Buckland, P. I., and Skidmore, P. (1998). Insect remains from GUS: An interim report. In J. Arneborg and H. C. Gulløv (eds.), Man, culture and environment in ancient Greenland. Copenhagen: Danish National Museum and Danish Polar Centre, 74-79.

Buckland, P. C., Sadler, J. P., and Sveinbjarnardóttir, G. (1992). Palaeoecological investigations at Reykholt, Western Iceland. In C. J. Morris and D. J. Rackham (eds.), Norse and later settlement and subsistence in the North Atlantic. Department of Archaeology, University of Glasgow, 149-168.

Buckland, P. C., Sveinbjarnardottir, G., Savory, D., McGovern, T. H., Skidmore, P., and Andreasen, C. (1983). Norsemen at Nipáitsoq, Greenland: A palaeoecological investigation. *Norwegian Archaeological Review* 16 (2), 86-98.

Buckland, P. I. (2000). *An introduction to palaeoentomology in archaeology and the BUGS database management system*. Umeå: Institute for Archaeology and Sami Studies, University of Umeå.

Buckland, P. I. and Buckland, P. C. (2006). *Bugs Coleopteran Ecology Package* (Versions: BugsCEP v7.61; Bugsdata v7.09; BugsMCR v2.0; BugStats v1.2). www.bugscep.com.

Bullock, J. A. (1993). Host plants of British beetles: A list of recorded associations. *Amateur Entomologist* 11, 1-24.

Burmeister, S. (2000). Archaeology and migration: Approaches to an archaeological proof of migration. *Current Anthropology* 41 (4), 539-567.

Buxton, K. and Howard-Davis, C. (2000). Bremetenacum: Excavations at Roman Ribchester 1980, 1989-1990. *Lancaster Imprints Series* 9. Lancaster University Archaeological Unit.

Cainé, L., Corte Real, F., Lima, G., Pontes, L., Abrantes, D., and Pinheiro, M. F. (2006). Genetic identification of forensically important Calliphoridae in Portugal. *International Congress Series* 1288, 846-848.

Cano, R. J., Poinar, H., and Poinar Jr, G. O. (1992a). Isolation and partial characterisation of DNA from the bee *Problebeia dominicana* (*Apidae*: *Hymenoptera*) in 25-40 million year old amber. *Medical Science Research* 20, 249-251.

Cano, R. J., Poinar, H. N., Pieniazek, N. J., Acra, A., and Poinar Jr, G. O. (1993). Amplification and sequencing of DNA from a 120-135-million-year-old weevil. *Nature* 363, 536-538.

Cano, R. J., Poinar, H. N., Roubik, D. W., and Poinar Jr, G. O. (1992b). Enzymatic amplification and nucleotide sequencing of portions of the 18S rRNA gene of the bee *Problebeia dominicana* (*Apidae*: *Hymenoptera*) isolated from 25-40 million year old Dominican amber. *Medical Science Research* 20, 619-622.

Cardoso, A. and Vogler, A. P. (2005). DNA taxonomy, phylogeny and Pleistocene diversification of the *Cicindela hybrida* species group (Coleoptera: Cicindelidae). *Molecular Ecology* 14, 3531-3546.

Carr, T. S. (1838). *The history and geography of Greece including its literature, forms of government, and the spread of Grecian civilization by colonies and conquests*. London: Simpkin Marshall and Co.

Carracedo, A., Bar, W., Lincoln, P., Mayr, W., Morling, N., Olaisen, B., Schneider, P., Budowle, B., Brinkmann, B., Gill, P., Holland, M., Tully, G., and Wilson, M. (2000). DNA commission of the international society for forensic genetics: Guidelines for mitochondrial DNA typing. *Forensic Science International* 110, 79-85.

Carrott, J., Akeret, Ö., Hall, A., Mant, J., Jaques, D., and Gardner, S. (2005). A review of, and statement of potential for, sediment samples and hand-collected shell and bone recovered from ongoing archaeological works at Spurriergate, York (site code: 2000.584). *Palaeoecological Research Services* 2005/20

Carrott, J., Dobney, K., Hall, A., Issitt, M., Jaques, D., Johnstone, C., Kenward, H., and Large, F. (1995a). An evaluation of biological remains from excavations at Keldgate, Beverley (site code: KEL94). *Reports from the Environmental Archaeology Unit, York* 95/3

Carrott, J., Hall, A., Issitt, M., Jaques, D., Kenward, H., and Large, F. (1995b). Evaluation of biological remains from excavations at Tower Street, Hull (site code: HCT95). *Reports of the Environmental Archaeology Unit, York* 95/37

Carrott, J. and Kenward, H. (2001). Species associations among insect remains from urban archaeological deposits and their significance in reconstructing the past human environment. *Journal of Archaeological Science* 28, 887-905.

Casale, A., Prüser, F., Arndt, E., and Mossakowski, D. (1998). Phylogenetic relationships in the subgenus *Platycarabus* Morawitz, 1886 (Coleoptera: Carabidae: Carabini). *Phylogeny and classification of Caraboidea* XX. I.C.E. (1996, Firenze, Italy), 429-448.

Chaddick, P. R. and Leek, F. F. (1972). Further Specimens of Stored Products Insects Found in Ancient Egyptian Tombs. *Journal of Stored Products Research* 8, 83-86.

Chamberlain, C. P., Blum, J. D., Holmes, R. T., Feng, X. H., Sherry, T. W., and Graves, G. R. (1997). The use of isotope tracers for identifying populations of migratory birds. *Oecologia* 109, 132–141.

Chang, J. H. (1958). *Ground Temperature*, vols. 1–2. Blue Hill Meteorological Observatory, Harvard University, Milton, Massachusetts.

Cheyne, I. A., Foster, W. M., and Spence, J. B. (1974). The incidence of disease and parasites in the Soay sheep population of Hirta. In P. A. Jewell, C. Milner, and J. Morton Boyd (eds.), *Island survivors: The ecology of the Soay sheep of St. Kilda*. London: Athlone Press, 338-359.

Chikatunov, V., Lillig, M., Pavlíček, T., Blaustein, L. and Nevo, E. (1997). Biodiversity of insects at a microsite, 'Evolution Canyon', Nahal Oren, Mt. Carmel, Israel. Coleoptera: Tenebrionidae. *Journal of Arid Environments* 37 (2), 367-377.

Childe, V. G. (1925). *The dawn of European civilization*. London: Kegan, Paul, Trench and Trubner.

Childe, V. G. (1957). *Piecing together the past: The interpretation of archaeological data*. London: Routledge and Kegan Paul.

Choi, W. J., Roa, H. M., and Hobbie, E. A. (2003). Patterns of natural 15N in soils and plants from chemically and organically fertilized uplands. *Soil Biology and Biochemistry* 35, 1493-1500.

Chowne, P., Girling, M., and Greig, J. (1986). Excavations at an Iron Age defended enclosure at Tattershall Thorpe, Lincolnshire. *Proceedings of the Prehistoric Society* 52, 159-188.

Chu, H. F. and Wang, L-Y. (1975). Insect carcasses unearthed from Chinese antique tombs. *Acta Entomologica Sinica* 18, 333-337.

Chuter, K. (2000). Some scarce beetles in Kent. *Coleopterist* 9 (1), 42-43.

Clark, J. G. D. (1966). The invasion hypothesis in British archaeology. *Antiquity* 40, 172-189.

Colledge, S., Conolly, J., and Shennan, S. (2004). Archaeobotanical evidence for the spread of farming in the Eastern Meditteranean. *Current Anthropology* 45, 35-58

Colledge, S., Conolly, J., and Shennan, S. (2005). The evolution of Neolithic farming from SW Asian origins to NW European limits. *European Journal of Archaeology* 8 (2), 137-156.

Compte, A. and Perales, J. (1984). Estudios de insectos coleópteros datados en el inicio de la iberización y pertenecientes al poblado de Siriguarach (Alcañiz, Teruel). *Kalathos* 3-4, 121-137.

Coombs, C. W. and Freeman, J. A. (1956). The insect fauna of an empty granary. *Journal of Entomological Research* 46, 399-417.

Coombs, C. W. and Woodroffe, G. E. (1963). An experimental demonstration of ecological succession in an insect population breeding in stored wheat. *Journal of Animal Ecology* 32, 271-279.

Coope, G. R. (1959). A late Pleistocene insect fauna from Chelford, Cheshire. *Proceedings of the Royal Society* London B 151, 70-86.

Coope, G. R. (1970). Interpretations of Quaternary insect fossils. In R. Smith and T. E. Mittler (eds.), *Annual review of entomology* 15. Palo Alto, California: Annual Reviews, Inc. and Entomological Society of America, 97-120.

Coope, G. R. (1977a). Fossil coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage. *Philosophical Transactions of the Royal Society of London* B 280, 313-340.

Coope, G. R. (1977b). Quaternary Coleoptera as aids in the interpretation of environmental history. In F. W. Shotton (ed.), *British Quaternary Studies*. Oxford University Press, 55-68.

Coope, G. R. (1978). Constancy of insect species versus inconstancy of Quaternary environments. In L. A. Mound and N. Waloff (eds.), *Diversity of insect faunas. Royal Entomological Society of London Symposium* 9, 176-187.

Coope, G. R. (1986a). Coleoptera analysis. In B. E. Berglund (ed.), *The Handbook of Holocene Palaeoecology and Palaeohydrology*. Chichester: Wiley, 703-715.

Coope, G. R. (1986b). The invasion and colonisation of the North Atlantic islands: A palaeoecological solution to a biogeographic problem. *Philosophical Transactions of the Royal Society London* B 314, 619-635.

Coope, G. R. (2000). The palaeoclimatological significance of Late Cenozoic Coleoptera: familiar species in very unfamiliar circumstances, pp. 303-315. In Culver, S. J. and Rawson, P. F. (eds.), *Biotic response to global change*. Cambridge: Cambridge University Press.

Coope, G. R. (2004). Several million years of stability among insect species because of, or in spite of, ice age climatic instability? *Philosophical Transactions of the Royal Society of London* B 359, 209-214.

Coope, G. R., Lemdahl, G., Lowe, J. J., and Walkling, A. (1998). Temperature gradients in northern Europe during the last glacial-Holocene transition (14-9 14C kyr BP) interpreted from coleopteran assemblages. *Journal of Quaternary Science* 13, 419-433.

Coope, G. R. and Osborne, P. J. (1968). Report on a coleopterous fauna of a Roman well at Barnsley Park, Gloucestershire. *Transactions of the Bristol and Gloucestershire Archaeological Society* 86, 84-87.

Cooper, A. and Poinar, H. (2000). Ancient DNA: Do it right or not at all. *Science* 289, 1139.

Cordy, J-M. and Stassart, M. (1982). La faune omalienne de la Place Saint-Lambert (Liège). *Notae Praehistoricae* 2, 105-110.

Cormie, A. B., Schwarcz, H. P., and Gray, J. (1994). Relation between hydrogen isotopic ratios of bone collagen and rain. *Geochimica et Cosmochimica Acta* 58, 377-391

Cox, C. B. and Moore, P. D. (2000). *Biogeography. An ecological and evolutionary approach* (sixth edition). Oxford: Blackwell Science Ltd

CP: Theophrastus' De Causis Plantarum. Einarson, B. and Link, G. K. K. (trans.) (1990). De *Causis Plantarum Book III-IV*. Cambridge: Harvard University Press.

Crabtree, P. J. (1990). Zooarchaeology and complex societies: Some uses of faunal analysis for the study of trade, social status, and ethnicity. In M. B. Schieffer (ed.), *Archaeology: Method and theory* 2. Tuscon: University of Arizona Press, 155-205.

Craig, H. and Gordon, L. I. (1965) Deuterium and oxygen-18 variations in the ocean and the marine atmosphere. In E. Tongiorgi (ed.), *Proceedings of a Conference on Stable Isotopes in Oceanographic Studies and Paleotemperatures*. Spoleto, Italy, 9–130.

Craig, O. E., Biazzo, M., O'Connell, T. C., Gamsey, P., Martinez-Labarga, C., Lelli, R., Salvadeli, L., Tartaglia, G., Nava, A., Renò, L. Fiammenghi, A., Rickards, O., and Bondioli, L. (2009). Stable isotopic evidence for diet at the Imperial Roman coastal site of Velia (1st and 2nd centuries AD) in Southern Italy. *American Journal of Physical Anthropology* 139, 572-583.

Crosby, A. (2004). *Ecological imperialism: The biological expansion of Europe, 900-1900.* New York: Cambridge University Press.

Crowson, R. A. (1958). Some observations on a coleopterological visit to Central Italy. *Entomologist's Monthly Magazine* 94, 248-251.

Cymorek, S. and Koch, K. (1969). Über Funde von Körperteilen des Messingkäfers Niptus hololeucus (Fald.). Auslagerungen aus dem 15-16 Jahrhundert (Neuss, Neiderrhein) und Folgerungen daraus für die Ausbreitungsgeschichte der Art in Europa. *Anzeiger für Schädlingskunde und Pflanzenschutz* 42, 185-186.

Dal Monte, G. (1956). La presenza di insetti dei granai in frumento trovato neg1i scavi di Ercolano. *Redia* 41, 23-28.

Dansgaard, W. (1964). Stable isotopes in precipitation. *Tellus* 16, 436-468.

Dansgaard, W., White, J. W. C., and Johnson, S. J. (1989). The abrupt termination of the Younger Dryas climate event, *Nature* 339*,* 532–534.

Darby, H. C., and Maxwell, I. S. (1978). *The Domesday geography of northern England*. Cambridge: Cambridge University Press.

Deagle, B., Eveson, J. P., and Jarman, S. N. (2006). Quantification of damage in DNA recovered from highly degraded samples – a case study on DNA in faeces. *Frontiers in Zoology* 3, 11.

DeNiro, M. J. and Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42, 495-506.

DeNiro, M. J. and Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* 45, 341-351.

DeSalle, R., Barcia, M., and Wray, C. (1993). PCR jumping in clones of 30-million-year-old DNA fragments from amber preserved termites (*Mastotermes electrodominicus*). *Experientia* 49, 906-909.

DeSalle, R., Gatesy, J., Wheeler, W., and Grimaldi, D. (1992). DNA sequences from a fossil termite in Oligo-Miocene amber and their phylogenetic implications. *Science* 257, 1933-1936.

DeSalle, R. and Grimaldi, D. (1994). Very old DNA. *Current Opinion in Genetic Development* 4, 810-815.

Dieckmann, B., Hoffstadt, J., Maier, U., and Spatz, H. (1997). The state of the excavations on the "Offwiesen" in Singen, Kreis Konstanz. *Archaeological Excavation in Baden-Württemberg*, 43-47

Dillon, D. S. and Dillon, L. S. (1972). *A manual of common beetles of eastern North America*. New York: Dover Publications.

Dobney, K., Hall, A., Issitt, M., Jaques, D., Kenward, H., and Shaw, T. (1995). Assessment of plant and animal remains from deposits at Higher Lane,

Fazakerley, Merseyside (site code FAZ94). *Reports from the Environmental Archaeology Unit, York* 95/22.

Donisthorpe, H. St. J. K. (1939). *A preliminary list of the Coleoptera of Windsor Forest*. London: Lloyd and Co.

Duff, A. (1993). *Beetles of Somerset: Their status and distribution*. Taunton: Somerset Archaeological and Natural History Society.

Earle, T. K. (1982). Prehistoric economies and the archaeology of exchange. In J. E. Ericson and T. K. Earle (eds.), *Contexts for prehistoric exchange*. New York and London Academic Press, 1-12.

Efremov, J. A. (1940). Taphonomy: New branch of palaeontology. *Pan-American Geologist* 74, 81-93.

Eggleton, P. and Belshaw, R. (1992). Insect parasitoids—an evolutionary overview. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 337, 1-20.

Elias, S. A. (1994). *Quaternary insects and their environments*. Washington, DC: Smithsonian Institution Press

Elton, C. S. (1927). *Animal ecology*. New York: Macmillan.

Elton, C. S. (1958). *The ecology of invasions*. New York: John Wiley and Sons Inc.

Elton, C. S. (1966). *The pattern of animal communities*. London: Methuen.

Estep, M. F. (1980). The uptake and incorporation of the hydrogen from water into the organic matter of plants. *Carnegie Institution Washington Yearbook* 79, 391–394.

Evans, F. C. (1956). Ecosystem as the basic unit in ecology. *Science* 123, 1127-1128.

Evans, D. E. (1983). The influence of relative humidity and thermal acclimation on the survival of adult grain beetles in cooled grain. *Journal of Stored Product Research* 19, 173-180.

Evans, G. (1977). *The life of beetles*. London: Allen and Unwin.

Eyre, K. (2000). A note on the feeding ecology of *Carabus problematicus* Herbst (Col., Carabidiae). *Entomologist's monthly Magazine* 136, 205.

Fasani, L. (1976). Presenza di *Sitophilus granarius* (Linnaeus, 1758) (Coleoptera Curculionidae Calandrinae) in depositi dell'età del bronzo dell'Italia settentrionale. *Tesi di Laurea di Scienze Naturali*, University of Ferrara.

Flanagan, L. B. and Ehleringer, J. R. (1991). Effects of mild water stress and diurnal changes in temperature and humidity on the stable oxygen and hydrogen

isotopic composition of leaf water in *Cornus stolonifera* L. *Plant Physiology* 97, 298- 305.

Flanagan, L. B., Bain, J. F., and Ehleringer J. R. (1991). Stable oxygen and hydrogen isotope composition of leaf water in C3 and C4 plant species under field conditions. *Oecologia* 88, 394–400.

Floyd, E. H. and Newsom, L. D. (1959). Biological study of the rice weevil complex. *Annals of the Entomological Society of America* 52, 687-695

Frankham, R., Lees, K., Montgomery, M. E., England, P. R., Lowe, E. H. and Briscoe, D. A. (1999). Do population size bottlenecks reduce evolutionary potential? *Animal Conservation* 2, 255-260.

Freeman, P. (1980). *Common insects pests of stored products*. London: British Museum (Natural History).

Friday, L. E. (1988). A key to the adults of British water beetles. *Field Studies* 7, 1-151.

Fry, B. and Sherr, E. B. (1984). $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science* 27, 13-47.

G. Virgil's Georgics. Goold, G. P. (ed.) (1999). *Virgil I*. Cambridge: Harvard University Press.

Galloway, J. A., Keene, D., and Murphy, M. (1996). Fuelling the city: Production and distribution of firewood and fuel in London's region, 1290-1400. *Economic History Review* 69 (3), 447-472.

Gardiner, L. (2008). *The carbon cycle*. Windows to the Universe. University of Michigan and University Corporation for Atmospheric Research. Page consulted on 28th July 2009. http://www.windows.ucar.edu/

Garnery, L., Mosshine, E. H., Oldroyd, B. P. and Cornuet, J-M. (1995). Mitochondrial DNA variation in Moroccan and Spanish honey bee populations. *Molecular Ecology* 4, 465-471.

Gauthier, E. and Richard, H. (2009). Bronze Age Lake Bourget (NW Alps France): Vegetation, human impact, and climatic change. *Quaternary International* 200, 111-119.

GBIF (2009a). *Dataset: Natural England- Invertebrate site register- England (Species collected 1950)*. UK Natural Biodiversity Network. Global Biodiversity Information Facility. Page consulted 28th August 2009. http://data.gbif.org/occurrences/149221689/

GBIF (2009b). *Dataset: Bugs (GBIF-SE:Artdatabanken)*. GBIF- Sweden. Global Biodiversity Information Facility. Page consulted 28th August 2009.

http://data.gbif.org/occurrences/173580057/

Gilbert, M. T. P., Moore, W., Melchior, L. and Worobey, M. (2007). DNA extraction from dry museum beetles without conferring external morphological damage. *PLoS ONE* 2 (3): e272. doi:10.1371/journal.pone.0000272.

Gilbert, M. T. P., Bandelt, H.-J., Hofreiter, M., and Barnes, I. (2005). Assessing ancient DNA studies. *Trends in Ecology and Evolution* 20, 541-544.

Girling, M. A. (1980). The fossil insect assemblage from the Baker Site. *Somerset Levels Papers* 6, 36-42.

Girling, M. A. (1983). The environmental implications of the excavations of 1974-76. In A. E. Brown, C. Woodfield and D. C. Mynard (eds.), Excavations at Towcester, Northamptonshire: The Alchester Road suburb. *Northamptonshire Archaeology* 18, 128-130.

Gleixner, G., Danier, H. J., Werner, R. A., and Schmidt, H. L. (1993). Correlations between the carbon-13 content of primary and secondary plant products in different cell compartments and that in decomposing Basidiomycetes. *Plant Physiology* 102, 1287–1290.

