



Taphonomy in palaeoecological interpretations

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ABSTRACT

The taphonomic history of single fossils or of fossil assemblages provides evidence additional to that given by taxonomic identification. Too often taphonomy is viewed as destructive processes biasing evidence of past life or restricting taxonomic diversity in the reconstruction of palaeoecology, but in reality it sheds light on circumstances of life and preservation of fossil organisms. Because recorded modifications of fossils are due to biotic or abiotic agents that may not be evident in a studied sequence, taphonomic modifications should be seen as providing a more dynamic view of the past rather than as destructive processes.

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1. What is taphonomy for?

Less than a century ago, excavations were performed with picks and shovels while a palaeontologist or archaeologist who surveyed these works decided which specimens should be kept and which discarded. All valuable items selected were indiscriminately wrapped together and taken to the laboratory or museum (Fig. 1). Far removed from these out-dated methods, today's excavations are performed by careful recovery of all finds and sediments with fine tools and controlling spatial coordinates. What is the significance of this change in methodology? The target is always the fossils or artefacts, but the main difference between the old and new way of recovering fossils concerns the amount of information that fossils provide about past environments, biological principles, the influence of the wider surroundings of the organisms, ethological implications as well as the basic knowledge of site formation, i.e. taphonomic information.

Taphonomy (etymologically from the Greek *taphos* = burial and *nomos* = laws) was created and defined by Efremov (1940, 1953) because of the difficulties of studying "...phylogeny of different groups of organisms, the interpretation of the biology of forms now extinct, paleozoography ... greatest difficulty in all palaeontological reconstructions is the desultory and incomplete character of the material and causality of its preservation in the rock" (Efremov, 1940; p. 81). Especially critical for Efremov was the application of palaeoecological methods on faunal remains, which frequently are not found at the place where they were living i.e. thanatocoenosis. This is especially prevalent in terrestrial organisms. Shipman

(1981) already emphasized that fossil sites cannot be interpreted as a snapshot of the past and that fossils no longer possess the social and biological traits, nor the metabolic activity that animals had in the past (Fernández López, 1991).

Taphonomy was originally created as a subdiscipline of palaeoecology (Efremov, 1940), but the new questions in palaeontology extends the subject beyond its traditional role (Behrensmeyer et al., 2000), and supplies palaeobiological information encoded in fossils that can only be deciphered by taphonomic analyses. Behrensmeyer and Kidwell (1985) denoted that sometimes, often intuitively, palaeontologists tend to choose well-preserved specimens to minimize taphonomic biases in the systematic description and interpretations of functional morphology. However, in population studies, processes such skeletal size sorting and time-averaging can affect morphometric parameters. Differential preservation of species plays an important role in palaeocommunity reconstructions and reworking in biostratigraphy. Similarly, considering a wide geographic range of localities and extended temporal record, some palaeontologists consider that taphonomic processes do not affect the application of palaeoecological methods. In order to reconstruct the past, palaeontologists have to use fossils, and the basic study sample, i.e. fossil or the fossil assemblage, is always affected by the way it was accumulated and preservation processes undergone. Therefore, palaeoecological reconstructions must take into account the effects of all the various preservation factors (Shipman, 1981). In summary, all processes that give raise to fossils provide information about past organisms that allow us to gain information about their palaeobiology, way of living and evolutionary traits (Fernández López, 1981, 1995, 1991, 2006).

Efremov (1953) considered that burial was the key to the preservation of organic remains and their fossilization. Processes

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Fig. 1. Past and present palaeontological excavations. The contrast between old and new methods of recovering fossils is dramatic. The old procedure (left) resembles mining for minerals where digging takes place in a penumbra, sediments are removed with picks and shovels, and a donkey carries the fossils away in bags. Modern systematic excavations (right) are performed in a metric grid, using fine tools and brushes to carefully uncover the fossils in well-lit conditions. They are labelled, listed and drawn and their spatial coordinates are recorded. The inter-relationship between sediment and fossil, artefact and fossil, and fossil and fossil, are described and these distributions are plotted. Sediments samples are labelled and their grid coordinates are recorded for later sieving and analysis of small vertebrates, invertebrates, charcoal, seeds, stone-tool debris, microfossils and other remains. The ultimate aim is to recover fossils in the context in which they were deposited and fossilized.

between death and burial were destructive, so burial was synonymous with preservation and fossilization, and laws of burial (taphonomy) meant the study of all processes by which past organisms become fossils. Later, during the 1970s, anthropologists and archaeologists rediscovered taphonomy as the means to obtaining further information and establish human behaviour and way of life through information recorded on the fossil bone surfaces as result of butchering, hunting or decoration.

