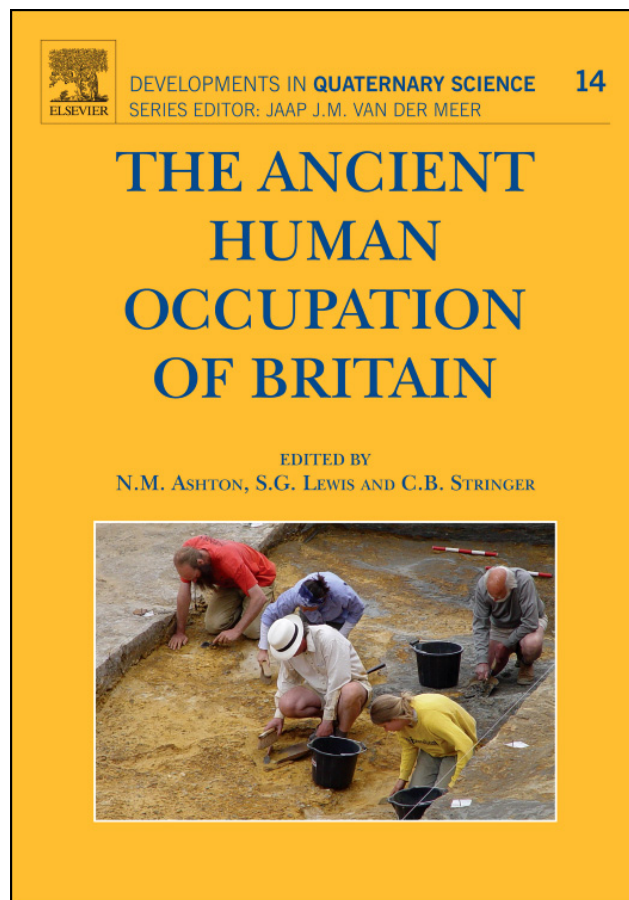


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Pleistocene Hyaena Coprolite Palynology in Britain: Implications for the Environments of Early Humans

Mark D. Lewis

*Department of Palaeontology, The Natural History Museum, Cromwell Road, London, SW7 5BD, United Kingdom
(e-mail: m.lewis@nhm.ac.uk)*

Abstract

Spotted hyaena (*Crocuta crocuta*) coprolites from four British Pleistocene sites were analysed for their pollen content. At the two open sites, the palynology was compared to that of the surrounding sediments. The results provide palynological data, supported by other lines of evidence, enabling reconstruction of human environments as well as providing insights into the taphonomic complexities of incorporation of pollen into coprolites. Pollen presence and preservation appear to be closely related to mammalian behaviour and post-depositional processes. Geological age does not seem to be a significant factor, as samples from two of these sites are amongst the earliest known from the Pleistocene to provide viable coprolite-derived pollen counts.

Keywords: Pollen; Hyaena; Coprolite; Britain; Pleistocene; Palaeolithic.

14.1. Introduction

Pollen analysis is one of the most successful and widely used tools in the reconstruction of past environments. Palynology can detect natural changes in vegetation, caused by factors such as climate change and plant succession, over broad spatial and temporal scales (Lowe and Walker, 1997). One successful application of palynology has been the reconstruction of the changing environments of early humans, providing critical information on their climatic tolerances and environmental preferences. In later prehistory, it also allows us to study the impact of human activities on vegetation and landscape. Pollen can be found in a wide range of contexts, the most conventional and commonly used being lake sediments and peats due to their excellent anaerobic preservational qualities; other sources include soils, cave deposits and ocean floor sediments. Additionally, within the last few decades, coprolites from hyaenas and other vertebrates have become increasingly recognized as a further potential source of fossil palynomorphs, particularly at sites where conventional pollen sources are absent (Martin and Sharrock, 1964; Bryant and Larson, 1968;

Scott, 1987, 1994, 2002; Reinhard *et al.*, 1991; Reinhard and Bryant, 1992; Scott and Brink, 1992; Scott *et al.*, 1995, 2003; Fernández Jalvo *et al.*, 1996; Carrión *et al.*, 1999a, 2000, 2001, 2005, 2007, 2008; Yll *et al.*, 2006). This potential can be extended to any site with stratified deposits, including caves where associated bone and coprolite accumulations by hyaenas can occur, as well as evidence of human occupation. The taphonomic problems of pollen analysis from cave sediments are well documented (e.g. Dumbleby, 1985; Turner, 1985; Coles *et al.*, 1989; Carrión *et al.*, 1999b, 2007, 2008), and an analysis of coprolite pollen can help avoid these difficulties due to the sealed nature of the context. Palynology of coprolites from stratified open sites can prove equally rewarding and should be seen as an important complementary line of evidence, especially when used in conjunction with pollen analysis of the surrounding sediments.

The extraction of pollen from faecal material is by no means new. Pollen analysis has been used to analyse dietary preferences of numerous mammalian taxa from herbivores (Moe, 1983; Carrión *et al.*, 1999a) to humans (Martin and Sharrock, 1964; Callen, 1965; Bryant and Larson, 1968; Trevor-Deutsch and Bryant, 1978; Reinhard *et al.*, 1991, 2006; Chaves and Reinhard, 2006). Comprehensive bibliographies have been provided by Reinhard and Bryant (1992), Carrión *et al.* (2004, 2005) and Davis (2006). However, analysis of pollen from Pleistocene hyaena coprolites only began relatively recently and appears to have first been undertaken in South Africa at the site of Equus Cave (Taung; Scott, 1987), continuing at Florisbad (Orange Free State; Scott and Brink, 1992) and Oyster Bay (Eastern Cape; Carrión *et al.*, 2000).

These first studies were performed mainly on coprolites belonging to the omnivorous brown hyaena (*Parahyaena brunnea* Thunberg, 1820). The Equus Cave deposits range from about 30 to 2.5 ka BP (Pta-2452; Beaumont *et al.*, 1984), the earlier layers being more problematic in dating terms, but with all units containing lithic artefacts. The study provided evidence for vegetation change over this time from open, shrubby grassland growing in a fairly cool, humid climate in the Late Pleistocene, to a thornveld vegetation with similar climatic conditions to today in the upper levels representing the last 7500 years. These changes were apparent in both the sediment

and coprolite pollen, but with some differences. The pollen from the cave sediment was more representative of local conditions, and it was concluded that the coprolite pollen spectra not only reflected the dietary behaviour of the animal, but also regional vegetation due to hyaenas ranging up to 50 km from their den sites (Scott, 1987).

The site of Florisbad is a spring mound with two distinct faunal assemblages, one of which is associated with a Middle Stone Age (MSA) living floor and artefacts. Palynological studies of the sediments have been undertaken periodically since the mid-1950s and site complexities such as unconformities and dating problems have been identified (Scott and Rossouw, 2005). These authors suggest that a more in-depth palynology, along with phytolith analysis, still needs to be done to clarify the relationships of the sediment pollen to the palaeontology and archaeology at Florisbad. However, Scott and Brink (1992) performed a successful pollen analysis of spotted hyaena (*Crocota crocota* Erxleben, 1777) coprolites from the lower section of the sequence. They noted, as at Equus Cave, that the coprolite pollen spectra were more representative of wider regional grassland than the local spring environment with a high representation of grass pollen.

At Oyster Bay, brown hyaena coprolites that were considered broadly contemporaneous with MSA artefacts and vertebrate faunal remains accumulated by hyaenas and humans (Carrión *et al.*, 2000) were analysed for pollen content. The coprolites contained pollen, although concentrations were not very high. The evidence suggested a cooler climate than at present and greater distance from the sea. The study also observed that pollen preservation appeared to be better in coprolites than sediment, due to the sealed nature of the coprolite context, although the dangers of modern contamination from pollen in cracks or on the coprolite surface also came to light.

Carrión and colleagues have continued the application of the technique in southern Europe, mainly in the Iberian Peninsula, throughout the past decade (Carrión *et al.*, 2001, 2004, 2007, 2008; Yll *et al.*, 2006), usually with *Crocota* coprolites, but with some exceptions, including badger (*Meles meles*) coprolites (Carrión *et al.*, 2005). Their most recent work was a successful palaeobotanical analysis of sediments and coprolites from Gorham's Cave, Gibraltar, an area of archaeological importance with potentially some of the latest Neanderthal remains in Europe (Finlayson *et al.*, 2006). The biological remains also provide evidence for a potential plant refugium in southern Iberia during Marine Isotope Stages (MIS) 3 and 2 (Carrión *et al.*, 2008). They analysed 30 coprolites from three distinct Pleistocene levels (Mousterian to Upper Palaeolithic) along with palynology of these deposits and, once again, the regional representation of pollen types in hyaena coprolites was emphasized. The coastal shelf area and the adjacent mountains were found to be a rich reservoir of biodiversity during this time, thus providing a resource capable of sustaining the Neanderthals and the animals they consumed. Their work has shown that although there are still undoubtedly some taphonomic uncertainties related to coprolite pollen spectra, it remains a useful technique, particularly when

able to complement conventional sediment pollen data. Locations of successful studies in all of these regions are shown in Fig. 14.1.

The case studies presented here of Pleistocene hyaena coprolites from four British locations, two caves and two open fluvial sites (Fig. 14.1A), were undertaken over the last 10 years and are the first from northern Europe, thus providing an important data set. In all cases, the coprolites were found in association with other biological evidence, including different mammalian taxa characteristic of the changing faunal composition of the British Isles during the Pleistocene, and in two cases, Palaeolithic artefacts also. The main aims of the study presented here are (1) to provide an insight into the palaeoenvironments at each site at the time of deposition and therefore, in some cases, those encountered by humans; (2) where possible, to compare the results with other complementary lines of evidence from the site in question; and (3) from the results of this and other studies, to see if this can lead to any further insights regarding the potential taphonomic complexities involved in incorporation of pollen into coprolites, and any consequent biases that may be inferred from these or from the different depositional processes between open and cave sites.

