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INSECT REMAINS AND THEIR TRACES: RELEVANT FOSSIL WITNESSES IN THE RECONSTRUCTION OF PAST FUNERARY PRACTICES

ABSTRACT: The combination of archaeoentomological and forensic analyses, known as "Funerary Archaeoentomology", yields important new insights into our knowledge of past burial practices: secondary body handling, taphonomy of the grave, delayed burial, grave reopening and anthropogenic mummification processes. After a detailed review of the sampling methods for insect remains retrieval, diagnostic identification criteria for the archaeoentomofauna are provided for a better understanding and interpretation of grave taphocenosis. The second part of this paper highlights how the ichnological approach, namely the study of trace fossils present on bones and on some various exogenous materials present in the grave, proved to be an efficient new tool to improve our knowledge of pre- and post-depositional taphonomic processes.

KEY WORDS: Archaeoentomology – Burial practices – Taphonomy – Ichnoarchaeology – Mineralization – Bone modification

INTRODUCTION

Archaeoentomology is the study of mainly synanthropic insect assemblages recovered during archaeological excavations. When these remains are issued from funerary contexts, they are transcribed according to forensic entomology principles and methods. The investigations conducted on these fossil thanatocenoses provide precious information on the treatment of the cadaver, its taphonomic history, and therefore on the funerary practices of ancient societies: prolonged exposure of the corpse prior to burial, anthropic mummifying processes, re-intervention in tombs, etc. When environmental conditions are not conducive to the preservation of the exoskeleton, an ichnological approach to traces or imprints present on bones or on diverse non-indigenous materials makes it possible to reconstitute, *a posteriori*, arthropod fossil activity in the tomb.

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METHODOLOGY

Preservation of insects in archaeological contexts

Insects have a propensity for conservation in very diverse environments and can, at times, be the only preserved organic remains (Ponel 1993). However, certain contexts are more conducive to insect preservation, such as very moist and anaerobic environments (bogs, trenches, latrines, etc.) or very cold and/or desert-like conditions. Speight (1974) showed that arthropod "sclerites" (the hardened plates constituting the arthropod exoskeletons), mostly made up of chitin, were chemically stable and particularly resistant to decomposition. The main causes of the degradation of insect exoskeletons are generally due to physical (fragmentation caused by sediment pressure) and biological (bacterial and/or fungal) processes. However, it is important to point out that entomofaunal assemblages from archaeological contexts only imperfectly reflect the original biocenoses as not all insects display the same aptitude for conservation (only the most chitinized taxa stand the test of time) (Kenward 1975). This differential preservation combined with a possible subsequent contamination by present-day taxa (burrowing species, pedotrophic nests, etc.) introduces a non-negligible bias into the *a posteriori* reconstitution and the interpretation of archaeological facts. Finally, necrophagous or saprophagous insects are often omitted during archaeological excavations, mostly due to unfamiliarity with potential results or methods of collecting.

In situ sampling and extraction of the entomological fraction in the laboratory

According to the cultural, geographic, and/or chronological contexts, funerary practices display marked diversity: primary or secondary, single or multiple burials, in empty or filled-in spaces, natural or anthropic mummification or incineration. It is thus necessary to adapt the sampling of the entomological fraction depending on cadaver treatment. The recovery of an archaeoentomofauna associated with human remains requires specific protocols used in other bioarchaeological disciplines (palynology, palaeoparasitology, etc.) and in forensic entomology. However, unlike in forensic investigations, the elements in question (inert, generally fragmented remains) can rarely be examined *in situ*. Sediment samples are thus taken from burials, focusing on the skeleton (namely the abdominal region, skull and thorax) but also on diverse zones of the tomb. This latter point is particularly important for burials in empty spaces (coffin, sarcophagus, funerary chamber) since fly larvae generally leave the cadaver to pupate in the perimeter delimited by the container. In the particular case of sarcophagi, the implementation of an internal grid (squares of 10 cm wide) provides the exact topography of each sample. Lastly, in cases where organic matter (skin, hair, wood, vegetal remains, etc.) but also textiles, metal artefacts or receptacles for offerings are preserved, each element is carefully studied in the laboratory.

Diagnostic identification criteria for the archaeoentomofauna

Beetles (Coleoptera)

In the majority of cases, beetles are preferentially preserved in archaeological sediments owing to the very resistant nature of their exoskeleton (*Figure 1*). Generally speaking, only fragments are preserved and taxa are thus determined through the comparative study of sclerites with homologous elements from extant specimens. Two specific methods are used for the estimation of the total number of individuals: the minimum number of individuals (MNI) obtained by counting single (head, thorax, abdomen, etc.) or lateralized elements (elytra, legs, etc.), and the number of identified specimens (NISP).

Flies (Diptera)

Unlike beetles, adult flies are relatively fragile insects and are generally badly conserved in archaeological contexts. In most cases, the only "fossil" evidence of fly activity is the presence of the small, rigid, ovoid envelopes linked to pupation: the puparia (Phipps 1983, 1984) (*Figure 2a–c*). The latter are generally well sclerified and have a propensity to be conserved over remarkably long periods, extending at times to several million years (Kitching 1959, 1980). The use of the SEM (Huchet, Greenberg 2010) combined with the examination of third instar larva mouthparts which are at times still present inside the sub-fossil puparia are valuable aids for refining sample determination. The value of the study of dipterous remains from an archaeological context has been clearly demonstrated by Panagiotakopulu (2004).

Mites (Acarina)

Although acari are not insects, they are remarkably well-preserved in sediments, as shown by the discovery of fossil forms dating back some 400 million years (Norton *et al.* 1988). The study of acari in archaeological contexts is relatively recent and resulted in the creation of a new branch of archaeozoology: "archaeo-acarology"

(Schelvis 1987). Although their small size requires specific sampling protocols reserved for specialists, this discipline is being progressively incorporated into the field of bioarchaeological sciences (e.g., Baker 2009, Morales Muñiz, Sanz Bretón 1994, Schelvis 1987, 1992a, b).

In funerary archaeological contexts, diverse mite species have been discovered on human mummies from different countries and periods (Aufderheide 2003, Baker 1990, Corrado 1899, Hidalgo-Argüello *et al.* 2003, Radovsky 1970). In 1990, Gutierrez described a case of diffuse acariasis (sarcoptic scabies) on the mummified remains of a Capuchin monk in Sicily. The clinical examination of the mummy revealed the presence of *ante mortem* applications of sulphur unguent destined to eradicate the skin infection.

ARCHAEOENTOMOLOGY AND FUNERARY PRACTICES

The aims of funerary archaeoentomology (Huchet 1996, Huchet, Gallis 1996) adopt the principles and methods of forensic entomology but nonetheless display diverse differences. An obvious convergence concerns the objects analyzed but their *a posteriori* transcription is carried out on a different level, linked to the archaeological space. Although certain results concern events, from an occasional application to a particular case, others are part of a quantitative analytical dimension, and add a historical dimension to the interpretation. By orienting its research, funerary archaeoentomology lays claims to the precepts of archaeothanatology or the "Archaeology of Death"

