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Six-legged Hitchhikers: An Archaeobiogeographical Account of the Early Dispersal of Grain Beetles

Gary A. King, Harry Kenward, Edith Schmidt, and David Smith
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Six-legged Hitchhikers: An Archaeobiogeographical Account of the Early Dispersal of Grain Beetles

Gary A. King1*, Harry Kenward2, Edith Schmidt3, and David Smith4

Abstract - Grain-associated insect species are economically important and archaeologically significant. Their dispersal around the globe and eventually across the North Atlantic region surely occurred through human transport rather than naturally. Most beetle cereal pests are now nearly cosmopolitan in their distribution, but their prehistoric ranges appear to have been more restricted. What is known or surmised of the early dispersal of these insect species is summarized, and the role of archaeobiogeographical data in investigating past human contact evaluated. Analysis of fossil and historic records of grain-associated beetles suggests that their dispersal corresponded with assumptions concerning human movement and interaction in the past. There is a significant fossil record for some grain beetles, but it is incomplete and predominantly from northwest Europe. More fossils are needed from across the Palaearctic and North Africa. The examination of pre-agricultural natural deposits in the Middle East, North Africa, and the Indian Subcontinent might reveal the original ranges of the pest species, the stages by which they entered into association with humans, and their earliest dispersal. With a more complete fossil record, the grain fauna may provide a useful proxy by which to evaluate cultural contact and human migration into the North Atlantic region in the past.

Introduction

Grain-associated insect pests play an important role in the reduction of human food resources in the present day (e.g., McFarlane 1989, Payne 2002, Tyler and Boxall 1984). Of these species, beetles (Order Coleoptera) are arguably the most socioeconomically significant. Additionally, beetles have been a critical factor leading to food depletion in the past (e.g., Fitch 1879, Kirby and Spence 1859, Munro 1966). These synanthropic beetles are of archaeological, biogeographical, and ecological importance as they are species that were dispersed alongside humans (often well beyond their naturally viable distributions), and thus can be used as secondary evidence of past human movement and/or trade (cf. King 2010b). But where did they originate, and when did they spread? How significant were they to past economies as people moved across the North Atlantic?

Dispersal pathways by which organisms spread between areas can be classified into corridor, filter, and sweepstakes routes (Cox and Moore 2000). In a corridor route, suitable habitats exist between the source and invaded areas. The majority of organisms would be able to disperse between the areas with little difficulty. A filter pathway presents a more limited range of habitats, so that only organisms that can exist in those habitats can disperse between the regions. The end regions in sweepstake dispersal are “islands” surrounded by a “sea” (sometimes literally) of unsuitable habitat. Depending on the scale at which habitats are examined, the dispersal of storage pest species can be placed in any one of these categories, but they are usually seen as undergoing the third type of dispersal, by hopping between isolated islands of artificial habitat (mainly food stores in temperate areas).

Elton (1958) introduced the concept of human activity as a mechanism for the passive distribution of animals and plants beyond their natural geographic ranges. Buckland (1981, 1990) attempted to trace the dispersal of stored-product pests by people on the basis of the archaeoentomological records available at the time. He successfully demonstrated that pests were transported in the past, but patterns of movement or origins for the evaluated species could only be guessed at in view of the paucity of fossil data, especially from beyond the British Isles. Buckland offered speculations and urged for more archaeoentomological investigations across Eurasia. The themes introduced by Buckland have subsequently been touched on and amplified by others (e.g., King 2010b; Panagiotakopulu 2000; Pfarrre 2010; Smith and Kenward 2011, 2012). Three decades after Buckland’s seminal 1981 paper, we use the currently available fossil and literary evidence to revisit Buckland’s review.

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The Archaeological Record of Storage Pests

Many thousands of samples from archaeological deposits have now been examined for insect remains, and although most have been from sites in the British Isles, a substantial number have come from Scandinavia, mainland Europe, the Middle East, and North America. These insect remains are usually preserved under anoxic conditions by “waterlogging”, and while typically disarticulated into individual sclerites, or groups of sclerites, they may be in superb condition, often bearing scales or setae, and sometimes containing male genitalia. Charred fossils are moderately common and represent the main source of information in more arid areas.

Storage pests appear early in the Holocene fossil record in the Middle East and North Africa, and their subsequent spread across Europe and into North America can be traced, albeit with some large gaps in time and space. For Britain, we have a fairly full record for the past two millennia, from which patterns of invasion, abundance, and species composition can be followed.

Good as the archaeological record often is, caution is essential in using it to trace the early history of insect species. We need to recognize that there are problems related to the presence of intrusive remains that can occur, post-dating the deposit in which they are found. Contamination of samples during excavation and storage, and during processing in the laboratory, have all been documented (Kenward 2009). There is also a danger of misidentification of fossils, which may be in poor condition, or of simple errors in recording and data handling. All of these have certainly occurred, so that special care is needed in evaluating the significance of published rare records of insects from unexpected periods. Unfortunately, some remains that (with hindsight at least) were clearly contaminants have been recorded from archaeological associations without comment; some other records are at least suspect. Were every archaeological record to be accepted unquestioningly, various Australasian beetles would now be regarded as originating in Europe, for example. Ideally, any suspect remains should be re-examined, but many have probably been lost. Insect remains from tombs need to be approached with particular caution, for recent invasion, especially during transport and museum storage, is not just possible, but highly likely, and not all such contaminants will appear recent.

The Grain Beetles

The beetle fauna associated with stored cereals includes, in addition to native species, a group of species which have been ecologically classified by Kenward (1997) in the context of northwest European archaeology as “strong synanthropes”, i.e. a species group comprising taxa that are mostly thermophilous and generally dependent on artificial habitats for survival in the region. However, as the classification is climate-dependent, certain species are able to survive beyond the boundaries of the human-created artificial environments in other regions. Information on the commonly recovered grain fauna is presented in Table 1.