Gobin, B., Peeters, C., Billen, J., and Morgan, E. D. (1998). Interspecific trail following and commensalism between the Ponerine ant *Gnamptogenys menadensis* and the Formicine ant *Polyrhachis rufipes*. *Journal of Insect Behavior* 11 (3), 361-369.

Golenberg, E. M. (1991). Amplification and analysis of Miocene plant fossil DNA. Philosophical Transactions of Royal Society London B 333, 419-426.

Golenberg, E. M., Giannasi, D. E., Clegg, M. T., Smiley, C. J., Durbin, M., Henderson, D., and Zurawski, G. (1990). Chloroplast DNA sequence from a Miocene magnolia species. *Nature* 344, 656-658.

Google Inc. (2009). *Google Earth* [online]. Page Consulted on 21st July 2009. http://earth.google.com/

Graham, N. P. H. and Taylor, K. L. (1941). Studies on the ectoparasites of sheep and their control. I. Observations on the bionomics of the sheep ked *Melophagus ovinus*. *Australian Council for Scientific and Industrial Research Pamphlet* 108, 9–26.

Grafenstein, U. von, Erlenkeuser, H., Muller, J., Jouzel, J., and Johnsen, S. (1998). The cold event 8200 years ago documented in oxygen isotope records of precipitation in Europe and Greenland. *Climate Dynamics* 14, 73–81.

Gray, M. W., Burger, G., and Lang, B. F. (1999). Mitochondrial evolution. *Science* 283, 1476-1481.

GRIN (2009). USDA, ARS, National Genetic Resources Program. *Germplasm Resources Information Network - (GRIN)* [Online Database]. National Germplasm Resources Laboratory, Beltsville, Maryland. Page consulted 10th September 2009. http://www.ars-grin.gov/cgi-bin/npgs/html/taxon.pl?17337

Grist, E. P. M. and Gurney, W. S. C. (1997). Seasonal synchronicity and stage-specific life cycles: Topp's beetles revisited. *Mathematical Biosciences* 145 (1), 1-25.

Gröcke, D. R., Schimmelmann, A., Elias, S., and Miller, R. F. (2006). Stable hydrogen-isotope ratios in beetle chitin: Preliminary European data and re-interpretation of North American data. *Quaternary Science Reviews* 25, 1850-1864.

Grootes, P. M., Steig, E. J., Stuiver, M., Waddington, E. D., Morse, D. L., and Nadeau, M. J. (2002). The Taylor Dome Antarctic d18O record and globally synchronous changes in climate. *Quaternary Research* 56, 289–298.

Gu, B., Schelske, C. L., and Hoyer, M. V. (1996). Stable isotopes of carbon and nitrogen as indicators of diet and trophic structure of the fish community in a shallow hypereutrophic lake. *Journal of Fish Biology* 49, 1233–1243.

Gullan, P. J. and Cranston, P. S. (2000). *The insects: An outline of entomology*. Malden: Blackwell Sciences Inc.

Hadley, N. F. (1986). The arthropod cuticle. *Scientific American* 255, 98-106.

Hagen, K. S., Dadd, R. H., and Reese, J. (1984). The food of insects. In C. B. Huffaker and R. L. Rabb (eds.), *Ecological entomology*. New York: John Wiley and Sons, 79-112.

Haggis, M. J. (1996). Forecasting the severity of seasonal outbreaks of African armyworm, *Spodoptera exempta* (Lepidoptera: Noctuidae) in Keyna from the previous year's rainfall. *Bulletin of Entomological Research* 86 (2), 129-136.

Hakbijl, T. (1988). Insektenresten. In W. Groenmann-van Waateringe and B. L. van Beek (eds.), De Romeinse castellan te Valkenburg ZH. *Studies in Prae- und Protohistorie* 2, 106-107.

Hakbijl, T. (1989). Insect remains from site Q, an early Iron Age farmstead of the Assendelver Polders Project. *Helenium* 24, 77-102.

Hall, A. and Kenward, H. (1998). Disentangling dung: Pathways to stable manure. *Environmental Archaeology* 1, 123-126.

Hall, A. and Kenward, H. (1999a). Plant and invertebrate remains from Anglo-Scandinavian deposits at 16-22 Coppergate, York: Technical report. Part 1: Period 3. *Reports from the Environmental Archaeology Unit, York* 99/30.

Hall, A. and Kenward, H. (1999b). Plant and invertebrate remains from Anglo-Scandinavian deposits at 16-22 Coppergate, York: Technical report. Part 2: Periods 4a and 4b. *Reports from the Environmental Archaeology Unit, York* 99/38.

Hall, A. and Kenward, H. (1999c). Plant and invertebrate remains from Anglo-Scandinavian deposits at 16-22 Coppergate, York: Technical report. Part 4: Period 5b. *Reports from the Environmental Archaeology Unit, York* 99/49.

Hall, A. and Kenward, H. K (1990). Environmental evidence from the Colonia. In P.V. Addyman (ed.), *The past environment of York. Archaeology of York* 14/6. London: Council for British Archaeology.

Hall, A., Kenward, K., Girvan, L. and McKenna, R. (2007). Investigations of plant and invertebrate macrofossil remains from excavations in 2004 at 62-8 Low Petergate, York. *Reports from the Centre for Human Palaeoecology, University of York.*

Hall, A. Rowland, S., Kenward, H., Jaques, D., and Carrott, J. (2000). Evaluation of biological remains from excavations of land to rear of 7-15 Spurriergate, York (site code: 2000.584). *Reports from the Environmental Archaeology Unit, York* 2000/80.

Hall, A. R. and Kenward, H. K. (1980). An interpretation of biological remains from Highgate, Beverley. *Journal of Archaeological Science* 7, 33-51.

Hall, A. R. and Kenward, H. K. (2003). Can we identify biological indicator groups for craft, industry and other activities?. In P. Murphy and P. E. J. Wiltshire (eds.), *The environmental archaeology of industry. Symposia of the Association for Environmental Archaeology* 20. Oxford: Oxbow, 114-130.

Hall, A. R., Kenward, H. K., and Williams, D. (1980). Environmental evidence from Roman deposits in Skeldergate. In P. V. Addyman (ed.), *The past environments of York*. *The Archaeology of York* 14/3. London: Council for British Archaeology.

Hall, A. R., Kenward, H. K., Williams, D., and Greig, J. R. A. (1983). Environment and living conditions at two Anglo-Scandinavian sites. *Archaeology of York* 14/4. Council for British Archaeology for York Archaeological Trust.

Hall, R. (1984). *The excavations of York: The Viking dig*. London: The Bodley Head.

Hammond, P. M. (1971). Notes on the British Staphylinidae 2 - On the British species of *Platystethus* Mannerheim, with one species new to Britain. *Entomologist's monthly Magazine* 107, 93-111.

Hammond, P. M. (1974). Changes in the British coleopterous fauna. In D. L. Hawksworth (ed.), *The changing flora and fauna of Britain. Systematics Association Special* 6. London: Academic Press, 329-369.

Handt, O., Höss, M., Krings, M., and Pääbo, S. (1994). Ancient DNA: Methodological challenges. *Experientia* 50, 524-529.

Hansen, M. (1987). The Hydrophiloidea (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* 18. Leiden: Scandinavian Science Press.

Hanski, I. (1991). North temperate dung beetles. In I. Hanski and Y. Cambefort (eds.), *Dung beetle ecology*, Princeton, NJ: Princeton University Press, 75-96.

Hantman, J. L. and Plog, S. (1982). The relationship of stylistic similarities to patterns of material exchange. In J. E. Ericson and T. K. Earle (eds.), *Contexts for prehistoric exchange*. New York and London Academic Press, 237-263.

Harde, K. W. (1984). *A field guide in colour to beetles*. London: Octopus.

Hardenbroek, M. R. van (2006). Stable isotope ratios in water beetle chitin: Towards a new palaeotemperature proxy. Unpublished MSc dissertation, Royal Holloway, University of London.

Hardenbroek, M. R. van, Gröcke, D. R., Elias, S. A. (2007). Stable hydrogen and oxygen isotope ratios in water beetle chitin. *Geophysical Research Abstracts* 9.

Härke, H. (1998). Archaeologists and migrations: A problem of attitude?. *Current Anthropology* 39 (1), 19-45.

Harpaz, I. (1973). Early entomology in the Middle East. *Annual Review of Entomology* 18, 21-36.

Hayes, J. M. (2001). Fractionation of carbon and hydrogen isotopes in biosynthetic processes. *Reviews in Mineralogy and Geochemistry* 43, 225–277.

Hebert, C. E. and Wassennar, L. I. (2001). Stable nitrogen isotopes in waterfowl feathers reflect agricultural land use in western Canada. *Environmental Science and Technology* 35 (17), 3482-3487.

Hebert, C. E., Weseloh, D. V. C., Idrissi, A., Arts, M. T., and Roseman, E. (2009). Diets of aquatic birds reflect changes in Lake Huron ecosystem. *Aquatic Ecosystem Health and Management* 12 (1), 37-44.

Helbaek, H. (1970). The plant husbandry of Haçilar. In J. Melaart (ed.), *Excavations at Haçilar* 1. Edinburgh University Press, 189-244.

Hellqvist, M. (1999). *Urban and rural environments from Iron Age to medieval time in Northern Europe. Evidence from insect remains from South Eastern Sweden and Novgorod, Russia*. Unpublished PhD. dissertation, Universitatis Uppsaliensis.

Henn, M. R. and Chapela, I. H. (2001). Ecophysiology of ^{13}C and ^{15}N isotopic fractionation in forest fungi and the roots of the saprothic-mycorrhizal divide. *Oecologia* 128, 480-487.

Henriksen, K. (1937). *Mallophaga and Anoplura. Zoology of the Faroes*. In S. Jensen, W. Lundbeck, T. Mortensen, and R. Spärck (eds.). Copenhagen: A. F. Høst and Son.

Hesslein, R. H., Capet, M. J., Fox, D. E. and Hallard, K. A. (1991). Stable isotopes of sulphur, carbon, and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie River Basin, Canada. *Canadian Journal of Fisheries and Aquatic Science* 48, 2258–2265.

Hewitt, C. G. (1914). *The house-fly, its structure, habits, development, relation to disease control*. Cambridge University Press

Hewitt, G. M. (1999). Post-glacial colonisation of European biota. *Biological Journal of the Linnean Society* 68, 87-112.

Hewitt, G. M. (2000). The genetic legacy of the Quaternary ice ages. *Nature* 405, 907-913.

Hewitt, G. M. (2004). Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society of London* B 359, 183-195.

HH: Herodotus' History: Below, W. (trans.) (1791). *The history of Herodotus, translated from the Greek.* Vol. 1. London. Based on information from *English Short Title Catalogue*. *Eighteenth Century Collections Online*. Gale Group. http://galenet.galegroup.com/servlet/ECCO

Hickin, N. E. (1968). *The insect factor in wood decay*. London: Hutchinson.

Hidayat, P., Phillips, T. W., and Ffrench-Constant, R. H. (1996). Molecular and morphological characters discriminate *Sitophilus oryzae* and *S. zeamais* and confirm their reproductive isolation. *Annals of the Entomological Society of America* 89, 645-652.

Higuchi, R., Bowman, B., Freiberger, M., Ryder, O. A., and Wilson, A.C. (1984). DNA sequences from the quagga, and extinct member of the horse family. *Nature* 312, 282-284.

Hilderbrand, G. V., Farley, S. D., Robbins, C. T., Hanley, T. A., Titus, K., and Servheen, C. (1996). Use of stable isotopes to determine diets of living and extinct bears. *Canadian Journal of Zoology* 74, 2080–2088.

Hill, D. S. (1994a). *Agricultural Entomology*. Oregon: Timber Press.

Hill, M. (1994b). Insect assemblages as evidence for past woodlands around York. In A. R. Hall and H. K. Kenward (eds.), *Urban-rural connexions: Perspectives from Environmental Archaeology, Symposia of the Association for Environmental Archaeology* 12. Oxford: Oxbow Books, 45-54.

Hill, M. J. (1993). Insect death assemblages and the interpretation of woodland history: Evidence from the Vale of York. Unpublished PhD thesis, University of York.

Hinton, H. E. (1945). *A monograph of the beetles associated with stored products* I. London: British Museum of Natural History.

Hinton, H. E. (1948). A synopsis of the genus *Tribolium* Mac Leay with some remarks on the evolution of the species-groups (Coleoptera, Tenebrionidae). *Bulletin of Entomological Research* 39, 13-55.

Hobbie, E. A., Macko, S. A., and Shugart, H. H. (1999). Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprotrophic fungi from isotopic evidence. *Oecologia* 118, 353–360.

Hobbie, E. A., Watrud, L. S., Maggard, S., Shiroyama, S., and Rygiewicz, P. T. (2003). Carbohydrate use and assimilation by litter and soil fungi assessed through stable isotopes and BIOLOG® assays. *Soil Biology and Biochemistry* 35, 303–311.

Hobson, K. A. (1990). Stable isotope analysis of marbled murrelets: Evidence for freshwater feeding and determination of trophic level. *Condor* 92, 897–903.

Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120, 314–326.

Hobson, K. A. and Wassenaar, L. I. (1997). Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia* 109, 142–148.

Hobson, K. A., Hughes, K. D., and Ewins, P. J. (1997). Using stable-isotope analysis to identify endogenous and exogenous sources of nutrients in eggs of migratory birds: Applications to Great Lakes contaminants research. Auk 114, 467-478.

Hobson, K. A., Schell, D. M., Renouf, D., and Noseworthy, E. (1996). Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive seals: Implications for dietary reconstructions involving marine mammals. *Canadian Journal of Fisheries and Aquatic Sciences* 53, 528–533.

Hobson, K. A., Wassenaar, L. I., and Taylor, O. R. (1999). Stable isotopes (δD and $\delta^{13}C$) are geographic indicators of natal origins of monarch butterflies in eastern North America. *Oecologia* 120, 397-404.

Hodder, I. (1982). Towards a contextual approach to prehistoric exchange. In J. E. Ericson and T. K. Earle (eds.), *Contexts for prehistoric exchange*. New York and London Academic Press, 199-211.

Hodges, R. (1982). *Dark Age economics: The origins of towns and trade AD 600-1000.* London: Academic Press.

Hoffman, A. (1954). Coléoptères Curculionides. *Faune de France* 59, Paris: Lechevalier.

Hoffmann, A. (1958). Coléoptères Curculionides 3. *Faune de France* 62. Paris.

Hoffman, A. (1986). Coléoptères Curculionides (Deuxième partie). *Faune de France* 59. Paris: Fédération Française des Sociétés de Sciences Naturelles.

Högberg, P., Plambœck, A. H., Taylor, A. F. S., and Fransson, P. M. A. (1999). Natural ^{13}C abundance reveals trophic status of fungi and host-origin of carbon in mycorrhizal fungi in mixed forests. *Proceedings of the National Academy of Sciences, USA* 96, 8534–8539.

Hogsette, J. A. (1996). Development of house flies (Diptera: Muscidae) in sand containing various amounts of manure solids and moisture. *Journal of Economic Entomology* 89, 940-945.

Hopf, M. and Zachariae, G. (1921). Determination of botanical and zoological remains from Ramat Matred and Arad. *Israel Exploration Journal*, 63-64.

Hopkins, T. L., and Kramer, K. J. (1992). Insect cuticle sclerotization. *Annual Review of Entomology* 37, 273-302.

Holdridge, L. R., Grenke, W. C., Hatheway, W. H., Liang, T., and Tosi Jr, J. A. (1971). *Forest environments in tropical life zones: A pilot study*. Oxford: Pergamon.

Horion, A. (1956). Faunistik der mitteleuropäischen Käfer, Band 5. *Heteromera*. Munich.

Horion, A. (1960). Faunistik der mitteleuropäischen Käfer, Band 7. *Clavicornia* 1, *Teil,* (*Sphaeritidae–Phalacridae)*. Überlingen-Bodensee.

Horion, A. (1961). Faunistik der mitteleuropäischen Käfer, Band 8. *Clavicornia* 2. Überlingen-Bodensee.

Horvitz, C., Pascarella, J., McMann, S., Freedman, A., and Hofsetter, R. H. (1998). Functional roles of invasive non-indigenous plants in hurricane-affected subtropical hardwood. *Ecological Applications* 8, 947-974.

Höss, M. and Pääbo, S. (1993). DNA extraction from Pleistocene bones by a silica-based purification method. *Nucleic Acids Research* 21, 3913-3914.

Howard, A. J., Smith, D. N., Garton, D., Hillam, J. and Pearce, M. (1999). Middle to Late Holocene environments in the Middle to Lower Trent valley. In A. G. Brown and T. A. Quine (eds.), *Fluvial processes and environmental change*. Chichester: J. Wiley and Sons, 165-178.

Howe, R. W. (1965). *Sitophilus granarius* (L.) (Coleoptera, Curculionidae) breeding in acorns. *Journal of Stored Product Research* 1, 99-100.

Howe, R. W. and Lefkovitch, L. P. (1957). The distribution of storage species of *Cryptolestes*. *Bulletin of Entomological Research* 48, 795-809.

Hoy, M. A. (2003). *Insect molecular genetics: An introduction to principles and applications*, second edition. San Diego: Academic Press.

Hubbard, R. N. L. (1979). Appendix 2: Ancient Agriculture and Ecology at Servia. In, Rescue Excavations at Servia 1971-1973: A Preliminary Report. *Annual of the British School of Archaeology at Athens* 74, 226-228.

Huey, R. B., Gilchrist, G. W., Carlson, M. L., Berrigan, D. and Serra, L. (2000). Rapid evolution of a geographic cline in size in an introduced fly. *Science* 287, 308-309.

Huffaker, C. B., Gordon, H. T., and Rabb, R. L. (1984). Meaning of ecological entomology—the ecosystem. In C. B. Huffaker and R. L. Rabb (eds.), *Ecological entomology*. New York: John Wiley and Sons, 3-18.

Hunter, F. A., Tulloch, J. B. M., and Lambourne, M. G. (1973). Insects and mites of maltings in the East Midlands of England. *Journal of Stored Products Research* 9, 119-141.

Hyman, P. S. (1992). *A review of the scarce and threatened Coleoptera of Great Britain*, Part 1. Peterborough: UK Joint Nature Conservation Committee.

Hyman, P. S. (1994). *A review of the scarce and threatened Coleoptera of Great Britain*, Part 2. Peterborough: UK Joint Nature Conservation Committee.

IAEA (2000). The global water cycle. What can isotopes tell us?. *GNIP Booklet*. Page consulted on July 28th 2009. http://www-naweb.iaea.org/napc/ih/GNIP/userupdate/description/Precip0.html

Iregren, E. (1988). Finds of brown bear (*Ursus arctos*) in Southern Scandinavia—indicators of local hunting or trade?. In B. Hårdh, L. Larsson, D. Olausson, and R. Petré (eds.), *Trade and exchange in prehistory: Studies in honour of Berta Stjernquist*. Lund: Lunds Univeritats Historika Museum, 294-308.

Jacob, T. A. (1988). The effect of temperature and humidity on the developmental period and mortality of *Typhaea stercorea* (L.) (Coleoptera: Mycetophagidae). *Journal of Stored Product Research* 24 (4), 221-224.

Jaques, D., Hall, A., Kenward, H., Rowland, S., and Carrott, J. (2001). Assessments of biological remains from excavations at 41-9 Walmgate, York. *Reports from the Environmental Archaeological Unit, York 2001/26*.

Jenkins, E. L. (2003). *Environmental reconstruction, the use of space, and the effect of sedentism on microfaunal communities: Case studies from Pinarbaşi and Çatalhöyük*. Unpublished PhD thesis, Cambridge University.

Jessop. L. (1986). Dung beetles and chafers (Coleoptera: Scarabaeodea). *Handbook for the identification of British insects* 5 (11). The Royal Entomological Society of London.

Jones, F. G. W. and Jones, M. G. (1974). *Pests of field crops* (2nd ed.). London: Arnold.

Jones, G. (1984). The LM 11 Plant Remains. In M. R. Popham, *The Minoan Unexplored Mansion at Knossos*, 303-306. British School at Athens, London: Thames and Hudson.

Jones, S. (1997). *The archaeology of ethnicity*, London: Routledge.

Jones, V., Collins, M. J., Penkman, K. E. H., Jaffé, R., and Wolff, G. A. (2005). An assessment of the microbial contribution to aquatic dissolved organic nitrogen using amino acid enantiomeric ratios. *Organic Geochemistry* 36, 1099-1107.

Joy, N. H. (1932). *A practical handbook of British beetles*. London.

Joy, N. H. (1976). *A practical handbook of British beetles*. Volume 1 Faringdon: E W Classey Ltd.

Juan, C., Ibrahim, K. M., Oromi, P., Hewitt, G. M. (1998). The phylogeography of the darkling beetle, *Hegeter politis*, in the Eastern Canary Islands. *Proceedings of the Royal Society London* B 265 (1391), 135-140.