14.2. Hyaenas and Coprolites

The earliest members of the family Hyaenidae are dated to approximately 25 million years and currently nearly 100 species have been named (Werdelin and Solounias, 1991). Some of the early forms had dental and cranial adaptations that indicate significant bone-cracking abilities and this includes the giant short-faced hyaena (*Pachycrocota brevirostris* Amyard, 1846), the largest hyaena ever recorded, which in Europe ranged from about 1.6 to 0.5 Ma (Turner and Antón, 1996), although its exact time of extinction is unclear. In Britain, fossil remains of *Pachycrocota* are recorded from the Cromer Forest-bed Formation (CF-bF) at Bacton, Mundesley and Sidestrand in Norfolk. In addition, bone-rich coprolites from the CF-bF attributed to this species are amongst the largest recorded for any fossil or extant hyaena (Parfitt and Larkin, 2010). During the Middle and Late Pleistocene, *C. crocota* was also present in Europe, and for at least part of the early Middle Pleistocene, the two species were present contemporaneously in Britain. The bone-cracking abilities of *Pachycrocota* mean, therefore, that it cannot be ruled out as the coprolite contributor at West Runton and Happisburgh, both before 0.5 Ma. Other factors discussed subsequently would, however, suggest *Crocota* to be the more likely candidate.

The evolutionary history of the genus *Crocota* is still contentious, but early forms are described from the early Pliocene of East Africa (Werdelin and Lewis, 2008). In Europe, *C. crocota* is known from early Pleistocene layers at Atapuerca (García and Arsuaga, 1999), and although the timing of its first appearance in Britain is uncertain, it is present by the early Middle Pleistocene at Pakefield and Corton Cliff in Suffolk together with Sea Palling and West Runton (Norfolk); the Pakefield



Fig. 14.1. The distribution of sites in the main areas where successful palynological analyses of hyaena coprolites have been performed. In (A) and (B), all sites involve *Crocota crocuta* coprolites. In (C), all sites involve *Parahyaena brunnea*, apart from Florisbad (*C. crocuta*). The asterisk on the north coast of Sicily represents San Teodoro Cave (Yll *et al.*, 2006).

remains possibly represent its earliest record in Britain (Parfitt *et al.*, 2005; Lewis *et al.*, 2010). *C. crocuta* continues in the British fossil record until late in MIS 3, with a recent ultra-filtered AMS radiocarbon date of $27,100 \pm 750$ BP (OxA-9673; Jacobi and Higham, 2010) at Nanna's Cave, Isle of Caldey, Wales.

Investigations into the morphological, physical and chemical characteristics of hyaena scats and coprolites are well documented (i.e. Kruuk, 1972; Horwitz and Goldberg, 1989; Larkin *et al.*, 2000). Hyaena scat and coprolite morphology is quite distinctive due to peristaltic movement of the digestive tract (Dietrich, 1951; Horwitz and Goldberg, 1989). This produces segmented scats with each segment, in *Crocota*, often having one concave end and the other more convex, although there is some variation (Fig. 14.2). The size of these segments can also vary, both within and between hyaena individuals. The coprolites used here (Table 14.1) varied in colour from those with a yellowish-brown exterior and whitish interior (Tornewton 01), to others which were dark brown both inside and out (Happisburgh 01; Fig. 14.2). Happisburgh 01 was the only sample measured here, with a length of 45.8 mm and width of 36.5 mm, which although large is within the range of *Crocota* coprolites



Fig. 14.2. Coprolite HSB 01 showing the convex feature at the bottom. Small units of scale bar = millimetres.

from other studies (e.g. Carrión *et al.*, 2001; Parfitt and Larkin, 2010).

Coprolites and scats of any taxon obviously reflect the diet of the animal and are therefore useful in studying the diet of shy or elusive, and also fossil, species. However,

Table 14.1. Summary of site locations and tests performed on samples.

Site and sample number	Lat/long	Depositional environment	Productive coprolites	Determination of Ca and P	XRD
Tornewton (TN 01)	50°29'40.00" N 03°40'07.00" W	Limestone cave	1 of 4	✓	✓
Pin Hole (LL.1900e)	53°15'43.27" N 01°12'05.35" W	Limestone cave	1 of 2		
West Runton (WR 01)	52°56'26.06" N 01°15'16.79" E	Slow-moving river	1 of 1	✓	✓
Happisburgh 3 (HSB 01)	52°49'35.68" N 01°31'57.43" E	Large river estuary	1 of 1	✓	✓

Productive coprolites are those containing sufficient pollen.

scats of most taxa may also contain other components acquired inadvertently or not directly related to diet such as parasites, phytoliths, minerals and pollen (Reinhard and Bryant, 1992). With bone-crushing hyaena taxa, there are a number of potential taphonomic pathways by which pollen can be incorporated into the coprolite, including drinking water, breathing atmospheric pollen and the consumption of herbivorous prey taxa. The characteristic that most distinguishes coprolites of *Crocota* from those of other carnivores is their chemical composition and mineralogy due to the very high bone content of *Crocota* diet (Kruuk, 1972, 1976). The coprolites are largely composed of apatite ($\text{Ca}_5(\text{PO}_4)_3(\text{OH})$), a complex mineral form of calcium phosphate, indicating digestion of all the organic constituents of the bone, leaving only the inorganic fraction in a reconstituted form. This high inorganic content makes the coprolites extremely durable, which is undoubtedly a factor in their preservation in the fossil record (Larkin *et al.*, 2000). The calcium and phosphorous composition of the coprolites was determined using wet chemistry and their mineralogy by X-ray diffraction (XRD; see Appendix).

From personal observation, bone consumed by other carnivore taxa such as wolf (*Canis lupus*) or wolverine (*Gulo gulo*) is usually visible as large splinters found in the scats, but there were no readily visible bone fragments present in any of the coprolites used here. *C. crocuta* is the only known extant taxon with the ability to break down bone in its digestive system. Therefore from the composition, size and shape of the coprolites used here (see Appendix), as well as evidence provided by *Crocota* bones or bones gnawed by the species at three of these sites, it is highly likely that this is the species responsible.

14.3. Palynological Method

Before processing, the exteriors of the coprolites were cleaned using scalpels, thereby avoiding contamination from surrounding sediments and during post-excavation. This ensures as far as possible that the pollen being examined is from a sealed context. With HSB 01, which showed more mineralization than the other samples, a circular 'plug' was removed from the exterior of the

coprolite and part of the interior excavated; the 'plug' was then replaced. A small amount of each coprolite was retained for calcium, phosphorous and XRD analyses.

The methods of laboratory pollen preparation followed those of Moore *et al.* (1991), using conventional HCl, HF and KOH treatment, as well as acetolysis. In the case of HSB 01, HCl and HF treatment were used, followed by 20 h immersion of the sample in Schulze solution (70% nitric acid and potassium chlorate), and finally washing and then brief ultrasound treatment (10 s) with Sobo pH 9 detergent. In all cases, safranin was used as a colour stain and the samples were mounted in glycerine jelly. Counting was done by equally spaced traverses across slides at 400× magnification, with phase contrast and oil immersion (1000×) used for more problematic identifications. Pollen identifications were made using the key of Moore *et al.* (1991); the reference collection from the Department of Botany, Natural History Museum, London, was also consulted. Plant nomenclature follows that of Stace (1997) and pollen types are in accord with Moore *et al.* (1991).

For the cave sites of Tornewton, Devon, and Pin Hole, Derbyshire, two coprolites were initially sampled for pollen, but in each case it was found that only one of the coprolites had any discernible pollen within it, and consequently these are the samples used in this study. From Tornewton this is sample TN 01 and from Pin Hole sample LL.1900e (from the Armstrong Collection at the Manchester Museum). A preparation of three further coprolites from Tornewton (TN 252, 258a, 258b) was performed later and these were found to have only very small amounts of pollen, numbers not viable for counts. West Runton and Happisburgh each had only one coprolite processed, and in both cases, they contained pollen; the samples are known here as WR 01 and HSB 01, respectively. With the Pin Hole and Tornewton samples, all palynomorphs found in each sample were counted. With the West Runton and Happisburgh samples, six slides were prepared from each; two slides from West Runton were counted as well as the richest slide from Happisburgh. The results are presented as a pollen and spore diagram (Fig. 14.3), with taxa expressed as percentages of the total land pollen and spore sum (sumP/calculation sum). Obligate aquatic taxa and other palynomorphs are presented as percentages of sum

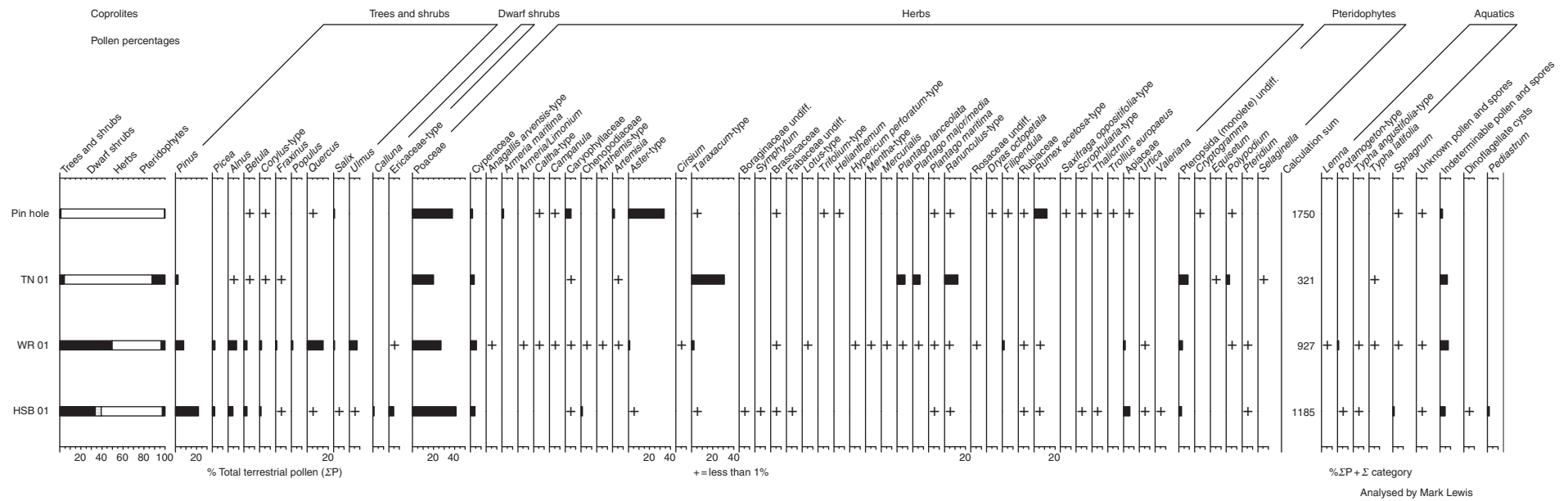


Fig. 14.3. Pollen diagram of the four coprolites, with taxa expressed as percentages of the total land pollen and spore sum (sumP/calculation sum). Obligate aquatic taxa and other palynomorphs are presented as percentages of sumP + the sum of the category to which they belong.