Based on their ability to infest or attack undamaged cereal kernels, grain beetles can be classified as primary or secondary pests. Primary pests are capable of successfully attacking, feeding, and multiplying on undamaged grains and often complete their entire development within a single grain (Semple et al. 1992). From archaeological contexts in temperate regions, four primary beetle pests of stored grains have been commonly recovered: the granary weevil, *Sitophilus granarius*; the rice weevil, *S. oryzae*; the maize weevil, *S. zeamais*; and the lesser grain borer, *Rhyzopertha dominica*. Most of these species have been recovered from non-synanthropic habitats, primarily in tropical and subtropical areas, and seem to be favored by high temperatures for completion of their development (see Table 1). In contrast, the flightless species *S. granarius* has yet to be found outside of human-created environments and is able to adjust to unheated indoor conditions in Northern Europe; indeed the granary weevil is not favored by high temperatures (perhaps indicating an origin in an upland area; see King, in press c; Plarre 2010).

Secondary pests are not capable of attacking previously undamaged grains and do not complete their development within a single grain. Beetle species in this category tend to attack a wider range of commodities than primary pests (Semple et al. 1992). Several of the commonly recovered secondary pests of archaeological interest, e.g., beetles of the genera *Oryzaephilus*, *Cryptolestes*, and *Palorus*, are thermophilous and may have originally exploited a habitat of loose bark and fungoid wood. Buckland (1990) posited that moulds were the link between the natural and artificial environments; the damp grain can mimmick the microhabitat of fungoid bark.

Some of the species that are generally listed among “pests” in the stored-products literature, e.g., the biscuit beetle, *Stegobium paniceum*, 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. Similarly, the large scavenger beetles, e.g., *Tenebrio* spp. and *Blaps*
spp., are regularly found with stored products but have also been noted in nature, such as in rotting bark and birds’ nests, and feed on a range of organic matter (see Koch 1989). Many other “pests” had a wider range of habitats in the past and are best just regarded as domestics in the context of archaeology (“house fauna” as defined by Kenward and Hall 1995; see also Carroll and Kenward 2001, Kenward and Carroll 2006). Notable among these domestics are the various spider beetles of the genera *Ptinus*, *Tipnus*, *Gibbium*, and *Niptus*. Other components of the “house fauna” which are now often found in storage habitats include various latridiids and cryptophagids, *Myctea subterranea* (F.) *(Endomychiidae)*, and *Typhaeus stercorea* (L.) *(Mycetophagidae)*, all mould feeders.

**Records of Storage Fauna in Space and Time**

**Setting the stage: The earliest records**

The archaeological as well as documentary evidence suggest that the principle grain pests first formed an association with human beings in the Middle East, but the origin of some species may have been much further east (King 2010b, in press c; Parre 2010). The archaeoentomological record for Eastern Asia is very limited. However, recent work by Obata et al. (2011) has revealed the earliest evidence for stored-product pests. Obata and associates discovered impressions of *Sitophilus zeamais* in early Jomon potsherds dating to ca. 9000 BP from the Sanbonmatsu site in Kagoshima Prefecture, Japan (Obata et al. 2011). Although recorded as *S. zeamais*, the species-level identification was based solely upon the length of the individuals and the claim that adult maize weevils are on average larger than adult rice weevils. However, size is not reliable in separating the two species, and genetic analysis is often necessary (see Hidayat et al. 1996); as such, the identifications may be safer if conservatively considered as *S. zeamais/oryzae*. 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.

As an aside, there are later records from the Eastern Asia. “Maize” weevil fossils have also been recovered from contexts at Fujiwara Palace (ca. 8th century AD) and Kiyosu Castle (ca. 16th century AD) (Mori 2001), and impressions have been noted from Late Jomon pottery in Kyushu (Yamazaki 2005). Chu and Wang (1975) reported *Trogoderma persicum* (Pic.) (i.e., *T. variabile* Ball.) and *Sitophilus oryzae* (i.e., *oryzae or zeamais*) from a tomb dated about 2100 BP in Hunan Province in China. The oldest writ-

<table>
<thead>
<tr>
<th>Species</th>
<th>Common name</th>
<th>Habitat</th>
<th>Temperature range (optimum)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alphitobius diaperinus (Panzer)</td>
<td>Lesser mealworm</td>
<td>Attacks dried animal and plant material (Rees 2007)</td>
<td>16–35 °C (30–33 °C)</td>
</tr>
<tr>
<td>Cryptolestes ferrugineus (Stephens)</td>
<td>Flat or rust grain beetle</td>
<td>Found in wheat, rape, maize, milk and flour as well as dried fruit (Horion 1960)</td>
<td>18–42.5 °C (33–35 °C)</td>
</tr>
<tr>
<td>Cryptolestes ferrugineus (Grouvelle)</td>
<td>Mediterranean flat beetle</td>
<td>Found in cereals and cereal products as well as dried fruit (Halstead 1993)</td>
<td>19–37 °C (30–35 °C)</td>
</tr>
<tr>
<td>Gnatocerus cornutus (Fabricius)</td>
<td>Broad-horned flour beetle</td>
<td>Attacks dried animal and plant material, especially grains and cereal products (Rees 2007)</td>
<td>16–32 °C (24–30 °C)</td>
</tr>
<tr>
<td>Oryzaephilus surinamensis (L.)</td>
<td>Saw-toothed grain beetle</td>
<td>Attacks a wide range of commodities including cereal and cereal products, dried fruit and nuts (Reed 1989)</td>
<td>20–38 °C (30–33 °C)</td>
</tr>
<tr>
<td>Palorus ratzeburgii (Wissman)</td>
<td>Small-eyed flour beetle</td>
<td>Attacks stored cereal products, particularly mouldy grain residues previously attacked by primary pests (Brendell 1975)</td>
<td>18–37 °C (30–32.5 °C)</td>
</tr>
<tr>
<td>Alphitobius diaperinus (Panzer)</td>
<td>Lesser grain borer</td>
<td>Attacks a range of stored products, especially cereal grains, and nuts (Hoffman 1954)</td>
<td>15–34 °C (26–30 °C)</td>
</tr>
<tr>
<td>Staphylinus cladidius (L.)</td>
<td>Cadelle</td>
<td>Feeds principally on dried material of plant origin, especially grains and cereal products (Brendell 1975)</td>
<td>15–38 °C (26–32 °C)</td>
</tr>
<tr>
<td>Tenebroides mauritanicus (Fabricius)</td>
<td>Khapra beetle</td>
<td>Attacks dried material of plant origin and plant products, including grains and cereal products (Brendell 1975)</td>
<td>15–34 °C (26–32 °C)</td>
</tr>
</tbody>
</table>
ten account of grain pests in China, the Ėryā, dates between the 5th and 2nd centuries BC (Kaletān 1931).