Junquiera, A. C., Lessinger, A. C. and Azeredo-Espin, A. M. (2002). Methods for the recovery of mitochondrial DNA sequences from museum specimens of myiasis causing flies. *Medical and Veterinary Entomology* 16, 39-45.

Katzenberg, M. A. and Pfeiffer, S. (2000). Stable isotope analysis: A tool for studying past diet, demography and life history. In M. A. Katzenberg, S. R. Saunders (eds.), *Biological Anthropology of the Human Skeleton*. New York: Wiley-Liss, 305–328.

Kelly, J. F. (2000). Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology − Revue Canadienne de Zoologie* 78, 1–27.

Kenward, H. and Carrott, J. (2006). Insect species associations characterise past occupation sites. *Journal of Archaeological Science* 33, 1452-1473.

Kenward, H. and Hall, A. (2000). Technical report: Plant and invertebrate remains from Anglo-Scandinavian deposits at the Queen's Hotel site, 1-9 Micklegate, York (site code 88-9.17). *Reports from the Environmental Archaeology Unit, York* 2000/14.

Kenward, H. and Tipper, J. (2008). Insect invaders of reconstructed Anglo-Saxon houses at West Stow, Suffolk, England. *Environmental Archaeology* 13(1), 51-57.

Kenward, H., Hall, A., Allison, E. P. and Carrott, J. (2000). Environment, activity and living conditions at Deer Park Farms: evidence from plant and invertebrate remains. *Reports from the Environmental Archaeology Unit, York* 2000/57.

Kenward, H. K. (1974). Methods for palaeo-entomology on site and in the laboratory. *Science and Archaeology* 15, 16-24.

Kenward, H. K. (1975a). Pitfalls in the environmental interpretations of death assemblages. *Journal of Archaeological Science* 2, 63-69.

Kenward, H. K. (1975b). The biological and archaeological implications of the beetle *Aglenus brunneus* (Gyllenhall) in ancient faunas. *Journal of Archaeological Science* 2, 63-69.

Kenward, H. K. (1976). Reconstructing ancient ecological conditions from insect remains: some problems and an experimental approach. *Ecological Entomology* 1, 7-17.

Kenward, H. K. (1978a). The analysis of archaeological insect assemblages: A new approach. *Archaeology of York* 19 (1). Council for British Archaeology for York Archaeological Trust.

Kenward, H. K. (1978b). The value of insect remains as evidence of ecological conditions on archaeological sites. In D. R. Brothwell, K. D. Thomas and J. Clutton-Brock (eds.), *Research problems in zooarchaeology*. Institute of Archaeology, University of London: Occasional Publication 3, 25-38.

Kenward, H. K. (1979). Five insect assemblages. In M. O. H. Carver, Three Saxo-Norman tenements in Durham City. *Medieval Archaeology* 23, 60- 67.

Kenward, H. K. (1985). Outdoors-Indoors? The outdoor component of archaeological insect assemblages. In N. R. J. Fieller, D. D. Gilbertson and N. G. A. Ralph (eds), Palaeoenvironmental investigations: Research design, methods and data analysis. *British Archaeological Reports* S266, 97-104. Oxford.

Kenward, H. K. (1988). Insect remains. In K. Griffin, R. H. Okland, A. K. G. Jones, H. K. Kenward, R. W. Lie, and E. Schia, Animal bones, moss, plant, insect and parasite remains. In E. Schia (ed.), *De arkeologiske utgravninger i Gamlebyen, Oslo* 5. Øvre Ervik: Alveheim and Eide, 115-140.

Kenward, H. K. (1992). Rapid recording of archaeological insect remains—a reconsideration. *Circaea, the Journal of the Association for Environmental Archaeology* 9, 81-8.

Kenward, H. K. (1997). Synanthropic decomposer insects and the size, remoteness and longevity of archaeological occupation sites: Applying concepts from biogeography to past 'islands' of human occupation. *Quaternary Proceedings* 5, 135-151.

Kenward, H. K. (1999). Insects as indicators of zonation of land-use and activity in Roman Carlisle, England. *Reports from the Environmental Archaeology Unit*, York, 99/43. York.

Kenward, H. K. (in press). *Invertebrates in archaeology in the north of England*. York: English Heritage. English Heritage e-publication.

Kenward, H. K. and Allison, E. (1994a). A preliminary view of the insect assemblages from the early Christian rath site at Deer Park Farms, Northern Ireland. In J. Rackham (ed.), Environment and economy in Anglo-Saxon England. *Council for British Archaeology Research Report* 89. London, 89-107.

Kenward, H. K. and Allison, E. (1994b). Rural origins of the urban insect fauna. In A. R. Hall and H. K. Kenward (eds.), *Urban-rural connexions: Perspectives from Environmental Archaeology, Symposia of the Association for Environmental Archaeology* 12. Oxford: Oxbow Books, 55-78.

Kenward, H. K. and Allison, E. (1995). Insect remains from the Roman fort at Papcastle, Cumbria. *Reports of the Environmental Archaeology Unit, York* 95/1.

Kenward, H. K. and Hall, A. R. (1995). Biological evidence from Anglo-Scandinavian Deposits at 16-22 Coppergate. In P.V. Addyman (ed.), *The archaeology of York: The past environment of York* 14 (3). London: Council for British Archaeology, 435-797.

Kenward, H. K. and Hall, A. R. (1997). Enhancing bio-archaeological interpretation using indicator groups: Stable manure as a paradigm. *Journal of Archaeological Science* 24, 663-673.

Kenward, H. K., Allison, E. P., Dainton, M. Kemenés, I. K. and Carrott, J. B. (2000). The insect and parasite remains. In M. R. McCarthy (ed.), *Roman and medieval Carlisle: The southern Lanes*. Department of Archaeological Sciences, University of Bradford, Research Report 1. Carlisle: Carlisle Archaeology Limited, 145-147.

Kenward, H. K., Engleman, C., Robertson, A., and Large, F. (1985). Rapid scanning of urban archaeological deposits for insect remains. *Circea* 3 (3), 163-173.

Kenward, H. K., Hall, A. R., and Jones, A. K. G. (1980). A tested set of techniques for extraction of plant and animal macrofossils from waterlogged archaeological deposits. *Science and Archaeology 22*, 3-15.

Kenward, H. K., Hall, A. R., and Jones, A. K. G. (1986). Environmental evidence from a Roman well and Anglian pits in the legionary fortress. In P. V. Addyman (ed.), *The past environment of York*. *The Archaeology of York* 14/5. London: Council for British Archaeology.

Kielty, J. P., Allen-Williams, L. J., and Underwood, N. (1999). Prey preferences of six species of Carabidae (Coleoptera) and one Lycosidae (Araneae) commonly found in UK arable crops. *Journal of Applied Entomology* 123, 193-200.

Kieser, D. (2005). *Minoan trade: Aspects and ambiguities*. Unpublished MA dissertation, University of South Africa.

King, G. A. (2006). *Infestations and pest control in Viking Age settlements*. Unpublished MA dissertation, University of York.

King, G. A. (2008). Establishing a foothold or six: Insect tales of trade and migrations. *Proceedings of Graduate Archaeology Organisation International Conference. Challenging Frontiers: Mobility, Transition and Change*. Oxford. 4th-5th April.

King, G. A. and Hall, A. (2008). Evaluation of biological remains from a Roman timber drain at 21 St Peters Street, Colchester (site code: 2007.124). *Reports from the Centre for Human Palaeoecology, University of York* 2008/15.

King, G. A., Bain, A., and Dussault, F. (2010). *Assessment of insect remains from a colonial well (JR2158; Structure 177) at James Fort, Jamestown, Virginia. Technical Report.* Laboratoire d'Archéologie Environnementale, CELAT, Université Laval, Québec.

King, G. A., Gilbert, M. T. P., Wilerslev, E., Collins, M. J., and Kenward, H. (2009). Recovery of DNA from archaeological insect remains: First results, problems and potential. *Journal of Archaeological Science* 36, 1179-1183

Kislev, M. E. (1991). Archaeobotany and storage entomology. In J. M. Renfrew (ed.), *New light on early farming. Recent developments in palaeoethnobotany*. Edinburgh: Edinburgh University Press, 121-136.

Kislev, M. E., Hartmann, A., Galili, E. (2004). Archaeobotanical and archaeoentomological evidence from a well at Atlit-Yam indicates colder, more humid climate on the Israeli coast during the PPNC period. *Journal of Archaeological Science* 31, 1301-1310.

Kislev, M. E. and Melamed, Y. (2000). Ancient infested wheat and horsebean from Horbat Rosh Zayit. In Z. Gal and Y. Alexandre (eds.), *Horbat Rosh Zayit, An Iron Age storage fort and village*. Jerusalem: Israel Antiquities Authority, 206-220.

Kitchen, K. A. (1991). The chronology of Ancient Egypt. *World Archaeology* 23 (2), 201-208.

Klitgaard-Kristensen, D., Sejrup, H.P., Haflidason, H., Johnsen, S., and Spurk, M. (1998). A regional 8200 cal yr BP cooling event in northwest Europe, induced by final stages of the Laurentide ice-sheet deglaciation? *Journal of Quaternary Science* 13 (2), 165–169.

Kloet, G. S. and Hincks, W. D. (1964-78). *A check list of British Insects*. London: Royal Entomological Society.

Knopf, A. A. (1980). *National Audubon Society: Field guide to insects and spiders*. New York: Chanticleer Press Inc.

Knörzer, K-H. (1970). Römerzeitliche Pflanzenfunde aus Neuss. Novaesium IV. *Limesforschungen* 10. Berlin: Mann.

Knutson, A., Boring III, E. P., Michaels Jr, G. J., and Gilstrap, F. (1993). Biological control of insect pests in wheat. *Texas Agricultural Extension Service* B-5044, 8.

Koch, K. (1971). Zur Untersuchung subfossiler Käferreste aus römerzeitlichen und mittelalterlichen Ausgrabungen im Rheinland. *Rheinische Ausgrabungen* 10, 378-448.

Koch, K. (1989a). Die Käfer Mitteleuropas. *Ökologie* 1. Krefeld: Goecke and Evers.

Koch, K. (1989b). Die Käfer Mitteleuropas, *Ökologie* 2. Krefeld: Goecke and Evers.

Koch, K. (1992). Die Käfer Mitteleuropas. *Ökologie* 3. Krefield: Goecke and Evers.

Kohzu, A., Yoshioka, T., Ando, T., Takahashi, M., Koba, K. and Wada, E. (1999). Natural ^{13}C and ^{15}N abundance of field-collected fungi and their ecological implications. *New Phytologist* 144, 323–330.

Körner, Ch. and Diemer, M. (1987). *In situ* photosynthetic responses to light, temperature and carbon dioxide in herbaceous plants from low and high altitude. *Functional Ecology* 1, 179-194.

Körner, Ch, Farquhar, G. D., and Roksandic, Z. (1988). A global survey of carbon isotope discrimination in plants from high altitude. *Oecologia* 74, 623-632.

Körner, Ch, Farquhar, G. D., and Wong, S. C. (1991). Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. *Oecologia* 88, 30-40.

Kotsakis K., Papanthimou-Papaefthymiou A., Pilali-Papasteriou A., Savopoulou T., Maniatis Y and Kromer B. (1989). Carbon 14 dates from Mandalo, W. Macedonia. In Y. Maniatis (ed.), *Proceedings of the 25th International Symposium on Archaeometry, 1986*. Amsterdam: Elsevier, 679-685.

Kranz, J., Schmutterer, H., and Koch, W. (1978). Diseases, pests, and weeds in tropical crops. Chichester: Wiley.

Krebs, C. J. (1972). *Ecology: The experimental analysis of distribution and abundance.* New York: Harper and Row.

Kuhne, R. (1995). Data on the biology of selected *Geotrupes* species - *G spiniger* Marsham, *G vernalis* Linne and *G stercorosus* Scriba (Coleoptera, Scarabaeidae, Geotrupini). *Deutsche Entomologische Zeitschrift* 42, 343-367.

Kuijper, W. J. and Turner, H. (1992). Diet of a Roman centurian at Alphen aan den Rijn, The Netherlands, in the first century AD. *Review of Palaeobotany and Palynology* 73, 187-204

Kuijt, I. and Finlayson, B. (2009). Evidence for food storage and predomestication granaries 11,000 years ago in the Jordan Valley. *Proceedings of the National Academy of Science of the United States of America* 106(27), 10966-10970

Landin, B. O. (1961). Ecological studies on dung-beetles. *Opuscula Entomologica*, Suppl. 19.

Landsberger, B. (1934). Die fauna des alten Mezopotamien nach der 14 Tafel der Serie Har-ra = Hubulu. Leipzig: Hizel.

Lang, B. F., Gray, M. W., and Burger, G. (1999). Mitochondrial genome evolution and the origin of the Eukaryotes. *Annual Review of Genetics 33*, 351-397.

Large, F., Kenward, H., Carrott, J., Nicholson, C. and Kent, P. (1994). Insect and other invertebrate remains from the Roman fort at Ribchester, Lancashire (site code RB89): Technical report. *Reports from the Environmental Archaeology Unit, York* 94/11.

Larsson, S. J. and Gígja, G. (1959). Coleoptera. *Zoology of Iceland* 43. Munksgaard, Copenhagen.

Leclercq, J. (1946). Insects brought with the hay from the meadows into the hayloft. *Entomologist's monthly Magazine* 82, 138.

Lee, M-Y. and Hall, H. G. (1996). Identification of mitochondrial DNA of *Apis mellifera* (Hymenoptera: Apidae) subspecies groups by multiplex allele-specific amplification with competing fluorescent-labeled primers. *Annals of the Entomological Society of America* 89, 20-27.

Leimar, O. (1996). Life history plasticity: Influence of photoperiod on growth and development in the common butterfly. *Oikos* 76 (2), 228-234.

Leo, N. P., Campbell, H. J. H., Yang, X., Mumcuoglu, K. and Barker, S. C. (2002). Evidence from mitochondrial DNA that head lice and body lice of humans (Phthiraptera: Pediculidae) are conspecific. *Journal of Medical Entomology* 39, 662-666.

LeSage, L. (1990). *Chaetocnema concinna* (Marsham 1802), a European flea beetle introduced in North America. *Canadian Entomologist* 122, 647-650.

Levinson, H. and Levinson, A. (1998). Control of stored food pests in the ancient orient and classical antiquity. *Journal of Applied Entomology* 122, 137-144.

Li, Y., An, C-C., and Zhu, Y-X. (1995). DNA isolation and sequence analysis of dinosaur DNA from Cretaceous dinosaur egg in Xixia Henan, China. *Acta Scientiarum Naturalium Universitatis Penkinensis* 31, 148-152.

Lindahl, T. (1993a). Instability and decay of the primary structure of DNA. *Nature* 362, 709-715.

Lindahl, T. (1993b). Recovery of antediluvian DNA. *Nature* 365, 700.

Lindstrom, T. C. and Kristofferson, S. (2001). Figure it out! Psychological perspectives on perception of Migration Period animal art. *Norwegian Archaeological Review* 34 (2), 65-84.

Lindroth, C. H. (1957). *Faunal connections between Europe and North America*. New York: Wiley and Sons.

Lindroth, C. H. (1974). *Coleoptera: Carabidae. Handbooks for the identification of British insects* IV, 2. Royal Entomological Society of London.

Lindroth, C. H. (1985). The Carabidae (Coleoptera) of Fennoscandia and Denmark, *Fauna Entomologica Scandinavica* 15.

Lindroth, C. H., Andersson, H., Bodvarsson, H., and Richter, S. H. (1973). Surtsey, Iceland. The development of a new fauna, 1963-1970. *Terrestrial Invertebrates*. *Entomologica Scandinavia*, Suppl.5.

Locke, M. (2001). The Wigglesworth lecture: Insects for studying fundamental problems in biology. *Journal of Insect Physiology* 47, 495-507.

Luff, M. L. (1998). *Provisional atlas of the ground beetles (Coleoptera, Carabidae) of Britain*. Abbots Ripton: Centre for Ecology and Hydrology, Biological Records Centre.

Lysyk, T. J. (1991). Effects of temperature, food, and sucrose feeding on longevity of the house fly (Diptera: Muscidae). *Environmental Entomology* 20, 1176-1180.

Lynsk, T. J. (1993). Adult resting and larval development sites of stable flies and house flies (Diptera: Muscidae) on dairies in Alberta. *Journal of Economic Entomology* 86, 1746-1753.

Magny, M., Begeot, C., Guiot, J., and Peyron, O. (2003). Contrasting patterns of hydrological changes in Europe in response to Holocene climate cooling phases. *Quaternary Science Reviews* 22, 1589–1596.

Manetho (1940). Manetho with English translations. G. W. Waddell (ed.) Loeb Classic Library 350. London and Cambridge: William Heinemann Ltd. and Harvard University Press.

Marinval, P. (1992). Approche carpologique de la néolithisation du sud de la France. In P. C. Anderson (ed.), *Préhistoire de l'Agriculture*. París: Éditions du C.N.R.S., 255–263.

Markoe, G. E. (2000). *Peoples of the past. Phoenicians*. Los Angeles: University of California Press.

Mason, D. J. P. (2003). *Roman Britain and the Roman navy*. Stroud: Tempus

Matisoo-Smith, E. and Allen, J. S. (1997). Ancient DNA from Polynesian rats: Extraction, amplification, sequence from single small bones. *Electrophoresis* 18, 1534-1537.

Matisoo-Smith, E. and Allen, J. S. (2001). Name that rat: Molecular and morphological identification of Pacific rodent remains. *International Journal of Osteoarchaeology* 11, 34-42.

Matisoo-Smith, E. and Robins, J. H. (2004). Origins and dispersal of Pacific peoples: Evidence from mtDNA phylogenies of the Pacific rat. *Proceedings of the National Academy of Sciences* 101 (24), 9167-9172.

Matterne, V., Yvinec, J-H., and Gemehl, D. (1998). Stockage des plantes alimentaires et infestation par les insects dans un grenier incendié de la fin de Iie siècle après J-C à Amiens (Somme). *Revue archéologique de Picardie* 3 (4), 93-122.

Matthews Jr, J. V. and Telka, A. (1997). Insect fossils from the Yukon. In H. V. Danks and J. A. Downes (eds.), *Insects of the Yukon: A biological survey of Canada (Terrestrial Arthropods)*. Ottawa, 911-962.

Mayr, E. (1963). *Animal species and evolution*. Cambridge, Massachusetts: Belknap Press.

McFarlane, J. A. (1989). Guidelines for pest management research to reduce stored food losses caused by insects and mites. *Overseas Development and Natural Resources Institute Bulletin* 22. Chatham, Kent, UK: HMSO

Meehan, T. D., Giermakowski, J. T., and Cryan, P. M. (2004). GIS-based model of stable hydrogen isotope ratios in North American growing-season precipitation for use in animal movement studies. *Isotopes in Environmental Health Studies* 40 (4), 291-300.

Merritt, R. (2006). Atlas of the water beetles (Coleoptera) and water bugs (Hemiptera) of Derbyshire, Nottinghamshire and South Yorkshire, 1993-2005. *Sorby Record Special Series* 14.

Merwe N. J. van der, Lee-Thorpe, J. A., Thackeray, J. F., Hall-Martin, A., Kruger, F. J., Coetzee, H., Bell, R. H. V., and Lindeque, M. (1990). Source-area determination of elephant ivory by isotopic analysis. *Nature* 346, 744-746.

Michener, R. M. and Schell D. M. (1994). Stable isotope ratios as tracers in marine aquatic food webs. In R. H. Michener and K. Lajtha (eds.), *Stable isotopes in ecology and environmental science*. Oxford: Blackwell, 138-157.

Miller, R. F. (1984). *Stable isotopes of carbon and hydrogen in the exoskeleton of insects: Developing a tool for paleoclimatic research*. Unpublished PhD Thesis, University of Waterloo.

Miller, R. F., Fritz, P., and Morgan, A. V. (1988). Climatic implications of D/H ratios in beetle chitin. *Palaeogeography, Palaeoclimatology, Palaeoecology* 66, 277-288.

Mlambo, S. S. (1980). Field and laboratory on population dynamics and dispersal of grain weevils (Coleoptera: Curculionidae). Unpublished PhD thesis. University of Adelaide.

Moret, P. and Martin Cantarino, C. (1996). L'utilisation des Coléoptères subfossiles dans la reconstruction des paléoenvironnements: L'exemple du port antique de Santa Pola (Espagne). *Bulletin de la Société entomologique de France* 101 (3), 225-229.

Morris, M. G. (1990). Orthocerous weevils. Coleoptera Curculionoidea (Nemonychidae, Anthribidae, Urodontidae, Attelabidae and Apionidae). *Handbooks for the identification of British insects* 5. Royal Entomological Society of London.