P+ the sum of the category to which they belong. Fungal spores were present in most of the samples, as expected with coprolites, but numbers are not recorded here.

14.4. Case Studies

Each case study is presented with a description of the site location, excavation history, environment, chronology and context, as well as the corresponding results for that site and a brief discussion of the palynology. Detailed stratigraphies used in this study have been published elsewhere and the most recent publication details are cited here. The sites are presented in chronological order, the most recent first, and their locations shown in Fig. 14.1A. A more detailed discussion on matters such as taphonomy is dealt with later.

14.4.1. Pin Hole, Creswell Crags

Pin Hole is near the western end of the northern (Derbyshire) face of Creswell Crags gorge (NGR: SK533742). It is a solutionally enlarged linear fissure some 46 m in length, and the lower cave-earth, the relevant context here, has been periodically excavated since the 1920s (Jacobi *et al.*, 1998, 2006). There is evidence for human presence at the cave, with Middle Palaeolithic artefacts spread through the deposit. This could be interpreted as implying visits over a long span of time (Jacobi *et al.*, 2006); there is also evidence in the upper layers for Later Upper Palaeolithic occupation. The large mammal fauna from the lower cave-earth is listed in Curran and Jacobi (2001) and forms the type locality for the Pin Hole Mammal Assemblage Zone. Recently obtained ultra-filtered radiocarbon dates on bones and teeth indicate that animal remains began to accumulate as early as 55 ka BP (Jacobi *et al.*, 2006) until about 38 ka BP, the first part of the Middle Devensian (Ballantyne and Harris, 1994), correlating with the first half of MIS 3 (Lowe and Walker, 1997; Jacobi *et al.*, 1998, 2006).

Cave sediment palynology is known to have taphonomic problems of preservation, percolation and reworking (Dimpleby, 1985; Turner, 1985; Coles *et al.*, 1989; Carrión *et al.*, 1999b, 2007, 2008). Previous pollen work on the sediments at Pin Hole was undertaken by Coles (1988) but this provided only low pollen numbers and mixing was noticed in some layers. The latter implies that recycled or contaminating material was present (Coles, 1988). The coprolite, however, provides a sealed context for the pollen from the relevant layer with little possibility of contamination.

The pollen-rich coprolite (Manchester Museum LL.1900e) is from level 10', of the east passage, the sediments of which are a continuation of the lower cave-earth of the main passage. Middle Palaeolithic (Mousterian) artefacts have been found in both these contexts (Jacobi *et al.*, 1998). The presence of neonatal hyaenas in parts of the cave, and also the abundance of gnawed animal bones, would suggest that at times Pin Hole had been a hyaena den. The additional presence of

artefacts, and therefore humans, would indicate intermittent occupation of the cave by both groups.

Twenty-nine different pollen and spore types were identified and the concentration of pollen was reasonable at approximately 200 grains per gram. Pollen preservation was fair with occasional ghosting of some grains and some degradation of *Artemisia* (mugwort). The results show an arboreal pollen (AP) percentage of just over 1%, with non-arboreal pollen (NAP) approaching 99%. The predominant NAP taxa were Poaceae (grasses, 38%) and *Aster*-type (daisy-type, 34%); Cyperaceae (sedges, 2%) are also present. The majority of the remainder of pollen types are all terrestrial herb taxa with differing ecological tolerances, all being common in mid-Devensian local or regional herb communities (West, 1977).

The very low AP count is the salient characteristic of this assemblage, the majority belonging to one genus *Salix* (willow, 1%). The pollen and macrofossils of *Salix* are present in a large number of other Quaternary cold stage samples, the most commonly represented being *Salix herbacea* (dwarf willow; West, 2000). *Betula* (birch), *Quercus* (oak) and *Corylus*-type (hazel/bog-myrtle) are also represented here but by only one grain each. A large proportion of the herb taxa present could be considered representative of grassland, including *Artemisia*, *Aster*-type, *Campanula* (bellflower), *Helianthemum* (rock-rose), Rubiaceae (bedstraw family) and *Rumex acetosa*-type (sorrel-type). Halophytes such as *Armeria maritima* (thrift) and *Plantago maritima* (sea plantain) are also present and their occurrence inland is well documented during Quaternary cold periods (Bell, 1969; West, 2000). Along with the high counts of Poaceae and low AP numbers, this would suggest open grassland conditions locally. The presence of fossils of woolly mammoth (*Mammuthus primigenius*), wild horse (*Equus ferus*), woolly rhinoceros (*Coelodonta antiquitatis*), reindeer (*Rangifer tarandus*) and bison (*Bison priscus*) in the lower cave-earth supports this argument, with open grassland being considered the likely predominant biotope regionally.

Implications of environment for humans during early MIS 3 are made difficult by the occurrence of a succession of interstadials, punctuated initially (until c. 45 ka) by brief cooler events, followed by a deterioration in climate with much colder Dnsgaard-Oeschger (D-O) events between 42 and 38 ka (van Andel, 2003). The coprolite pollen is possibly representative of one of these cool events, which is borne out by the very low AP numbers and the high proportions of grass and herb pollen. This horizon therefore probably represents a cold period when the cave was visited by hyaenas, their presence inferring that the cave was not in use by humans at exactly that time, or that there was possibly intermittent use by both groups.

14.4.2. Tornewton Cave, Devon

Tornewton Cave, in the Torbryan Valley near Buckfastleigh, Devon (NGR: SX817674), is a site containing one of the most complete late Middle and Late

Pleistocene sequences in Britain. It is currently considered to span from MIS 7 or earlier to MIS 3 (Currant, 1998, pers. comm.; Gilmour *et al.*, 2007). Tornewton was first excavated by James Widger in the latter part of the nineteenth century, although the main account of the site is still that of Sutcliffe and Zeuner (1962) who undertook excavations from 1953 onwards. There are deposits both inside and outside the cave and correlations between them are difficult. The picture is made more confusing when it comes to distinguishing undisturbed external deposits from those that are spoil from the Widger excavations. Gilmour *et al.* (2007) give a comprehensive description of the internal stratigraphy as it is currently understood, as well as an up-to-date interpretation of previous site descriptions. They also provide a number of U-series dates from an *in situ* stalagmite boss from the inner chamber of the cave, which spans a significant part of the internal Late Pleistocene sediment sequence.

No previous palynological work has been published from Tornewton. The stratigraphic context of the two coprolites initially processed for pollen (TN 01 and 02) is unclear but is believed to be Unit 1 of Gilmour *et al.* (2007), equivalent to the 'Hyaena Stratum' of Sutcliffe and Zeuner (1962) or the 'Great Bone Bed' of Widger.

Two of the three further coprolite samples (TN 258 a and b) were also from this layer and the other (TN 252) from the 'Dark Earth' (Fig. 14.4).

Evidence of humans in and around the cave is sparse. A human right incisor was found by Sutcliffe and Zeuner (1962) at the top of the external Reindeer Stratum and has more recently been dated to the Neolithic at 4680 ± 60 BP (OxA-5684). Two flint blades were also found by them in this layer and are considered to be Magdalenian (Jacobi, pers. comm.) as well as one further broken blade found in the Middle Tunnel in Widger's 'Diluvium' layer. There is also what appears to be a Lower Palaeolithic flake from the 'Glutton Stratum', although this layer is disturbed by sludging and other processes (Sutcliffe and Zeuner, 1962). Probably the most interesting artefact is what appears to be a handaxe trimming flake of Cretaceous Lower Greensand chert, possibly Middle Palaeolithic (Mousterian) in age, found in the external 'Elk' Stratum (Jacobi, pers. comm.). In summary, the evidence for humans at the cave is scant and is further confused by problems of the stratigraphy of the deposits. The cave may have been visited occasionally by humans but there is no evidence of occupation.

Unit 1 is dominated by faunal remains of spotted hyaena, brown bear (*Ursus arctos*), water vole (*Arvicola*