In the Middle East, G.A. King (unpubl. data) has noted holes that resemble the characteristic damage made by Sitophilus weevils in charred wild einkorn from the Natufian era Abu Hureyra I site in modern Syria, ca. 13,000 BP. (However, bubbling during charring can produce similar damage; Kenward et al. 2008.) Interestingly, the damaged einkorn grains were recovered from a sample containing acorns, perhaps furthering the hypothesis that acorns were a pathway for the introduction of the species into artificial habitats (Buckland 1981, Howe 1965, Zohary 1969). The earliest fossils of grain pests in the Middle East came from layer VI at Hacilar, SW Anatolia, dated to 7700–7550 BP, in the Pre-Pottery Neolithic C period (Helbaek 1970). Helbaek described charred fragments of several adult Sitophilus in small heaps of charred wheat and barley. Additionally, one of the grains contained an adult weevil, and some kernels showed evidence of lengthwise tunnelling. As early evidence of S. oryzae and S. zeamais has yet to be recovered in the region, the unidentified Sitophilus are likely to have been S. granarius. More conclusive evidence for the presence of the granary weevil in the region at the time came from a near-contemporaneous well at Atlit-Yam, Israel (ca. 7500 BP) where Kislev et al. (2004) recorded 27 specimens of Sitophilus granarius.

Moving substantially forward in time, the Harra Hubullu Tablets XI–XV provide the earliest written zoological account of stored-product species, listing 33 names of crop and stored-product pests, e.g., uh.sē.kū and uh.zī(d).da (Landsberger 1934; see also King 2010b). While believed to have been compiled during the 9th century BC in bilingual Sumero-Akkadian script, the tablets are thought to be derived from Hammurabian period lists (ca. 3792–3750 BP), which were in turn developed from even older ones (Harpaz 1973). The grain pests are also mentioned in other literature of the period, for example, the Sumero-Akkadian proverb “A piece of linen is spread for a flea, a tissue for a moth, a granary for grain pests” (Bodenheimer 1947). Helbaek (1970) referred to weevil-ravaged grain, providing indirect evidence for the presence of S. granarius in Assyrian and Hellenistic barley from Nimrud. Hopf and Zachariae (1971) recorded the grain weevil in grain deposits dating to around 3000 years ago from Tel Arad in the Northern Negev, Israel. Kislev and Melamed (2000) discovered insect remains of about the same date 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 in association with charred wheat, Triticum parvicolossum. Other storage pests were also noted, including: Alphitophagus bifasciatus (Say), Oryzaephilus surinamensis (adult and pupa), and an adult and whole larva of Tenebroides mauritianus.

As with the Sumero-Akkadians, the ancient Egyptians left a scant documentary record of grain pests. Egyptian inscriptions include images of some invertebrates that can be identified to genus (cf. Harpa 1973, Levinson and Levinson 1998), but the ancient Egyptian language, like biblical Hebrew, apparently lacked a comprehensive term for “insect” (King 2010b). The Ebers Papyrus is an Egyptian medical document (ca. 3552 BP) describing magical formulae and remedies and is one of the earliest written records containing methods for controlling pests. The Ebers Papyrus XCIII contains instructions for deterring kkt-animals using burnt gazelle dung diluted in water. The kkt-animals may be a reference to grain weevils (Panagiotakopulu et al. 1995). However, kkt transliterates as small animal, and the species identification is purely speculative, based on context (King 2010b).

The earliest archaeological accounts for Egyptian grain pests were made by Helbaek (cited in Solomon 1965), who recorded Sitophilus granarius from the ca. 4900 BP Tomb in Saqqarah. Solomon (1965) also mentions that S. granarius was recovered from the tomb beneath the Step Pyramid of Saqqarah, ca. 4300 BP. Sitophilus granarius and Stegobium panicum were recovered at the tomb of Queen Ichetis at Saqqarah, ca. 4334–4150 BP (Chadick and Leek 1972).

Several specimens each of Trogoderma granarium and Stegobium panicum (the earliest fossil evidence for both), were identified in a wheat deposit from a Middle Kingdom tomb at el-Gebelein (4181–4055 BP) (Panagiotakopulu 2003). A Tribolium species was noted in a mid-3rd millennium BC (5000–4000 BP) Egyptian tomb by Alfieri (in Andre 1931). Tribolium confusum was reported from an offering pot from ca. 3000 BP (Alfieri 1976). Zachar (1937) recorded T. castaneum from Egypt ca. 3500 BP. Rhyzopertha dominica and S. panicum were present in Liverpool Museum collections from Twelfth Dynasty Kahun, 3990–3800 BP (Panagiotakopulu 1998). R. dominica was recovered from a small sample of barley and is the earliest on record; it was also noted in a botanical sample from a vessel in Tutankhamun’s tomb, ca. 3345 BP (Alfieri 1931), while Zacher (1937) recorded T. castaneum, S. panicum, Oryzaephilus surinamensis, and R. dominica from another vessel from the tomb.

Samples from the Workmen’s Village at Tell el-Amarna (thought to be dated between 3350–3323
BP on pottery) yielded grain pests in probable pigsty deposits—fossils of *Sitophilus granarius* and *Rhizopertha dominica* were recovered. Moreover, Panaggiotakopulu (1999) discusses the remains of *S. granarius* and *Palorus ratzburgii* from coprolites at the site. Panaggiotakopulu (2001) lists *Tribolium confusum*, *T. castaneum*, *Palorus subdepressus* (Wollaston) and *Cryptolestes turcicus* from Pharoanic Amarna. Zacher (1934a, b) noted *Oryzaephilus surinamensis* (L.) from a Minoan period vessel, 3350 BP. Panaggiotakopulu and Buckland (2010) provide a recent review of insect remains from Egyptian archaeological sites.