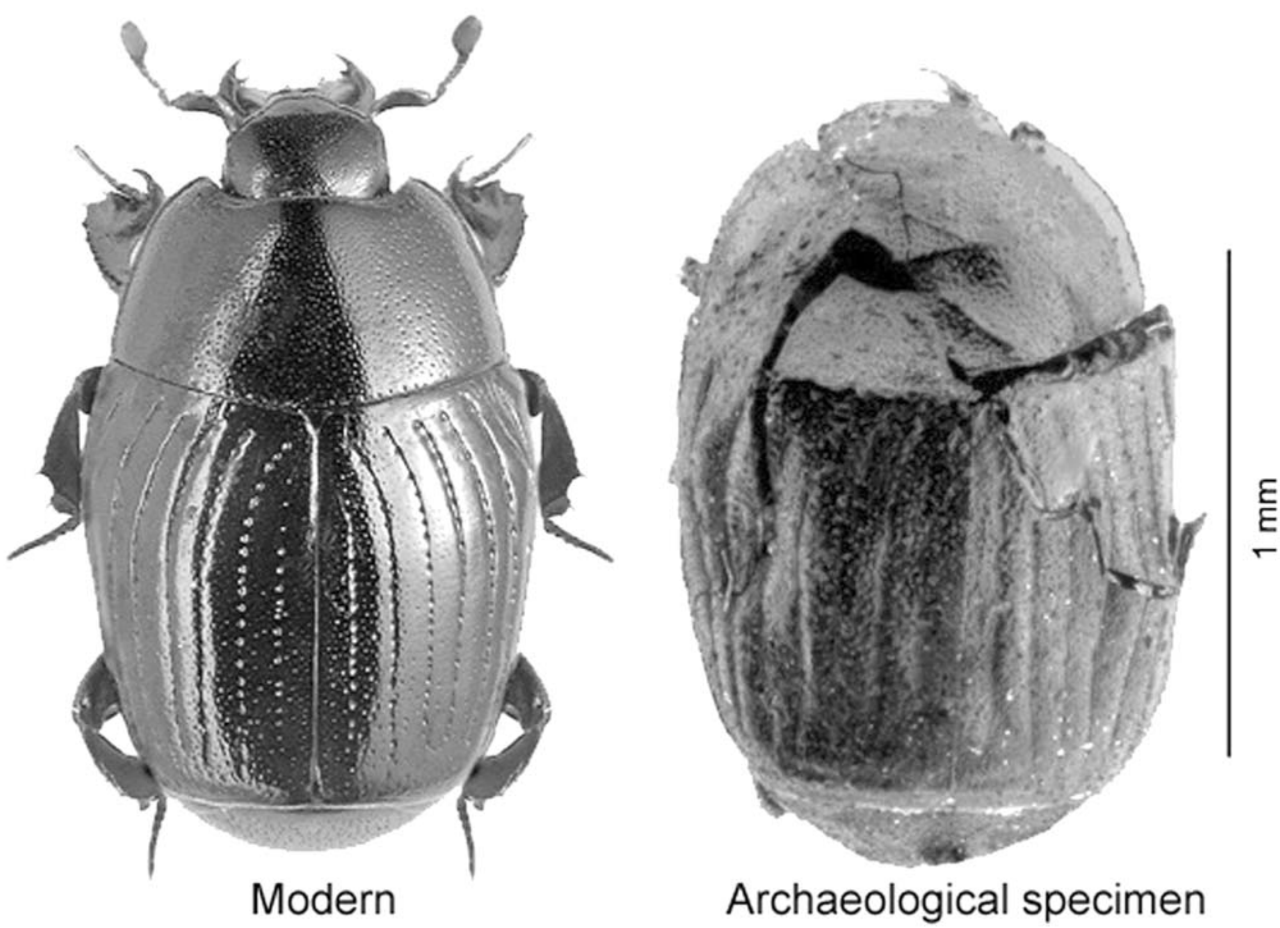

FIGURE 1. Comparison between a present-day specimen of the house fly predator *Carcinops pumilio* (Er.) (Coleoptera: Histeridae) (photo by M. E. Smirnov, modified) with an archaeological specimen of the same genus (*Carcinops tenella* (Er.)) (Mochica civilization, 100–750 AD, Huaca de la Luna, Peru) (photo by J.-B. Huchet).

(Boulestin, Duday 2005, Duday 2005, 2009) in that the main objectives target the reconstitution of funerary practices and customs in past populations.

Component and interpretation of taphocenosis

The presence of insect remains in funerary contexts results from two distinct modes of colonization. The first phase, called pre-depositional, mainly concerns necrophagous insects that colonize human cadavers and animal carcasses shortly after the death of the individual. This "open-air" phase implies that the remains are exposed above ground for a certain period of time before being buried. The second "post-depositional" phase occurs underground, and involves specialized ecological groups with a propensity for colonizing buried remains.

The characterization of these two categories is of major interest in the *a posteriori* reconstitution of the taphocenosis of the tomb or buried human remains. In this respect, unlike in certain erroneous representations, the presence of fly puparia associated with human remains in an archaeological context does not necessarily imply that the individual remained exposed above ground for a considerable time before being buried. Different taxa, including notably certain muscid or phorid flies are morphologically adapted to colonizing corpses buried at depths reaching two meters (Bourel *et al.* 2004).

In most cases, human remains from archaeological contexts come from burials and investigations concerning skeletonized individuals. In addition to the vicissitudes linked to the *in situ* preservation of organic matter, the entomofauna of buried cadavers is incomparably less diversified than that of surface species (Bourel *et al.* 2004, Gunn, Bird 2011). For these reasons, interpretations concerning insect remains cannot be equated with the precision and the predictability of forensic expertise on present-day cadavers.

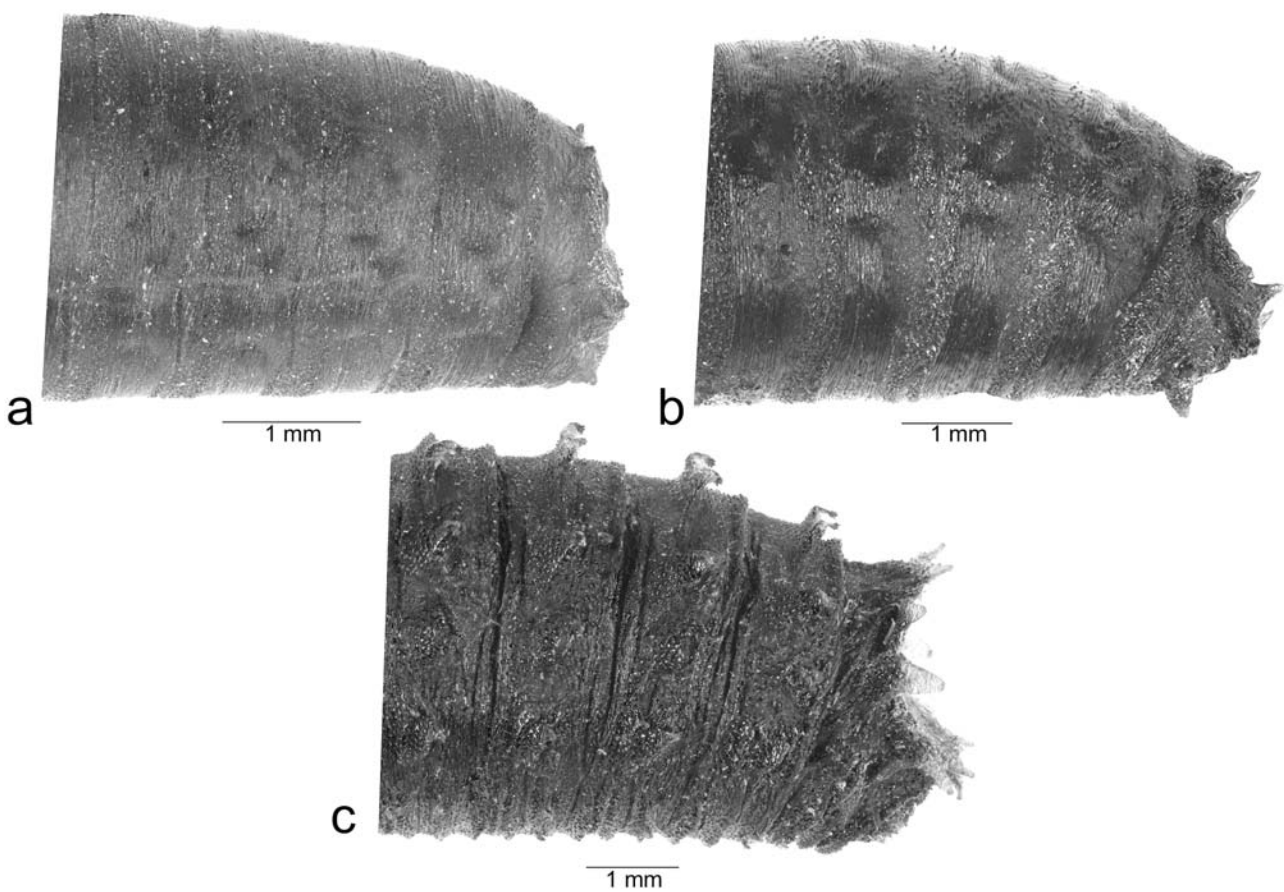

FIGURE 2. Posterior end (in lateral view) of the puparia of three modern calliphorid species of forensic importance. a, *Calliphora vomitoria* (L.); b, *Protophormia terraenovae* (R.-D); c, *Chrysomya rufifacies* (Macq.). Photo by J.-B. Huchet.