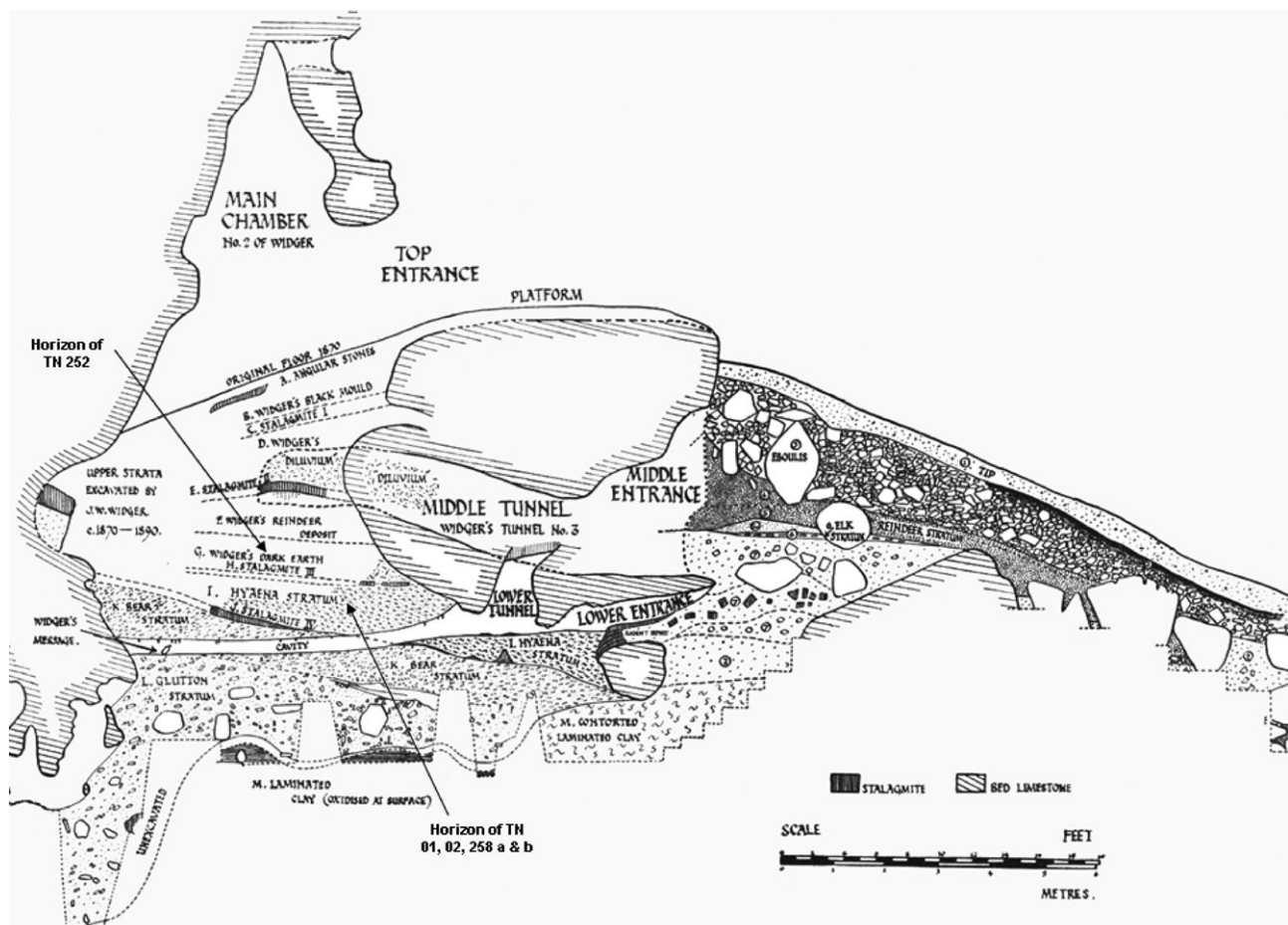


Fig. 14.4. Partial reproduction of the original profile of Tornewton Cave (from Sutcliffe and Zeuner, 1962) showing the stratigraphy of deposits both inside the cave and outside (to the right of 'Middle Entrance') with the find horizon locations of all coprolites. The exact locations of TN 01 and 02 are unknown but thought to be the 'Hyaena Stratum'. Reproduced by kind permission of the Devon Archaeological Society.

terrestris cantiana) and northern vole (*Microtus oeconomus*); bank vole (*Clethrionomys glareolus*) and wood mouse (*Apodemus sylvaticus*) are also present. Sutcliffe and Zeuner (1962) claim to have found remains of hippopotamus (*Hippopotamus amphibius*) in this layer, but more recently doubt has been cast on the provenance of these finds (Currant, 1998; Gilmour *et al.* 2007). Undoubtedly, there are complexities in the stratigraphy of the cave and its interpretation. The deposit is considered to be MIS 5, but it is suggested that the abundance of *M. oeconomus* signifies that the fauna is unlikely to belong to MIS 5e (Currant and Jacobi, 2001; Gilmour *et al.*, 2007), the latter authors suggesting that Unit 1 more likely represents a later part of MIS 5.

The AP content of this sample is very small, totalling only about 4%. The only two taxa with more than one grain are *Pinus* (pine) and *Fraxinus* (ash), with single grains of *Alnus* (alder), *Betula* and *Corylus*-type. The NAP makes up the majority of this assemblage, although the overall taxonomic diversity of the sample is poor, with only 18 taxa. Undifferentiated Pteropsida (ferns, 9%), Poaceae (20%) and Cyperaceae (4%) account for a large proportion of this category. *Taraxacum*-type (dandelion-type, 31%) is also well-represented as is *Ranunculus*-type (buttercup-type, 13%). The remaining taxa are *Plantago lanceolata* (ribwort plantain), *Plantago major/ media* (greater or hoary plantain), *Polypodium* (polypody), *Artemisia* and Caryophyllaceae (pink family). The aquatic group has only two taxa represented by one grain each, *Equisetum* (horsetail) and *Typha latifolia* (bulrush). There is also a single spore of *Selaginella* (lesser club moss).

Interpretation of this assemblage is made difficult by the low pollen numbers and species diversity. The low AP content may only be a taphonomic anomaly and would still suggest some woodland regionally, if not locally. The presence of pteridophytes tends to support this. More importantly, there is an absence of thermophilous indicators, which would be expected if the sample were of MIS 5e age, as proposed by Sutcliffe (1985). Whatever the exact time period represented by the coprolite pollen, it is unlikely to have been during a period of human presence, as an absence of humans in the British Isles is currently postulated from MIS 6 throughout MIS 5 and into MIS 4 (Ashton and Lewis, 2002). In effect, further pollen-rich coprolite samples with a more precise provenance need to be analysed before any further interpretation can be made, which would help to clarify the vegetational, faunal and stratigraphic record of the cave deposits.

14.4.3. West Runton

The early Middle Pleistocene site of West Runton (NGR: TG193430) is situated on the north Norfolk coast and is one of a number of sites in this area which form the CF-bF, a series of freshwater and marine deposits ranging from the Pliocene to Middle Pleistocene. The highly fossiliferous CF-bF is exceedingly important in enabling reconstructions of palaeoecology, climate and sea-level during the 'Cromerian Complex', the composite

temperate period preceding the MIS 12 glaciation (West, 1980). Although there is at present no evidence for early humans at West Runton, other CF-bF sites, such as Pakefield and Happisburgh (Parfitt *et al.*, 2005; 2010), have provided the earliest evidence for humans in northern Europe. West Runton remains an important location as it exposes the fossil-rich fluvial organic sediments known as the West Runton Freshwater Bed (WRFB), the type locality for the Cromerian Interglacial Stage. This is currently placed within the early part of the Cromerian Complex, probably either MIS 15 or 17 (Prece *et al.*, 2009).

In 1995, an excavation of an approximately 85% complete skeleton of *Mammuthus trogontherii* from the WRFB was undertaken, which also yielded a rich vertebrate fauna, including mammals, birds, herpetofauna and fish; the WRFB mammals currently number some 53 taxa (Tony Stuart, pers. comm.; Stuart and Lister, 2010). Along with the mammoth bones, some of which had been gnawed by hyaenas, were a number of associated hyaena coprolites scattered on and around the skeleton (Stuart, 1996; Larkin *et al.*, 2000), one of which was used for this analysis (see Larkin *et al.*, 2000, for location of coprolites). An edited volume (Turner, 1996) summarizes much of the work done on the CF-bF, including the WRFB. More detailed and up-to-date descriptions of the site, the mammoth excavation, its chronology and finds can be found in a special edition of Quaternary International (Stuart and Lister, 2010). The palynology of the coprolite can be compared with that of the surrounding sediment undertaken by Peglar (Field and Peglar, 2010) and to extensive studies by West (1980).

The pollen and spores of 47 different plant taxa are present in the WR coprolite sample, with a rich diversity of trees, shrubs and herbs represented, and a few aquatics. Palynomorph concentration is high at approximately 830 grains/g. Trees and shrubs account for almost 50% of the total land pollen and spores, the most common taxa being *Quercus* and *Alnus*, followed by *Pinus* and *Ulmus* (elm). The tree taxa are largely characteristic of mixed deciduous and coniferous woodland. Including the Poaceae and Cyperaceae, there are 28 herb taxa present accounting for just over 50% of the total land pollen, although the numbers of many amount to less than 1% each. However, these taxa are characteristic of a range of habitat types, from grassland (i.e. some Asteraceae taxa, *Hypericum perforatum*-type (St. John's wort-type), *R. acetosa*-type (Rubiaceae and Poaceae)) to wetter, marshier areas (i.e. some Apiaceae (carrot family), *Caltha/Aquilegia* (marsh marigold/columbine), *Mentha*-type (mint-type), *Valeriana* (valerian, i.e. possibly *V. dioica*, marsh valerian) and Cyperaceae). There are also small numbers of taxa of woodland (*Mercurialis* (mercury) and Pteropsida) and disturbed ground (Brassicaceae (cabbage family), *Plantago major/media*, *Urtica* (nettle)), as well as halophytes such as *P. maritima*. Aquatics are poorly represented with only 4 taxa in small numbers, the most common being *Potamogeton*-type (pondweed-type).

Palynology of the sediments surrounding the elephant skeleton found the pollen assemblage to be very similar throughout the sequence, probably as a result of the

sediment being mixed due to heavy trampling (Field and Peglar, 2010). The majority of the taxa present in the coprolite sample are also present in their study. However, there are some interesting differences between the assemblages and also those of West (1980), which could be related to taphonomy or hyaena behaviour. One of the most striking features of the coprolite pollen assemblage is the relatively high AP content at almost 50%. *Quercus* is the predominant tree genus found in the coprolite, whereas Field and Peglar found *Alnus* to be the most common type in samples from the surrounding sediment. The other tree taxa are present in all three studies, apart from *Populus* (poplar) in the coprolite sample. The coprolite also has a very small number of aquatics and a lack of *Pediastrum* (a green alga).

The arboreal and NAP types present show a richness and diversity of taxa from a range of habitat types. Undoubtedly, there is mixed deciduous and coniferous woodland close by, with pollen of more hydrophilous taxa such as *Alnus* probably originating from the banks of the channel. The NAP taxa mirror these habitats with the addition of grassland either locally or regionally.

14.4.4. Happisburgh 3

A number of sites at Happisburgh, Norfolk, have been excavated since 2005, following the discovery of a handaxe in 2000 protruding from organic muds underlying Happisburgh Till. The sediments at Happisburgh are also part of the CF-bF and represent pre-Anglian (MIS 12) cold and warm deposits. The coprolite was found in September 2008 at Happisburgh 3 (NGR: TG380313) in sand and gravel sediments associated with the estuary of a large river and currently dated at >0.78 Ma (Parfitt *et al.*, 2010). These sediments are the equivalent of Bed 'j' of West's (1980) borehole HC at Happisburgh. The coprolite was found in association with a number of knapped flint flakes, currently under study at the British Museum, and also fossils of large herbivores, including southern mammoth (*Mammuthus cf. meridionalis*), as well as extinct horse (*Equus suessenbornensis*), extinct elk (*Cervalces latifrons*) and red deer (*Cervus elaphus*). As at West Runton, the palynology of the coprolite can be compared with that of the surrounding sediment, undertaken by S. Peglar (Parfitt *et al.*, 2010) and to studies by West (1980).