Moving westward: records from prehistoric Europe

How soon the grain pests were carried to Europe is uncertain. The earliest evidence of cereal pests in the region comes from bandkeramic wells in Eythra village in the Leipzig region of Germany from Well 2 (cal. radiocarbon dated 7269–7180 BP) and Well 1 (dendro-date 7034 BP) (Schmidt 2005a). The oldest records for the golden spider beetle, *Niptus hololeucus* (Fald.), and for *Gibbium psylloides* (Czemp.) are reported from the bandkeramik well in Eythra (Leipzig) (Schmidt 2005a). Large numbers of granary weevils have also been recorded from the well at Plaussig, near Leipzig, dated dendrochronologically to 7219 BP (Schmidt, in press a) and from a well at Erkelenz-Kückhoven near Cologne dendro-dated 7040 BP and 7007 ± 5 BP (Schmidt 1998, in press b) (Fig. 1). Büchner and Wolf (1997) have also recorded *S. granarius* from an underground pit, at Göttingen, Germany, dated 6030 BP.

Populations of the granary weevil were well established in central Europe less than 500 years after the earliest known fossil appearance of the species in the Middle East. However, the pathway that it followed is unclear, although it was surely introduced via human migration or exchange rather than natural dispersal (see King 2010b for discussion). The only other Neolithic evidence for *S. granarius* comes from a cast in a piece of pottery from Servia (6700 BP) in south Macedonia, Greece (Hubbard 1979).

Although the fossil record for the granary weevil in Neolithic Europe is sparse, it is even more limited for the other stored-cereal pests. A single charred head of *Oryzaephilus surinamensis* was reported from Mandalo in western Macedonia, Greece, dating 5490 ± 55 BP (Kotsakis et al. 1989, Valamoti and Buckland 1995). Additionally, the cadelle *Tenebroides mauritanicus* has been recovered from Erkelenz-Kückhoven (Schmidt 1998, in press b) and Plaussig (Schmidt, in press a) in Germany (Fig. 1).

*Figure 1. Illustrations of intact insects from Reitter (1911) and Jamestown photos from Keng et al. (2010).*
the Singen-Offwiese, Germany, which is associated with the Groß Gartach culture dendro-date 6950 BP (Dieckmann et al. 1997, Schmidt 2007).

The fossil evidence of grain pests continues to be limited for the Bronze and Iron Ages. *Sitophilus granarius* was found in a Middle Bronze Age site in Northern Italy (Fasani 1976), and in Late Bronze Age France at the site of Lake Bourget (Pecreaux 2008). Moreover, Middle Bronze Age contexts at Cova Punta Farisa in Fraga Huesca, Spain yielded the remains of *Rhyzopertha dominica* (Alonso Martinez and Buxo Capdevilla 1993). The biscuit beetle *Stegobium panicum* has been recovered from sites dating to Late Bronze Age Britain: Runnymede Bridge, Staines, Surrey (Robinson 1991) and Wilsford, Wiltshire (Osborne 1989). Chowne et al. (1986) reported the biscuit beetle from an Iron Age site in Britain (Tattershall Thorpe, Lincolnshire). *S. granarius*, *R. dominica*, and *Tribolium* sp. have been recovered from Siriguarch, Alcañiz, Teruel, Spain (Compte and Perales 1984). There is a record of *Tenebrio molitor* L. from prehistoric Britain, dated 4000 BP (Howard et al. 1999), notable in view of its rarity in the later fossil record.

**The northern Mediterranean shore**

While the grain pests almost certainly spread into Europe via the Mediterranean shores, early fossil records from that area do not yet exist; the contrast in known archaeological evidence of grain pests from southern compared to central Europe is probably at least in part a result of different cultural and preservational circumstances (particularly the lack of known waterlogged deposits in the south). There is a modest amount of evidence from later periods.

The fossil record for insects from pre-Roman Greece is remarkably limited. A carbonized specimen of *Sitophilus granarius* was recovered from a sample of barley at the “unexplored” mansion complex at Knossos, with a Late Minoan date, around 3425 BP (Jones 1984). Shaw and Shaw (1995) noted *S. granarius* and *Tribolium confusum* from a contemporaneous site at Kommos. Panagiotakopoulou and Buckland (1991) identified the remains of *S. granarius*, *Rhyzopertha dominica*, *Stegobium panicum*, and *Oryzaephilus* sp. in samples from the West House, Akrotiri Santorini, Thera, ca. 3500 BP. In literature, the Greek terms κίς, κορίς, φθείρ, σής, ἵν, σκοίν, and θρίψ were used to refer to small insect pests, and Κίς, in particular, is believed to have been associated principally with insects that infest grains or pulses (Beavis 1988, King 2010b).

**Expanding to the Atlantic seaboard: The Roman Empire in Europe**

There is abundant documentary evidence for the Roman period, which dates back to Cato’s *De Re Rustica*, ca. 235 BC (Ag. XCII). The Roman authors express particular concern over a grain pest called *curculio*—an insect that was capable of ravaging enormous heaps of grain (e.g., G. Virgil I.CLXXXVI). The term was even used by Plautus to portray a greedy, gluttonous, and unscrupulous character (PC. 219–221). Several authors also provide insight into the construction of granaries and methods for preventing contamination of cereals by *curculio* (e.g., Arch. Vitruvius VI,VI,IV, RR. Varro I.L.VII; RR., Columella I.VI.XV). Both Varro and Columella depict *curculio* as a primary pest of stored cereals, capable of infesting undamaged grains, and King (2010b) suggests that the term may have been applied to both *Sitophilus granarius* and *Rhyzopertha dominica*, with the former being more commonly associated.

Fossil records for the early Roman period are rare. However, Cappadocia, Thrace, Carthaginian, and Oscensian districts in Hither Spain, and Apulia adopted pest control measures against infestations of *curculio* (RR. Varro I.L.VII). In the absence of an established fossil record for 36 BC, Varro’s text affords the best evidence for the distribution of *curculio* at that time, implying that the species was established along most of the Mediterranean coast of southern Europe during the Roman Republic (see Carr 1838, SG. Strabo VI.III in King 2010b).