Past living organisms may or may not lose or change their original biological information content during fossilization (e.g. fossil-Lagerstätten, bog bodies, natural mummification). However, remains of these past organisms always gain information on other contemporary past living organisms interacting with their dead remains (e.g. predators, scavengers, saprophages, vegetation), on past environments acting before and during burial (e.g. physical or chemical weathering) and physico-chemical processes occurring through time generally after burial (Fernández López, 1981, 1991; Behrensmeyer and Kidwell, 1985; Soligo and Andrews, 2005).

Taphonomic research is not only focused on the fossil, it also encompasses trace fossils and signs of activity of life forms of the past (e.g. footprints, coprolites, pellets, tooth marks, digestion traits, insect damage, stone tool cuttings, trampling marks, root marks, etc.). These sources of evidence tell us about the life and behaviour of these species and such information could never be recovered without taphonomy. This aspect is of key importance when interpreting past ecosystems and palaeoecology, and is a requisite to confirm dating (Grün et al., 2006) and to identify contemporary species in a given site. Taphonomy is an integrative and multidisciplinary investigation that aims to reconstitute the past in all details. The investigation of reworking, i.e. mixtures of fossils of different time periods, is another crucial aspect of taphonomy. Evolutionary studies cannot be successfully done if taphonomic studies do not confirm or exclude the occurrence of mixtures and establish the degree of mixing (Fernández-López, 1990; Fernández-López and Meléndez, 1995; Fernández-López et al., 2002; Andrews, 2006). Therefore, taphonomy also has implications in biostratigraphy and evolutionary investigations, as well as a wide application in a variety

of fields that includes geology, archaeology, palaeobotany and forensics studies. Taphonomy is not only part, but key in palaeobiological and palaeoecological investigations.

2. Palaeoecological interpretations

The species composition of floras and faunas from palaeontological sites differ to some degree from the original sources from which they were derived in the past. Establishing past climatic sequence of environmental conditions requires information provided by botanical remains or other archives, but biotic and abiotic factors of accumulation and preservation may affect species composition. This may result in altered species representation, either by reduction in species richness, when certain elements or groups are selected against, or by increase in richness when species from more than one source are mixed together or preserve better than others (Andrews, 2006). Both forms of bias may operate together. In addition, community and palaeocommunity attributes are not equivalent, because the palaeocommunity is described using time-averaged data and is not only affected by biological factors but equally affected by abiotic taphonomic factors.

Three major issues have to be addressed when seeking to reconstruct the palaeoecology of any combination of fauna or flora: habitat complexity arising from mixed faunas, biases arising from processes of accumulation and preservation, and the problem that past habitats may have no modern counterpart with which to compare them. The first issue of habitat complexity, “whereby animal/flora species in fossil assemblages are almost always derived from more than one habitat...” (Andrews, 2006, p. 572). This issue can be approached by combining modern faunas from a variety of habitat types and in different proportions in order to see the effects this has on the ecological signal of the faunas (Andrews et al., 1979; Kovarovic et al., 2002; Andrews, 2006). Mixing of source habitats should be considered the norm rather than the exception, so that some degree of faunal mixing should be expected in most fossil faunas. Different combinations or mixes may be due to ecological causes because many animal and botanical species

occupy different habitat types, and they do not always die or end up in their optimal habitat. Mixing of faunal assemblages from widely different habitats can readily be identified, for example mixing of animals from tropical forest and savanna habitats: these retain a strong forest signal but the savanna element is apparent in the increase in non-forest elements (Andrews, 2006). In contrast, mixtures of various types of savanna ecosystem, such as woodland with grassland, are hard to identify, for the differences between them are not great. For botanic remains (e.g. flowers, pollen) the external environment (e.g. wind, rain, animals) and their own abundance, shape, size or buoyancy will determine degrees of mixtures.