A total of 37 different plant taxa were identified in the sample, including nine tree types, with the remainder mainly being herb taxa, but once again there were few aquatics. Palynomorph concentration was reasonably high at approximately 600 grains/g. Dinoflagellate cysts were also present. Of the tree genera, *Pinus* was the most common at almost 22%, followed by *Alnus* at about 5% and smaller numbers of *Betula* and *Picea* (spruce). The AP percentage at approximately 34% is far lower than at West Runton, and also differs in being dominated by conifers. Apart from the Poaceae (41%) and Cyperaceae (4%), there are 18 herb taxa, with the Apiaceae (6%) being the only other taxon with a percentage $>1\%$. There are herbs that could be considered characteristic of grassland, such as *Aster*-type, *Taraxacum*-type,

Helianthemum, *R. acetosa*-type, Rubiaceae and Poaceae, and also of wetter, marshier areas such as some Apiaceae, *Scrophularia*-type (figwort-type), *Thalictrum* (meadow rue), *Valeriana* (i.e. *dioica*), *Symphytum* (comfrey) and Cyperaceae. There are smaller numbers of disturbed ground taxa such as Brassicaceae and *Urtica*, and the presence of the halophyte *P. maritima* would suggest the sea to be in close proximity.

The two foremost characteristics of the coprolite pollen assemblage are the dominance of *Pinus* amongst the tree taxa and the high numbers of Poaceae pollen. The first of these can be explained by comparison with results of palynology of the sediment associated with the coprolite and of West's (1980) equivalent samples from Bed 'j' in borehole HC. The former shows a dominance of *Pinus* (up to 60% of the land pollen) with AP of about 80% in all comparable layers; West (1980) had AP percentages of about 85%, with about 70% conifers, *Pinus* being the dominant taxon. Were it not for the high Poaceae numbers, the coprolite *Pinus* percentage would be similar. With the exception of one grain each of *Tsuga* (hemlock) and *Acer* (maple) in the sediment around the coprolite, all of the tree taxa in the coprolite pollen were also present in the sediment. The high Poaceae numbers are likely to result from taphonomic factors, which will be discussed.

The palynology of the coprolite indicates boreal woodland, with low numbers of deciduous tree pollen also, possibly suggesting the later part of an interglacial. There was grassland in the vicinity, as shown by high numbers of Poaceae pollen, and also the presence of both herb and tree (*Alnus*) taxa of wetter habitats, as would be expected in a river estuary. The exploitation by humans of coastal/estuarine environments during temperate episodes of the Lower Palaeolithic is documented at sites such as Boxgrove (Roberts and Parfitt, 1999). Coniferous woodland is generally fairly dense, and it is suggested that humans also preferentially targeted fluvial environments as they were usually more open due to the grazing, browsing, trampling and tree-felling activities of elephants and other large herbivores (Ashton *et al.*, 2006), remains of which are present at Happisburgh in these deposits. It is inferred then that the grassland environments suggested from the Poaceae pollen were perhaps nearby riparian fluvial habitats, with herbivores feeding and watering there. This would enable passage both for themselves and humans through the landscape, facilitating potential opportunities for human hunting as well as access to flint resources from the river.

14.5. Discussion and Taphonomic Considerations

14.5.1. Hyaena Coprolites as Sealed Contexts

One notable benefit of the hyaena coprolite as a reservoir for pollen, and a medium for its preservation, is its nature as a sealed contextual unit. The durability of *Crocota* coprolites, largely because of their significant apatite content, has been demonstrated by Larkin *et al.* (2000) and the encasement of the pollen within can often serve to aid its preservation and give initial

protection from damaging external factors such as sunlight and large fluctuations in moisture (Scott *et al.*, 2003). There were small numbers of corroded grains in the analyses presented here, although in general, preservation was good. The reasons for this type of damage remain unclear, as was noted by Scott *et al.* (2003), although these authors also suggest that pollen survival may be related to age, with older coprolites having little or no pollen. This does not seem to be the case here with the presence of well-preserved pollen in the two oldest samples, West Runton and Happisburgh. Scott *et al.* (2003) also note, however, that preservation may be related to fluctuating, often unfavourable, conditions during very long burial histories. Their observation that preservation may be related to a lack of oxidizing conditions, both within the coprolite and sedimentary contexts, seems more probable, but further experimental work is undoubtedly needed. These conditions may also be seen as a contributory factor in the presence or absence of pollen in coprolites (Scott *et al.*, 2003), although other factors such as viscera consumption are considered more likely here.

The sealed context of *Crocota* coprolites has particular relevance to cave sites where there are problems, amongst others, of preservation, percolation, stratigraphic resolution and reworking of pollen grains (Carrión *et al.*, 2008). These problems are likely to be less significant factors in coprolite assemblages. With regard to open sites such as West Runton and Happisburgh, the sealed context has enabled comparison with sedimentary palynology and, from any differences observed, allows the investigation of other more difficult taphonomic factors related to *Crocota* behaviour and also that of its prey. There appear to be no notable preservational differences in coprolite pollen between the cave and fluvial sedimentary contexts presented here, although larger numbers of coprolites would need to be tested to substantiate this.

14.5.2. Taphonomic Pathways

There are a number of potential taphonomic pathways by which pollen can be incorporated into *Crocota* coprolites (Fig. 14.5). The first is through direct ingestion of plant material. Although both the striped hyaena (*Hyaena hyaena*, Linnaeus, 1758) and the brown hyaena are known to have omnivorous diets (Kruuk, 1976; Scott, 1987, respectively), studies on *Crocota* by Kruuk (1972, 1976) showed plant material to be completely absent from their diet. Stuart (1976) noted, however, that isolated individuals have been observed to feed on cucurbitid fruit, albeit in areas with few large game mammals for most part of the year, and consequently, it is likely that these populations tended to be more opportunistic in their feeding habits. As well as this, direct ingestion of substantial amounts of pollen would usually require ingestion of the flowering part of the plant, including the anther, which considering the behaviour of *C. crocuta*, is very unlikely (see Kruuk, 1972). However, what appeared to be part of an anther of *Aster*-type

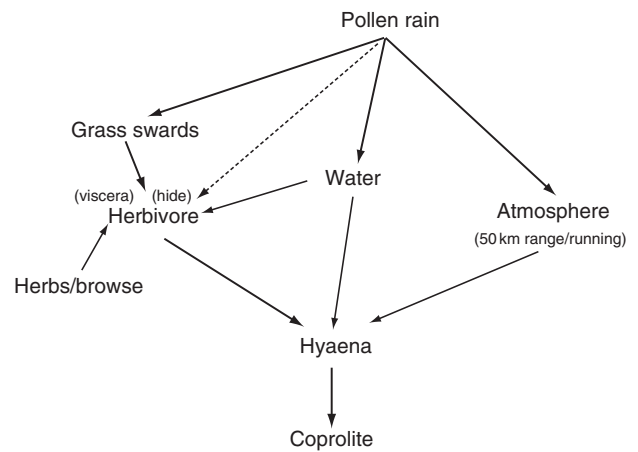


Fig. 14.5. Flow diagram showing potential taphonomic pathways involved in incorporation of pollen into *Crocota* coprolites. Direct ingestion of plant food by *Crocota* is not considered likely. The atmospheric component refers to the large ranges of *Crocota*, up to 50 km per day, and to inhalation of pollen with the proximity of their heads to the ground.

was observed in the Pin Hole sample but this is considered to be secondary, the result of feeding on herbivores.

Secondly, pollen may be derived through drinking water, which may contain both local and regional pollen, the latter depending on the size of the hydrological catchment area (Birks and Birks, 1980). Spotted hyaenas are known to drink water regularly (Kruuk, 1972) and Carrión *et al.* (2001) note the presence of zygospores of the filamentous green algae *Spirogyra* and *Zygnema* in *Crocota* coprolites from Las Ventanas, possibly derived from drinking water by either hyaena or prey. Only one of the four samples here, HSB 01, contained any similar material, in the form of cells, or fragments of cells, of the green alga *Pediastrum* (2%), showing a possible contribution of drinking water to the pollen assemblage of this coprolite. However, very low numbers of aquatic taxa in this and the other samples in this study, would tend to suggest that drinking water is an unlikely, or at least minor, pollen source in most cases here.

Two final potential pathways by which pollen may be incorporated into *Crocota* coprolites are strongly dependent on aspects of behaviour, both of the hyaena and of its prey. First, pollen may certainly be derived by inhalation of atmospheric pollen and subsequent ingestion of mucus. The atmospheric pollen component in hyaena coprolites has been documented by Scott (1987), Scott and Brink (1992) and Scott *et al.* (2003) who concluded that in these cases, the pollen spectra in question were representative of the wider, regional surroundings away from den sites. *Crocota* are known to range up to 50 km from their dens (Mills and Bester, 2005; Yll *et al.*, 2006) and in the Namib Desert their range is thought to be associated with the locations of freshwater pools, providing a link with the freshwater pollen spectra component already mentioned. More recent work at Villacastín and Los Torrejones (Carrión *et al.*, 2007) and Gibraltar (Carrión *et al.*, 2008) has noted differences in

pollen spectra from coprolites collected from the same contexts at a site, these differences they suggest being representative of the mosaic of phytogeographical traits and complexities of landscapes visited by the hyaenas. The almost complete lack of tree taxa at Pin Hole, and also the presence of *Populus* in the West Runton coprolite but absence in sediment samples, are two possible examples of this taphonomic factor at work.

The last, but probably most relevant, taphonomic pathway in terms of *Crocota* behaviour is through ingestion of the hide or guts of the hyaena's prey. This is bound to present difficulties and potential taphonomic bias due to the diet, foraging and other behaviours of the differing prey species, the prey of spotted hyaenas being numerous and varied. The most comprehensive studies of *Crocota* diet have been undertaken by Kruuk (1972, 1976) who observed that, in East Africa, they subsist primarily on large mammals such as wildebeest, zebra, gazelle and buffalo depending on seasonal availability. More recent evidence from several southern African locations also suggests large to medium-sized ungulates to be their main prey (Mills and Bester, 2005, p. 375). However, there have also been occasional observations of them eating small mammals, birds, fish, reptiles, crabs, snails, termites, fruit (Mills and Bester, 2005) as well as ostrich eggs and bone evidence of ostriches themselves (Henschel *et al.*, 1979).

Atmospheric pollen can adhere to the hides of most prey animals (Groenman-van Waateringe, 1998) and also from disturbed substrate during hyaena feeding. Although some of the hair and skin are often regurgitated, the pollen may remain in the alimentary tract and subsequently be passed to the intestine. Spotted hyaenas have even been known to consume prey hides discarded by other carnivore species as too tough (Smithers, 1983). The presence of a peak of quartz in the XRD of HSB 01 may be related to ingestion of substrate (at 2θ 45 in Fig. 14.6B. Also see appendix).