Later Roman sites have yielded abundant fossil records of the grain pests, the frequency of recovery apparently reflecting the intensity of research, so that the archive for Britain greatly exceeds that for mainland Europe.

**Fossil records from the first century AD.** The earliest evidence of Roman-age grain pests (i.e., *Oryzaephilus surinamensis* and *Sitophilus granarius*), dating to 30 AD, was reported from Neuss (Novaesium) in Germany (Cymorek and Koch 1969, Koch 1970). Knörzer (1970) also identified the rice weevil *S. oryzae* in a sample containing charred rice from early first century AD contexts from Neus-Novaesium IV, Germany. From Touffréville Calvados, France, Ponel et al. (2000) reported *S. granarius*, *Stegobium panicum*, *Tenebrio obscurus*, and *Oryzaephilus* sp., dated ca. 75 AD. From beneath the AD 79 tephra at Herculaneum, Naples, Italy, Dal Monte (1956) noted larval, pupal, and adult *S. granarius* as well as a single *Oryzaephilus* sp. in infested charred wheat. Additionally, *Sitophilus granarius* was recovered from first-century AD contexts at Alphen aan den
Rijn, Netherlands (Kuijper and Turner 1992) and Valkenburg fort (Hakbijl 1988).

The grain pests appear to have entered Britain following the arrival of the Roman legions. It is now three decades after Buckland’s (1981) review, and there are still no records to support the presence of grain pests in Britain prior to the arrival of the Roman military forces (King 2010b, Smith and Kenward 2011). At the Poultry site in central London, a number of buildings, workshops, yards, and pits dating to just after 47 AD—the start of the Roman occupation—and sealed by the 60 AD “fire horizon”, interpreted as the burning of London during the Boudican revolt, have yielded myriad insect remains, including: *Sitophilus granarius, Oryzaephilus surinamensis, Cryptolestes ferrugineus, Palorus ratzeburgii, Alphitobius diaperinus, Tenebrio molitor*, and *Tenebroides mauritanicus* L. (Rowsome 2000, Smith 2011). Similarly, deposits at 20–30 Gresham Street, London, dated to 50–75 AD, produced large numbers of individuals of *C. ferrugineus, S. granarius, A. diaperinus, O. surinamensis*, and *P. ratzeburgii* (Smith and Tetlow 2004). The same range of species was identified from a timber drain at 21 Saint Peters Street, Colchester, constructed immediately following the Boudican revolt (King and Hall 2008).

The grain pests arrived in northern England in the later part of the first century AD. The Roman Fort at the Millennium site at Carlisle Castle, dated before and shortly after 72/73 AD, yielded *Cryptolestes ferrugineus, Sitophilus granarius, Oryzaephilus surinamensis, Tribolium castaneum*, and *Palorus ratzeburgii* (Smith 2010). Grain pests have been noted at other sites in and near the Roman fortress at Carlisle (Kenward and Carrott 2006; Robinson 2002, 2003; see also Smith and Kenward 2011) and have been found as far north as Invereskgate in West Lothian, Scotland (Smith 2001, 2004) until the end of the fourth century AD. The second century provides more evidence of *Tribolium castaneum* (Hall and Kenward 1990, Hall et al. 1980), as well as the arrival of *A. diaperinus* (Hall and Kenward 1990; Kenward and Allison 1995; Kenward et al. 1986, 2000) and *Sitophilus paniceum* (Hall and Kenward 1990) in Northern England. Furthermore, *P. subdepressus* (Osborne 1971), *C. turcicus*, and *Tribolium confusum* (Girling 1983) appear to have been introduced to England by the third and fourth centuries AD. South of the Mediterranean, *Oryzaephilus* sp. and *C. turcicus* have been recovered from a second-century quarry site at Mons Claudianus in Egypt (Panagiotakopulu and van der Veen 1997).

The later Roman period also provides the earliest archaeological evidence for the movement of grain pests as stowaways in ships. Pals and Hakbijl (1992) recovered *Sitophilus granarius, O. surinamensis, C. ferrugineus, P. ratzeburgii, Tenebrio molitor*, *Alphitobius bifasciatus* Say, and the parasitoid wasp *Lariophagus distinguendus* (Förster) from the remains of a late second-century ship near the presumed Roman fort of Laurium in Woerden, Zuid-Holland. *Sitophilus* sp. (probably *S. granarius*) was reported from a third-century ship wreck near Guernsey (Rule and Monaghan 1993). The presence of cereal pests in these vessels shows that grain was still a traded commodity in the outer reaches of the Roman Empire during the second and third centuries, and that it was insect contaminated.

**A curious rarity of grain pests: The early medieval period**

The early medieval period (5th–11th centuries AD) is considered as a unit because there are no clearly authentic British records of the main grain pests from it (and incidently because *Tipus unicolor* (Piller and Mitterpacher), characteristic of many Roman sites, was rare, or more often absent; see Kenward 2009, Kenward and Whitehouse 2010).
Both the grain pests and *T. unicolor* were present in a few samples from Anglo-Scandinavian Coppergate, York, but there are good reasons to regard them as quite probably contaminant, including their rarity, sometimes their preservational condition, and the regrettable fact that samples from sites rich in grain pests were processed concurrently in the same laboratory (Kenward and Hall 1995:760–762). *Tipus unicolor* was, however, rather abundant at an Early Christian rath site of Deer Park Farms, Antrim, Northern Ireland (Kenward et al. 2011). While not considered to be a typical stored-product pest, *T. unicolor* is part of the “house fauna” species group and is generally an indicator of long-lived, high-status buildings, with proportions of this spider beetle believed to increase with the improved cleanliness of buildings (Kenward 2009). Kenward and Hall (2000) reported the presence of eggs of thecestode genus *Hymenolepis* in Anglo-Scandinavian deposits from Walmgate, York. The life cycle of *Hymenolepis* is known to be able to include grain pests, particularly *Tenebrio* and *Tribolium*, as intermediate hosts (see King and Henderson, in press).