Morris, M. G. (1997). Broad-nosed weevils. Coleoptera: Curculionidae (Entiminae). *Handbooks for the Identification of British Insects* 5. London: Royal Entomological Society.

Motz, J. (2000). *Oxygen and hydrogen isotopes in fossil insect chitin as palaeoenvironmental indicators*. Unpublished Ph.D. Thesis, University of Waterloo.

Mound, L. (1989). Common insect pests of stored food products: A guide to their identification. *British Museum (Natural History) Economic Series* 15. London: British Museum (Natural History).

Moya, O., Contreras-Diaz, H. G., Oromi, P., and Juan, C. (2004). Genetic structure, phylogeography and demography of two ground-beetle species endemic to the Tenerife laurel forest (Canary Islands). *Molecular Ecology* 13, 3153-3167.

Mullis K. B. and Faloona F. (1987). Specific synthesis of DNA in vitro via a polymerasecatalysed chain reaction. *Methods in Enzymology* 155, 335-350.

Mundy, C. A., Allen-Williams, L. J., Underwood, N., and Warrington, S. (2003). Prey selection and foraging behaviour by *Pterostichus cupreus* L. (Col., Carabidae) under laboratory conditions. *Journal of Applied Entomology* 124, 349-358

Munro, J. W. (1966). *Pests of stored products*. London: Hutchinson.

Murphy, G. and Fraser, H. (2006). DNA—a new tool for insect identification. *Greenhouse Canada* 26 (10), 36-37.

Murphy, P., Albarella, A., Germany, M., and Locker, A. (2000). Production, imports, and status: Biological remains from a Late Roman Farm at Great Holts Farm, Boreham, Essex, UK. *Environmental Archaeology* 5, 35-48.

Murray, H. (1983). Viking and early medieval buildings in Dublin: A study of the buildings excavated under the direction of A B Ó Ríordáin in High Street, Winetavern Street and Christchurch Place, Dublin, 1962-63, 1967-76. In A. R. Hands and D. R. Walker (eds.), *BAR British Series 119*. Oxford: BAR.

Murray, M. D. (1957a). The distribution of the eggs of mammalian lice on their hosts II. Analysis of the oviposition behaviour of *Damalinia ovis* (L.) on the sheep. *Australian Journal of Zoology* 5 (1), 19-29.

Murray, M. D. (1957b). The distribution of the eggs of mammalian lice on their hosts III. The distribution of the eggs of *Damalinia ovis* (L.) on the sheep. *Australian Journal of Zoology* 5 (2), 173-182.

Murray, M. D. (1960a). The ecology of lice on sheep I. The influence of skin temperature on populations of *Linognathus pedalis* (Osborne). *Australian Journal of Zoology* 8 (3), 349-356.

Murray, M. D. (1960b). The ecology of lice on sheep II. The influence of temperature and humidity on the development and hatching of the eggs of *Damalinia ovis* (L.). *Australian Journal of Zoology* 8 (3), 357-362.

Muzzarelli, R. A. (1977). *Chitin*. Oxford: Pergamon Press.

National Weather Service (n.d.). The water cycle. Corpus Christi, TX: The National Weather Forecast Office. Page Consults on 28th July 2009. http://www.srh.noaa.gov/crp/weather/education/water_cycle.html

Nealis, V. G., Oliver, D., and Tchir, D. (1996). The diapause response to photoperiod in Ontario populations of *Cotesia melanoscela* (Ratzeburg) (Hymenoptera: Braconidae). *Canadian Entomologist* 128 (1), 41-46.

NH: Pliny the Elder's Natural History: Holland, P. (trans.) (1635). The historie of the vvorld: Commonly called, the naturall historie of C. Plinius Secundus. London: Adam Islip.

Nice, C., Anthony, N., Gelembiuk, G., Raterman, D. and Ffrench-Constant, R. (2005). The history and geography of diversification within the butterfly genus *Lycaeides* in North America. *Molecular Ecology* 14, 1741-1754.

O'Connell, T. C. and Hedges, R. E. M. (1999). Investigations into the effect of diet on modern human hair isotopic values. *American Journal of Physical Anthropology* 108, 409–425.

O'Connor, T. P. (1994). 8th- 11th century economy and environment in York. In J. Rackham (ed.), Environment and economy in Anglo-Saxon England. *CBA Research Report* 89. York: Council for British Archaeology, 136-147.

O'Connor, T. P. (2000). *The archaeology of animal bones*. Stroud: Sutton.

O'Connor, T. P. (2001). On the interpretation of animal bone assemblages from wics. In D. Hill and R. Cowie (eds.), *Wics. The early medieval trading centres of northern Europe*. Sheffield: Sheffield Academic Press, 54-60.

Oeggl, K., and Eicher, U. (1989). Pollen and oxygen isotope analyses of late and postglacial sediments from the Schwemm raised bog near Walchsee in Tirol, Austria. *Boreas* 18, 245–253.

Olausson, D. (1988). Dots on a map—thoughts about the way archaeologists study prehistoric trade and exchange. In B. Hårdh, L. Larsson, D. Olausson, and R. Petré (eds.), *Trade and exchange in prehistory: studies in honour of Berta Stjernquist*. Lund: Lunds Univeritats Historika Museum, 15-24.

Osborne, P. J. (1971). An insect fauna from the Roman site at Alcester, Warwickshire. *Britannia* 2, 156-165.

Osborne, P. J. (1983). An insect fauna from a modern cesspit and its comparison with probable cesspit assemblages from archaeological sites. *Journal of Archaeological Science* 10, 453-463.

Osborne, P. J. (1989). Insects. In P. Ashbee, M. Bell, and E. Proudfoot (eds), *Wilsford Shaft: excavations 1960-2. English Heritage Archaeological Report* 11. London, 96-99.

Ostrom, P. H. and Fry, B. (1993). Sources and cycling of organic matter in modem and prehistoric food webs. In M. H. Engel and S. A. Macko (eds.), *Organic geochemistry*. New York: Plenum, 785-798.

Ostrom, P. H, Colunga-Garcia, M., and Gage, S. H. (1997). Establishing pathways of energy flow for insect predators using stable-isotope ratios: Field and laboratory evidence. *Oecologica* 109 (1), 108-113.

Pääbo S. (1985a). Preservation of DNA in ancient Egyptian mummies. *Journal of Archeological Science* 12, 411-417.

Pääbo S. (1985b). Molecular cloning of ancient Egyptian mummy DNA. *Nature*. 314, 644-645.

Pääbo S. (1986). Molecular genetic investigations of ancient human remains. *Cold Spring Harbour Symposium Quantative Biology* 51, 441-446.

Palm, T. (1959). Die Holz und Rindenkäfer der sud-und mittelschwedischen Laubbaume. *Opuscula Entomologica Suppl.* 16.

Pals, J. P. and Hakbijl, T. (1992). Weed and insect infestation of a grain cargo in a ship at the Roman fort of Laurium in Woerden (Province of Zuid-Holland). *Review of Palaeobotany and Palynology* 73, 287-300.

Panagiotakopulu, E. (1998). An insect study from Egyptian stored products in the Liverpool Museum. *Journal of Egyptian Archaeology* 84, 231-234.

Panagiotakopulu, E. (1999). An examination of biological materials from coprolites from XVIII Dynasty Amarna, Egypt. *Journal of Archaeological Science* 26, 547-551.

Panagiotakopulu, E. (2001). New records for ancient pests: Archaeoentomology in Egypt. *Journal of Archaeological Science* 28, 1235-1246.

Panagiotakopulu, E. (2003). Insect remains from the collections in the Egyptian Museum of Turin. *Archaeometry* 45 (2), 355-362.

Panagiotakopulu, E. and Buckland, P. C. (1991). Insect pests of stored products from Late Bronze Age Santorini, Greece. *Journal of Stored Product Research* 27 (3), 179-184.

Panagiotakopulu, E., Buckland, P. C., and Day, P. M. (1995). Natural insecticides and insect repellents in antiquity: A review of the evidence. *Journal of Archaeological Science* 22, 705-710.

Panagiotakopulu, E. and Van der Veen, M. (1997). Synanthropic insect faunas from Mons Claudianus, a Roman quarry site in the Eastern Desert, Egypt. In A. C. Ashworth, P. C. Buckland and J. P. Sadler (eds.), *Studies in Quaternary Entomology - An inordinate fondness for insects. Quaternary Proceedings* 5, 199-206.

Pasteels, J. M., Dobler, S., Rowell-Rahier, M., Ehmke, A., and Hartmann, T. (1995). Distribution of autogenous and host-driven chemical defenses in *Oreina* leaf beetles (Coleoptera: Chrysomelidae). *Journal of Chemical Ecology* 21 (8), 1163-1179.

Payne, T. S. (2002). Harvest and storage management of wheat. In B.C. Curtis, S. Rajaram and H. Gómez Macpherson (eds), *Bread wheat Improvement and Production*. *FAO Plant Production and Protection Series 30.* Rome: Food and Agriculture Organization of the United Nations. Accessible at http://www.fao.org/DOCREP/006/Y4011E/y4011e0u.htm#bm30

Payre, F. (2004). Genetic control of epidermis differentiation in *Drosophila*. *International Journal of Developmental Biology* 48, 207-215.

PC: Plautus' Curculio: Nixon, P. (trans.) (1917). *Plautus II.* London: William Heinemann Ltd.

Pecreaux, D. (2008). *Potentialités de l'entomologie appliquée aux sites archéologiques subaquatiques – L'exemple du Bronze final du la du Bourget (Savoie, France)*. Unpublished Doctoral Thesis, Muséum national d'Histoire naturelle

Pentz, P. (1992). Changing patterns of Late Roman/ Early medieval exchange in the Western Mediterranean. In *Medieval Europe 1992: Preprinted papers volume 5, exchange and trade*. York: Medieval Europe, 1-8.

Perez, V. R., Godfrey, L. R., Nowak-Kemp, M., Burney, D. A., Ratsimbazafy, J., and Vasey, N. (2005). Evidence of early butchery of giant lemurs in Madagascar. *Journal of Human Evolution 49,* 722-742.

Perlès, C. (2001). *The Early Neolithic in Greece. The first farming communities in Europe*. Cambridge: Cambridge University Press.

Perry, D. W., Buckland, P. C., and Snæsdóttir, M. (1985). The application of numerical techniques to insect assemblages from the site of Stóraborg, Iceland. *Journal of Archaeological Science* 12, 335-345.

Peterson, B. J. and Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18, 293-320.

Pfeiffer, I., Volkel, I., Taubert, H., and Brenig, B. (2004). Forensic DNA-typing of dog hair: DNA-extraction and PCR amplification. *Forensic Science International* 141, 149–151.

Poinar, H. N., Schwarz, C., Qi, J., Shapiro, B., MacPhee, R. D. E., Buigues, B., Tikhonov, A., Huson, D. H., Tomsho, L. P., Auch, A., Rampp, M., Miller, W., and Schuster, S. C. (2006). Metagenomics to paleogenomics: large-scale sequencing of mammoth DNA. *Science* 311, 392–394.

Ponel, P., Matterne, V., Coulthard, N. and Yvenic, J. H. (2000). La Tène and Gallo-Roman natural environments and human impact at the Touffréville rural settlement, reconstructed from Coleoptera and plant macroremains (Calvados, France). *Journal of Archaeological Science* 27, 1055-1072.

Preston-Mafham, K. (2005). *Identifying bugs and beetles*. London: New Burlington Books.

Price, P. W. (1975). *Insect Ecology*. New York: John Wiley and Sons.

Price, P. W. (1984). The concept of the ecosystem. In C. B. Huffaker and R. L. Rabb (eds.), *Ecological entomology*. New York: John Wiley and Sons, 19-50.

Rausling, G. (1988). The Silk Road: Some reflections during two short walks in the Karakorum in 1963 and in 1986. In B. Hårdh, L. Larsson, D. Olausson, and R. Petré (eds.), *Trade and exchange in prehistory: Studies in honour of Berta Stjernquist*. Lund: Lunds Univeritats Historika Museum, 177-185.

Rees, D. (2004). *Insects of stored products*.Victoria: CSIRO Publishing.

Rees, D. (2007*). Insects of stored grain: A pocket reference*. Collingwood, Australia: CSIRO Publishing.

Reiss, R. A. (2006). Ancient DNA from ice age insects: proceed with caution. *Quaternary Science Reviews* 25, 1877-1893.

Reiss, R. A., Ashworth, A. C. and Schwert, D. P. (1999). Molecular genetic evidence for the post-Pleistocene divergence of populations of the arctic-alpine ground beetle *Amara alpina* (Paykull) (Coleoptera: Carabidae). *Journal of Biogeography* 26, 785-794.

Reitter, E. (1911). *Fauna Germanica - Die Käfer des Deutchen Reiches*. Stuttgart.

Reynard, L. M. and Hedges, R. E. M. (2007). Stable hydrogen isotopes of bone collagen in palaeodietary and palaeoenvironmental reconstruction. *Journal of Archaeological Science* 35, 1934-1942.

Richards, J. D. (1991). *Book of Viking Age England*. London: B.T. Batsford Ltd and English Heritage.

Richards, O. W. (1926). Studies on the ecology of English heaths. III. Animal communities of the felling and burn successions at Oxshott Heath, Surrey. *Journal of Ecology* 14, 244-281.

Roaf, M. and Postgate, N. (1991). *The cultural atlas of Mesopotamia and the Ancient Near East*. New York: Equinox Books.

Robinson, M. A. (1979). The biological evidence. In G. Lambrick and M. A. Robinson (eds.), *Iron Age and Roman riverside settlements at Farmoor, Oxfordshire. Council for British Archaeology Research Report* 32. London, 77-133.

Robinson, M. A. (1981). The use of ecological groupings of Coleoptera for comparing sites. In M. Jones and G. Dimbleby (eds.), The Environment of Man: The Iron Age to the Anglo-Saxon period. *British Archaeological Reports* 87. Oxford, 279-286.

Robinson, M. A. (1983). Arable/pastoral ratios from insects?. In M. Jones (ed.), Integrating the subsistence economy. Symposia of the Association for

Environmental Archaeology 4, *British Archaeological Reports International Series* 181. Oxford, 19-55.

Robinson, M. A. (1991). The Neolithic and Late Bronze Age insect assemblages. In S. Needham (ed.), *Excavation and salvage at Runnymede Bridge, 1978: the Late Bronze Age waterfront site*. London: British Musuem, 277-327.

Robinson, M. A. (2001). Insects as palaeoenvironmental indicators, pp 121-133. In D. R. Brothwell and A. M. Pollard (eds.), *Handbook of archaeological sciences*.

Roden, J. S. and Ehleringer, J. R. (1991). Observations of hydrogen and oxygen isotopes in leaf water confirm the Craig-Gordon model under wide-ranging environmental conditions. *Plant Physiology* 120, 1165-1173.

Roeder, C. (1899). Recent Roman discoveries in Deansgate and on Hunt's Bank, and Roman Manchester re-studied (1897-1900). *Tranactions of the Lancashire and Cheshire Antiquarian Society* 17, 147-189.

Rosenfeld, A. (1965). *The inorganic raw materials of antiquity*. London: Weidenfeld and Nicolson.

Roslund, M. (1992). The strife for power: Interregional contacts and trade in Sigtuna, CA 970-1200 AD. *Medieval Europe 1992: Preprinted papers volume 5, exchange and trade*. York: Medieval Europe, 145-151.

Roth, J. (1999). *The logistics of the Roman army at war (264 B.C.-A.D. 235)*. Boston: Brill.

Rouse, I. (1986). *Migrations in prehistory: Inferring population movement from cultural remains*. New Haven: Yale University Press.

Rousseau, M. (2009). *Understanding the (in)efficiency of paraffin floatation for archaeoentomological work : Methodological test, reasons, and implications*. Unpublished Masters dissertation, University of York.

Rowsome, P. (2000). *Heart of the city: Roman, medieval and modern London revealed by archaeology at 1 Poultry*. London: Museum of London Archaeology Service.

Rowan, Y. M. and Golden, J. (2009). The Chalcolithic Period of the southern Levant: A Synthetic Review. *Journal of World Prehistory* 22 (1), 1-92.

RR: Columella's *De Re Rustica:* Ash, H. B. (trans.) (1941). *Columella De Re Rustica I-IV*. London: William Heinemann Ltd.

RR: *Varro's De Re Rustica*: Hooper, W. D. and Ash, H. B. (trans.) (1935). *Marcus Porcius Cato On Agriuculture; Marcus Terentius Varro On Agriculture*. London: William Heinemann Ltd.

Rubenstein, D. R. and Hobson, K. A. (2004). From birds to butterflies: Animal movement patterns and stable isotopes. *Trends in Ecological Evolution* 19, 256-263.

Rule, M. and Monaghan, J. (1993). Insect remains- grain weevils. In M. Rule and J. Monaghan (eds.), A Gallo-Roman trading vessel from Guernsey. The excavation and recovery of a third century shipwreck. *Guernsey Museum Monograph* 5, pl. 20.

Ruttner, F., Milner, E., and Dews, J. E. (1990). *The dark European honey bee, Apis mellifera mellifera Linnaeus 1758*. The British Isles Bee Breeders Association.

Sacktor, B. (1970). Regulation of intermediary metabolism with special reference to control mechanisms in insect flight muscle. *Advances in Insect Physiology* 7, 267-347.

Sadler, J. P. (1988). *The analysis of insect remains from Norse sites in the former Western Settlement of Greenland*. Unpublished MSc dissertation, University of Birmingham.

Sadler, J. P. (1991a). Beetles, boats and biogeography. Insect invaders of the North Atlantic. *Acta Archaeologica* 61, 1999-211.

Sadler, J. P. (1991b). *Archaeological and biogeographical implications of Palaeoentomological studies in Orkney and Iceland*. Unpublished PhD thesis, University of Sheffield.

Sadler, J. P. and Skidmore, P. (1995). Introductions, extinctions or continuity? Faunal change in the North Atlantic islands. In R. A. Butlin and N. Roberts (eds.), Ecological relations in historical times. Human impact and adaptation. *Institute of British Geographers Special Publication* 32. Oxford: Blackwell, 206-255.

Saiki, R. K., Gelfand, D. H., Stoffel, S., Scharf, S. J., Higuchi, R., Horn, G. T., Mullis, K. B., and Erlich, H. A. (1988). Primer-directed enzymatic amplification of DNA with thermostable DNA polymerase. *Science* 239, 487-491.

Sailer, R. I. (1983). History of insect introductions. In C. L. Wilson and C. L. Graham (eds.), *Exotic plant pest and North American agriculture*. Academic Press: New York, 15-38.

Saki, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., McCauley, D. E., O'Neil, P., Parker, I. M., Thompson, J. N., and Weller, S. G. (2001). The population biology of invasive species. *Annual Review of Ecological Systems* 32, 305-332.

Salmond, K.F. (1957). The insect and mite fauna of a Scottish flour mill. *Bulletin of Entomological Research* 47, 621-630.

Savage, S. H. (1998). AMS Radiocarbon dates from the Predynastic Egyptian cemetery, N7000, at Naga-ed-Dêr. *Journal of Archaeological Science* 25, 235-249.

Schaffner, F. C. and Swart, P. K. (1991). Influence of diet and environmental water on the carbon and oxygen isotopic signatures of seabird eggshell carbonate. *Bulletin for Marine Science* 48, 23-38.

Schelvis, J. and Koot, C. (1995). Sheep or goat? *Damalinia* deals with the dilemma. Experimental and applied entomology. *Proceedings of the Netherlands Entomological Society* 6, 161-162.

Schimmelmann A. (1991). Determination of the concentration and stable isotopic composition of nonexchangeable hydrogen in organic matter. *Analytical Chemistry* 63, 2456-2459

Schimmelmann, A. and DeNiro, M. J. (1986). Stable isotope studies in chitin. III. The D/H and $^{18}O/^{16}O$ ratios in arthropod chitin. *Geochimica et Cosmochimica Acta* 50, 1485-1496.

Schimmelmann, A. and Miller, R. F. (2002). Review of methods for the determination of deuterium/hydrogen stable isotope ratios in chitin. In R. A. A. Muzzarelli and C. Muzzarelli (eds.), Chitosan in pharmacy and chemistry. Atec Edizioni, Grottammare, Italy, 469–474.

Schimmelmann A., Miller, R. F., and Leavitt, S. W. (1993). Hydrogen isotopic exchange and stable isotope ratios in cellulose, wood, chitin, and amino compounds. In P. K. Swart, K. C. Lohmann, J. McKenzie, and S. Savin (eds.), Climate change in continental isotopic records. *Geophysical Monograph* 78. American Geophysical Union, Washington, DC, 367–374.

Schmidl, A., Allison, E., Jaques, D., Carrott, J., Gardner, S., (2006). Evaluation of Biological Remains from Excavations at Park View School, Chester-le-Street, County Durham (Site Code: PVC06). Palaeoecological Research Services 2006/47.