Perhaps to a greater extent than the hides, the stomach contents of the large herbivore prey of spotted hyaenas are likely to be a major and significant source of pollen within coprolites. There are reports of *Crocota* avoiding consumption of the viscera of herbivorous prey (Smithers, 1983), but this is probably unlikely in colder Pleistocene environments. Pleistocene coprolite pollen studies in Iberia by Carrión *et al.* (2007) suggest the likelihood of viscera consumption, citing the lack of other competitive carnivores as a possible reason for this, and the consumption of viscera would help to explain a number of anomalies seen in the pollen spectra of the samples presented here. The first of these is the very high representation of particular taxa, notably grasses, in two samples (Pin Hole and HSB 01), also noted at Villacastín by Carrión *et al.* (2007). Large numbers of grass pollen may be due to the hyaena being close to the ground whilst running, but the consumption of viscera at present seems a more likely explanation. This would also help to answer another anomaly, that of the variable pollen abundance or absence in coprolites. Although differential preservation because of post-burial processes may be seen as a contributory factor to this (Carrión *et al.*,

2001; Scott *et al.*, 2003), this may also be explained by viscera consumption. This in turn may be related to the order of accessibility to a carcass for hyaenas, perhaps the subordinate individuals being those eating the viscera, or even the dominant ones if viscera are favoured. One of the many peculiar aspects of *Crocota* biology is that of female dominance, the adult females being considerably larger and heavier than males, although there is some overlap in size range (Kruuk, 1972). Adult females are known to have priority of access to carcasses (Henschel and Skinner, 1987) and even if the order is not strictly observed, the larger animals are most likely to gain access first; male offspring of the alpha females are also known to be less submissive than other males towards the normally dominant females (Werdelin and Solounias, 1991). Further work is needed looking at correlations of size of coprolites with pollen content, as body-size of the individual, and therefore possibly accessibility to kills and also gender, can be inferred from coprolite size. If viscera consumption is a substantial contributory factor, then the feeding behaviour and range of the prey animal may in turn affect the composition of plant types and diversity shown in the pollen spectra. The presence of large numbers of tree pollen in the West Runton sample may, for instance, indicate consumption of forest dwelling mammals such as deer. There is also evidence to suggest that grass swards are excellent traps of regional pollen (Gutiérrez *et al.*, 1998; Carrión *et al.*, 2001) and therefore, even with principally grass-eating mammals such as horse, a representation of regional pollen should still be reflected in coprolites with visceral contents of such taxa.

14.5.3. Coprolite Palynology and Implications for Early Human Environments

There is an undoubted significance for Pleistocene archaeology in the interaction between early humans and bone-crushing hyaenas. They are both considered to have been part of the larger carnivore guild (Turner, 1984, 1992) and their inter-relations would have existed on a number of levels. These included scavenging and hunting competition (Turner, 1988, 1992), and possibly competition for other resources such as protection from the elements through the use of caves, as can be seen here at Pin Hole. At such cave sites with cultural evidence of humans, in this case through the presence of Mousterian artefacts and coprolites rich in pollen, this allows important inferences to be made concerning early hominid environments. Pin Hole provides a vegetational signature which is consistent with the faunal assemblage found at the site in providing a picture of a largely open grassland habitat with plants and animals characteristic of mid-Devensian environments, in which Neanderthals were also present, possibly only intermittently. This produces a snapshot in time and although ideally one would prefer a number of coprolites, perhaps in a well-stratified sequence within the cave, as presented by Carrión *et al.* (2008) from Gorham's Cave, Gibraltar, such scenarios are unfortunately rare.

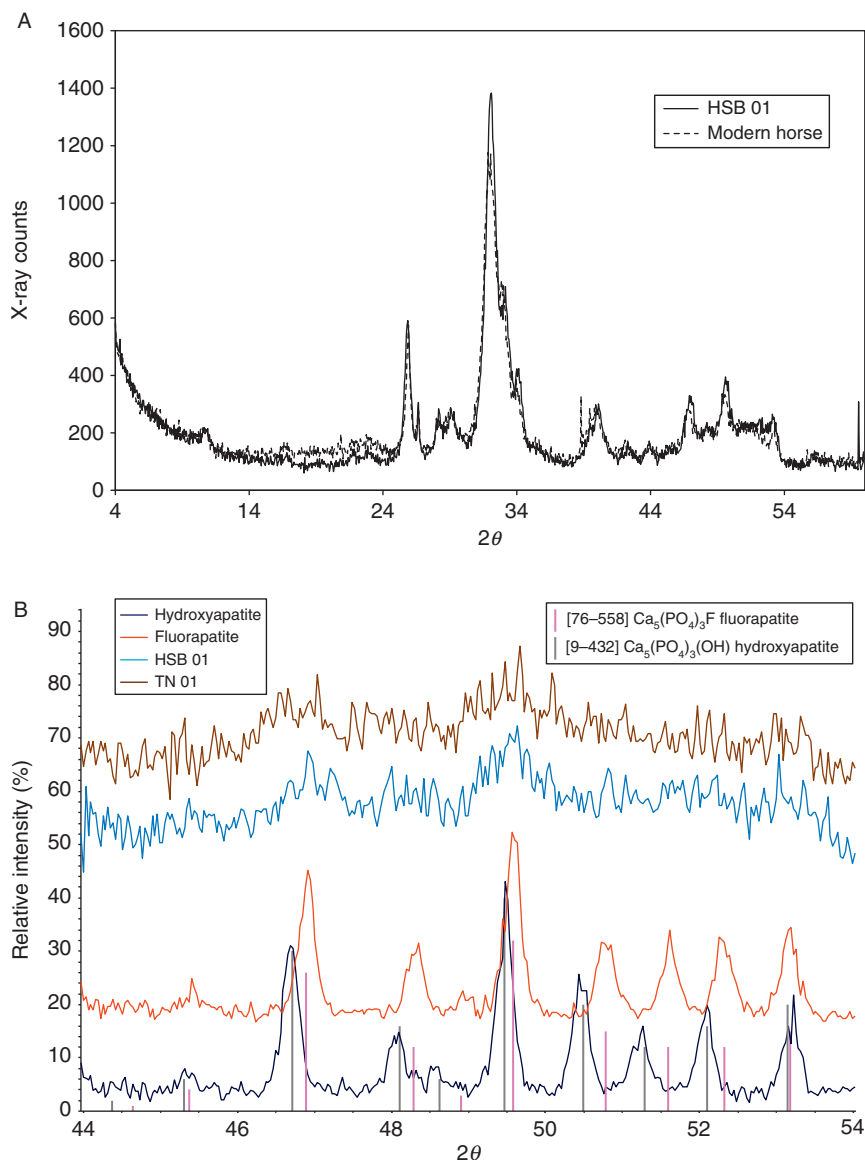


Fig. 14.6. (A) XRD of sample HSB 01, with a comparative sample of modern horse bone, showing clear apatite peaks for both but those of the coprolite slightly offset. This is most likely due to diagenetic alteration of hydroxyapatite to fluorapatite through groundwater processes. (B) Enlargement of the 2θ 44–54 region showing standards for hydroxyapatite (bottom) and fluorapatite (next), with the two coprolite samples, HSB 01 and TN 01, at the top. The two standard samples clearly show, in the peaks, the shift between the hydroxyapatite and fluorapatite phases, and this is also reflected in the difference in peaks between the two coprolite samples. The vertical lines on the x-axis represent the positions of peaks for these two phases of apatite, taken from the International Centre for Diffraction data (ICDD) database, and substantiate that the standard samples have the structures of pure end-member hydroxyapatite and fluorapatite, respectively. See Appendix for details.

At open archaeological sites such as Happisburgh, pollen from hyaena coprolites can provide an important vegetational record that differs from that of the sedimentary pollen. These differences reflect pollen taphonomy and the behavioural and ranging activities of both the hyaena and its prey. In this case, the abundance of Poaceae pollen indicates that grassland was present, probably along the river or its estuary. These riparian habitats were important for, and probably favoured by, humans in enabling them to travel with relative ease through what would otherwise be fairly densely forested areas, as well

as providing opportunities for hunting and access to water and lithic resources (Ashton *et al.*, 2006).

14.6. Conclusions

This study has provided palynological data from hyaena coprolites in more northern latitudes than has been previously reported. The results demonstrate that the extraction of pollen from hyaena coprolites is a viable tool in palynology, either in circumstances where there is an

absence of conventional sources, or in comparison or contrast to those conventional sources where they are available. There appears to be a mixture of factors determining the presence, abundance and preservation of pollen within coprolites, involving aspects of depositional environment and of the behaviour of the mammalian taxa involved. Consumption of the hides or viscera of prey animals is seen here as being a major contributory factor. The age of the coprolites does not seem to affect pollen preservation, although this is probably related to burial conditions. Most of the taphonomic variables should still be considered as needing further experimental work, although observational studies on wild animals and subsequent collection of their scats are likely to prove extremely challenging.

Appendix A. Calcium and Phosphorous Determinations and X-Ray Diffraction (XRD)

All coprolites, except Pin Hole, were analysed for calcium (Ca) and phosphorous (P) content and/or mineralogy to determine their composition and confirm their attribution to *Crocuta*. Comparisons were made with some modern *Crocuta* scats from Colchester Zoo (Col 01 and 02). The Ca and P determination of the coprolites was performed using wet chemistry (see Method below). Modern comparative data from Kruuk (1976) are also presented (Table 14.2). Details of Colchester Zoo samples can be found in Larkin *et al.* (2000).

The coprolites of bone-cracking hyaenids can be differentiated from those of other carnivore taxa by high values of Ca and P due to their bone-rich diet (Kruuk, 1972, 1976; Larkin *et al.*, 2000). The results presented in Table 14.2 clearly show that the WR 01 and TN 01 samples have very similar values to those of the modern comparative *Crocuta* samples. The striped hyaena has a more omnivorous diet which is apparent here.