The second issue to be considered when reconstructing palaeoecology is the processes of accumulation and preservation that concerns alterations to which most fossil faunas or floras are subject during its natural taphonomic history, such as trophic or food chain, traps or transport (bringing animal/plant remains and species together from different geographic areas), or differential preservation due to environmental conditions and susceptibility to decay. Other taphonomic processes may entail preservation of animal species and this aspect has been extensively studied (see Lyman, 1994 for references), for it has long been recognized that processes of preservation and destruction can so alter faunas and floras that they may give a misleading picture of past environments (Weigelt, 1927; Efremov, 1940; Olson, 1981; Brain, 1981; Shipman, 1981; Klein and Cruz-Urbe, 1984; Behrensmeyer and Hill, 1988; Andrews, 1990; Behrensmeyer et al., 1992; Lyman, 1994). The emphasis here has been on the identification of the processes and the descriptions of the bias produced, but in most of these cases little attention has been given to recognizing the degree to which the ecological signal of fossil taxa may have been changed by these processes. Again this issue may be approached by altering recent species in such a way as to reproduce the effects of habitat mixing and species loss. One of the most common types of mixing in faunas is by body size, and this can be investigated by removing species from modern comparative faunas in order to simulate the effects of species loss (e.g. Dreyer, 1984; Foote, 1992; Andrews, 1996; Robb, 2002). Rarefaction in this case is measured by weighted averages, a simple ordination method described by Gauch (1989). Species reductions are based on the ecological ordination scores for the altered faunas, combining species presence/absence with weighting derived from an ecological scale based on those species habitat preferences (Andrews, 2006). An example is shown here in Fig. 2, where small mammals have been progressively removed from faunas representing a series of habitats. Most mammal species occupy variable ranges of habitat, some more than others, but the botanic record is influenced by natural trophic sequences and also influenced by animal behaviour and interaction (e.g. pollination, bird nesting, grazing).

Another approach is to test community structure of fossil species against the ranges of patterns seen in extant species, which can provide an approximation of the extent by which the fossil species are preserved or altered (Soligo and Andrews, 2005; Behrensmeyer et al., 1992). Deviation from an expected community pattern due to taphonomic selection may be identified by the absence (or over-abundance) of specific groups, but it could also be due to a real difference in community structure, and this may be identified easily if the comparative samples are based on general biological principles, as was done, for example, for several of Olduvai faunas (Fernández-Jalvo et al., 1998).

When predation is the agent of taphonomic change, the species representation is influenced by consumer behaviour and selective incorporation of species in their diet. This affects both vertebrate species and botanic taxonomy. Vegetation is consumed by herbivores, which in turn may fall prey to predators. Even in the most

generalist herbivores, palatability of plants may vary greatly, because some species of prey are ignored and others heavily consumed (Marquis and Batzli, 1989). Similarly, the species composition of small and large mammals taken by predators is selected by hunting strategies and prey choice, and even in the most generalist predators, preference is observed due to prey–predator relative size or nocturnal–diurnal prey–predator activity when compared with their natural occurrence (Kruuk, 1972; Mikkola, 1983; Andrews, 1990).