Schmidt, E. (1998). Der Kornkäfer *Sitophilus granarius* Schoen. Curculionidae aus der Schuttshicht des bandkeramischen Brunnens con Erkelenz-Kuchoven. In H. Koschic (ed.), *Brunnen der Jungsteinzeit, Internationales Symposium Erkelenz, 27-29 Oktober 1997, Materialien zur Bodenkmalpflege im Rheinisches* 11. Landschaftsverband Rheinland, Rheinland-Verlag, Köln, 261-269.

Schmidt, E. (2001). Wirbellosenreste in Schutt- und Verfüllschichten des bandkeramischen Brunnens in Erkelenz-Kückhoven, Kreis Heinsberg. Unpublished manuscript.

Schmidt, E. (2005). Insektenreste aus drei bandkeramischen Brunnen aus Eythra / Zwenkau (Kr. Leipziger Land). Unpublished manuscript.

Schmidt, E. (2006). Insektenreste aus drei römischen Brunnen der Grabung Hambach 512. In T. Kaszab-Olschewski, *Siedlungsgenese im Bereich des Hambacher Forstes 1.-4.Jn. n. Chr. Hambach 512 and Hambach 516. BAR International Series 1585*, Oxford, 153-171.

Schmidt, E. (2007). Käferreste aus der Grabung Singen Offwiesen. *Research Report for Landesamt für Denkmalpflege, Feuchtboden- und Unterwasserarchäologie Hemmenhofen, Ref. 115, Stuttgart.*

Schmidt, E. (2010a). Insektenreste aus der bandkeramischen Brunnenanlage Leizig-PlauBig. *Veröffentlichungen des Landesamtes f. Archäologie mit Landesmuseum f. Vorgeschichte Sachsen 2010 (in press).*

Schmidt, E. (2010b). *Wirbellosenreste in Schutt- und Verfüllschichten des bandkeramischen Brunnens in Erkelenz-Kückhoven, Kreis Heinsberg*. *Rheinische Ausgrabungen 2011 (in press 2011).*

Schoeninger, M. J. (1995). Stable isotope studies in human evolution. *Evolutionary Anthropology* 4, 83–98.

Schrey, N. M., Reeve, J. D. and Anderson, F. E. (2005). Mitochondrial DNA analysis of the bark beetle predatory *Thanasimus dubius* F. (Coleoptera: Cleridae) reveals regional genetic differentiation. *Molecular Ecology* 14, 3317-3324.

Seifert, P. (1987). Die Käfer aus der Mumie. In J. Boessneck, Die Münchner Ochsenmumie. *Hildersheimer ägyptologie* 25, 73-78

Semple, R. L., Hicks, P. A., Lozare, J. V., and Castermans, A. (1992). Towards integrated commodity and pest management in grain storage. *Proceedings and selected papers from the Regional Training Course on Integrated Pest Management Strategies in Grain Storage Systems, conducted by the National Post Harvest Institute for Research and Extension (NAPHIRE), Department of Agriculture, June 6-18, 1988, Philippines.* Rome: FAO and REGNET.

SG: Strabo's Geography: Meineke, A. (ed.) (1877). *Strabonis Geographica*. Lipsiae: B.G. Teubneri

Shackleton, N. J. and Opdyke, N. D. (1973). Oxygen isotope and palaeomagnetic stratigraphy of equatorial Pacific core V28–238, oxygen isotope temperatures and ice volumes on a 105 year and 106 year scale. *Quaternary Research* 3, 39–55.

Shaw, J. W. and Shaw, M. C. (1995). Insects. In J. W. Shaw and M. C. Shaw (eds.), Kommos, an excavation on the south coast of Crete. I. Part 1, 277-278.

Shigehara, N., Matsu'ura, S., Nakamura, T., and Kondo, M. (1993). First discovery of the ancient Dingo-type dog in Polynesia (Pukapuka, Cook Islands), *International Journal of Osteoarchaeology* 3, 315-320.

Shirt, D. B. (ed.) (1987). *British Red Data Books*. *Insects* 2. Peterborough: Nature Conservancy Council.

Simmons, A. H. (1988). Extinct pygmy hippopotamus and early man in Cyprus, *Nature* 333, 554-557.

Sinha, R. N. (1991). Storage ecosystems. In R. J. Gorman (ed.), *Ecology and management of food-industry pests*. Arlington, Virginia: Association of Official Analytical Chemists, 17-30.

Sinha, R. N. and Watters, F. L. (1985). Insect pests of flour mills, grain elevators, and feed mills and their control. *Agriculture Canada Publication 1776E*. Ottawa, Ontario: Canadian Government Publications Centre

Skidmore, P. (1996). *A dipterological perspective on the Holocene history of the North Atlantic Area*. Unpublished PhD thesis, University of Sheffield.

Small, R. W. (2005). A review of *Melophagus ovinus* (L.), the sheep ked. *Veterinary Parasitology* 130, 141-155.

Smith, C. I. and Farrell, B. D. (2005). Phylogeography of the longhorn cactus beetle *Moneilema appressum* LeConte (Coleoptera: Cerambycidae): Was the differentiation of the Madrean sky islands driven by Pleistocene climate changes?. *Molecular Ecology* 14, 3049–3065.

Smith, C. I., Chamberlain, A. T., Riley, M. S., Stringer, C. B., and Collins, M. J. (2003). The thermal history of human fossils and the likelihood of successful DNA amplification. *Journal of Human Evolution* 45, 203–217.

Smith, D. and Tetlow, E. (n.d.). *The insect remains from the Roman deposits at the Carlisle Millennium Site.* The University of Birmingham Environmental Archaeology Services Report 53.

Smith, D., Gaffney, V., Grossman, D., Howard, A. J., Milošević, A., Ostir, K., Podobnikar, T., Smith, W., Tetlow, E., Tingle, M., and Tinsley, H. (2006). Assessing the late prehistoric environmental archaeology and landscape development of the Cetina Valley, Croatia. *Environmental Archaeology* 11 (2), 171-186.

Smith, D. N. (1996a). Hebridean blackhouses and a speculative history of the 'culture favoured' Coleoptera of the Hebrides. In D. Gilbertson, M. Kent and J. Grattan (eds.), *The Outer Hebrides: The last 14,000 years*. Sheffield: Sheffield Academic Press, 207-217.

Smith, D. N. (1996b). Thatch, turves and floor deposits: A survey of Coleoptera in materials from abandoned Hebridean blackhouses and the implications for their visibility in the archaeological record. *Journal of Archaeological Science* 23, 161-174.

Smith, D. N. (2000). *The insect remains from One Poultry, London*. The University of Birmingham Environmental Archaeology Services Report 13.

Smith D. N. (2001). The insect remains from Invereskgate. *The University of Birmingham Environmental Archaeology Services Report* 30, Report to AOC Scotland.

Smith, D. N. (in press). The insect remains. In J. Hill and P. Rowsome (eds), *Roman London and the Walbrook stream crossing: Excavations at 1 Poultry and vicinity, City of London.* MoLAS Monograph Series

Smith, D. N. and Howard, A. J. (2004). Identifying changing fluvial conditions in low gradient alluvial archaeological landscapes: Can Coleoptera provide insights into changing discharge rates and floodplain evolution? *Journal of Archaeological Science* 31, 109-120.

Smith, M. R. (1936). Distribution of the Argentine ant in the United States and suggestions for its control and eradication. *Circulation Report U.S. Department of Agriculture* 387, 1-39.

Snodgrass, R. E. (1935). Principles of insect morphology. New York: McGraw-Hill.

Solomon, M. E. (1965). Archaeological records of storage pests: *Sitophilus granarius* (L.) (Coleoptera, Curculionidae) from an Egyptian pyramid tomb. *Journal of Stored Product Research*, 1, 105-107.

Solomon, M. E. and Adamson, B. E. (1955). The powers of survival of storage and domestic pests under winter conditions in Britain. *Bulletin of Entomological Research* 46, 311-355.

Somerville, E. M. (1999). Some aspects of the palaeoecology of commensals. *Quaternary Proceedings* 7, 605-613.

Speight, M. R., Hunter, M. D., and Watt, A. D. (1999). *Ecology of insects: Concepts and applications*. Malden: Blackwell Science Inc.

Stäuble, H. (1995). Radiocarbon dates of the earliest Neolithic in central Europe. *Radiocarbon* 37 (2), 227-237.

Stead, J. (1982). The uses of urine. *Old West Riding* 2, 1-9.

Suidas' lexicon. Souidas. Suidæ lexicon, Græce & Latine. Textum Græcum cum manuscriptis codicibus collatum a quamplurimis mendis purgavit, notisque perpetuis illustravit: versionem Latinam Æmilii Porti ... correxit; indicesque auctorum & rerum adjecit Ludolphus Kusterus, ... Vol. 2. Cantabrigiæ, 1705. Eighteenth Century Collections Online. Gale Group. http://galenet.galegroup.com/servlet/ECCO

Taanman J-W. (1999). The mitochondrial genome: Structure, transcription, translation and replication. *Biochemica et Biophysica Acta* 1410, 103-123.

Talbot, M. R. (1990). A review of the paleohydrological interpretation of carbon and oxygen isotope ratios in primary lacustrine carbonates. *Chemical Geology* 80, 261–279.

Tansley, A. G. (1939). *The British islands and their vegetation.* London: Cambridge University Press.

Tautz, D., Arctander, P., Minelli, A., Thomas, R. A. and Vogler, A. P. (2003). A plea for DNA taxonomy. *Trends in Ecology and Evolution* 18, 70-74.

Tawil, H. (1977). A curse concerning crop-consuming insects in the Sefîre Treaty and in Akkadian: A new interpretation. *Bulletin of the American Schools of Oriental Research* 225, 59-62.

Tchernov, E**.** (1994). An early Neolithic village in the Jordan Valley, Part II: The Fauna of Netiv Hagdud. *American School of Prehistoric Research Bulletin* 44. Cambridge: Peabody Museum of Archaeology and Ethnology, Harvard University.

Telnov, D. (n.d.). *Lucanidae (Coleoptera) of the Baltic Sea region and adjacent territories*. Entomological Society of Lativa: Section of Coleopterology. Page consulted on 21st August 2009.
http://www.zin.ru/animalia/Coleoptera/addpages/lucanidb/lucanidb.htm

Tieszen, L. L. and Boutton, T. W. (1988). Stable isotopes in terrestrial ecosystem research. In P. W. Rundel, J. R. Ehleringer, and K. A. Nagy (eds.), *Stable isotopes in ecological research*. New York: Springer, 167-195.

Tipper, J. (2004). *The Grubenhaus in Anglo-Saxon England*. Yedingham: Landscape Research Centre.

Topp, W. (1990). Selection for an optimal monovoltine life cycle in an unpredictable environment. Studies on the beetle *Catops nigricans* Spence (Col., Catopidea). *Oecologia* 84 (1), 134-141.

Tsao, C. H. and Richards, A. G. (1952). Studies on arthropod cuticle – IX. Quantitative effects of diet, age, temperature and humidity on the cuticle of five representative species of insects. *Annals of the Entomological Society of America* 45. 585-599.

Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M. and Webb, D. A. (eds.) (1964-80). *Flora Europaea* 1-5. Cambridge: University Press.

Tyler, P. S. and Boxall, R. A. (1984). Post-harvest loss reduction programmes: a decade of activities: what consequences?. *Tropical Stored Product Information* 23, 13-28

Valamoti, S. M. and Buckland, P. C. (1995). An early find of *Oryzaephilus surinamensis* (L.) (Coleoptera: Silvanidae) from final Neolithic Mandalo, Macedonia, Greece. *Journal for Stored Product Research* 31 (4), 307-309.

Vasconcelos, H. L. and Casimiro, A. B. (1997). Influence of *Azteca alfari* ants on the exploitation of *Cecropia* trees by a leaf-cutting ant, *Biotropica* 29, 84-92.

Vasilev, I. V. (1914). The major pests of alfalfa. Part 2. *Otiorrhynchus* (*Cryphiphorus*) *ligustici* L., its description, mode of life and control measures. *Proceedings of the Bureau of Entomology* 8 (2). St. Petersburg: Bureau of Entomology.

Villa, J. D. and Rinderer, T. E. (1993). Coldroom thermoregulation, store consumption, and survival of Africanized and European honey bees (*Apis mellifera* L). *Apidologie* 24, 411-423.

Vogel, J. C., Eglington, B., and Auret, J. M. (1990). Isotope fingerprints in elephant bone and ivory. *Nature* 346, 747-749.

Wada E., Terazaki, M., Kabaya, Y., and Nemoto, T. (1987). 15N and 13C abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. *Deep Sea Research* 5 (6), 829-841

Wassenaar, L. I. and Hobson, K. A. (1998). Natal origins of migratory monarch butterflies at wintering colonies in Mexico: New isotopic evidence. *Proceedings of the National Academy of Sciences, USA* 95, 15436–15439.

WatkinsHire (n.d.). *Average temperature/ relative humidity data for UK Ireland*. Page consulted on 21 July 2009. http://www.watkinshire.co.uk/assets/File/uk-weather-average-data.pdf.

Weightman, C. (n.d.). *Heather honey*. Beedata. Page consulted on 15th August 2009. http://www.beedata.com/data2/nutshell_heather_honey.html

Wells, P. S. (1980). *Culture contact and culture change: Early Iron Age central Europe and the Mediterranean world*. Cambridge: Cambridge University Press.

Wells, J. D. and Sperling, F. A. H. (2001). DNA-based identification of forensically important Chrysomyinae (Diptera: Calliphoridae). *Forensic Science International* 120, 110-115.

West, S. (1985). West Stow, the Anglo-Saxon village (*East Anglian Archaeology* 24). Ipswich: East Anglian Archaeology.

West, S. E. (1969). The Anglo-Saxon village of West Stow: An interim report of the excavations. *Medieval Archaeology* 13, 1–20.

White, J. W. C. (1988). Stable hydrogen isotope ratios in plants: a review of current theory and some potential applications. In P. W. Rundel, J. R. Ehleringer, and K. A. Nagy (eds.), *Stable isotopes in ecological research.* New York: Springer, 142-162.

White, J. W. C. and Gedzelman, S. D. (1984). The isotopic composition of atmospheric water vapor and the concurrent meteorological conditions. *Journal of Geophysical Research* 89, 4937–4939.

Whitehead, P. F. (1999). Further observations on *Tribolium castaneum* (Herbst) (Col., Tenebrionidae), especially in arboreal contexts. *Entomologist's monthly Magazine* 135, 76.

Whitehead, P. F. (2006). The puparium of *Onthophagus joannae* Goljanm 1953 (Col., Scarabaeidae). *Entomologist's Monthly Magazine* 142, 52.

Whitehouse, N. J. (2006). The Holocene British and Irish ancient forest beetle fauna: Implications for forest history, biodiversity and faunal colonisation. *Quaternary Science Reviews* 25, 1755-1789.

Whittle, A. (1996). Europe in the Neolithic. The creation of new worlds. Cambridge University.

Will III, O. H., Tieszen, L. L., Kellen, M., and Gerlach, T. (1986). Stable carbon isotope discrimination in the smut fungus *Ustilago violacea*. *Experimental Mycology* 10, 83–88.

Willerslev, E., Cappellini, E., Boomsma, W., Nielsen, R. Hebsgaard, M. B., Brand, T. B., Hofreiter, M., Bunce, M., Poinar, H. N., Dahl-Jensen, D., Johnsen, S., Steffensen, J. P., Bennike, O., Schwenninger, J., Nathan, R., Armitage, S., de Hoog, C., Alfimov, V., Christl, M., Beer, J., Muscheler, R., Barker, J., Sharp, M., Penkman, K. E. H., Haile, J., Taberlet, P., Brochmann, C., Gilbert, M. T. P., Casoli, A., Campani, E., and Collins, M. J. (2007). Ancient biomolecules from deep ice cores reveal a forested southern Greenland. *Science* 317, 111-114.

Willerslev, E., Hansen, A. J., Binladen, J., Brandt, T. B., Gilbert, M. T. P., Shapiro, B., Bunce, M., Wiuf, C., Gilichinsky, D. A., and Cooper, A. (2003). Diverse plant and animal genetic records from Holocene and Pleistocene sediments. *Science* 300, 791-795.

Wojciechowski, M. F. and Mahn, J. (2006). *Nitrogen fixation and the nitrogen cycle*. The Tree of Life web project. Environmental Protection Agency, USA. Page consulted on 28th July 2009. http://tolweb.org/notes/?note_id=3920.

Woodward, S. R., Weyand, N. J., and Bunnell, M. (1994). DNA sequence from Cretaceous period bone fragments. *Science* 266, 1229-1232.

Wooller, M. J., Francis, D., Fogel, M. L., Miller, G. H., Walker, I. R., and Wolfe, A. P. (2004). Quantitative paleotemperature estimates from d18O of chironomid head capsules preserved in arctic lake sediments. *Journal of Paleolimnology* 31, 267–274.

Yapp, C. J. and Epstein, S. (1982). A re-examination of cellulose carbon-bound hydrogen D measurements and some factors affecting plant-water D/H relationships. *Geochimica et Cosmochimica Acta* 46, 955-965.

Yeo, C. A. (1946). Land and sea transportation in Imperial Italy. *Transactions of the American Philosphical Association* 77, 221-244.

Yong, Z., Fournier, P-E., Rydkina, E. and Raoult, D. (2003). The geographical segregation of human lice preceded that of *Pediculus humanus capitis* and *Pediculus humanus humanus*. *Comptes Rendus Biologies* 326, 565-574.

Yurtsever, G. and Gat, J. R. (1981). Atmospheric waters. In J. R. Gat and R. Gonfiantini (eds.), *Stable isotope hydrology, deuterium and oxygen 18 in the water cycle.* IAEA Technical Reports Series 210, Vienna, 103-142.

Yvinec, J-H. (1997). Infestation par les insectes d'un grenier carbonisé de la fin du IIe siècle A.D. à Amiens (Somme). *L'Entomologiste (Paris)* 53, 113-128.

Zacher, F. (1927). *Die Vorrats-, Speicher- und Materialschadlinge und ihre Bekämpfung*. Berlin.

Zacher, F. (1934a). Beiträge zur Geschichte, Verbreitung und Oekologie der Vorratsschädlinge. *Entomologische Beihefte Berlin-Dahlem* 1, 83-86.

Zacher, F. (1934b). Vorratsschädlinge und Speicherwirtschaft im alten und neuen Ägypten. *Forschung und Fortschritte* 10, 347-348.

Zacher, F. (1937). Vorratschadlinge und Vorratschutz, ihre Bedeutung für Volksernährung und Weltwirtschaft. *Zeitschrift für hygienische Zoologie und Schädlingsekämpfung* 29, 193-202.

Zacher, F. (1938). Die Einwirkung oberflichenaktiver Stoffe auf Insekten. Verh. VII. *International Congress of Entomology (Berlin, Germany),* 2884-2891.

Zakharov, E. V., Chelomina, G. N., and Zhuravlec, I. uN. (2000). Isolation of DNA from museum exhibits of butterflies (Lepidoptera, Papilionidae) and PCR analysis with random and universal genes-specific primers. *Genetika* 36, 1221-1229.

Zazula, G. D., Froese, D. G., Telka, A. M., Mathewes, R. W., and Westgate, J. A. (2002). Plants, bugs, and a giant mammoth tusk: Paleoecology of Last Chance Creek, Yukon Territory. *Yukon Exploration and Geology* 2002, 251-258

Ziegler, H. (1988). Hydrogen isotope fractionation in plant tissues. In P. W. Rundel, J. R. Ehleringer, and K. A. Nagy (eds.), *Stable isotopes in ecological research.* New York: Springer, 105-123.