Given that puparia are among the most frequently preserved structures associated with human remains, it is imperative to take account of several important parameters for their interpretation, namely: their number, location, the taxonomic diversity of the sample and lastly whether or not they are empty or complete (non-hatched) pupae.

Quantitative representation

Although it is not a secondary effect of differential conservation, the quantity of puparia should be taken into consideration. A large quantity of puparia is a good indicator of cadaver accessibility (in the pre-sepulchral phase or after burial). Depending on the taxa and the burial mode, it may sometimes be possible to advance hypotheses concerning the burial period (seasonality) or the possibility of pre-depositional exposure and the duration of this exposure. The absence of any traces of insects in an environment propitious to conservation can also be significant (extreme climatic conditions (cold) at the time of death, taphonomic incidences, fast filling in of the body, etc.).

Location

The location of the puparia within the tomb can provide data on the funerary structure (namely burial in an empty or filled in space). In archaeological contexts, certain perishable structures (such as coffins) are only conserved over a limited period of time. The collapse and subsequent disintegration of the container can, in some cases, complicate the identification of the initial funerary structure. The topographic location of the fly puparia (in contact with or at a distance from the skeleton), combined with the archaeothanatological study of the human remains can thus provide pertinent data on inhumation modes.

Taxonomic diversity

As mentioned above, the fauna of buried cadavers is generally sparse and displays little diversity. The marked presence of particular species, including namely several non-burrowing necrophagous, necrophile or parasitoid species, suggests that the corpse was subject to prolonged open-air exposure before burial (Huchet, Greenberg 2010) or that the layer of sediment covering the corpse was thin and permeable enough to allow for a subsequent colonization by surface entomofauna.

Empty and complete pupae

In the absence of adult remains in the sediment, the presence of empty (hatched) puparia associated with human remains suggests that the complete cycle took place before burial.

When the empty puparia are from "pioneer" species intervening immediately after death (namely calliphorid flies), the specific identification of the species can sometimes provide an estimate of the minimum duration of the pre-sepulchral phase. However, as the third instar larvae usually moved from the body to pupate, only a non-representative sample of the original colonization is generally accessible to the archaeoentomologist.

Complete puparia are generally of less importance as they only indicate that the environmental conditions or burial mode (mainly directly in the ground) inhibited the completion of the cycle. Finally, we should bear in mind that preservation of insect remains is variable and a low representation of puparia in a grave might be linked to lower number of larvae/puparia from the beginning or poor conditions for preservation of organic material in the sediments.

The most frequent species in archaeological funerary contexts

In archaeological contexts, certain species of diptera are excellent indicators of burial in empty spaces (coffins, sarcophagi) or else point towards the presence of non-filled in zones in contact with the skeletons. Among these taxa, we can cite notably the muscid fly *Ophyra capensis* (Wiedemann). This species is a classic host of buried cadavers and is frequently found during legal exhumations (Bourel *et al.* 2004). It intervenes at a late stage of the decomposition process. In our latitudes, *O. capensis* (*Figure 3*), but also *O. leucostoma* (Wied.), are without doubt among the most common species in archaeological contexts (Couri *et al.* 2008, 2009, Huchet 1996, Masetti *et al.* 2008, Robinson 2001, Scharrer-Liska, Grassberger 2005, 2010, Turner-Walker, Scull 1997). Given their relatively modest size and their capacity to penetrate closed places, *Ophyra* species (but also different phorid flies) are frequently the only species present on corpses that are generally inaccessible for other sarco-saprophagous flies.

"Exotic" contexts are infinitely more diversified and, unlike in our latitudes, beetles are often more widely represented than diptera.

Several application examples

Exposure of the corpses before inhumation

The first studies focusing on the interpretation of insect remains associated with human remains in an archaeological context appear to date to the second half of the 20th century (Hincks 1966).

In modern western societies, the exposure of corpses before inhumation is often associated with criminal acts,

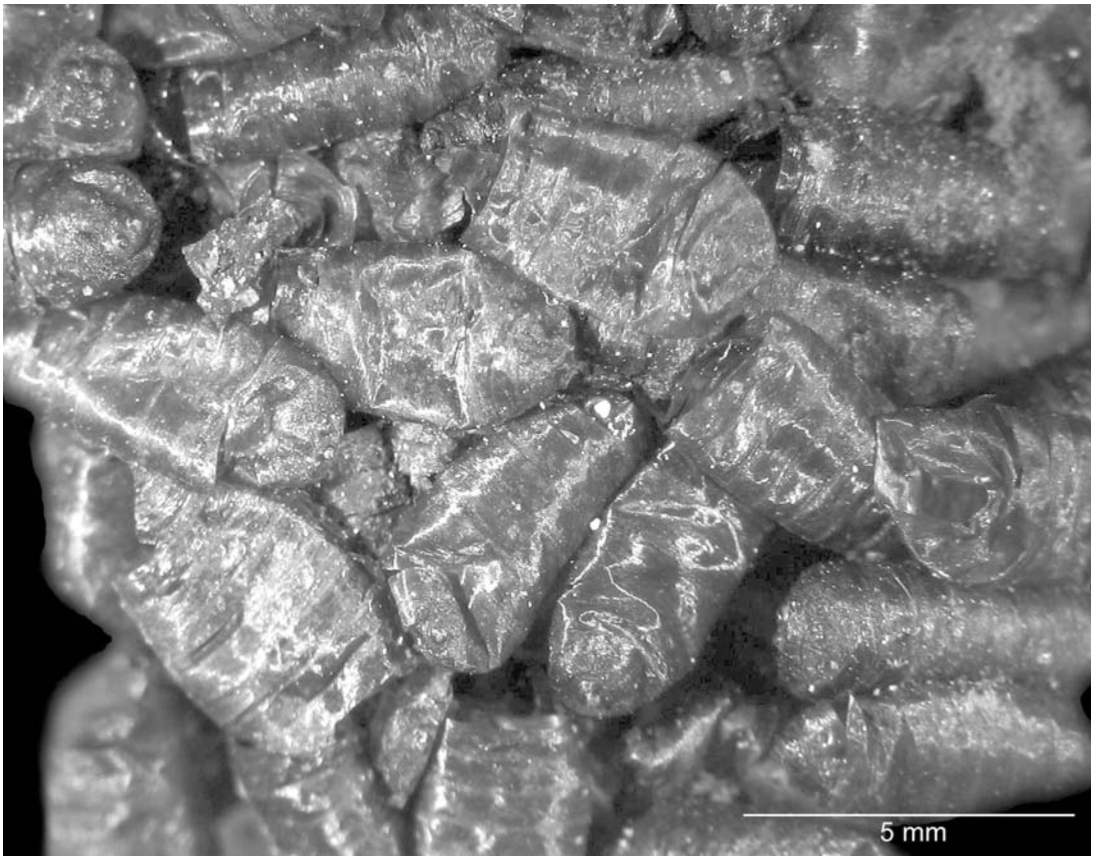

FIGURE 3. Archaeological puparia of the muscid fly *Ophyra capensis* (Wied.) recovered from the grave of a pilgrim at Saint-Julien-de-Brioude (15th century AD) (Haute-Loire, France). Photo courtesy of F. Gauthier, INRAP, France.

whereas this singular treatment of the dead is intentionally practiced in many civilizations.