Pollen transport/deposition may not be fully subjected to insect-pollination or hydrodynamic/aerodynamic properties, but to predator–prey physiological relationships and consumer preferences (browser-grazing). Vegetation in the surroundings can be also inferred indirectly from the taxonomy, predominance of prey in the site and their usual diet (browser/grazer). The herbivore diet can also be deduced from fossil bone isotopic ($\delta^{13}\text{C}/\delta^{14}\text{C}$) analyses. Taphonomic investigation of pollen in coprolite/pellets provides more detailed information of preservation and the local environment. For instance, palynological records especially in cave deposits where faunal remains occur are usually not preserved. This is because of aerated damp local conditions prevailing in the sediment and resulting in oxidation and microbial decay of microfossils (Fig. 3) (Scott, 2003). A strategy that, however, produced some success in finding pollen in caves is to inspect dung material such as coprolites, which seems to be representing local capsules that are slightly better sealed off from local adverse environmental conditions that favour preservation (Scott, 1987; Fig. 4). Coprolites contain richer and more diverse pollen than the surrounding sediment or surface dust i.e. pollen rain (Scott, 1987, 2000; Scott and Brink, 1992; Carrión et al., 2000, 2001; Scott et al., 2003). The microenvironment that may favour pollen preservation in coprolites and the ecological meaning and the source of both pollen from the environment (pollen rain) and pollen from feeding and/or predation are currently under investigation (Fernández-Jalvo et al., 2010, Scott et al., in preparation).

Environmental parameters that modify bone/pollen and its preservation are important taphonomic factors. Vertebrate and floral remains are affected by soil corrosive (acidic or alkaline) compounds, bacterial or fungal attack, and by weathering factors, such as solar radiation or changes in temperature and humidity. These factors, or more probably a combination of characteristics, are critical to the preserving or destruction of bones/palynomorphs, but they also record taphonomic agents that changed the nature (surface and histological traits) of fossils. A combination of experimental studies, and investigation of modern analogues together with analyses of fossil remains provide the information needed to interpret what happened in the past and how it happened.

Taphonomic agents may act together or may be time successive. Similarly, fossil accumulations may be deposited as a single event, or they may occur over considerable lengths of time, and it is important to distinguish between them. Earlier accumulations may be subjected to a different combination of taphonomic agents to later accumulating bones, and if the two sets are mixed together in the sediment this can give rise to confusion as to the manner of accumulation. Time-averaging may be important in the interpretation of certain sites, and climatic and environmental interpretations are seriously influenced by time-averaging.

The third issue that concerns the analysis of past ecosystems is the possibility that past habitats may have no modern counterpart. This is assumed in geological ancient ages (Palaeozoic or Mesozoic), but not regarded as important in more modern times like the Quaternary, although in all probability it is highly relevant during this period which has experienced complex and rapid climate change (Wright et al., 1993). This is probably a widespread problem