Appendices

Appendix 1

Mutual Climatic Range Data

Appendix 1A:

MCR Species from 7-15 Spurriergate York

Species	TmaxHi	TMaxLo	TminHi	TminLo	TRangeHi	TrangeLo
Dyschirius globosus (Hbst.)	31	9	16	-47	57	8
Trechus obtusus/ quadristriatus (Er.)/ (Schr.)	36	10	31	-11	30	5
Pterostichus melanarius (Ill.)	26	10	11	-37	49	7
Helophorus aquaticus/ grandis (L.)/ (Ill.)	36	10	31	-20	36	5
Cercyon tristis (Ill.)	24	9	9	-44	53	9
Megasternum obscurum (Marsham)	26	9	13	-17	30	7
Xylodromus concinnus (Marsham)	29	10	17	-16	30	7

Anotylus rugosus (F.)	28	11	10	-23	39	8
Anotylus sculpturatus (Grav.)	30	15	17	-13	32	8
Anotylus nitidulus (Grav.)	33	10	17	-43	53	8
Platystethus arenarius (Geoff.)	18	9	7	-47	56	8
Platystethus nitens (Sahl.)	33	15	15	-33	48	8
Leptacinus pusillus (Steph.)	27	12	17	-27	44	9
Tachinus laticollis (Grav.)	27	9	14	-35	44	7
Aphodius fimetarius (L.)	29	9	15	-40	54	8

(formulated using Buckland and Buckland 2006)

Appendix 1B:

MCR for 3 Roman Age Sites

Site	TMaxLo	TMaxHi	TMinLo	TMinHi	TRangeLo	TrangeHi	NSPEC	Overlap	Environmental Report
Bedern Well	16	18	-8	6	11	24	37	97.30	Kenward *et al.* 1986
Alcester, Warwickshire	15	18	-7	6	11	24	15	93.33	Osborne 1971
Copthall Ave., London	15	18	-7	6	11	22	30	100	Allison and Kenward 1987

(adapted from Table 1, King 2008)

Appendix 1C:

MCR Period 4B Tenement C16-22 Coppergate Samples

Species	TmaxHi	TMaxLo	TminHi	TminLo	TRangeHi	TrangeLo
Clivina fossor (L.)	29	9	18	-42	54	11
Trechoblemus micros (Hbst.)	25	13	10	-26	43	10
Bembidion gilvipes (Sturm)	23	15	9	-34	49	11
Bembidion biguttatum (F.)	29	15	16	-18	33	10
Harpalus rubripes (Duft.)	29	14	13	-19	37	9
Pterostichus melanarius (Ill.)	26	10	11	-37	49	7
Megasternum obscurum (Marsham)	26	9	13	-17	30	7

Hydrobius fuscipes (L.)	26	8	13	-53	62	8
Omalium rivulare (Payk.)	28	9	18	-21	30	7
Xylodromus concinnus (Marsham)	29	10	17	-16	30	7
Anotylus rugosus (F.)	28	11	10	-23	39	8
Anotylus sculpturatus (Grav.)	30	15	17	-13	32	8
Anotylus nitidulus (Grav.)	33	10	17	-43	53	8
Platystethus arenarius (Geoff.)	18	9	7	-47	56	8
Platystethus nitens (Sahl.)	33	15	15	-33	48	8

Leptacinus pusillus (Steph.)	27	12	17	-27	44	9
Gyrohypnus fracticornis (Müll.)	27	11	15	-17	30	8
Tachinus rufipes (L.)	27	9	15	-27	36	7
Aphodius prodromus (Brahm)	29	12	14	-23	41	8

(calculated using Buckland and Buckland 2006)

Appendix 1D:

MCR data from three Neolithic Age sites in Germany

Site	TMaxLo	TMaxHi	TMinLo	TMinHi	TRangeLo	TRangeHi	NSPEC	Overlap	Environmental Report
Erkelenz-Kückhoven	15	25	-11	9	10	28	8	100	Schmidt 1998, 2010b
Plaußig	16	24	-11	9	11	27	11	100	Schmidt 2010a
Eythra	17	24	-10	9	13	30	7	100	Schmidt 2005

(determined using Buckland and Buckland 2006)

Appendix 2

Evaluation of Biological Remains from a Roman Timber Drain at 21 St Peters Street, Colchester (site code: 2007.124)

Modified from the Reports from the Centre for Human Palaeocology publication

Evaluation of biological remains from a Roman timber drain at 21 St Peters Street, Colchester (site code: 2007.124).

Reports from the Centre for Human Palaeoecology, University of York 2008/15.

(2008).

Gary A. King and Allan Hall

Appendix 2A:

Evaluation of biological remains from a Roman timber drain at 21 St Peters Street, Colchester (site code: 2007.124)

Gary Andrew King and Allan Hall

Department of Archaeology, University of York, The King's Manor, YO1 7EP

Summary

A subsample from a Roman timber drain was selected for detailed evaluation for its bioarchaeological potential, primarily insect remains. Both plant and insect taxa were present and in excellent condition, though rather sparse. Analysis of the plant remains revealed the presence of both wild and domestic occupation taxa including the presence of an exotic, fig. The insect fauna was largely synanthropic in nature and resembled the indicator group associated with stable manure. Given the context, the synanthropes are believed to be primarily background fauna suggesting the redeposition of the material, most likely during the in-filling of the drain. The insect fauna also revealed some of the earliest evidence for the presence of grain pests in Britain.

Keywords: COLCHESTER; ROMAN DRAIN; INSECT REMAINS; PLANT REMAINS

Evaluation of biological remains from a Roman timber drain at 21 St Peters Street, Colchester (site code: 2007.124)

Introduction

In 2008, Colchester Archaeological Trust Ltd. excavated a nine metre long and 101.6 cm wide timber drain at the 21 St Peter's Street site, within the town's Dutch Quarter. Using dendrochronology, the construction of the drain has been dated to approximately AD 62, and the investigating field archaeologists place the in-filling around 65-80 AD. Because of the presence on the site of some deposits with waterlogged preservation (a very rare phenomenon in Roman Colchester), a 1.5 kg subsample (Context 127) was submitted to the Centre for Human Palaeoecology, University of York for evaluation of bioarchaeological potential, primarily through insect remains.

Methods

The sediment sample was inspected in the laboratory broadly following the procedures of Kenward *et al*. (1980; 1985), for the recovery of plant and invertebrate macrofossils (three cycles of admixture paraffin, 3 floatations). Plant and invertebrate remains in the resulting residue and washover were recorded by 'scanning' using a low-power binocular microscope. Identification of insect remains was carried out through comparison with material in the reference collection of the former Environmental Archaeology Unit, University of York. Taxonomy and nomenclature for the insects follow Kloet and Hincks (1977). Data were recorded on paper before being transferred to personal computer.

Results

Context 127 (organic lowest fill of timber drain; silts sealed by *in situ* timber lid)

Sample 6 (1.5 kg sieved to 300 microns with paraffin floatation)

Moist, light-dark brown, stiff to crumbly, sandy-silt.

The washover yielded some mammalian bone fragments (a charred sheep ulna with coloration suggesting firing temperatures around 700 degrees centigrade, an ungulate scapula, as well as ungulate rib with evidence of butchery), eggshell, and oyster shell. Plant remains in the flot and residue both consisted of 'waterlogged' seeds and fruits in a moderate state of preservation. The flot also contained ample insect remains.

Most of the wild plant taxa recovered, including spike rush (*Eleocharis* sp.), lesser spearwort (*Ranunculus flammula* L.), and *Glyceria* sp., are typical of wet places of various kinds. Orache (*Atriplex* sp.) knotgrass *Polygonum* and docks (*Rumex* sp.) commonly inhabit disturbed ground. There were a few taxa indicative of occupation and here, probably, domestic waste: traces of seeds of fig (*Ficus carica* L.), fruitstone fragments of *Prunus* (sloe, plum, etc.) and nutshell fragments of *Corylus avellana* L. (hazel). Some sclerotia (resting bodies) of the soil-dwelling fungus *Cenococcum* may simply have arrived in imported soil or have formed from fungal mycelia that lived in the deposit at some stage after formation.

The flot contained a relatively small number of insect remains. The fauna were primarily synathropic (defined here as species associated with human occupation). The flot yielded one heavily fragmented chrysomelid (leaf beetle) elytron, potentially representing a non-synanthropic species, although this cannot be conclusively deduced due to the condition of the fossil. Additionally, the presence of *Phyllodrepa*

?floralis/salicis could represent a nearby woodland environment or equally be evidence of a more human-associated habitat through haystack refuse or stable dung (Koch 1989). Given the context, it is also interesting to note the lack of aquatic invertebrates.

A high percentage (84 %) of the recovered insect remains consisted of synanthropic taxa, presumably representative of the fauna of nearby buildings. *Ptinus ?fur* and *Tipnus unicolor* are both characteristic of this category. While it has been found to inhabit bird nests, *Ptinus fur* is common in mouldy straw and hay in barns and stables as well as cereal debris (Koch 1989). *Tipnus unicolor* is found to frequent similar environments (Koch 1989) but is typical of older buildings. The recovery of individuals of *Lathridius minutus* group and *Gyrohypnus ?fracticornis* is further evidence to support the presence of mouldy decaying vegetation, particularly straw or hay (Böcher 1988; Koch 1989). Although not necessarily indicative of the presence of hay or straw, *Cercyon analis* has been found in decomposing plant debris and has been recovered from compost heaps and leaf litter (Hansen 1987). Although *Aphodius granarius* has been recorded in rotting vegetation, the dung beetle is common in stable manure heaps and may indicate the presence of foul matter.

While the drain fauna consisted primarily of facultative synanthropes (those forms most commonly found in artificial environments but capable of surviving in nature), 27 % of the synanthropic assemblage itself was contributed by strong synanthropes. The single individual of *Sitophilus granarius* is evidence for the presence of cereal grains. *S. granarius* is capable of feeding on damaged as well as undamaged grain, although it has been noted to have difficulty breaching husked kernels. *Cryptolestes ferrugineus* is regarded as a secondary pest of cereals and is often found in grains that have been worked or damaged. *Palorus ratzeburgi* is a

scavenger of very spoiled grain and is known to prey upon other grain pests. Both *C. ferrugineus* and *P. ratzeburgi* are also found in other stored products, including flour, bran meal, and non-cereals such as dried fruit (Salmond 1957; Hunter *et al.* 1973; Freeman 1980).

Discussion

Pests of stored products

One of the most interesting features of the Roman timber drain at 21 St Peter's Street is the presence of species associated with cereals and other stored products. *Sitophilus granarius*, the granary weevil, is a common pest in granaries where both larvae and adults feed on whole cereals (Hoffman 1986). *S. granarius* is considered a major pest of cereals and is noted to be very destructive, resulting in considerable loss of stored grain. In the United Nations Food and Agriculture Organisation's report of 1947, it was suggested that 10 % of the world's cereal production was lost to insect attack; five decades ago 5 % of the loss was attributed to infestation by the granary weevil (Munro 1966).

Whilst the granary weevil has been known to feed on grains in the early stages of spoilage (Coombs and Woodroffe 1963), the other species present are often considered pests of cereals that have been broken and become wet and mouldy, often as a result of attack by *S. granarius*. Observing the natural succession of the infestation of stored grains, Coombs and Freeman (1955) have considered species such as *Cryptolestes ferrugineus* and *Palorus ratzeburgi* to be secondary pests of stored product cereals.

Although these stored product pests are believed to be able to overwinter successfully in the unheated grain stores of Britain today as a result of the warmer-

than-ambient temperatures existing in the internal microhabitats (Solomon and Adamson 1955), the archaeological record indicates that they were absent from Britain prior to the Roman invasion. Buckland (1978) proposes that this pre-Roman absence is due to a combination of minimal importation of grain from the continent during the Iron Age and the storage of grains in pits which would create a sealed carbon dioxide-rich environment inhibiting infestation. The mass importation of cereals by the Roman army and civil administration as well as the use of ventilated above-ground granaries may have enabled the pests to survive and flourish.

The pre-Boudiccan deposits at One Poultry, London (Smith 2000) suggest that the species entered Britain almost immediately after the Roman invasion. Moreover, having seemingly entered Britain with the Romans, biogeographical mapping (*c.f.* King in press) suggests that the species spread across England along with the Roman legions, entering the Roman Fort at the Millennium site at Carlisle Castle by AD 72/3 (Smith and Tetlow n.d.) and the fort at Ribchester, Lancashire, by AD 71-4 (Large *et al.* 1994; Buxton and Howard-Davis 2000). Furthermore, with the Roman departure from Britain, the granary beetles become notably absent from the record until the Norman Conquest.

At a minimum, the presence of the grain pests at the site in question here suggests the mass storage of grains in the area and puts forth the possibility that the cereals may have been imported rather than native.

Origin and deposition of material

Although the recovery of grain pests indicates the storage of grains near the site, they are not necessarily evidence of the timber drain having serviced a granary, as was similarly proposed for the Roman sewer in York (Buckland 1976). Kenward

and Hall (1997) have also proposed that the presence of grain pests along with 'hay' fauna, house fauna, and decomposers is characteristic of stable manure, most likely equine. The grains would have served directly as a part of the mammals' diet or, less possibly, the grain pests could have invaded residue grain in straw or chaff that was used for bedding (Kenward forthcoming). Osborne (1983) demonstrated that insect fragments could successfully pass through a human dietary tract without damage; it seems plausible that the same would hold true for large non-ruminant herbivores.

An indicator group of organisms for stable manure is now recognised (Kenward and Hall 1997). From the invertebrates, stable manure can often be recognised through a combination of grain pests, 'hay' insects, house fauna from the stables, and decomposers often associated with foul matter. Along with the grain pests, the sample from 21 St Peters Street contained two commonly associated house fauna taxa (*Tipnus unicolor* and *Ptinus ?fur*) and the dung beetle *Aphodius granarius* which is strongly associated with stable manure. It also produced a range of fauna associated with plant debris, particularly decaying hay and straw. This combination of fauna strongly supports the origin deposit as stable manure.

While the presence of a stable manure indicator fauna in the timber drain could be indicative of contemporaneous runoff and redeposition from the stable, the lack of aquatic insects supports the possibility for in-fill or deliberate dumping as appears to be the case for the Roman deep wells at Skeldergate and Bedern in York (Hall *et al.* 1980; Kenward *et al.* 1986).

Most of the plant remains were taxa likely to have been part of a local weed flora or to have been imported with cut wetland vegetation (as litter for stables?), though with evidence from hazel nut and fig for some material from domestic occupation. In the case of the fig, an exotic origin for the fruit seems highly likely.

The lack of evidence for cereals in a deposit containing grain pests is not especially problematic since the routes by which such remains can travel on their way to a forming deposit are complex (Hall and Kenward 1998).

Acknowledgements

I am grateful to Ben Holloway and Philip Crummy of the Colchester Archaeological Trust for the opportunity to work on this material, to Harry Kenward for his assistance with this project and comments on the draft, and to Terry O'Connor for assistance with identification of mammalian fragments.

Appendix 2B:

Complete list of invertebrate remains recorded from the 'detail' recorded subsample from the Roman timber drain at 21 St Peter's Street, Colchester.

Order and nomenclature follow Kloet and Hincks (1964-77) for insects. Ecological codes used in calculating statistics and minimum number of individuals (MNI) are given (they are explained in Appendix 1C). The remains were of adults unless stated. 'Sp.' indicates that record was probably an additional taxon, 'sp. indet.' that the material may have been of a taxon listed above it.

Taxon	**MNI**	**Ecological Code**
Arachnida		
Acarina sp.	1	--
Insecta		
Diptera		
Diptera sp. (pupa)	3	--
Coleoptera		
Cercyon analis (Paykull)	2	Rt
Phyllodrepa ?floralis/salicis	1	Rt
Gyrohypnus ?fracticornis (Muller)	1	Rt
Aleochara sp.	1	U
Aphodius granarius (Linn.)	2	ob-rf
Tipnus unicolor (Piller & Mitterpacher)	1	rd
Ptinus ?fur (Linn.)	2	Rd
Cryptolestes ferrugineus (Steph.)	2	G
Lathridius minutus group (Linn.)	1	Rd
Palorus ratzeburgi (Wiss.)	4	G
Chrysomelidae sp. indet.	1	--
Sitophilus granarius (Linn.)	1	G
Coleoptera sp.	1	--
Coleoptera (larvae)	1	--
Hemiptera		
Psylloidea sp. (nymph)	1	--

Appendix 2C:

Abbreviations for ecological codes used for interpretation of insect remains in text and tables.

Lower case codes in parentheses are those assigned to taxa and used to calculate the group values (the codes in capitals). Indivs - individuals (based on MNI); No - number.

No 'certain' outdoor taxa (oa) SOA
No 'certain' outdoor indivs NOA
No OA and probable outdoor taxa (oa + ob) SOB
No OB indivs NOB
No aquatic taxa (w) SW
No aquatic indivs NW
No damp ground/waterside taxa (d) SD
No damp D indivs ND
No strongly plant-associated taxa (p) SP
No strongly P indivs NP
No heathland/moorland taxa (m) SM
No M indivs NM
No wood-associated taxa (l) SL
No L indivs NL
No decomposer taxa (rt + rd + rf) SRT
No RT indivs NRT
No 'dry' decomposer taxa (rd) SRD
No RD indivs NRD
No 'foul' decomposer taxa (rf) SRF
No RF indivs NRF
No synanthropic taxa (sf + st + ss) SSA
No synanthropic indivs NSA
No facultatively synanthropic taxa
SSF
No SF indivs NSF
No typical synanthropic taxa SST
No ST indivs NST
No strongly synanthropic taxa SSS
No SS indivs NSS
No uncoded taxa (u) SU
No indivs of grain pests (g) NG

Appendix 2D:

Complete list of plant remains and some other components of the residue from the subsample of St Peters Street, Colchester.

All material was preserved by anoxic 'waterlogging' unless otherwise indicated. Nomenclature and taxonomic order follow Tutin et al. (1964-80) for vascular plants. Abundance is presented using a four-point semi-quantitative scale from 1—one or a few fragments or individuals (or a very small component of the original sample volume) to 4—abundant remains or a large component of the sample volume.

Name	**Vernacular**	**Abundance**
Eleocharis sp.	Spike rush	2
Ranunculus flammula L.	Lesser spearwort	2
Glyceria sp.	Sweet grass	1
Atriplex sp.	Orache	2
Polgonum	Knotgrass	1
Rumex sp.	Docks	2
Ficus carica L.	Fig	1
Prunus	Sloe, plum, etc	1
Corylus avellana	Hazel	1

Appendix 3

Stable-Isotopic Assays Relating to Modern *Sitophilus granarius*, Cereals, and Quality Control Procedures

Appendix 3A:

Nitrogen-15 and Carbon-13 Results: *Sitophilus granarius* L.

Sample	Elemental N	Result δ-$^{15}N_{AIR}$	Mean δ-$^{15}N_{AIR}$	Elemental C	Result δ-$^{13}C_{V\text{-}PDB}$	Mean δ-$^{13}C_{V\text{-}PDB}$
Ident.	**(%)**	**(‰)**	**(‰)**	**(%)**	**(‰)**	**(‰)**
S20091	2.19	1.71		20.16	-27.09	
"	1.88	1.70	1.70	18.97	-27.21	-27.15
S20092	3.66	1.08		28.86	-28.00	
"	2.95	0.57	1.08	23.76	-27.98	-27.99
S20093	2.90	-1.23		26.22	-26.03	
"	-	-	-1.23	-	-	-26.03
S20094	2.82	2.15		21.79	-24.04	
"	-	-	2.15	-	-	-24.04
S20095	4.12	1.40		30.44	-24.23	
"	4.86	1.62	1.51	35.06	-24.56	-24.39
S20096	2.89	2.55		20.73	-26.16	
"	3.13	2.76	2.65	22.12	-26.39	-26.27
S20097	5.10	1.65		34.77	-20.44	
"	4.75	2.01	1.83	32.25	-20.96	-20.70
S20098	4.89	2.04		33.95	-20.25	
"	4.01	3.07	2.56	29.46	-20.16	-20.21

Appendix 3B:

Nitrogen-15 and Carbon-13 Results: Cereals

Sample	Elemental N	Result δ-$^{15}N_{AIR}$	Mean δ-$^{15}N_{AIR}$	Elemental C	Result δ-$^{13}C_{V\text{-}PDB}$	Mean δ-$^{13}C_{V\text{-}PDB}$
Ident.	(%)	(‰)	(‰)	(%)	(‰)	(‰)
S20099	1.11	2.69		40.56	-27.59	
"	1.30	3.18	2.94	41.79	-27.79	-27.69
S200910	1.56	2.75		43.24	-28.30	
"	1.85	2.94	2.85	42.87	-28.55	-28.42
S200911	1.13	2.12		38.86	-24.94	
"	1.13	2.14	2.13	38.45	-24.79	-24.87
S200912	1.33	2.47		38.95	-24.50	
"	1.01	2.38	2.42	37.32	-24.61	-24.55
S200913	1.59	2.38		41.07	-26.21	
"	1.62	2.51	2.45	41.29	-26.11	-26.16
S200914	1.61	2.32		41.61	-26.49	
"	1.23	2.62	2.47	40.15	-26.43	-26.46
S200915	2.19	3.08		39.86	-22.63	
"	2.04	2.99	3.03	39.75	-22.52	-22.57
S00916	2.20	3.56		39.73	-21.95	
"	2.05	3.31	3.43	38.82	-21.83	-21.89

Appendix 3C:

Quality Control: Reference Standards Nitrogen-15 and Carbon-13

	IA-R042		IA-R045	IA-R046	IA-R005	IA-R006
	Bovine Liver		Ammonium Sulphate	Ammonium Sulphate	Beet Sugar	Cane Sugar
	$\delta^{15}N_{Air}$ (‰)	$\delta^{13}C_{V\text{-}PDB}$ (‰)	$\delta^{15}N_{Air}$ (‰)	$\delta^{15}N_{Air}$ (‰)	$\delta^{13}C_{V\text{-}PDB}$ (‰)	$\delta^{13}C_{V\text{-}PDB}$ (‰)
	7.76	-21.53	-4.74	21.89	-26.08	-11.83
	7.47	-21.68	-4.64	21.91	-26.07	-11.80
	7.77	-21.61	-4.70	22.28	-26.19	-11.86
	8.01	-21.68	-5.15	22.26	-26.28	-11.72
	7.47	-21.69	-5.01	22.14	-26.20	-11.79
	7.65	-21.61		21.85	-26.00	-11.75
	7.25	-21.58			-26.03	
	7.71	-21.50			-26.02	
	7.88	-21.63				
Mean	7.66	-21.61	-4.85	22.05	-26.11	-11.79
1 s.d.	0.23	0.07	0.22	0.20	0.10	0.05
n	9	9	5	6	8	6
Accepted	7.65	-21.60	-4.71	22.04	-26.03	-11.64

Appendix 3D:

Deuterium Results: *Sitophilus granarius* L.