The presence of numerous hatched *Calliphora* sp. puparia in textiles from a Viking tomb in the Isle of Man (Irish Sea), incited the entomologist W. Hincks (1966) to suggest that the body was probably exposed for at least twenty days. On the basis of the presence of blowfly puparia (Calliphoridae) and hide beetle remains (Trogidae), Ubelaker and Willey (1978) showed that the Amerindian corpses in Arikara graves in Dakota were exposed prior to burial for at least three weeks. Analogous conclusions were advanced by Teskey and Turnbull (1979) for a "prehistoric" tomb in New Brunswick (Canada), dating between 2000 and 2500 years, following the discovery of several hundred puparia belonging to six distinct species of necrophagous and saprophagous diptera (Calliphoridae, Muscidae, and Heleomyzidae).

Since these pioneering studies in funerary archaeology, other estimates of the duration of a pre-sepulchral phase or the identification of bodies without signs of funerary treatment prior to burial have been carried out. In this respect, we can cite the study of fourteen mutilated individuals at Pacatnamu by Faulkner (1986) (Peru: 1270 ± 110 AD), Vanin *et al.* (2009) concerning a soldier from the first world war (Italy), Huchet and Greenberg (2010) for a Mochica tomb (Peru, 1st–7th century AD) and lastly, Lynch and Reilly (2011) in relation to a double grave from the medieval period (Kildimo, Ireland).

In other cases, it is not through the composition of insect assemblages but rather through the absence of certain ecological groups that certain *post mortem* information regarding individuals is revealed. Investigations on Lindow Man, the famous naturally mummified corpse form a bog in Lindow Moss (England) (Dinnin, Skidmore 1995, Girling 1986, Skidmore 1986), revealed the excellent conservation of the abundant insects characterizing the immediate environment of the cadaver when it was deposited. The total absence of necrophagous species led certain authors to suggest that the body was swiftly submerged in the bog.

Seasonality of death

Although it is not possible to establish the *post mortem* interval (PMI) with arthropod sclerites from archaeological funerary contexts, the knowledge of the phenology (periods of activity) of insects of forensic interest allows us to advance hypotheses concerning the time of year of death. Gilbert (1966), then Gilbert and Bass (1967), showed through the study of insect remains from native American tombs (Arikara indians) in Dakota (calliphorid flies), that it was possible to estimate burial seasonality, albeit with a relatively broad chronological range. In France, the study of an abundant series of insects from a 10th century sarcophagus, ascribed to Guillaume Taillefer, Count of Toulouse, showed that death (unknown to historians) probably occurred in early spring (March–April) (Huchet 1996, Huchet, Gallis 1996). The combined presence of *Ophyra leucostoma* (Wiedemann) and a lepidoptera chrysalide *Cydia splendana* (Hubner) (Tortricidae) in the plant filling used to embalm Cardinal Giulio della Rovere (1533–1578) incited the authors (Masetti *et al.* 2008) to advance a date of death during the summer. These results were corroborated by historical sources indicating that the Cardinal died on the 3rd September 1578. Other estimates for death seasonality issued from studies conducted on thanatophagous insect series were proposed recently by Fugassa *et al.* (2008) on human remains in Argentina dating to 212 ± 35 years and on an Italian soldier from the first world war (Vanin *et al.* 2009).

Imprints and insect traces in funerary contexts: the ichnological approach

When environmental conditions are not conducive to the preservation of insect exoskeletons, the presence of the latter is sometimes revealed by imprints and/or traces of activity on diverse materials present in the tomb (textiles, metals, ceramic) as well as on bones. The analysis, the description and the interpretation of these artefacts are part of the field of ichnology (from the Greek *iknos*: "imprint, trace"), a discipline studying the interactions between the organism and the substratum in which the imprint is conserved. The application of the principles and methods of this science to the domain of archaeology led Baucon *et al.* (2008) to propose the term ichnoarchaeology. In a funerary context, recorded insect traces or imprints can be of a physico-chemical nature (mineralization) or result from pre or post-depositional processes linked to the activity of diverse hexapods. The identification of biotic agents is of major interest and can lead to the *a posteriori* reconstitution of the taphocenosis of the tomb.

Mineralization

The corrosion of certain metals, namely copper, iron or bronze, produces metallic salt solutions during degradation, which cover, impregnate and eventually replace organic matter in a mineralized form. These mineralization processes also occur in diverse environments rich in calcium phosphates or in limestone, such as latrines or trenches with bone remains, pottery shards or excrements (Green 1979, Ruas 1986). The meticulous examination of metal artefacts present in certain tombs can at times reveal insect imprints, which are evidence of insect "fossil" activity on buried human remains (Grote, Benecke 2001, Hirst 1985, Janaway 1987, Robinson 2001). These substitutions of organic matter by inorganic matter, accurately reproducing the primitive organism, are called pseudomorphs. When the diagenetic processes lead to the complete dissolution of the skeleton, the latter are sometimes the only indicator of the presence of a corpse (Huchet unpublished).

Depending on the type of metal, corrosion produces distinct artefacts: negative imprints of external structures in contact with iron (Keepax 1975) or positive replicas of organic remains in the presence of copper alloys (Gillard, Hardman 1996). In certain cases, the preservation of certain taxonomically informative external structures authorizes the specific identification of mineralized species.

In the literature, the oldest citation of fly puparia fixed by corrosion seems to be that attributed to Hochstetter (1878). The imprints present on a bronze belt buckle are from a tomb from the Hallstatt period (ca. 750 BC). In 1956, the entomologist M. Beier conducted a detailed study of the artefacts and identified these impressions as those of calliphorid flies. The additional examination of two spearheads from the same context reveals the existence of abundant pseudomorphs attributable to fanniid flies (*Fannia canicularis*?). Beier suggests that the latter appear to be linked to the presence of animal offerings which would have decomposed on site.

Rich assemblages of necrophagous insects preserved by corrosion have been described in diverse Anglo-Saxon tombs (6th–8th centuries AD) (Turner-Walker, Scull 1997). Grote and Benecke (2001) also brought to light the mineralized remains of abundant puparia attributable to blowflies (Calliphoridae) in medieval graves in Wesel-Bislich (Germany). The recurrent presence of funerary metal accessories deposited in contact with the deceased