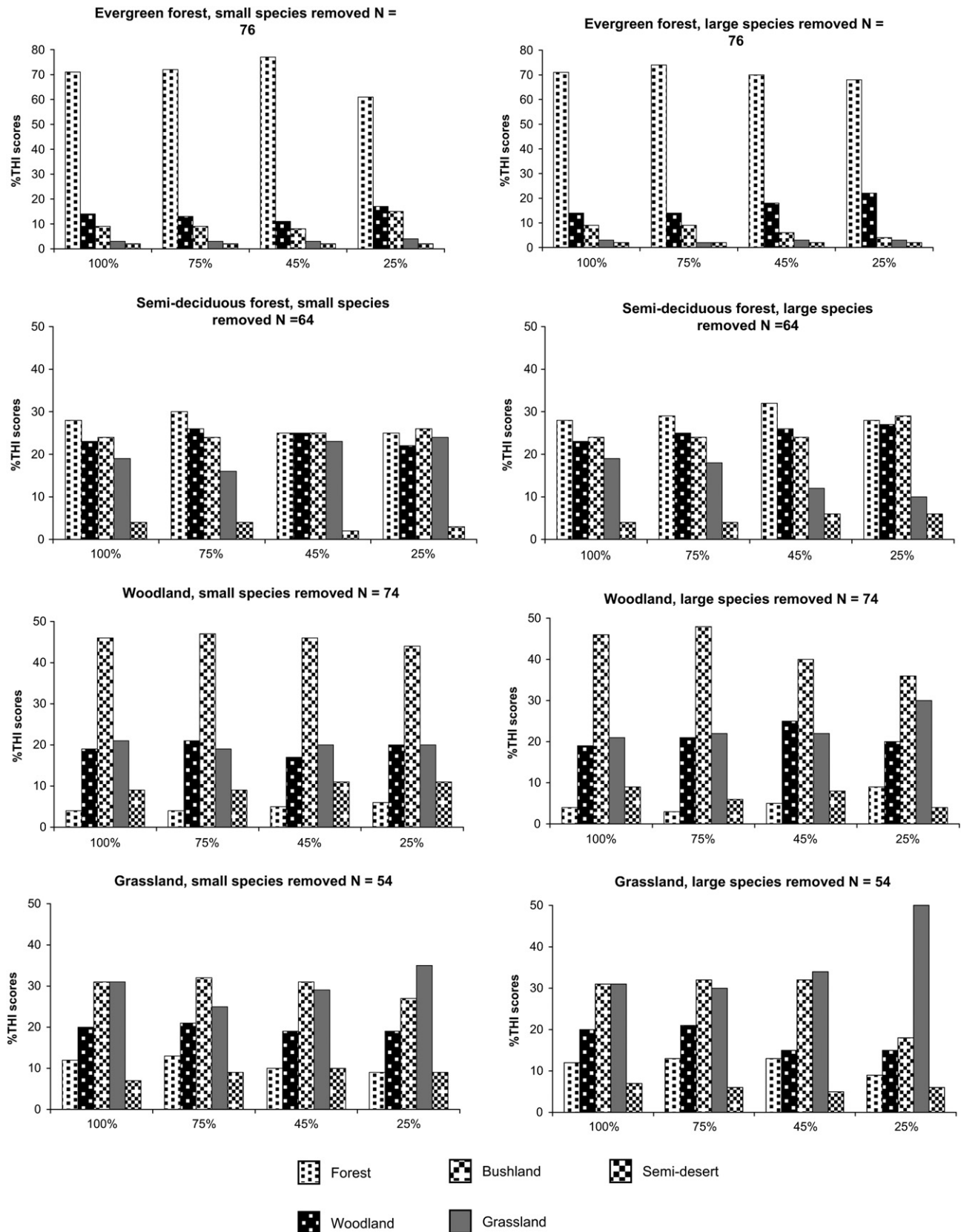


Fig. 2. Weighted averages scores for modern faunas with species progressively removed, from left to right on each bar chart: 100% (no reduction), 75%, 45% and 25% removal of species. The figures down the left side show the effects of removal of small-bodied species, while those on the right show the effects of removal of large-bodied species (from Andrews, 2006).

Preservation of fossil plant remains

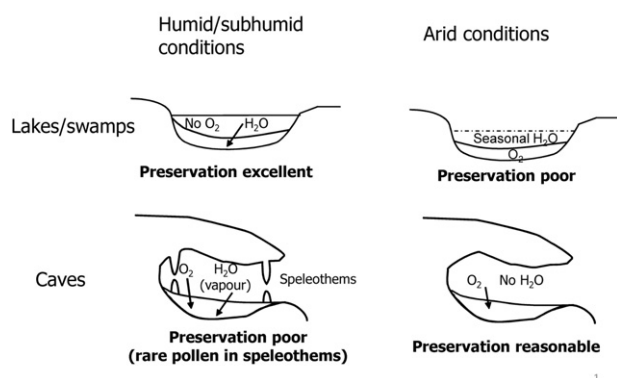


Fig. 3. Scheme of conditions in the past that eventually destroyed pollen by oxidation associated with perennial dampness in sediments, sun exposure and/or temperature oscillations (from Scott, 2003).

for all forms of environmental reconstruction, however, and it can be approached by methods that seek to reconstruct the structure of past environment, such as ecomorphology, which investigates the functional adaptations of groups of mammal species (e.g. Kappelman, 1988), or community ecology, which investigates the ranges of community structure of mammalian faunas (Andrews et al., 1979). In our earlier analysis of the Bed I Olduvai faunas, we found that several of the middle Bed I faunas were intermediate between forest and woodland and appeared to represent an unknown habitat with no modern counterpart (Fernández-Jalvo et al., 1998).