No grain pests were found in numerous samples from 11th-century Viborg, Denmark, though *Ptinus raptor* (Sturm) and *P. fur* (L.) (the latter a common species in stored products) were present (Kenward 2005a, b). Similarly, the distinctive *P. raptor* has been identified from the Viking-Age site in Kaupang, Norway (Barrett et al. 2004, 2007). From the same Norwegian site, Buckland et al. (2001) recorded *Ptinus* remains as *P. pusillus* (Sturm) and *P. palliatus* (Perr); however, neither was found in the subsequent study. These investigations underline the rarity or absence of the classic pests in northwest Europe during the early medieval period. However, a Merovingian grave near Pattonville, Ludwigsburg, SW Germany, from the late 6th to the middle of the 7th century exhibited large numbers of *C. ferrugineus* found in a byzantine bowl (Bofinger and Ebinger-Rist 2009, Schmidt 2010). From the coffin of the Ottonian queen Editha (died 946), which was found in Magdeburg, Germany, Schmidt (2012) recovered large numbers of *C. ferrugineus*, *Sitophilus granarius*, *P. fur*, and *Tipus unicolor*. By the 9th century, the large scavenger beetles appear to have arrived in Ireland; Reilly (2003) reports *Tenebrio molitor/obscerus* from Essex Street West site in Dublin. A contemporaneous site, Wood Quay in Dublin, also yielded *Blaps lethifera* Marsham (O’Connor 1979).

In contrast to the lack of convincing records from northern England, *Sitophilus granarius*, *O. surinamensis*, *C. ferrugineus*, and *T. obscurus* were present in small numbers in late 10th- and early 11th-century deposits at the Poultry site (Smith 2011). However, deposits at this site appear to have been extensively reworked in the past, and so these fragments could be intrusive from later medieval deposits. The same explanation could be advanced for the single individual of *S. granarius* recovered from deposits of a similar age at the Guildhall site, London (Smith and Morris 2008). Alternatively, perhaps this find was a result of differences in trade links, the demands of London being great enough to necessitate at least occasional imports of foreign grain, but further investigation of tightly dated and securely sealed waterlogged deposits of the period is desirable.

Emerging beyond the sphere of prior Roman influence: The later medieval to early modern periods

There are numerous records of grain pests from Britain after the Norman Conquest, especially of *S. granarius*, *O. surinamensis*, and *C. ferrugineus*, set against a background of generally declining urban faunal diversity. Amongst the pests, there is—subjectively—a broad tendency for *S. granarius* to become relatively more abundant, perhaps because grain was cleaned better (it is hard to sieve out weevils, both because of their larger size which more closely approximates the size of the grains they infest, and their presence inside the grains). Roman sites, such as those at Ribchester, Carlisle, and York, mentioned above, typically yield assemblages in which *S. granarius* is appreciably less abundant than *C. ferrugineus*, and especially *O. surinamensis* (for example, at Tanner Row, *O. surinamensis*, *C. ferrugineus*, and *S. granarius* were in the approximate ratio 5: 2: 1; Hall and Kenward 1990). By contrast, *S. granarius* may be proportionally much more abundant in later deposits, such as the post-medieval site at Coffee Yard in York, where there were more than twice as many *S. granarius* as *O. surinamensis*, and no records of other storage pests apart from spider beetles, probably best seen as domestics at this site (Robertson et al. 1989). At another site in York, The Bedern, grain pests were present in pit-fill deposits dated 13th to early 17th century, but only *O. surinamensis* and *S. granarius* were found, in roughly equal numbers (Hall et al. 1993). It is worth noting that the medieval deposits at The Bedern also yielded the eggs of the tapeworm *Hymenolepis* sp. (Hall et al. 1993).

A similar trend towards predominance of *S. granarius* may have occurred in Germany, although the evidence so far is slight: a large and varied fauna from 15–16th century Neuss included a range of domestic and storage beetles, but only *S. granarius*...
among the classic grain pests (Koch 1970). This site was unusual for its records of *Ptinus latro* (F.), *P. cf. clavipes* (Panzier), and *Niptus hololeucus* (Fald.) as well as the commonly encountered *P. fur* (L.) and *Tipus unicolor*. In a 14th-century cesspit in Con-
stance (Germany), *S. granarius* and *O. surinamensis* were found in great numbers (Schmidt 2005b). There are two records of the rice weevil *S. oryzae* from northern England during this period: one from early modern Hull (Carrott et al. 1995), and the other from a 19th-century drain fill in the center of York (Hall et al. 2006), in the latter case together with *R. dominica*. The presence of insects in sieved samples from the wreck of an 18th-century AD merchantman off the Red Sea coast of Egypt at Sadana Island is implied, and a jar with an insect-proof neck described (Ward 2001).

Beyond the sphere of prior Roman influence, the grain pests found their way to Scandinavia and Ireland. A single *S. granarius* was recorded from a cess-
pit fill dated 1275–1300 in Oslo, Norway (Kenward 1988), and the granary weevil was also present in a medieval context from the Lofoten Islands (Vågon), Norway (Buckland and Panagiotakopulu 1995). From medieval Gothenburg, Sweden, Andersson (1992) reported *S. granarius* and *Tenebrio obscurus*. The stored-product pests, *S. granarius* and *P. fur*, were recovered from the remains of a 13th-century shipwreck of the frame-timbered vessel Oskarshamn
off the coast of Sweden (Lemdahl 1991). Moreover, holes attributed to emergence of *S. granarius* were found in charred barley grains in a cesspit deposit of the early 14th century AD in Svendborg, Denmark (Jørgensen 1986), although, as mentioned earlier, “bubbling” during charring can produce holes strongly resembling those caused by weevils. Remains named as *S. oryzae* were identified from the wreck of the “Amsterdam” by Hakbijl (1987). King (unpublished) found *S. granarius* in 13th-century latrine deposits in Riga, Latvia. Deposits dated to the 14th-century in Novgorod, Russia, yielded equal, though very small, numbers of *S. granarius* and *O. surinamensis*. *Ptinus villiger* (Reitter) was also recovered from the site (Hellqvist 1999).