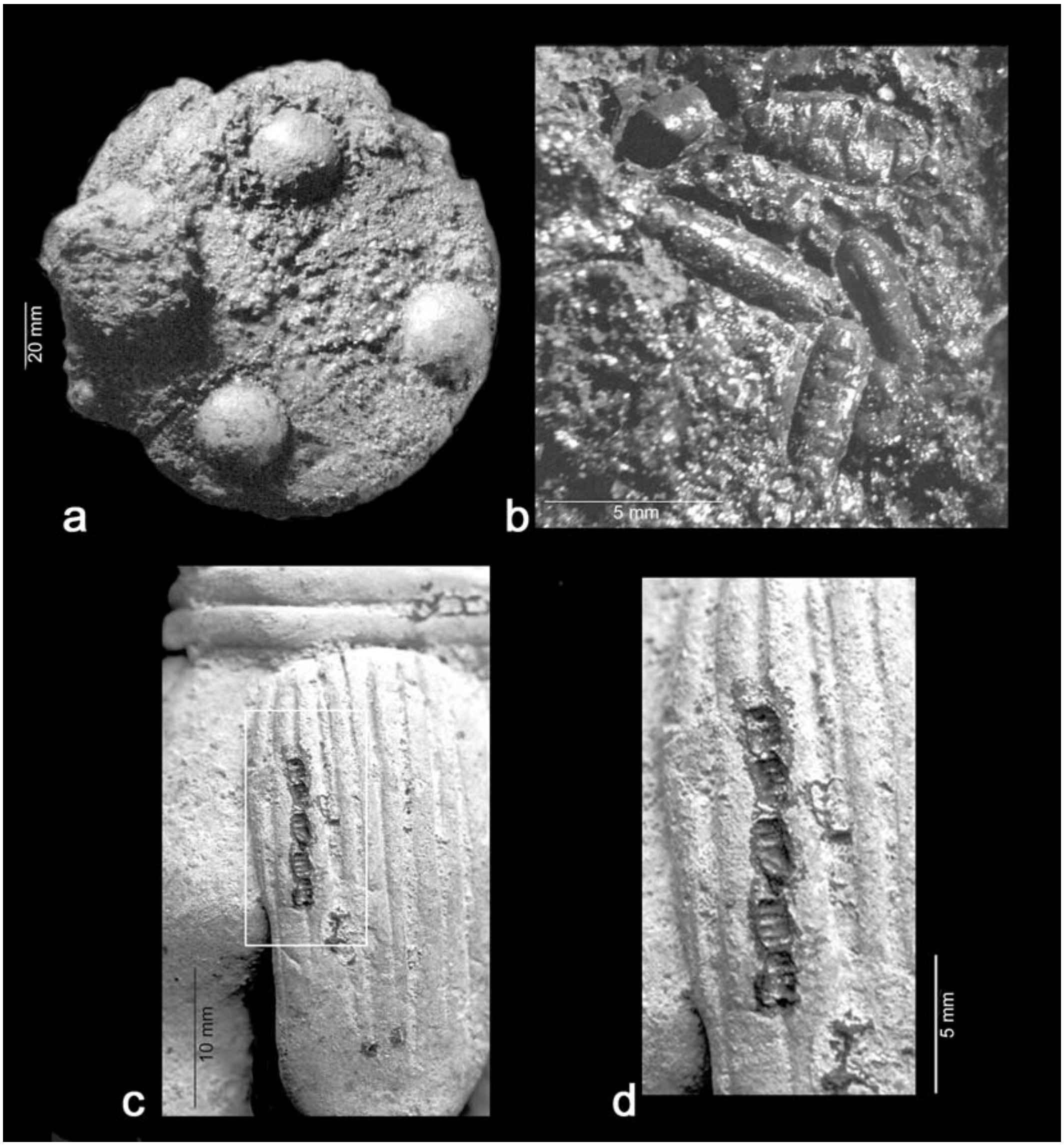

FIGURE 4. a, Medieval iron belt buckle corroded by rust allowing the mineralization of fly puparia (Tomb 628, Wesel-Bislich, Germany) (after Grote, Benecke 2001); b, detail of mineralized puparia preserved by iron corrosion; c, fly puparia mineralized by manganese deposits on the outer part of a two millennian pottery from a west Mexican shaft tomb at Huitzilapa; d, *idem*, detail of the puparia. a, b, Photo courtesy of Mark Benecke; c, d, photo courtesy of Robert B. Pickering.

(swords, decorative elements, belt plates, etc.) greatly contributed to the mineralization of the organic structures (*Figure 4a, b*). Unlike for certain taxa with the propensity to colonize deeply buried cadavers (certain muscid and phorid flies…), the oviposition of Calliphoridae can only occur if the corpse is accessible or buried at a depth of less than several decimetres (Lundt 1964, Nuorteva 1977, Rodriguez, Bass 1985). Their presence in deep graves indicates that colonization took place during the pre-burial phase. In the example cited here, inhumation in an empty space (wooden funerary chambers or hollowed-out tree trunks) allowed for the ontogenic development of diptera in the tomb and their mineralized imprints have been conserved up until now. Although certain calliphorid flies (namely the genus *Calliphora*) have been shown to be active during cold periods (e.g., Charabidze *et al.*

2012, Faucherre *et al.* 1999, Wyss *et al.* 2003), their main period of activity is from the spring to the autumn. These biological facts led Grote and Benecke (2001) to suggest that the deaths of the individuals appear to have occurred during this period of time.

In the absence of direct contact with metals, certain physico-chemical processes combined with specific bacteria activity (*Metallogenium*, *Leptothrix discophora*) can also lead to the mineralization of organic matter on very varied materials. The anthropologist R. Pickering (Pickering 1997, Pickering, Cuevas 2003a, b, Pickering *et al.* 1998) identified the presence of numerous ovoid structures, at least five millimetres long, solidly attached to the ceramic offerings deposited in two thousand year-old shaft-tombs (Huitzilapa, Mexico) (*Figure 4c, d*). In this particular case, he demonstrated that the mineralization of the puparia on the ceramics was due to the joint action of bacteria and the percolation of water laden with dissolved metals into the tomb. N. Haskell, responsible for the identification of fossil imprints on pottery, established that the latter appear to correspond to Phoridae diptera (R. Pickering, pers. comm. 2013). The presence of organic elements (in the present case puparia) allows for the application of combined dating methods (e.g., thermoluminescence for pottery and ^{14}C for the immature diptera stages) and thus to propose reliable elements for pottery dating. Lastly, the preservation of puparia on pottery is a discriminating element for authenticating pre-Columbian funerary ceramics, in view of the presence of numerous forged copies (Pickering 1998, Pickering *et al.* 1998).

Osteolytic lesions perpetrated by certain insects on human remains

Although the role of necrophagous insects as "biological clocks" is well-known and widely used in forensic science (e.g., Anderson 2001, Byrd, Castner 2009, Smith 1986), the implication of these insects in the taphonomic processes of osteolytic degradation remains poorly documented. However, different orders of arthropods could be responsible for significant bio-erosion on bones from fauna and human skeletons. The identification of these lesions, which are often spectacular, is of the utmost importance in the comprehension and the interpretation of certain pre- or post-depositional taphonomic phenomena. Moreover, the effects of these lesions on the bone matrix sometimes simulate certain degenerative or infectious bone pathologies (pseudopathologies), which require identification during the retrospective etiologic diagnosis (Huchet in press). Some of these artefacts, such as certain circular perforations present on skulls, can also be suggestive of traumatic damage, or even imitate certain *peri-* or *post mortem* anthropic interventions (projectile impacts, trepanation, etc.).

Most of the data concerning the osteophagy of certain insects are from the domain of palaeontology. Many "palaeoichnologists", according to the terminology used, described multiple osteolytic lesions on dinosaur bones (e.g., Bader *et al.* 2009, Britt *et al*. 2008, Chin, Bishop 2008, Paik 2000, Roberts *et al*. 2007) or on extinct forms of terrestrial mammals (e.g., Dominato *et al.* 2009, Kaiser 2000, Laudet, Antoine 2004, Martin, West 1995). Four orders of insects have been identified as taphonomic agents of bone damage on human remains: isoptera (subterranean termites), coleoptera (dermestid beetles), hymenoptera (wasps and burrowing bees), and lastly certain sarco-saprophagous diptera larvae.

Subterraenan termites (Isoptera)

Derry (1911) was the first author to reveal proof that certain bone modifications on human skeletons in Nubia were due to termite action. Previous observations of these lesions had led the anthropologists Fouquet (1897) and then Lortet (1907) (*Figure 5*) to interpret this damage as obvious evidence of the existence of syphilis on the African continent during prehistoric periods.