Sample Name	Sample Descript.	Weight	Hydrogen	$\delta^2H_{V\text{-}SMOW}$	Mean $\delta^2H_{V\text{-}SMOW}$	$\delta^2H_{V\text{-}SMOW}$ (BWB Adjusted)	Mean δ^2H (BWB Adjusted)
		(mg)	(%)	(‰)	(‰)	(‰)	(‰)
G1	Beetle remains	0.67	2.26	-116.21		-119.13	
G2	Beetle remains	0.52	3.07	-115.61		-118.51	
G3	Beetle remains	0.47	2.70	-101.92		-104.48	
G4	Beetle remains	0.77	2.62	-101.72		-104.27	
G5	Beetle remains	0.84	2.47	-111.43		-114.22	
G6	Beetle remains	0.81	2.13	-73.22		-75.06	
G7	Beetle remains	0.90	2.91	-99.84		-102.34	
G8	Beetle remains	0.85	2.47	-91.66		-93.96	
G9	Beetle remains	0.80	3.55	-91.07		-93.36	
G11	Beetle remains	0.57	2.46	-95.75		-98.15	
G12	Beetle remains	0.30	4.50	-111.98		-114.79	
G13	Beetle remains	0.67	2.49	-88.71		-90.93	
G14	Beetle remains	1.30	2.05	-91.53		-93.82	
G15	Beetle remains	0.47	2.53	-84.66		-86.78	
G16	Beetle remains	0.98	2.08	-89.55		-91.80	
G17	Beetle remains	1.35	2.17	-96.09		-98.50	
G18	Beetle remains	0.78	2.15	-108.54		-111.27	
G19	Beetle remains	---	---	---		---	
G20	Beetle remains	1.63	1.65	-112.63		-115.45	

G21	Beetle remains	0.83	2.22	-89.96		-92.22	
G22	Beetle remains	---	---	---		---	
G23	Beetle remains	1.05	1.68	-96.23		-98.65	
"	"	0.86	1.74	-93.77	-95.00	-96.12	-97.38
G24	Beetle remains	1.16	2.53	-108.30		-111.01	
G25	Beetle remains	1.15	2.07	-101.41		-103.95	
G26	Beetle remains	0.73	2.16	-98.36		-100.82	
G27	Beetle remains	1.05	2.57	-111.24		-114.03	
G28	Beetle remains	0.64	2.67	-97.67		-100.11	
G29	Beetle remains	0.76	2.40	-90.52		-92.79	
G30	Beetle remains	1.02	2.34	-99.34		-101.83	
G31	Beetle remains	1.08	1.33	-107.16		-113.22	
"	"	1.02	1.52	-101.24	-104.20	-106.96	-110.09
G32	Beetle remains	1.08	1.43	-92.93		-98.18	
"	"	0.93	1.58	-94.04	-93.49	-99.36	-98.77
G33	Beetle remains	1.26	1.36	-101.82		-107.57	
G34	Beetle remains	1.24	1.94	-83.26		-87.96	
G35	Beetle remains	1.1	2.43	-97.99		-103.53	
G36	Beetle remains	1.04	2.09	-105.46		-111.43	
G37	Beetle remains	1.31	1.93	-93.93		-99.24	
G39	Beetle remains	0.98	2.45	-89.67		-94.74	
G40	Beetle remains	0.94	2.22	-94.93		-100.30	
G41	Beetle remains	1.13	2.22	-93.40		-98.68	
"	"	0.91	2.36	-89.19	-91.29	-94.23	-96.45

Appendix 3E:

Deuterium Results: Cereals

Sample Name	Sample Descript.	Weight	Hydrogen	$\delta^2H_{V\text{-}SMOW}$	Mean $\delta^2H_{V\text{-}SMOW}$	$\delta^2H_{V\text{-}SMOW}$ (BWB Adjusted)	Mean δ^2H (BWB Adjusted)
		(mg)	(%)	(‰)	(‰)	(‰)	(‰)
G42	Cereal kernels	1.18	5.27	-87.68		-92.64	
"	"	1.25	5.86	-99.33	-93.51	-104.95	-98.80
G43	Cereal kernels	0.93	5.43	-102.49		-108.28	
"	"	0.90	5.25	-101.05	-101.77	-106.76	-107.52
G44	Cereal kernels	1.10	5.06	-70.86		-74.87	
G45	Cereal kernels	1.06	5.09	-78.87		-83.33	
G46	Cereal kernels	1.20	5.02	-87.21		-92.14	
"	"	1.10	5.03	-88.02	-87.62	-93.00	-92.57
G47	Cereal kernels	1.10	5.58	-97.98		-103.51	
G48	Cereal kernels	0.97	5.18	-124.05		-131.06	
"	"	1.17	5.03	-127.79	-125.92	-135.02	-133.04
G49	Cereal kernels	0.92	5.59	-113.06		-119.45	
"	"	1.13	4.94	-118.51	-115.78	-125.21	-122.33
G50	Cereal kernels	1.08	5.15	-81.91		-86.54	
G51	Cereal kernels	1.06	5.42	-86.44		-91.33	
G52	Cereal kernels	1.06	5.12	-59.65		-63.02	

Appendix 3F:

Deuterium Results: Water

Water			
Sample Name	Sample Description	δ^2H_{VSMOW}	Mean δ^2H_{VSMOW}
		(‰)	(‰)
Water	Used to rinse samples	-47.43	
		-47.73	-47.58

Appendix 3G:

Quality Control Reference Standards: Deuterium

Check Sample	Replicate	$\delta^2H_{V\text{-}SMOW}$	$\delta^2H_{V\text{-}SMOW}$ (BWB Adjusted)
		(‰)	(‰)
IA-R002	1	-112.81	
(mineral oil)	2	-109.06	
	3	-107.51	
	4	-110.68	
	5	-110.59	
	6	-112.15	
	7	-111.60	
	8	-111.29	
	9	-110.78	
	10	-111.50	
	Mean	-110.80	
	St. Dev.	1.53	
	Accepted value	-111.2	
IAEA-CH-7	1	-100.23	
(polyethylene)	2	-101.11	
	3	-102.82	
	4	-102.32	
	5	-102.20	
	6	-101.64	
	7	-101.67	
	8	-101.89	
	9	-103.10	
	10	-100.70	
	11	-100.31	
	12	-101.78	
	Mean	-101.65	
	St. Dev.	0.92	
	Accepted value	-100.3	
BWB-II	1	-106.64	-109.31
(whale baleen)	2	-104.08	-106.69
	3	-103.05	-108.88
	4	-102.22	-107.12
	Mean	-104.00	-108.00
	St. Dev.	1.92	1.29
	Accepted value		-108

Appendix 3H:

Quality Control Reference Standards: Deuterium Water

Check Sample	Replicate	δ^2H_{VSMOW}
		(‰)
IA-R053	1	-61.05
(natural water)	2	-62.39
	Mean	-61.72
	St. Dev.	0.95
	Accepted value	-61.97

Appendix 3I:

Stable-Carbon and Nitrogen Bradford Analyses

Sample	Weight	%N	$\delta^{15}N$	%C	$\delta^{13}C$	C/N
Sit1	1.03	6.3	5.61	33.9	-25.89	6.26
Sit2	1.54	6.5	5.70	36.4	-26.05	6.56
Sit3	1.23	5.3	7.00	28.6	-27.92	6.31
Sit4	1.55	5.7	6.28	35.0	-27.89	7.12
Sit5	1.18	4.9	6.52	26.8	-25.68	6.40
Sit6	0.97	6.5	6.27	43.9	-25.75	7.93

Appendix 4

Stable-Isotopic Assays for Insect Remains Recovered from Erkelenz-Kückhoven, Eythra, Plaußig, and West Stow

Appendix 4A:

Nitrogen-15 and Carbon-13 Results

Sample Ident.	Elemental N (%)	Result δ-$^{15}N_{AIR}$ (‰)	Elemental C (%)	Result δ-$^{13}C_{V\text{-}PDB}$ (‰)	Site
Sit27	1.22	5.85	10.44	-23.39	Plaußig
Sit28	0.45	1.06	4.77	-25.87	Plaußig
Sit29	1.67	4.66	13.61	-24.74	Plaußig
Sit30	-	-	3.22	-26.88	Plaußig
Sit31	-	-	9.37	-27.54	Plaußig
Sit32	0.96	2.73	8.39	-21.89	Plaußig
Sit33	-	-	4.88	-18.28	Eythra
Sit34	-	-	-	-	Eythra
Sit35	-	-	6.09	-24.62	Eythra
Sit36	0.41	6.89	4.12	-22.96	Eythra
Sit46	2.09	4.02	19.74	-25.16	West Stow
Sit47	2.55	21.10	15.64	-24.76	West Stow
Sit48	1.62	6.86	15.91	-27.29	West Stow
Sit49	0.53	3.91	6.24	-27.39	West Stow
Sit50	3.82	-1.86	33.91	-27.88	West Stow
Sit51	1.13	-1.25	11.88	-26.09	West Stow
Sit52	0.33	-6.02	4.22	-25.23	Erkelenz-Kückhoven
Sit53	0.35	-2.16	4.44	-26.25	Erkelenz-Kückhoven
Sit54	0.35	-5.99	4.14	-28.20	Erkelenz-Kückhoven
Sit55	4.73	-1.60	43.09	-25.42	Erkelenz-Kückhoven
Sit56	0.51	2.28	5.92	-29.38	Erkelenz-Kückhoven
Sit57	-	-	-	-	Erkelenz-Kückhoven
Sit58	9.30	10.10	46.35	-25.91	Erkelenz-Kückhoven
Sit59	1.65	3.09	11.56	-29.37	Erkelenz-Kückhoven
Sit60	-	-	6.66	-26.21	Erkelenz-Kückhoven
Sit61	2.49	0.80	15.64	-23.30	Erkelenz-Kückhoven
Sit62	0.48	-1.66	4.50	-25.65	Erkelenz-Kückhoven

Appendix 4B:

Deuterium Results

	un-corrected	BWB II corrected			
Sample	**Result δ-$^{2}H_{V\text{-}SMOW}$**	**Result δ-$^{2}H_{V\text{-}SMOW}$**	**equilibration**	**mean BWB II value**	**Site**
Ident.	**(‰)**	**(‰)**	**correction factor**	**(‰)**	
Sit28	-119.68	-119.98	1.0026	-107.72	Plaußig
Sit32	-106.18	-106.45	1.0026	-107.72	Plaußig
Sit36	-100.73	-100.99	1.0026	-107.72	Eythra
Sit46	-84.46	-84.68	1.0026	-107.72	West Stow
Sit48	-97.33	-97.58	1.0026	-107.72	West Stow
Sit49	-84.47	-84.69	1.0026	-107.72	West Stow
Sit51	-73.50	-76.17	1.0363	-104.21	West Stow
Sit52	-123.49	-123.81	1.0026	-107.72	Erkelenz-Kückhoven
Sit53	-121.46	-121.78	1.0026	-107.72	Erkelenz-Kückhoven
Sit54	-154.69	-160.31	1.0363	-104.21	Erkelenz-Kückhoven
Sit56	-125.88	-130.46	1.0363	-104.21	Erkelenz-Kückhoven
Sit58	-68.23	-70.71	1.0363	-104.21	Erkelenz-Kückhoven
Sit62	-101.07	-104.74	1.0363	-104.21	Erkelenz-Kückhoven

Appendix 4C:

Quality Control Reference Standards: Deuterium

	IAEA-CH-7	BWB II	IA-R002
	(PEF)	(Whale Baleen)	(Mineral oil)
	δ-$^2H_{V\text{-}SMOW}$ (‰)	δ-$^2H_{V\text{-}SMOW}$ (‰)	δ-$^2H_{V\text{-}SMOW}$ (‰)
	-101.78	-107.30	-112.51
	-101.67	-108.14	-111.38
	-102.99	-103.93	-109.30
		-104.50	-111.09
Mean	-102.15	-105.97	-111.07
1 s.d.	0.73	2.07	1.33
n	3	4	4
Expected	-100.3	-108	-111.2

Appendix 5

Raw Data from Amino Acid Racemization (AAR) Analyses of Beetle Remains from Waterlogged Archaeological Contexts

The experiments were carried out in collaboration with the Kirsty Penkman of the North East Amino Acid Racemization (NEAAR), Departments of Chemistry and Archaeology, University of York. The methods used for analysis followed those outlined in Jones *et al*. 2005. Palaeoentomological materials were retrieved from samples from Park View Schools, Chester-le-Street, County Durham.

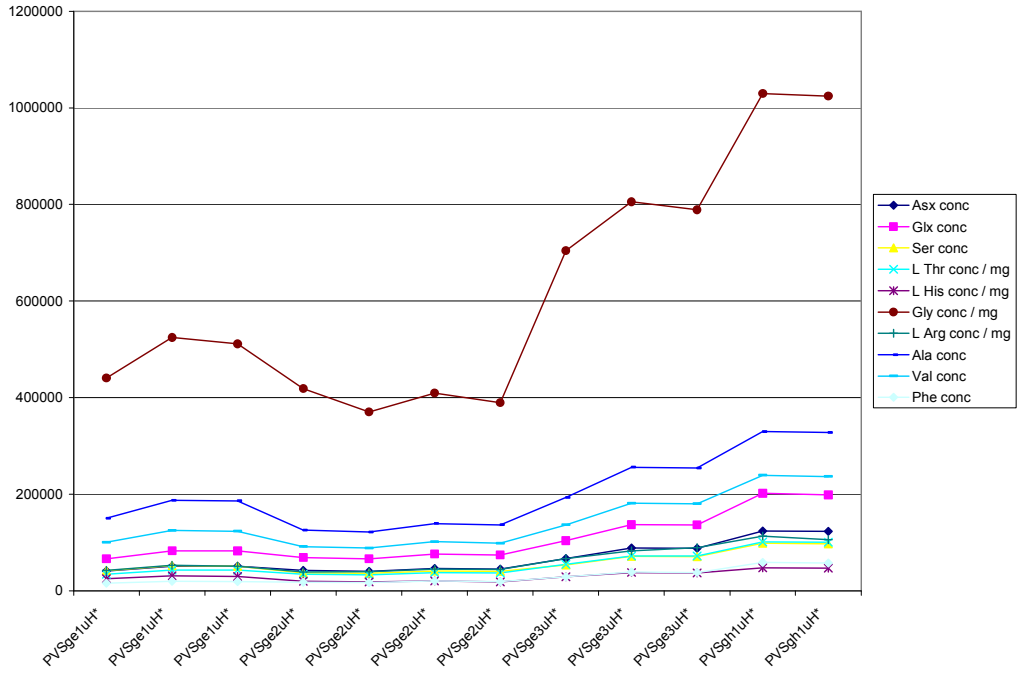
Appendix 5A:

AAR Raw Results

SampleName	File	D Phe	D Phe	L Leu	L Leu	D Ile	D Ile	D Leu	D Leu	ddd	ddd	
0.167d/H2O	G271-6140.xls	Area	MeasRetTime	Area	MeasRetTime	Area	MeasRetTime	Area	MeasRetTime	Area	MeasRetTime	
0.167d/H2O	G271-6150.xls	1648.05	81.07	8883.18	84.70	2131.75	86.33	1737.17	89.37			
0.167d/H2O	G271-6159.xls	2856.13	81.11	14100.27	84.73	3594.50	86.37	2767.36	89.42			
0.167d/H2O	G271-6167.xls	1113.65	81.07	5712.18	84.74	1439.08	86.33	1124.86	89.38			
4588uH*	G271-5241.xls	1149.58	80.99	5916.96	84.65	1486.71	86.26	1193.07	89.28			50
4588uH*	G271-5251.xls	222.75	81.06	16623.25	84.66	743.26	86.32	668.84	89.39	PVSge1uH*	0.1	100
4588uH*	G271-5260.xls	115.10	81.04	8623.87	84.70	390.49	86.32	341.94	89.36	PVSge1uH*	0.1	100
4589uH*	G271-5136.xls	121.03	81.07	9184.90	84.73	331.29	86.36	321.36	89.41	PVSge1uH*	0.1	50
4589uH*	G271-5148.xls	129.72	80.97	7420.45	84.63	420.89	86.26	342.74	89.28	PVSge2uH*	0.07	50
4589uH*	G271-5157.xls	134.82	81.10	7861.26	84.78	400.61	86.39	287.70	89.43	PVSge2uH*	0.07	100
4589uH*	G271-5166.xls	68.63	81.03	3818.83	84.72	152.14	86.33	135.46	89.34	PVSge2uH*	0.07	100
4590uH*	G271-5343.xls	77.74	81.02	4026.96	84.70	214.93	86.29	180.79	89.35	PVSge2uH*	0.07	50
4590uH*	G271-5353.xls	344.44	81.07	15292.79	84.69	1119.99	86.33	661.02	89.38	PVSge3uH*	0.08	100
4590uH*	G271-5362.xls	177.69	81.05	7887.92	84.69	570.82	86.30	344.88	89.34	PVSge3uH*	0.08	100
4591uH*	G271-5445.xls	187.20	81.07	8373.39	84.73	511.17	86.35	287.29	89.39	PVSge3uH*	0.08	50
4591uH*	G271-5455.xls	69089.25	81.04	127358.55	84.52	828.35	86.29	27300.17	89.37	PVSgh1uH*	0.2	500
4591uH*	G271-5464.xls	109.43	81.04	4533.60	84.71	334.44	86.30	209.61	89.37	PVSgh1uH*	0.2	500
7Mbk130607	G271-5547.xls	105.90	81.04	4318.07	84.74	327.27	86.34	209.28	89.39	PVSgh1uH*	0.2	50
LhArgbk150607	G271-6433.xls			16.87	84.81							
LhArgbk180607	G271-6558.xls			20.16	84.72	27.28	87.02	184.21	88.13			
				14.66	84.82							

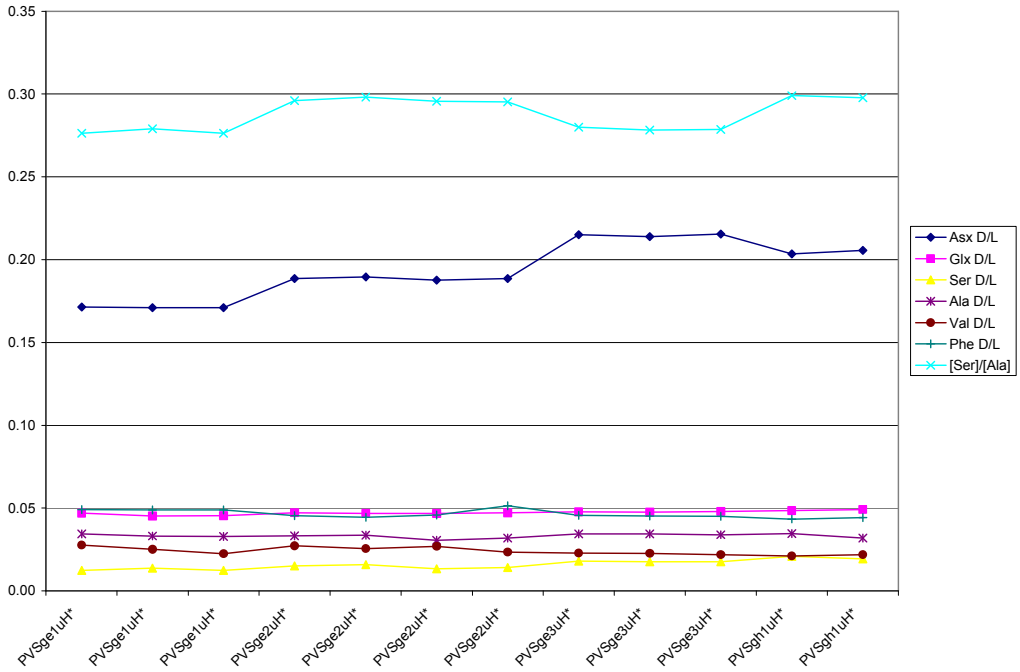
Appendix 5B:

Amino Acid Concentrations



Appendix 5C:

D/L Ratios



Appendix 6

Supplementary Data and Figures Pertaining to the Genetic Experiments Discussed in Chapter 8

Appendix 6A.