A.1. XRD Results

In the HSB 01 and TN 01 coprolite samples, the only apparent mineral phase is apatite, with all the major peaks in the trace corresponding to those generated by an

apatite mineral. In HSB 01, this is confirmed by the fact that an XRD trace generated by a modern bone sample (*Equus*) was almost identical to that generated by the coprolite sample (Fig. 14.6A). A wide range of apatite mineral phases exists and although this coprolite (HSB 01) is undoubtedly apatite, the closest match to the XRD trace is fluorapatite (Fig. 14.6B). The two standard samples clearly show, in the peaks, the shift between the hydroxyapatite and fluorapatite phases, and this is also reflected in the difference in peaks between the two coprolite samples. This would suggest that diagenetic alteration, common in fossil bone, has taken place during burial with the addition of fluorine to HSB 01, most likely through groundwater processes. TN 01 still retains some hydroxyapatite and the peaks appear to be midway between hydroxyapatite and fluorapatite, suggesting that the diagenetic alteration is in process but not yet complete. The inference from this is that diagenesis is occurring in both open and cave environments, but that it may be related to time and possibly also burial environment, with the Tornewton sample (TN 01) being far younger than HSB 01. It is notable that Tornewton Cave has water running through it, and the presence of flowstone and stalagmites (Gilmour *et al.*, 2007) would suggest that this has been the case for a considerable part of its Pleistocene history. The West Runton (WR01) sample also showed apatite peaks offset from the hydroxyapatite standard towards the fluorapatite region.

A.2. Method of Wet Chemistry Determination of Calcium and Phosphorous

Approximately 0.5 g of each of the fossil samples and 2.0 g of the two modern samples were ground to a fine powder using an agate pestle and mortar. After Loss on Ignition was performed, phosphate was separated from the other constituents by passing the filtrates through columns of cation exchange resin (Amberlite 120 (H⁺)) and then precipitated from the effluents as MgNH₄PO₄. This was ignited at 1000 °C and weighed as Mg₂P₂O₇ (to convert Mg₂P₂O₇ to P = 62/222.64).

Calcium was recovered from the cation exchange resin by leaching with 1:1 HCl and sesquioxides removed from the effluents by double precipitation with

Table 14.2. Results of calcium (Ca) and phosphorous (P) percentages for some *Crocuta* and *H. hyaena* scat and coprolite samples.

	Col 01	Col 02	WR 01	WR 04	TN 01	Kruuk (1976) Crocuta n=20	Kruuk (1976) H. hyaena n=20
% Ca	26.93	26.56	28.71	26.17	28.41	25.54 ± 10.76	12.07 ± 7.2
% P	11.34	11.95	10.94	11.91	13.36		

Col, Colchester Zoo; WR, West Runton, TN 01; Tornewton. Kruuk's (1976) values show standard deviations. WR 04 is additional data from another West Runton coprolite.

ammonium hydroxide and subsequently ignited and weighed. Calcium was precipitated from the sesquioxide filtrates as the oxalate, ignited at 500 °C and weighed as CaCO₃ (to convert CaCO₃ to Ca=40.08/100.08).

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References

- Ashton, N.M. & Lewis, S.G., 2002. Deserted Britain: declining populations in the British Late Middle Pleistocene. *Antiquity* 76, 388–396.
- Ashton, N.M., Lewis, S.G., Parfitt, S.A., & White, M.J., 2006. Riparian landscapes and human habitat preferences during the Hoxnian (MIS 11) Interglacial. *Journal of Quaternary Science* 21, 497–505.
- Ballantyne, C.K. & Harris, C., 1994. *The Periglaciation of Great Britain*. Cambridge University Press, Cambridge.
- Beaumont, P.B., van Zinderen Bakker, E.M., & Vogel, J.C., 1984. Environmental changes since 32 000 BP at Kathu Pan, northern Cape, South Africa. In: Vogel, J.C. (Ed.), *Late Cainozoic Palaeoclimates of the Southern Hemisphere*. Balkema, Rotterdam, 329–338.
- Bell, F.G., 1969. The occurrence of southern, steppe and halophyte elements in Weichselian (Last-Glacial) floras from southern Britain. *New Phytologist* 68, 913–922.
- Birks, H.J.B. & Birks, H.H., 1980. *Quaternary Palaeoecology*. Edward Arnold, London.
- Bryant, V.M. Jr. & Larson, D.L., 1968. Pollen analysis of the Devil's Mouth site, Val Verde County, Texas. In: Sorrow, B. (Ed.), *The Devil's Mouth Site: The Third Season, Papers of the Texas Archaeological Salvage Project 14*, Austin, 57–70.
- Callen, E.O., 1965. Food habits of some pre-Columbian Indians. *Economic Botany* 19, 335–343.
- Carrión, J.S., Scott, L., & Vogel, J.C., 1999a. Twentieth century changes in montane vegetation in the eastern Free State, South Africa, derived from palynology of hyrax dung middens. *Journal of Quaternary Science* 14, 1–16.
- Carrión, J.S., Munuera, M., Navarro, C., Burjachs, F., Dupré, M., & Walker, M.J.C., 1999b. The palaeoecological potential of pollen records in caves: the case of Mediterranean Spain. *Quaternary Science Reviews* 18, 1061–1073.
- Carrión, J.S., Brink, J.S., Scott, L., & Binneman, J.N.F., 2000. Palynology and palaeoenvironment of Pleistocene hyaena coprolites from an open-air site at Oyster Bay, Eastern Cape coast, South Africa. *South African Journal of Science* 96, 449–453.
- Carrión, J.S., Riquelme, J.A., Navarro, C., & Munuera, M., 2001. Pollen in hyaena coprolites reflects late glacial landscape in southern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 176, 193–205.
- Carrión, J.S., Yll, R., Riquelme, J.A., & González, P., 2004. Perspectivas del análisis polínico de coprolitos y otros depósitos biogénicos útiles en la inferencia paleoambiental. In: Baquedano, E., Rubio Jara, S. (Eds.), *Miscelanea en Homenaje a Emiliano Aguirre, Vol. II. Paleontología*. Museo Arqueológico Regional, Alcalá de Henares, 129–140.
- Carrión, J.S., Gil, G., Rodríguez, E., Fuentes, N., García-Antón, M., & Arribas, A., 2005. Palynology of badger coprolites from central Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 226, 259–271.
- Carrión, J.S., Scott, L., Arribas, A., Fuentes, N., Gil-Romera, G., & Montoya, E., 2007. Pleistocene landscapes in central Iberia inferred from pollen analysis of hyena coprolites. *Journal of Quaternary Science* 22, 191–202.
- Carrión, J.S., Finlayson, C., Fernández, S., Finlayson, G., Allué, E., López-Sáez, J.A., López-García, P., Gil-Romera, G., Bailey, G., & González-Sampériz, P., 2008. A coastal reservoir of biodiversity for Upper Pleistocene human populations: palaeoecological investigations in Gorham's Cave (Gibraltar) in the context of the Iberian Peninsula. *Quaternary Science Reviews* 27, 2118–2135.
- Chaves, S.A.M. & Reinhard, K.J., 2006. Critical analysis of coprolite evidence of medicinal plant use, Piauí, Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology* 237, 110–118.
- Coles, G.M., 1988. Aspects of the application of palynology to cave deposits in the Magnesian Limestone region of North Nottinghamshire. Unpublished PhD thesis. University of Sheffield, Sheffield, UK.
- Coles, G.M., Gilbertson, D.D., Hunt, C.O., & Jenkinson, R.D. S., 1989. Taphonomy and the palynology of cave deposits. *Cave Science* 16, 83–89.
- Currant, A.P., 1998. Tornewton Cave. In: Campbell, S., Hunt, C. O., Scourse, J.D., Keen, D.H., Stephens, N. (Eds.), *Quaternary of South-West England*. Chapman and Hall, London, 138–145.
- Currant, A.P. & Jacobi, R.M., 2001. A formal mammalian biostratigraphy for the Late Pleistocene of Britain. *Quaternary Science Reviews* 20, 1707–1716.
- Davis, O.K. (Ed.), 2006. *Advances in the Interpretation of Pollen and Spores in Coprolites*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 237.
- Dietrich, W.O., 1951. Koproolithen aus dem Pleistozan Ostafrikas. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 310–314.
- Dimbleby, G.W., 1985. *The Palynology of Archaeological Sites*. Academic Press, London.
- Fernández Jalvo, Y., Scott, L., & Denys, C., 1996. Pollen Composition in Owl Pellets and Their Environmental Implications, Vol. 323. *Comptes rendus de l'Académie des Sciences, Paris série II a*, 259–265.
- Field, M.H. & Peglar, S.M., 2010. A palaeobotanical investigation of the sediments from the West Runton mammoth site. In: Stuart, A.J., Lister, A.M. (Eds.), *The West Runton Elephant and its Cromerian Environment*. *Quaternary International*, doi:10.1016/j.quaint.2010.05.013.
- Finlayson, C., Pacheco, F.G., Rodríguez-Vidal, J., Fa, D.A., Gutierrez López, J.M., Pérez, A.S., Finlayson, G., Allue, E., Baena Preysler, J., Cáceres, I., Carrión, J.S., Fernández Jalvo, Y., Glead-Owen, C.P., Jimenez Espejo, F.J., López, P., López Sáez, J.A., Riquelme Cantal, J.A., Sánchez Marco, A., Guzman, F.G., Brown, K., Fuentes, N., Valarino, C.A., Villalpando, A., Stringer, C.B., Martínez Ruiz, F., & Sakamoto, T., 2006. Late survival of Neanderthals at the southernmost extreme of Europe. *Nature* 443, 850–853.
- García, N. & Arsuaga, J.L., 1999. Carnivores from the Early Pleistocene hominid-bearing Trinchera Dolina 6 (Sierra de Atapuerca, Spain). *Journal of Human Evolution* 37, 415–430.
- Gilmour, M., Currant, A.P., Jacobi, R.M., & Stringer, C.B., 2007. Recent TIMS dating results from British Late Pleistocene vertebrate faunal localities: context and interpretation. *Journal of Quaternary Science* 22, 793–800.