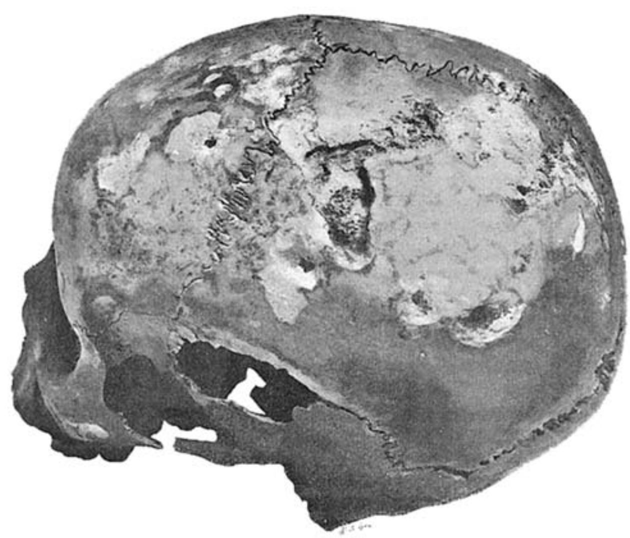

FIGURE 5. Skull of a young Egyptian woman (Roda) described as "syphilitic" by Lortet (1907: 212). The osteolytic lesions visible on this picture, causing the wrong retrospective diagnosis (pseudopathologic case), refer to subterranean termites activity. Adopted from Lortet (1907).

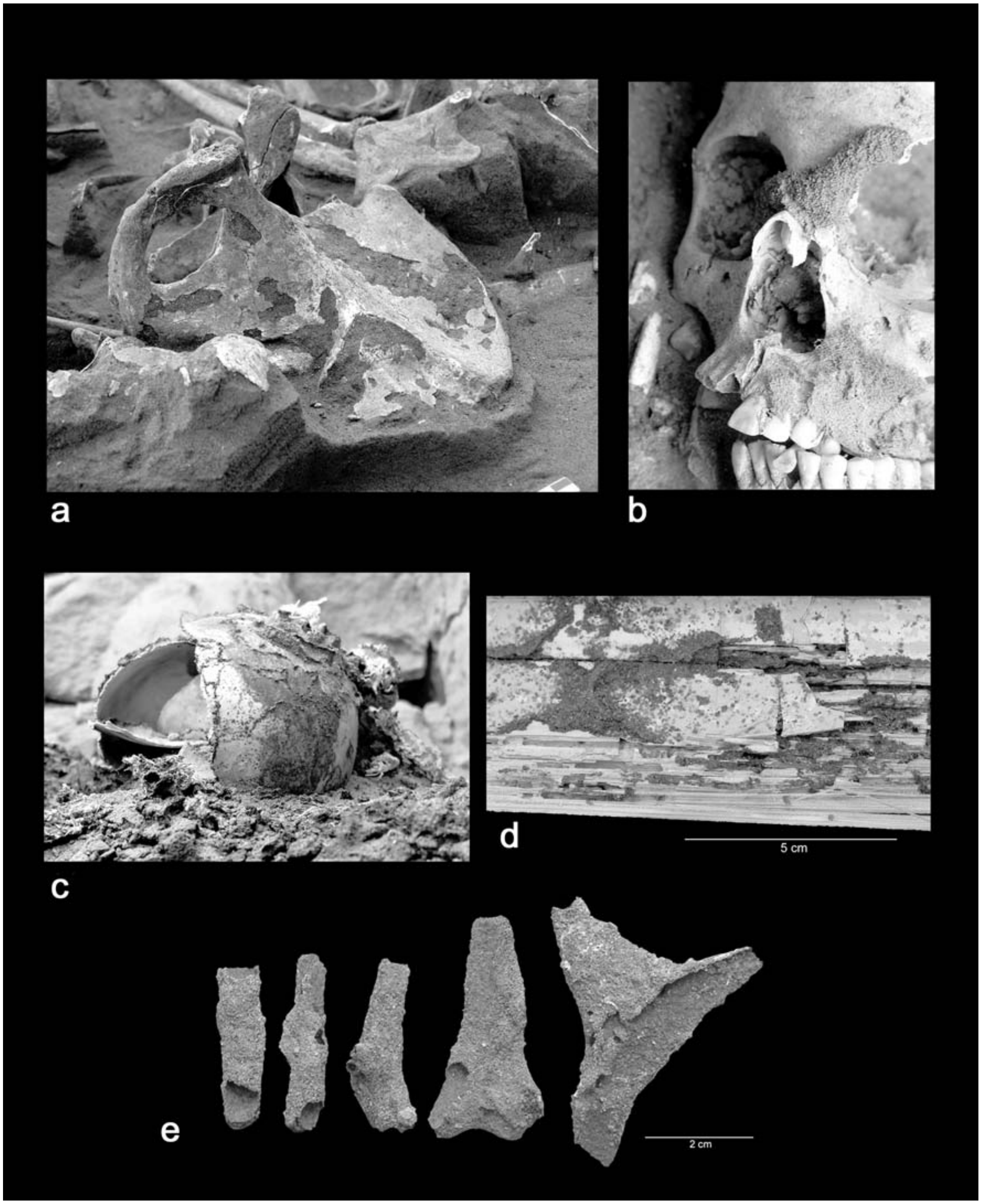

FIGURE 6. a, Human coxal bone *in situ* showing distinct activity of subterranean termites (Mochica civilization, Huaca de la Luna, Peru); b, a distinct subterranean termite "shelter tube" on the outer surface of the skull of an adult individual (Mochica civilization, Peru); c, skull of an immature individual (Mochica civilization, Peru) showing distinct traces of activity on the outer surface due to the subterranean termite *Amitermes lunae* Scheffr. (Isoptera: Termitidae); d, similar damage due to the same species on a piece of bambo (Huaca de la Luna, Peru); e, shelter tube fragments of the subterranean termite *A. lunae* Scheffr. recovered from a Mochica grave (Huaca de la Luna, Peru). a, b, c, Photo courtesy of C. Chauchat; d, e, photo by J.-B. Huchet.

Since Derry's publication, several similar cases have been described in different parts of the world: Asia (Light 1929), Africa (Dastugue, Gervais 1992: pl. II, Sampson 1964), Australia (Bonney, Clegg 2011, Wood 1976, Wylie *et al.* 1987), and South America (Guapindaia 2008, Huchet *et al.* 2011, Scheffrahn, Huchet 2010).

In a more recent archaeological context, the anthropologist D. Danielson (2005), responsible for the repatriation of American soldiers killed in airplane crashes (Vietnam, Laos, Papua New Guinea), showed that all the skeletons presented major osteolytic damage linked to termite action. The presence of numerous isoptera in the medullar cavity of long bones at the time of the discovery of the human remains left no doubt as to the identity of the agent responsible for the lesions.

Termites are traditionally divided into three ecological groups: dry wood termites, damp wood termites and subterranean termites. Investigations concerning the osteophagous behaviour of certain isoptera show that this activity appears to be specific to subterranean termites. According to Thorne and Kimsey (1983), the occasional exploitation of bone remains by these termites compensates for nitrogen deficiencies not easily met with strictly xylophagous diets (cellulose). Although fresh bones seem to be generally more attractive for termites (Backwell *et al.* 2012, Haynes 1991, Watson, Abbey 1986), termites also alter bones in the process of diagenesis, whether they are buried or not (Huchet in press) (*Figure 6a*).

The analysis of bones degraded by termites leads to the identification of different gradients of osteolytic alterations, classified by ascending order of destruction: superficial imprints of mud galleries (i.e., shelter tubes) on the cortex (*Figure 6b–e*), local, more or less generalized abrasion of the compact bone which can reach the diploe (*Figure 7a*), deeper effects including notably cupules, fossae, perforations and galleries beneath the cortex (*Figure 7b–d*), and lastly, the complete destruction of certain bones. Among the most characteristic signatures of termite activity on bones are surface "star-shaped" traces, which correspond to the furrows left by mandibles on the bone surface and on the periphery of the perforations (*Figure 7e*).