Details of methodology

The archaeological specimens were removed from the alcohol and dried overnight at 55 °C. Afterwards, the fossil and modern specimens were placed in 2 ml Eppendorf Biopur tubes, fully immersed in digestion buffer (400 µl), and incubated overnight at 55 °C with gentle agitation. As in Gilbert *et al.* (2007), the buffer was modified from Pfeiffer *et al.* (2004) and consisted of 5 mM $CaCl_2$, 1 % sodium dodecyl sulphate (SDS), 40 mM dithiotreitol (DTT), 2.5 mM ethylenediamine tetraacetic acid (EDTA), 250 mg/ml proteinase K, 10 mM Tris buffer pH 8, and 10 mM NaCl (final concentrations). After incubating with gentle agitation for 16-20 hours, the nucleic acids were purified from the solution using Qiaquick PCR Clean-up kit.

At this stage, 2 ml of Qiagen PB buffer were added to the 400 µl digestion buffer and vortexed gently. Once mixed, 650 µl aliquots were added to the spin column, spun at 6000 g for 1 minute, and the collection tube emptied. After repeating this step three times to ensure that the extraneous non-DNA material had been separated and removed and that the remaining DNA had sufficiently bound to the silica filter, 500 µl PE buffer was added to the column and spun for 1 minute at 10000 g to rinse the filter. The collection tube was emptied and the column spun again at maximum speed for 3 minutes to dry the filter. The filter was transferred to a clean new 1.5ml Eppendorf Biopur tube and 50 µl of AE Elution buffer was placed on the filter and left for 5 minutes to initiate the release of the DNA from the silica filter. The column was spun again at >10000 g for 1 minute allowing the solution to migrate to the base of the new tube.

The presence of amplifiable mitochondrial (mtDNA) and nuclear DNA (nuDNA) in the extract was assayed through PCR. The mtDNA was assayed through the amplification of a range of short (98 bp-256 bp; see Table 8.1) fragments of the

conserved cytochrome oxidase I (CO1) mtDNA gene (GenBank ID# AY131101) using primers designed by MTPG. Each extract was assayed with four primer sets (to account for degradation within the mtDNA gene). The forward primers SitCO1F1 (5' GCCTTCCCACGATTAAACAA; annealing temperature 56 °C) and SitCO1F2 (5' TCGTTACTGCTCACGCATTT; annealing temperature 56 °C) were paired with reverse primers SitCO1R1 (5' GAAAAAGGTGCTGGAACAGG; annealing temperature 56 °C) and SitCO1R3 (5' ATTGCCCATGAAGGAGCTT; annealing temperature 56 °C).

NuDNA was assayed through short (57 bp-88 bp; see Table 8.1) fragments of the multicopy 18s ribosomal RNA gene (GenBank ID# AF389038). The short (57 bp) primer set used the forward primer Sit18sF1 (5' GTTGGTGGAGCGATTTGTCT) and the reverse Sit18sR1 (5' GCAGGCTAGAGTCTCGTTCG; annealing temperature 56 °C). The 88 bp primer set paired forward primer Sit18sF3 (5' CACCGGAAGGATTGACAGAT) with reverse Sit18sR3 (5' AGACAAATCGCTCCACCAAC; annealing temperature 56 °C).

Each 25 µl PCR reaction contained 1 µl extracted DNA, 2.5 µl 10x PCR buffer, 1 µl 2.5mM $MgCl_2$, 1 µl of each primer, 0.2 µl 25 mM mixed dNTPs, 0.2 µl HiFi enzyme, and 1 µl bovine serum albumin (BSA), and was cycled 50 times. To briefly investigate the quantity of usable DNA extracted from each specimen, the PCR products were tested on 2 % gels stained with ethidium bromide. The amplified PCR products were purified using an Invitek purification kit (PCRapace) and cloned with Invitrogen Topo TA cloning kit.

New PCRs were performed on the *Escherichia coli* colonies which contained the inserted PCR extracts. The forward M13F and reverse M13R primers were amplified for 35 cycles with an annealing temperature of 53 °C, purified using Invitek Vario Cleanup, and sequenced several times with an ABI 3730x1 capillary sequencer

(Applied Biosystems), in both directions, using BigDye Terminator v. 3.1 chemistry (Applied Biosystems). For sequence information see Appendices 2-5.

Data authenticity

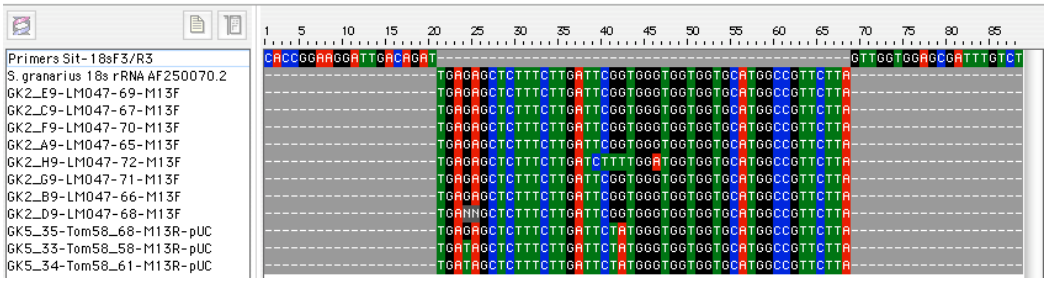
Although we did not adopt all the criteria for authenticity as outlined by Cooper and Poinar (2000), notably independent replication of the results and amino acid racemization, as following the arguments of Gilbert *et al*. (2005) we believe that a number of factors support the data authenticity. Firstly, the ancient samples fall within the time frame that DNA survival can be expected. Secondly, the data demonstrated appropriate molecular behavior. Specifically, while all the mtDNA and nuDNA PCR products could be amplified from the younger (medieval samples), only the shortest mtDNA products could be amplified from the older Roman sample. This is consistent with what is to be expected due to the effect of DNA degradation increasing with time. Thirdly, all DNA sequences were generated from multiple cloned PCR products, with sufficient sequences produced from each cloning reaction to ensure that DNA degradation will not have erroneously affected the sequence. Fourthly the amplified aDNA sequences were direct matches with *S. granarius,* with the exception of a small amount of variation observed in the 88bp 18s nuDNA sequences. We believe this likely to arise from natural variation within the species, although until future samples confirm the observation this hypothesis remains unproven. Fifthly, PCR and extraction blanks were consistently empty, indicating cross or background contamination of the target is unlikely. Sixthly it is extremely hard to argue for a plausible alternative source of modern *S. granarius* DNA contamination in the work. Lastly, no previous work had been done on the target species in the aDNA (or modern DNA) laboratories in Copenhagen. To conclude, we believe that the data fully supports the authenticity of the findings.

Appendix 6B:

Graphical representation of aligned mtDNA sequences

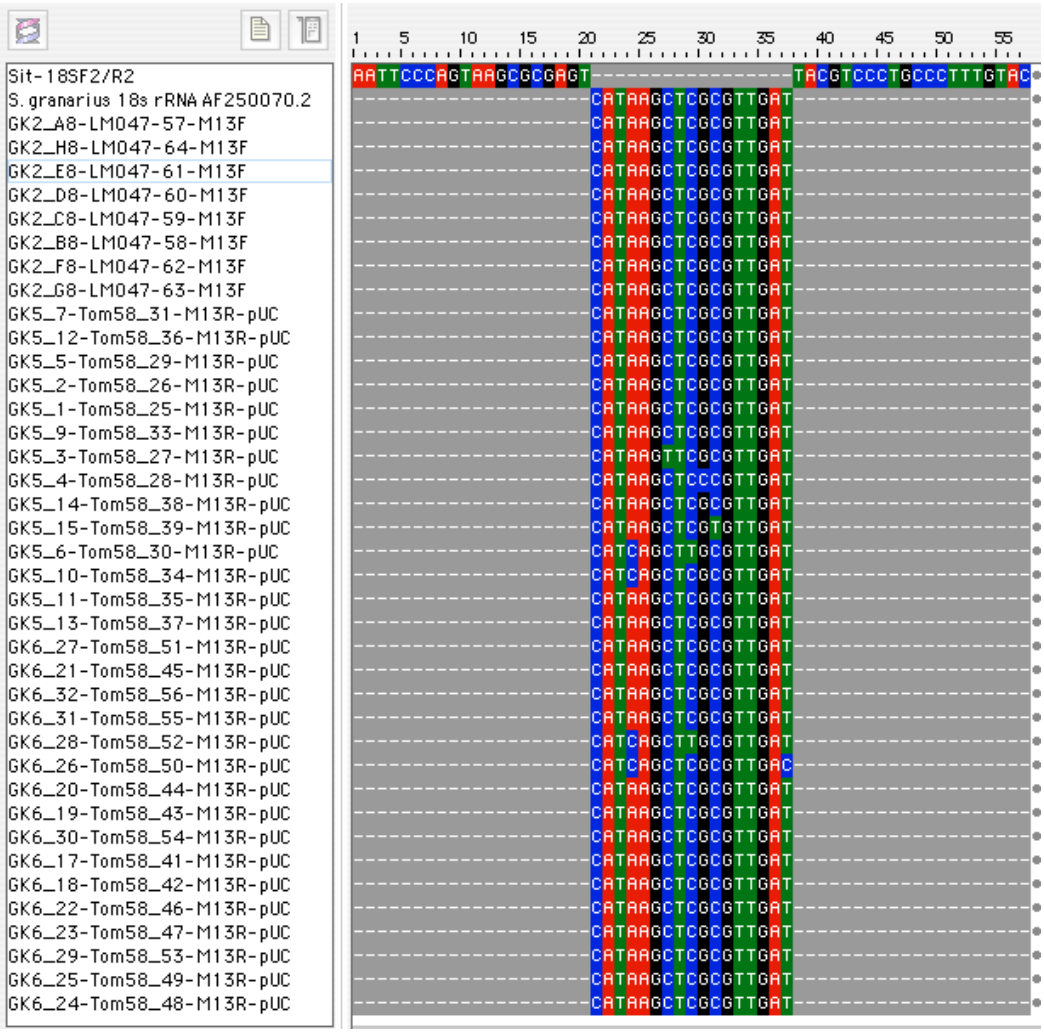
Appendix 6C:

Graphical alignment of 88bp nuDNA sequences



Appendix 6D:

Graphical alignment of 57bp nuDNA sequences



Appendix 6E:

FASTA sequence alignments of primer sequences and sequences of cloned PCR products for mtDNA amplifications

Data is presented aligned in FASTA format. A small minority of sequences are incomplete due to poor sequencing electropherograms.

>Primer_Sit_CO1F2
TCGTTACTGCTCACGCATTT----------

>Primer_Sit_CO1R3

----------ATTGCCCATGAAGGAGCTT
>GK1_92_2007-10-17

ATTATAATTTTTTTTATAGTTATACCTATCATAATTGGAGGATTCGGAAAT
TGACTAATTC
CATTAATATTAGGAGCCCCAGATATAGCCTTCCCACGGTTAAACAATATG
AGATTCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTA
TTGAAAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCC
AAT----------
>GK1_90_2007-10-17

ATTATAATTTTTTTTATAGTTATACCTATCATAATTGGAGGATTCGGAAAT
TGACTAATTC
CATTAATATTAGGAGCCCCAGATATAGCCTTCCCACGGTTAAACAATATG
AGATTCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTA
TTGAAAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCC
AAT----------
>GK1_93_2007-10-17

ATTATAATTTTTTTTATAGTTATACCTATCATAATTGGAGGATTCGGAAAT
TGACTAATTC
CATTAATATTAGGAGCCCCAGATATAGCCTTCCCACGGTTAAACAATATG
AGATTCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTA
TTGAAAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCC
AAT----------
>GK1_91_2007-10-17

ATTATAATTTTTTTTATAGTTATACCTATCATAATTGGAGGATTCGGAAAT
TGACTAATTC
CATTAATATTAGGAGCCCCAGATATAGCCTTCCCACGGTTAAACAATATG
AGATTCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTA

TTGAAAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCC
AAT----------
>GK1_94_2007-10-17

CCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATTGAAAAAGGTGCT
GGAACAGGGTGAACAGTT
TACCCACCTCTATCATCCAAT----------
>GK1_52_2007-10-17

CCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATTGAAAAAGGTGCT
GGAACAGG----------
>Primer_Sit_CO1R1

GAAAAAGGTGCTGGAACAGG----------
>Primer_Sit_CO1F1

----GCCTTCCCACGATTAAAC
AA----------
>GK1_54_2007-10-17

CTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----------
>GK1_51_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK1_55_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK1_53_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK1_56_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK7_PV113 _50_2007-10-17

----------TATGAGAT

TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK7_PV113 _46_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK7_PV113 _48_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK7_PV113 _49_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK8_PV144 _60_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK8_PV144 _61_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK8_PV144 _58_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK8_PV144 _59_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCTATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK6_PETER4977B_85_2007-10-17

ATTATAATTTTTTTTATAGTTATACCTATCATAATTGGAGGATTCGGAAAT
TGACTAATTC
CATTAATATTAGGAGCCCCAGATATAGCCTTCCCACGGTTAAACAATATG
AGATTCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTA
TTGAAAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCC
AAT----------
>GK6_PETER4977B_83_2007-10-17

ATTATAATTTTTTTTATAGTTATACCTATCATAATTGGAGGATTCGGAAAT
TGACTAATTC

CATTAATATTAGGAGCCCCAGATATAGCCTTCCCACGGTTAAACAATATG
AGATTCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTA
TTGAAAAAGGTGCTGGAACAGTGTGAACAGTTTACCCACCTCTATCATCC
AAT----------
>GK6_PETER4977B_81_2007-10-17

ATTATAATTTTTTTTATAGTTATACCTATCATAATTGGAGGATTCGGAAAT
TGACTAATTC
CATTAATATTAGGAGCCCCAGATATAGCCTTCCCACGGTTAAACAATGTG
AGATTCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTA
TTGAAAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCC
AAT----------
>GK6_PETER4977B_71_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATTGA
AAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCCAAT---

>GK6_PETER4977B_69_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATTGA
AAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATTCAAT---

>GK6_PETER4977B_72_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATTGA
AAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCCAAT---

>GK6_PETER4977B_74_2007-10-17

----------TATGAGAT
TCTGACTACCTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATTGA
AAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCCAAT---

>GK6_PETER4977B_70_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATTGA
AAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCCAAT---

>GK6_PETER4977B_40_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK6_PETER4977B_39_2007-10-17

----------TATGAGAT

TCTGACTACTTCCCCCATCTTTAGTTCTTCTATTAATAAGAAGATTTATT----

>GK6_PETER4977B_42_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK6_PETER4977B_41_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK5_PETER4977A_63_2007-10-17

----------CT
ACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATTGAAAAAGG
TGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCCAAT----------

>GK5_PETER4977A_66_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATTGA
AAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCCAAT---

>GK5_PETER4977A_64_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATTGA
AAAAGGTGCTGGAACAGGATGAACAGTTTACCCACCTCTATCATCCAAT---

>GK5_PETER4977A_68_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATTGA
AAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCCAAT---

>GK5_PETER4977A_67_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATTGA
AAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCCAAT---

>GK5_PETER4977A_65_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATTGA
AAAAGGTGCTGGAACAGGGTGAACAGTTTACCCACCTCTATCATCCAAT---

>GK5_PETER4977A_34_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK5_PETER4977A_38_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK5_PETER4977A_37_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK5_PETER4977A_35_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK5_PETER4977A_36_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

>GK5_PETER4977A_33_2007-10-17

----------TATGAGAT
TCTGACTACTTCCCCCATCTTTAATTCTTCTATTAATAAGAAGATTTATT----

Appendix 6F:

Primer sequences and sequences of cloned PCR products for 57bp nuDNA amplifications

>Sit-18SF2/R2
AATTCCCAGTAAGCGCGAGT----------TACGTCCCTGCCCTTTGTAC
>S. granarius 18s rRNA AF250070.2
----------CATAAGCTCGCGTTGAT----------
>GK2_A8-LM047-57-M13F
----------CATAAGCTCGCGTTGAT----------
>GK2_H8-LM047-64-M13F
----------CATAAGCTCGCGTTGAT----------
>GK2_E8-LM047-61-M13F
----------CATAAGCTCGCGTTGAT----------
>GK2_D8-LM047-60-M13F
----------CATAAGCTCGCGTTGAT----------
>GK2_C8-LM047-59-M13F
----------CATAAGCTCGCGTTGAT----------
>GK2_B8-LM047-58-M13F
----------CATAAGCTCGCGTTGAT----------
>GK2_F8-LM047-62-M13F
----------CATAAGCTCGCGTTGAT----------
>GK2_G8-LM047-63-M13F
----------CATAAGCTCGCGTTGAT----------
>GK5_7-Tom58_31-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK5_12-Tom58_36-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK5_5-Tom58_29-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK5_2-Tom58_26-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK5_1-Tom58_25-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK5_9-Tom58_33-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK5_3-Tom58_27-M13R-pUC
----------CATAAGTTCGCGTTGAT----------
>GK5_4-Tom58_28-M13R-pUC
----------CATAAGCTCCCGTTGAT----------
>GK5_14-Tom58_38-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK5_15-Tom58_39-M13R-pUC
----------CATAAGCTCGTGTTGAT----------
>GK5_6-Tom58_30-M13R-pUC
----------CATCAGCTTGCGTTGAT----------

>GK5_10-Tom58_34-M13R-pUC
----------CATCAGCTCGCGTTGAT----------
>GK5_11-Tom58_35-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK5_13-Tom58_37-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK6_27-Tom58_51-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK6_21-Tom58_45-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK6_32-Tom58_56-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK6_31-Tom58_55-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK6_28-Tom58_52-M13R-pUC
----------CATCAGCTTGCGTTGAT----------
>GK6_26-Tom58_50-M13R-pUC
----------CATCAGCTCGCGTTGAC----------
>GK6_20-Tom58_44-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK6_19-Tom58_43-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK6_30-Tom58_54-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK6_17-Tom58_41-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK6_18-Tom58_42-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK6_22-Tom58_46-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK6_23-Tom58_47-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK6_29-Tom58_53-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK6_25-Tom58_49-M13R-pUC
----------CATAAGCTCGCGTTGAT----------
>GK6_24-Tom58_48-M13R-pUC
----------CATAAGCTCGCGTTGAT----------

Appendix 6G:

Primer sequences and sequences of cloned PCR products for 88bp nuDNA amplifications

>Primers Sit-18sF3/R3
CACCGGAAGGATTGACAGAT----------
GTTGGTGGAGCGATTTGTCT
>S. granarius 18s rRNA AF250070.2

TGAGAGCTCTTTCTTGATTCGGTGGGTGGTGGTGCATGGCCGTTCTTA----------
>GK2_E9-LM047-69-M13F

TGAGAGCTCTTTCTTGATTCGGTGGGTGGTGGTGCATGGCCGTTCTTA----------
>GK2_C9-LM047-67-M13F

TGAGAGCTCTTTCTTGATTCGGTGGGTGGTGGTGCATGGCCGTTCTTA----------
>GK2_F9-LM047-70-M13F

TGAGAGCTCTTTCTTGATTCGGTGGGTGGTGGTGCATGGCCGTTCTTA----------
>GK2_A9-LM047-65-M13F

TGAGAGCTCTTTCTTGATTCGGTGGGTGGTGGTGCATGGCCGTTCTTA----------
>GK2_H9-LM047-72-M13F

TGAGAGCTCTTTCTTGATCTTTTGGATGGTGGTGCATGGCCGTTCTTA----------
>GK2_G9-LM047-71-M13F

TGAGAGCTCTTTCTTGATTCGGTGGGTGGTGGTGCATGGCCGTTCTTA----------
>GK2_B9-LM047-66-M13F

TGAGAGCTCTTTCTTGATTCGGTGGGTGGTGGTGCATGGCCGTTCTTA----------
>GK2_D9-LM047-68-M13F

TGANNGCTCTTTCTTGATTCGGTGGGTGGTGGTGCATGGCCGTTCTTA----------
>GK5_35-Tom58_68-M13R-pUC

TGAGAGCTCTTTCTTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTA-------

>GK5_33-Tom58_58-M13R-pUC

TGATAGCTCTTTCTTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTA-------

>GK5_34-Tom58_61-M13R-pUC

TGATAGCTCTTTCTTGATTCTATGGGTGGTGGTGCATGGCCGTTCTTA-------