In Ireland, the period following the Norman Conquest heralded the first appearance of the classic grain beetles. The earliest fossil record of the granary weevil in Ireland is from late Viking/early Anglo-Norman deposits at Waterford (Reilly 1994). The scavenger *B. lethifera*, present in Viking Age deposits, was found in late 12th-century layers at Essex Street West, Dublin, and *S. granarius* was re-
covered from early 13th-century deposits at the same site (Reilly 2003). The granary weevil has also been recovered from late 13th/early 14th-century layers of a medieval ditch at Iveagh Market (Reilly 2001) and a 16th-century context from George’s Quay, Limer-
ick (O’Donovan 2002).

**Crossing the Atlantic: Records from Iceland, Greenland, and North America**

Numerous insects, mostly synanthropes, were carried across the Atlantic to Iceland and Greenland (e.g., Forbes et al. 2010, Konráðsdóttir 2007, Sadler 1991, Sveinbjarnardóttir et al. 2007). Among them were occasional storage pests, though none seem to have become established, which is hardly surprising in areas where cereals could rarely be grown successfully. There are a few records from Iceland. *Oryzaephilus surinamensis* was found at late medieval Holt (Sveinbjarnardóttir 1983). Both *Sitophilus granarius* and *O. surinamensis* were found in post-medieval deposits in a high-status farm at Reykholt, Iceland, indicating storage of grain, though the grain may have been imported (Sveinbjarnardóttir et al. 2007). *Sitophilus granarius* was present at post-medieval Stóraborg (Buckland et al. 1992, Sveinbjarnardóttir et al. 1981), and post-medieval layers at Bessastaðir contained *O. surinamensis* and *S. granarius* (Amorosi et al. 1992). Remarkably, both *Sitophilus* and *Oryzaephilus*—surely carried in supplies of grain—have been found in later Norse deposits, apparently pre-dating the mid-14th century, at Nipaatsoq in Greenland (Panagiotakopulu et al. 2007).

It is hardly surprising that a range of Old World synanthropes arrived in North America with provi-
sions carried by the European colonists as well as in the lively trade that followed. Evidence for this importation is particularly notable in the recently examined well fill deposits dated 1611–1617 from James Fort, Colonial Jamestown, Virginia, USA, which have revealed a range of invasive stored prod-
uct species, e.g., *O. surinamensis*, *Sitophilus granarius*, *S. oryzae/zeamais*, *C. ferrugineus*, *Palorus sp.*, *B. lethifera*, *Alphitophagus bifasciatus*, *Typhae a stercorea* (L.), and *Mycteola subterraneus* (Marsh.), as well as native fauna, i.e., cf. *Lasioderma serricorne* (F.) (King et al. 2010) (Fig. 1). Additionally, a privy used at the English settlement at Ferryland, Newfoundland, Canada, dated 1621–1673, yielded a fauna with a range of European synanthropes, including *O. surinamensis* and *S. granarius* (Bain and King 2011, Bain and Prévost 2010, Prévost and Bain 2007). Both *S. granarius* and *Tenebrio obscu-
rus* were recovered from a mid-17th-century shipyard in Québec City in southeastern Canada (King, in press b). Analysis of late 17th-century deposits in Colonial Boston produced more assemblages rich in imported insects, among them *Tenebroides maurus
tanicus*, *Oryzaephilus* sp., *Gnatocerus cornutus*
(F.), and both S. granarius and S. oryzae (Bain 1998, Bain and King 2011). Deposits dating from the 18th century in Québec City yielded S. grana-
rarius, Tenebrio molitor, Alphitobius bifasciatus, and Ptinus fur (Bain et al. 2009). Also, Bain (2001) recorded Rhyzopertha dominica, Sitophilus oryzae, S. grana-
rarius, Cryptolestes, Tribolium castaneum, T. confusum, Tenebrio molitor, and T. obscurs from deposits from Québec City dated to the 19th century, in assemblages dominated by Old World species. In early to mid-19th-century deposits from Toronto in Ontario, Canada, cf. Blaps sp., Ptinus cf. clavipes, P. fur, Sitophilus granarius, and O. surinamensis/mercator were recovered alongside the house fauna beetles Mycetaea subterranea and Typhaea stercor (King 2010a). Moreover, by the 18th century, certain grain species had arrived on the west coast of North America; Essig (1927) reported evidence of S. grana-
rarius and S. oryzae in abode bricks of Santo Domingo Mission in lower California, dated to 1775.

The spread of storage pests to the rest of the world

Analyses of archaeological fossil insects are lacking for other lands colonized by Europeans, but early collections and published records show the arrival of the storage pests with colonists, and subsequently with trade—hardly surprising as the majority are now cosmopolitan. Many alien insects are certainly established in Australasia, especially in New Zealand (e.g., Cumber 1961, Kuschel 1979, Moed 1993). Archaeological investigation in Australia and New Zealand may well produce evidence of the early arrival of the grain pests, and also of the various other insects that have entered the ecology of those countries. The situation is similar for South America: archaeological investigation of colonial period sites is awaited, but worthwhile results can surely be anticipated.

Discussion and Future Directions

How good is the fossil record?

We have already issued a caveat concerning corruption of the evidence by contaminants and misidentifications. There may also be a taphonomic (preservational) effect. The different potential for preservation in different regions has already been alluded to. In addition, the more delicate taxa are potentially under-represented. In general, this probably does not undermine the record since storage insects preserved by anoxic waterlogging, desicca-
tion, and charring all contribute. There may be some bias, however. Charring may favor Sitophilus over the other common grain pests because it is tough and often protected within grains. In experiments, a range of insects survived charring in good condition up to moderate temperatures, though they were severely damaged above around 400 °C (Kenward et al. 2008). Nevertheless, while the charred insects appear to be in superb condition, with appendages and even hairs and setae entire, they are very fragile and easily broken into fragments small enough to evade recovery. Are we even losing the tiny sclerites of waterlogged Cryptolestes through our sieves? There may be problems of this kind; nevertheless we can certainly piece together a worthwhile story, albeit with many gaps.

What was the infested grain intended for?