The lesions are more or less generalized to the whole skeleton or localized on the bone surface in contact with the substratum, depending respectively on whether the bones were buried or remained exposed to open-air.

Dermestid beetles (Coleoptera)

The final phase of decomposition of a corpse exposed to open-air attracts a certain category of very specialized insects: the skin beetles (genus *Dermestes* Linnaeus: Dermestidae). These mainly dermatophagous and keratophagous insects and their larvae attack tissues, skin appendages and other desquamations by gnawing and shredding them. At the time of pupation, the larva digs out an ovoid or elliptical cell (pupation chamber) in the adjacent substratum, whatever the latter may be made from: plaster, wood but also bone. Characteristic perforations are visible on bones when they are totally defleshed.

Traces resulting from *Dermestes* action on fossil bone have been studied in detail by Martin and West (1995). They have also been identified on Jurassic (Hasiotis *et al.* 1999) and Cretaceous dinosaur bones (Rogers 1992). As for mammals, the oldest ichnofossils are from the Tertiary period (Rhinocerotidae from the Quercy Phosphorites) (Laudet, Antoine 2004). As underlined by these authors, these interactions between insects and vertebrates are extremely rare.

The duration of the *Dermestes* larval cycle is intricately linked to temperature, humidity and the type and quantity of food available (Hinton 1945). Although certain adult *Dermestes* have sometimes been observed on human cadavers in the early stages of decomposition (Early, Goff 1987, VanLaerhoven, Anderson 1999), optimal larval activity occurs on bodies in an advanced state of desiccation (Byrd, Castner 2009, Kulshrestha, Satpathy 2001, Voss *et al.* 2008). Colonization generally intervenes one to two weeks after death (Martin, West 1995, Richards, Goff 1997). However, depending on certain external factors (temperature, season of death, etc.), infestation sometimes intervenes several months after death (Anderson, VanLaerhoven 1996, Kulshrestha, Satpathy 2001). In order to be exploited by *Dermestes*, skin and muscles must subsist for the whole of the cycle and temperatures must be superior to 15°C (Richardson, Goff 2001). The total duration of the biological cycle varies from 5 to 15 weeks (from 42 to 46 days on average when conditions are optimal) (Hinton 1945). In order to avoid intra-larval predation or cannibalism, mature larvae dig a pupal chamber in the nearest substratum (Archer, Elgar 1998). These chambers have an external diameter of 3 to 4 mm, and are often clustered together (Martin, West 1995).

The recent study of Bronze Age human remains (Israel) (2100–1550 BC) (Huchet *et al.* 2013) brought to light evidence of analogous pupation chambers to those described on bones from fauna (e.g., Bader *et al.* 2009,

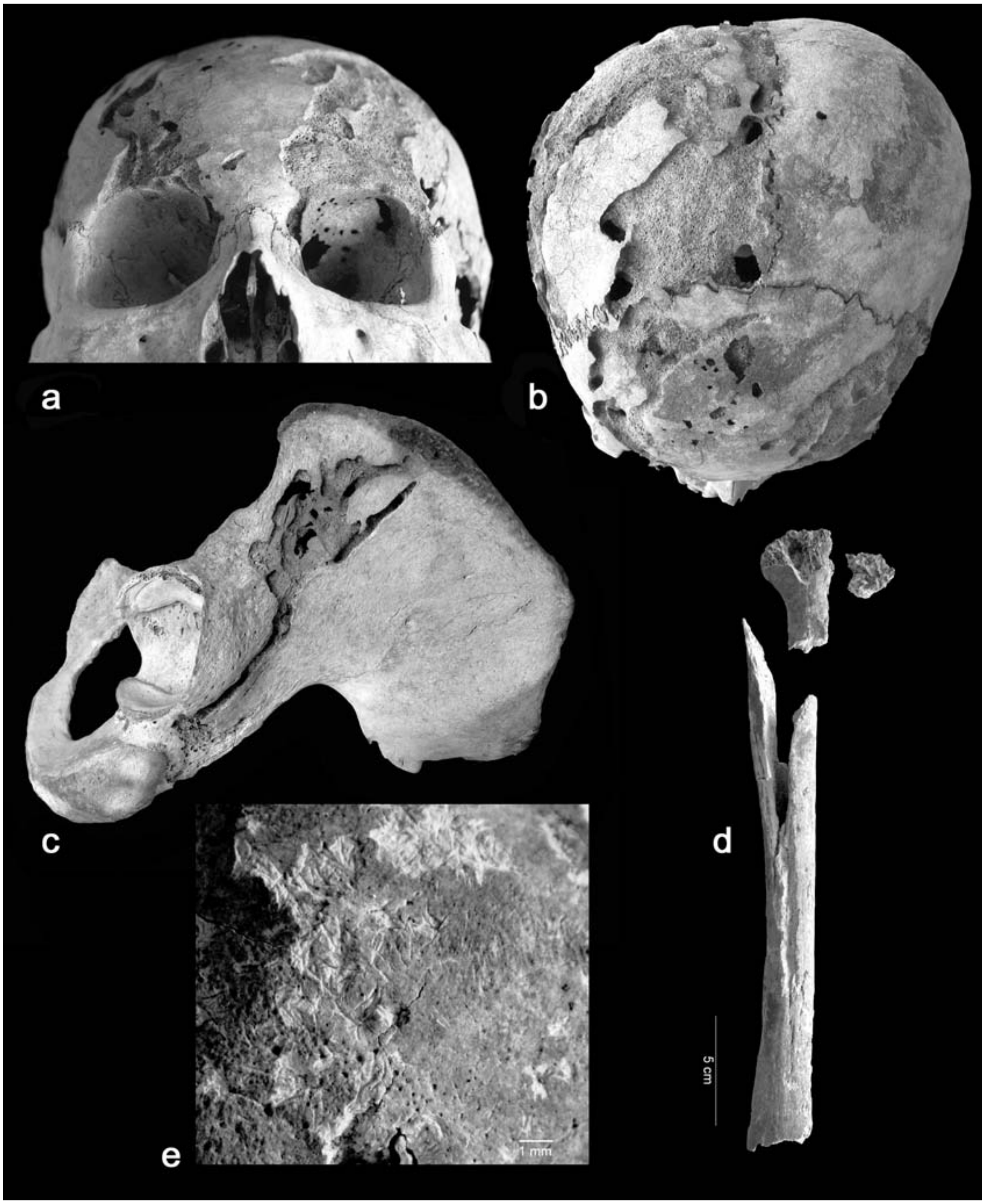

FIGURE 7. a, Partial view of the skull of an adult individual showing network of cavities and subterranean termite tunnelling on the frontal bone and orbital floor perforations (Mochica civilization, Peru) (photo by D. Deverly); b, the same skull (superior view) showing deeply incised areas of cortical bone, bores, large furrows and sub-circular perforations on the frontal and parietal bones (after Huchet *et al.* 2011); c, iliac fossa of left *os coxae* (same individual as described in *Figure 7a, b*) bearing a distinct network of deep cavities and termite tunnelling extending inferiorly (after Huchet *et al.* 2011); d, right tibia of an immature individual (anterior view) partially destroyed consecutively to subterranean termite activity (Mochica civilization, Peru) (photo by C. Favart / J.-B. Huchet); e, characteristic "star-shaped" traces on the surface of a parietal bone, signature of subterraenan termites activity (Mochica civilization, Peru) (photo by C. Favart / J.-B. Huchet).