- Groenman-van Waateringe, W., 1998. Pollen in animal coats and bird feathers. *Review of Palaeobotany and Palynology* 103, 11–16.
- Gutiérrez, A., Díez, M.J., & Carrión, J.S., 1998. Primeros datos sobre la deposición de polen actual en el Parque natural de los Alcornocales, Cádiz, a través de la evaluación de cepelones de gramíneas. In: Fombella, M.A. (Ed.), *Actas XII Simposio APLE León, León*, 118.
- Henschel, J.R. & Skinner, J.D., 1987. Social relationships and dispersal patterns in a clan of spotted hyaenas *Crocuta crocuta* in the Kruger National Park. *South African Journal of Zoology* 22, 18–24.
- Henschel, J.R., Tilson, R., & Von Blottnitz, F., 1979. Implications of a spotted hyaena bone assemblage in the Namib desert. *South African Archaeological Bulletin* 34, 127–131.
- Horwitz, L.K. & Goldberg, P., 1989. A study of Pleistocene and Holocene hyaena coprolites. *Journal of Archaeological Science* 16, 71–94.
- Jacobi, R.M., Rowe, P.J., Gilmour, M.A., Grün, R., & Atkinson, T.C., 1998. Radiometric dating of the Middle Palaeolithic tool industry and associated fauna of Pin Hole Cave, Creswell Crags, England. *Journal of Quaternary Science* 13, 29–42.
- Jacobi, R.M., Higham, T.F.G., & Bronk Ramsey, C., 2006. AMS radiocarbon dating of Middle and Upper Palaeolithic bone in the British Isles: improved reliability using ultrafiltration. *Journal of Quaternary Science* 21, 557–573.
- Jacobi, R.M. & Higham, T.F.G., 2010. The British Earlier Upper Palaeolithic: settlement and chronology. In: Ashton, N. M., Lewis, S.G., Stringer, C.B. (Eds.), *The Ancient Human Occupation of Britain*. Elsevier, Amsterdam, 181–222.
- Kruuk, H., 1972. *The Spotted Hyaena: a Study of Predation and Social Behaviour*. University of Chicago Press, Chicago.
- Kruuk, H., 1976. Feeding and social behaviour of the striped hyaena (*Hyaena vulgaris* Desmarest). *East African Wildlife Journal* 14, 91–111.
- Larkin, N.R., Alexander, J., & Lewis, M.D., 2000. Using experimental studies of recent faecal material to examine hyaena coprolites from the West Runton Freshwater Bed, Norfolk, U.K. *Journal of Archaeological Science* 27, 19–31.
- Lewis, M.D., Pacher, M., & Turner, A., 2010. The larger Carnivora of the West Runton Freshwater Bed. In: Stuart, A.J., Lister, A.M. (Eds.), *The West Runton Elephant and its Cromerian Environment*. *Quaternary International*, doi:10.1016/j.quaint.2010.06.022.
- Lowe, J.J. & Walker, M.J.C., 1997. *Reconstructing Quaternary Environments*, 2nd ed. Longman, London.
- Martin, P.S. & Sharrock, F.W., 1964. Pollen analysis of prehistoric human feces: a new approach to ethnobotany. *American Antiquity* 30, 168–180.
- Mills, M.G.L. & Bester, M.N., 2005. Carnivora. In: Skinner, J. D., Chimimba, C.T. (Eds.), *The Mammals of the Southern African Subregion*. 3rd ed. Cambridge University Press, Cambridge, 358–526.
- Moe, D., 1983. Palynology of sheep's faeces: relationship between pollen content, diet and local pollen rain. *Grana* 22, 105–113.
- Moore, P.D., Webb, J.A., & Collinson, M.E., 1991. *Pollen Analysis*. Blackwell Scientific, London.
- Parfitt, S.A. & Larkin, N.R., 2010. Appendix: Exceptionally large hyaena coprolites from West Runton and the possible presence of the giant short-faced hyaena (*Pachycrocuta brevirostris*). In: Stuart, A.J., Lister, A.M. (Eds.), *The West Runton Elephant and its Cromerian Environment*. *Quaternary International*, doi:10.1016/j.quaint.2010.06.022.
- Parfitt, S.A., Barendregt, R.W., Breda, M., Candy, I., Collins, M. J., Coope, G.R., Durbridge, P., Field, M.H., Lee, J.R., Lister, A.M., Mutch, R., Penkman, K.E.H., Preece, R.C., Rose, J., Stringer, C.B., Symmons, R., Whittaker, J.E., Wymer, J.J., & Stuart, A.J., 2005. The earliest record of human activity in northern Europe. *Nature* 438, 108–1012.
- Parfitt, S.A., Ashton, N.M., Lewis, S.G., Abel, R.L., Coope, G.R., Field, M.H., Gale, R., Hoare, P.G., Larkin, N.R., Lewis, M.D., Karloukovski, V., Maher, B.A., Peglar, S.M., Preece, R.C., Whittaker, J.E., & Stringer, C.B., 2010. Early Pleistocene human occupation at the edge of the boreal zone in northwest Europe. *Nature* 466, 229–233.
- Preece, R.C., Parfitt, S.A., Coope, G.R., Penkman, K.E.H., Pönel, P., & Whittaker, J.E., 2009. Biostratigraphic and aminostratigraphic constraints on the age of the Middle Pleistocene glacial succession in north Norfolk, UK. *Journal of Quaternary Science* 24, 557–580.
- Reinhard, K.J., Hamilton, D.L., & Hevly, R.H., 1991. Use of pollen concentration in paleopharmacology: coprolite evidence of medicinal plants. *Journal of Ethnobiology* 11, 117–132.
- Reinhard, K.J. & Bryant, V.M., 1992. Coprolite analysis: a biological perspective on archaeology. *Archaeological Method and Theory* 4, 245–288.
- Reinhard, K.J., Edwards, S., Damon, T.R., & Meier, D.K., 2006. Pollen concentration analysis of ancestral pueblo dietary variation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 237, 92–109.
- Roberts, M.B., & Parfitt, S.A. (Eds.), 1999. *Boxgrove: a Middle Pleistocene Hominid Site at Earham Quarry, Boxgrove, West Sussex*. English Heritage, London.
- Scott, L., 1987. Pollen analysis of hyaena coprolites and sediments from Equus Cave, Taung, Southern Kalahari (South Africa). *Quaternary Research* 28, 144–156.
- Scott, L., 1994. Palynology of late Pleistocene hyrax middens, south-western Cape Province, South Africa: a preliminary report. *Historical Biology* 9, 71–81.
- Scott, L., 2002. Grassland development under glacial and interglacial conditions in southern Africa: review of pollen, phytolith and isotope evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* 177, 47–57.
- Scott, L. & Brink, J.S., 1992. Quaternary palaeoenvironments of pans in central South Africa. *South African Geographer* 19, 22–34.
- Scott, L., Steenkamp, N., & Beaumont, P.B., 1995. Palaeoenvironmental conditions in South Africa at the Pleistocene–Holocene transition. *Quaternary Science Reviews* 14, 937–994.
- Scott, L., Fernández Jalvo, Y., Carrión, J., & Brink, J., 2003. Preservation and interpretation of pollen in hyaena coprolites: taphonomic observations from Spain and southern Africa. *Palaeontologia Africana* 39, 83–91.
- Scott, L. & Rossouw, L., 2005. Reassessment of botanical evidence for palaeoenvironments at Florisbad, South Africa. *South African Archaeological Bulletin* 60, 96–102.
- Smithers, R.H.N., 1983. *The Mammals of the Southern African Subregion*. University of Pretoria Press, Pretoria.
- Stace, C., 1997. *New Flora of the British Isles*, 2nd ed. Cambridge University Press, Cambridge.
- Stuart, C.T., 1976. Plant food in the diet of the spotted hyaena. *South African Journal of Science* 72, 148.
- Stuart, A.J., 1996. Vertebrate faunas from the early Middle Pleistocene of East Anglia. In: Turner, C. (Ed.), *The Early Middle Pleistocene in Europe*. Balkema, Rotterdam, 9–24.
- Stuart, A.J. & Lister, A.M., 2010. The West Runton Freshwater Bed and the West Runton Mammoth: Summary and Conclusions. In: Stuart, A.J., Lister, A.M. (Eds.), *The West*

- Runton Elephant and its Cromerian Environment. *Quaternary International*, doi:10.1016/j.quaint.2010.07.033.
- Sutcliffe, A.J., 1985. On the Track of Ice Age Mammals. British Museum (Natural History), London.
- Sutcliffe, A.J. & Zeuner, F.E., 1962. Excavations in the Torbryan Caves. Devonshire I. Tornewton Cave. *Proceedings of the Devon Archaeological Exploration Society* 5–6, 127–145.
- Trevor-Deutsch, B. & Bryant, V.M., 1978. Analysis of suspected human coprolites from Terra Amata, Nice, France. *Journal of Archaeological Science* 5, 387–390.
- Turner, A., 1984. Hominids and fellow travellers: human migration into high latitudes as part of a large mammal community. In: Foley, R. (Ed.), *Hominid Evolution and Community Ecology*. Academic Press, London, 193–217.
- Turner, A., 1988. Relative scavenging opportunities for East and South African Plio-Pleistocene hominids. *Journal of Archaeological Science* 15, 327–341.
- Turner, A., 1992. Large carnivores and earliest European hominids: changing determinants of resource availability during the Lower and Middle Pleistocene. *Journal of Human Evolution* 22, 109–126.
- Turner, A. & Antón, M., 1996. The giant hyaena, *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). *Geobios* 29, 455–468.
- Turner, C., 1985. Problems and pitfalls with the application of palynology to Pleistocene archaeological sites in Western Europe. In: Renault-Miskovsky, J. (Ed.), *Palynologie, Archéologie. Notes et Monographies Techniques*, Centre des Recherches Archéologiques 17, 347–372.
- Turner, C. (Ed.), 1996. *The Early Middle Pleistocene in Europe*. Balkema, Rotterdam.
- van Andel, T.H., 2003. Glacial Environments I: the Weichselian Climate in Europe between the End of the OIS-5 Interglacial and the Last Glacial Maximum. In: van Andel, T.H., Davies, W. (Eds.), *Neanderthals and modern humans in the European landscape during the last glaciation*. McDonald Institute Monographs, Cambridge, 9–19.
- Werdelin, L. & Lewis, M.E., 2008. New species of *Crocuta* from the Early Pliocene of Kenya, with an overview of Early Pliocene hyenas of eastern Africa. *Journal of Vertebrate Paleontology* 28, 1162–1170.
- Werdelin, L. & Solounias, N., 1991. The Hyaenidae: taxonomy, systematics and evolution. *Fossils and Strata* 30, Universitetsforlaget, Oslo.
- West, R.G., 1977. Early and Middle Devensian Flora and Vegetation. *Philosophical Transactions of the Royal Society of London Series B* 280, 229–246.
- West, R.G., 1980. *The pre-glacial Pleistocene of the Norfolk and Suffolk Coasts*. Cambridge University Press, Cambridge.
- West, R.G., 2000. *Plant Life of the Quaternary Cold Stages: Evidence from the British Isles*. Cambridge University Press, Cambridge.
- Yll, R., Carrión, J.S., Marra, A.C., & Bonfiglio, L., 2006. Vegetation reconstruction on the basis of pollen in Late Pleistocene hyena coprolites from San Teodoro Cave (Sicily, Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology* 237, 32–39.