3. Palaeoecology and taphonomy of human sites

Sites with evidence of human occupation are the specific subject of this special volume, for we have a particular interest in reconstructing ecological scenarios in relation to human evolution. Humans, however, are yet another agent of disturbance in terrestrial fossil sites, arising out of their social behaviour, omnivorous diet, versatile living strategies and highly destructive activity at occupied sites all of which produce a final mixed assemblage that needs intensive investigation to distinguish human distortion from ecological occurrence. The most common association of human remains in the fossil record is with mammal faunas, and it is on these that emphasis is placed in interpreting palaeoecology. Flora is usually interpreted from palynology (e.g. pollen, spores and phytoliths), and plant remains (e.g. lives, seeds, wood or charcoal) and these are also affected by human factors.

Pollen and plant remains that are directly linked to environmental conditions may be altered and chosen by humans that bring a variety of plants and fruits from different habitats together mixing them with those that accumulate naturally by other animals or abiotic agents. Caves are not the best location to preserve pollen (Scott et al., 2003; Carrión et al., 2009) but caves are frequent occupation sites by humans, especially in Europe. An example of pollen record associated with humans is the Middle Pleistocene Galeria sequence which forms part of the series of sites at Atapuerca, Spain (García-Antón and Sainz-Ollero, 1991). However, pollen preservation was not ideal and 85 out of 119 samples were sterile (other Atapuerca sites were even poorer, García-Antón, 1989). Indications of poor preservation in Atapuerca sites can be confirmed by 14 samples collected in 1995 by YFJ and LS from other accumulations like Penal, Gran Dolina and Elefante, where only minute organic fractions could be extracted with almost no pollen except for