Britt *et al.* 2008, Hasiotis *et al.* 1999, Martin, West 1995, West, Martin 2002) (*Figure 8a*). As *Dermestes* pupation takes place on the surface, the presence of these pupal chambers suggests that the excarnation phase of these individuals took place in open air and that the cadavers (or part of the cadavers) were thus exposed for several weeks before being buried in tombs or ossuaries.

Wasps and burrowing bees (Hymenoptera)

Certain post-depositional bio-erosions result from purely fortuitous processes, linked in particular to the burrowing activity of diverse insects nesting in the ground. During the excavation of a Roman necropolis (4th–5th century AD) in Sardinia, the anthropologist E. Pittoni (2009) showed that the enigmatic osteolytic lesions observed on more than half of the skeletons resulted from the excavating activity of Sphecidae and Halictidae hymnoptera, still active at the site. In this particular case, the bones had been weakened by diagenesis processes and were thus an ideal material for digging out nesting chambers. Although several parts of the skeleton were affected, the most remarkable bioerosions are on the skull. They appear as superficial or piercing circular perforations, with a diameter ranging between 2 and 20

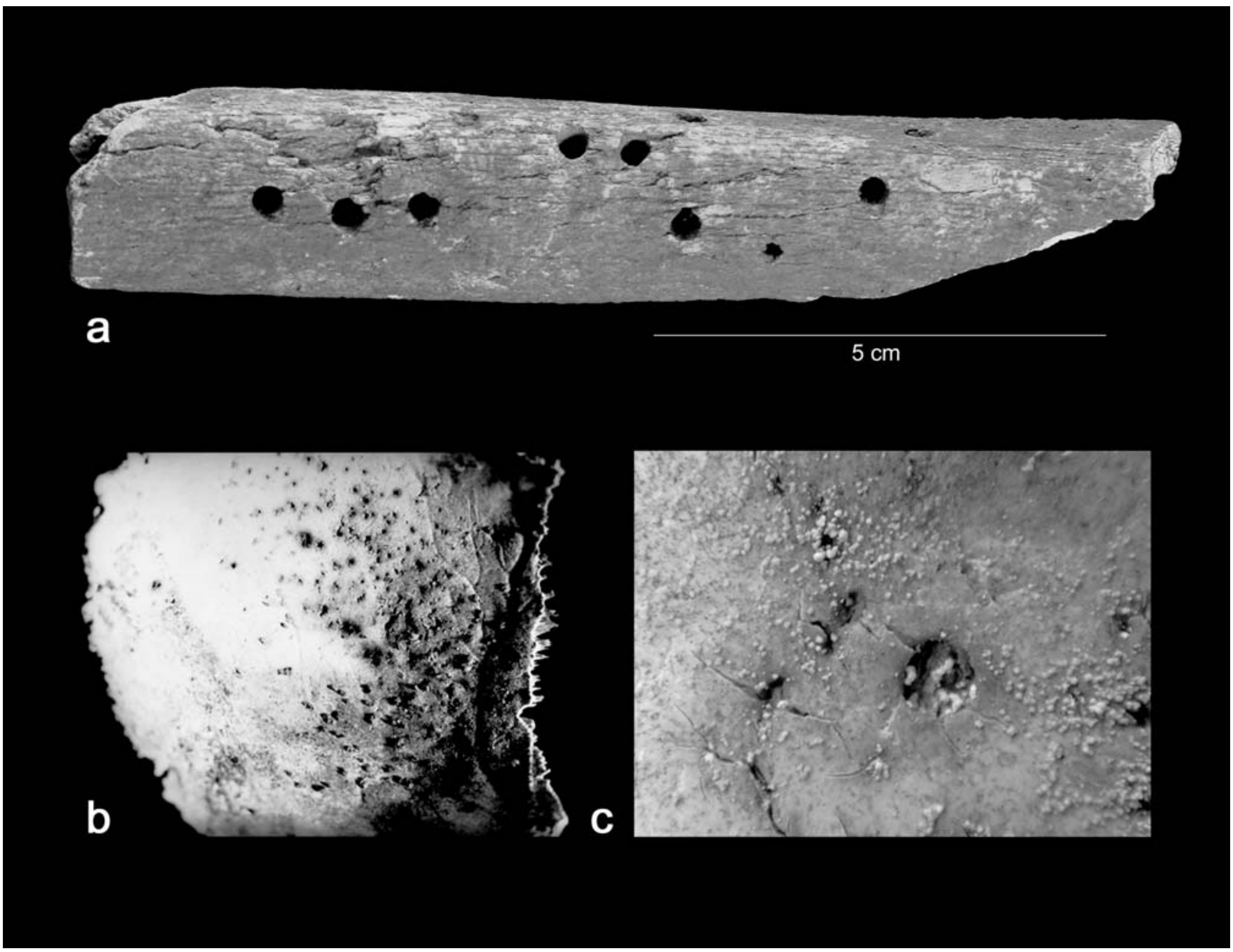

FIGURE 8. a. *Dermestes* pupal chambers on a Middle Bronze Age human tibial diaphysis fragment (tomb 641, Munhata, Israel, after Huchet *et al.* 2013) (photo by J. Perrot); b, parietal bone of an immature individual (internal view) showing multiple osteolytic lesions attributed to the corrosive action of necrophagous fly larvae digestive juices (St. John church, Gdansk, Poland, 18th century AD) (after Gładykowska-Rzeczycka, Parafiniuk 2001) (photo courtesy of M. Parafiniuk); c, *idem*, macroscopic view (×10) (after Gładykowska-Rzeczycka, Parafiniuk 2001) (photo courtesy of J. Gładykowska-Rzeczycka).

mm, depending on the corporal dimensions of the incriminated taxa. Due to their conformation and topography, the identification of these osteolytic lesions is of the utmost importance as they can simulate certain degenerative or infectious bone pathologies (periostitis, osteomyelitis, syphilis, multiple bone myeloma, etc.) which can result in an erroneous retrospective diagnosis.

Fly larvae (Diptera)

The larvae of necrophagous flies possess an extra-oral digestion (exodigestion), which means that they reject their digestive juices directly onto the substratum, which liquefies in reaction to the enzymes present in the salivary glands. Pollak and Reiter (1988) demonstrated that these gastric regurgitations could sometimes cause perforating osteolytic lesions on certain lamellar bone regions imitating the impacts of certain arms. In an archaeological context, Gładykowska-Rzeczycka and Parafiniuk (2001) suggested that certain atypical lesion areas on the internal surface of the cranial vault and the cervical vertebrae of an immature individual (Poland, 8th century) appeared to result from the corrosive action of digestive juices from diptera larvae (*Figure 8b, c*). The presence of diptera puparia was attested *in situ*.

CONCLUSION

Within the broad range of bioarchaeological sciences, archaeoentomology remains an under-developed, marginal discipline. However, as shown by the examples exposed in this paper, this disciplinary field offers huge potential and the study of entomofaunal species is a particularly effective tool for the comprehension and interpretation of archaeological events (Pringle 2010). In the vast majority of cases, interpretations are founded on fragments of insect exoskeletons discovered *in situ*, but the presence of the latter can also be revealed through the identification of traces or imprints preserved through physico-chemical processes (mineralization) or with regard to the bio-erosive activity of certain taxa (osteophagy). In this respect, the identification and characterization of these osteolytic lesions is of major interest to anthropologists and palaeopathologists, as they sometimes mimic certain pathologies (pseudopathologies). In the same way, depending on the incriminated taxa, these traces of activity can contribute in an original way to the reconstitution of certain mortuary practices of ancient societies.

Funerary archaeoentomology is at the interface of natural and environmental sciences, forensic sciences and human sciences, but is becoming increasingly important in the archaeological disciplines related to the study of the World of the Dead. The evolution of observation techniques in the characterization of certain taxonomically informative structures (electronic microscopy, tomography), combined with recent advances in molecular and metagenomic biology enables us to envisage innovative applications in the near future.

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