What do the records of grain pests tell us about the past? It may seem obvious that they were important in damaging stored grain intended for people. But did they appreciably reduce the availability of food? Hall and Kenward (1976) suggested that the structure at Coney Street in York mentioned above may have been a transit shed and thus a serious source of infection for the grain passing through it, leading to contamination in the main granary. This explanation now seems far less certain in view of our understanding of the overwhelming presence of stable manure in Roman towns and military centers, with grain pests being part of the characteristic “indicator group” for this material (Kenward and Hall 1997). For Roman and Post-Conquest Britain, many, if not most, records of grain beetles now seem to be from horse feed deposited as stable manure (Ken-
ward 2009; Kenward and Hall 1997; King, in press e; Smith and Kenward 2011). We are left to wonder whether horse feed was specially stored, with little regard to infestation, or whether perhaps grain originally intended as human food was routinely diverted to equines if it became infested. If so, the abundant grain pests would be of far less significance in our reconstructions of past human life; this question and the wider issue of the routes by which grain pests entered deposits, have been discussed by Smith and Kenward (2011, 2012).

Fortunately, not all of the fossil grain pest as-
semblages seem to have been from animal feed, as those from a number of Roman and Post-Conquest deposits lack key components of Kenward and Hall’s (1997) stable-manure indicator group. For example, the grain pests recovered from the In-
vereskegate well (Smith 2004) are more indicative of grain dumping rather than conversion to foder. Moreover, the infested cereals may not have always been intended for consumption. Analysis of the modern insect fauna from The Oldest House at West Stow, Sussex suggests that grain pests may
enter along with stored, unprocessed cereals used as thatch (King 2010b, 2012). Archaeologically, this may offer a possible explanation for the presence of grain pests in Smith et al.’s (1999) late medieval thatch from Southern England, and similarly on the other side of the Atlantic, in the colonial fort at Jamestown, Virginia (King et al. 2010).

Another significant route by which grain pests, and particularly Sitophilus, appears to have entered archaeological deposits is in human feces, for it has been shown that grain pests can pass relatively undamaged through the human gut (Osborne 1983). Certainly, grain pests are common enough in cesspits (cf. Smith 2013).

**Efficacy and reliability of the archaeobiogeographical approach**

When married to the archaeology, biogeography can serve as an effective tool for investigating a wealth of past human activities. By studying the fossil record for distributional changes in grain fauna over time, a number of archaeologically significant themes, such as past patterns of human migration, cultural contact, and trade, can be elucidated, for example. Unfortunately, an archaeobiogeographical approach also suffers from limitations, with the reliability of results hedged by the quality of the fossil record.

The study of insect remains from archaeological contexts is still rarely carried out outside of the British Isles, an issue addressed by Buckland (1981). The resulting lack of data continues to pose problems, particularly in attempting to ascertain shifts in species’ distributional ranges. Thus, although Sitophilus granarius has been recovered from early Holocene occupation sites in central Europe, the next record of the species in northern or central Europe does not occur until the Roman occupation. Was the granary weevil absent from the region during the Bronze and Iron Ages? Or did central Europe remain a potential source for the diffusion of the species into later prehistoric sites in the rest of Europe? It is only when numerous archaeological analyses have been made that the species’ absence from the region between the Neolithic and Roman Periods can be inferred. For example, trade and cultural contact between Britain and mainland Europe during the Bronze and Iron Ages would potentially have provided opportunities for the introduction of extant populations of the granary weevil to Britain prior to the Roman Era, were it at all common at mainland sites. Certainly, the grain pests seem to have spread easily enough in the Mediterranean region, and much more recently around the North Atlantic.

A current limitation of the archaeobiogeographical approach is that it is unable to differentiate between multiple introductions of a species, as it does not distinguish between different populations of the same species. The Roman garrisons appeared to have been receiving cereal supplies from several provinces during the early Roman conquest and occupation of Britain. As populations of Sitophilus granarius presumably existed in stores around the Mediterranean and further north, the species was probably transported to Britain from multiple regions on many occasions. However, an archaeobiogeographical study of S. granarius would be blind to these introductions, so that details of trade connections to regions with early Roman settlements would be obscured. Thus, in areas such as 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, the records give only the crudest view of culture contact. However, the recovery of other grain fauna might provide further insight towards any potential trade connections, which may enhance the efficacy of the archaeobiogeographical approach but which would perhaps also risk placing undue confidence or faith in the currently patchy fossil accounts of species’ distribution.

Closer analysis of the fossils might be rewarding. The suspected “contaminants” from the early medieval era in Britain mentioned above might be AMS dated to determine if they are redeposited or intrusive, and thus if pests survived or were only re-introduced after the Norman Conquest. Analyses of genetic diversity in fossils in the Roman and Norman period onwards might give clues. DNA has been recovered from Roman and later fossils of Sitophilus from English sites (King et al. 2009), suggesting the approach might be feasible. Are Roman and Norman populations genetically distinct? Investigating this would necessitate the recovery of abundant exceptionally well-preserved fossils from numerous sites. In many areas, and probably in most towns, the buried organic heritage is under threat (Kenward and Hall 2008), and needs to be protected so that the available stock of such remains does not diminish before it can be examined.

Regarding the status of the pests in towns and military establishments—whether they were depleting resources for human consumption or exploiting low-grade cereals primarily intended for livestock—we might examine the relationship of the grain community to decomposer and domestic fauna in deposits where preservation is good and insects abundant. Such analysis at some British sites has
proved informative, sometimes strongly suggesting that they indeed originated in stable manure, and occasionally hinting that they came from some other source (Kenward and Carrott 2006, Smith and Kenward 2012). Similarly, the application of stable isotope analyses to insect fossils in parallel with the remains of domestic vertebrate fauna may prove useful as a means of approaching this question (see King, in press a).

In conclusion, we have a very substantial fossil record for a range of grain beetles, but it is very patchy and predominantly from northwest Europe; no area yet has an adequate record. If we are to understand their origin and dispersal, fossils are needed from across the Palaeartic and North Africa. The analysis of pre-agricultural natural deposits in the Middle East, North Africa, and the Indian Subcontinent might greatly advance our understanding of the original ranges of the pest species and the stages by which they entered into association with humans. And finally, further research along these lines could address the question: have any of the storage pest species, and especially Sitophilus granarius, actually evolved in response to human activity?

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