Equus Cave: brown hyena den

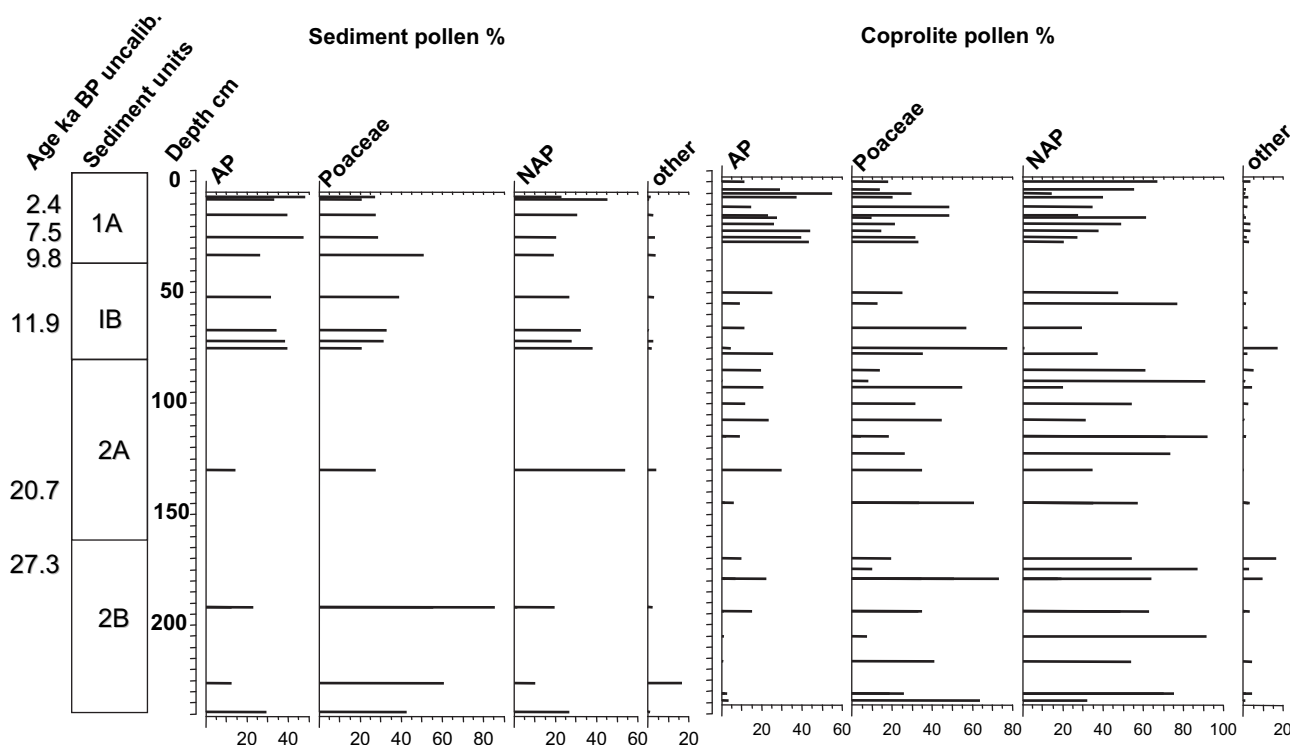


Fig. 4. Pollen spectrum from Equus Cave (South Africa, from Scott, 1987). Note pollen content recovery in sediment is poorer than in coprolites. Sediment samples covered larger depth intervals but also yielded lower numbers (not indicated).

a few in one sample at Elefante. Together with the problem of poor preservation when pollen content is low there is the effect of amplification of contaminants from the surroundings that inadvertently also capture modern microscopic material. This should always be considered as a possible flaw in such pollen sequences (Scott and Bonnefille, 1986; Scott, 1995; Carrión and Scott, 1999).

The composition of faunal remains found in human occupation areas can be also ecologically distorted by human feeding preferences and hunting/scavenging activities, but contrary to pollen, cave sites may be less destructive to bone. Another example, this time for faunal remains is Boxgrove (Sussex, UK – dated ca. 500 ka). The extensive excavations at Boxgrove have exposed a middle Palaeolithic landscape on the south coast of England. The deposits formed quickly and are preserved intact beneath low energy fine-grained beach sediment with little or no disturbance. The human tibia, assigned to *Homo heidelbergensis*, was found in isolation, but it and other animal bones have carnivore-chewing marks showing that they were exposed on the surface of the ground long enough for carnivore scavenging.

The fossil hominins, or signs of hominin presence, occur throughout the sequence above the beach deposits and below cold climate slope deposits (Roberts and Parfitt, 1999). The time period of deposition is not known, but there is no indication of faunal variations within the sequence. The majority of implements are bifacially flaked hand axes, and waste flakes can be refitted to reconstruct the original flint nodule. In some cases, flint implements are associated with bones with cut marks.

The fauna from Boxgrove has many elements that can be attributed to the early Middle Pleistocene, probably MIS 13, and includes an abundance of both large and small mammals. Many species of deer and carnivore are found alongside very large mammals such as elephant, rhino and bison, and alongside these is a diverse assemblage of small mammals (Roberts and Parfitt, 1999). Some species appear likely to have been living at or near the coastal plain on which the site is situated, but evidence of association with other taxa, and in particular the association of small mammals with the large mammals, is so far lacking. The palaeoecological analysis that can be presented here is therefore of limited value, for all faunal elements have been lumped together regardless of potential taphonomic bias. The results of the analysis are shown in Fig. 5, which is unusual in showing a higher than expected Mediterranean component in the Taxonomic Habitat Index (THI) analysis. This suggests a warmer than present climate prevailing at Boxgrove at the time of accumulation of the fauna. Warm deciduous and evergreen woodlands are strongly suggested by this analysis.

Most interesting is the period when humans are highly influenced by the environment and the surrounding ecosystems that

might influence hominin speciation. If that happened, researchers should be able to establish cause–effect relationships and this needs highly reliability undistorted evidence. The degree of distortion has to be recognized and calibrated before applying models and evolutionary trends.

4. Final remarks

The final aim of obtaining reliable palaeoecological reconstructions is to obtain a reliable indication of climatic sequence and to an extent, global climatic conditions and fluctuations along time. Long-term cyclic trends and detailed fluctuations in climate should be understood as far as possible as background scenario's that influenced the taphonomic setup at sites. But how precisely are climate and ecological interpretations obtained from terrestrial deposits? Some prejudices have been resolved by Western and Behrensmeyer (2009) who found strong correlation between dead/living populations and high fidelity ecological information preserved in bone assemblages. These results applied to fossil assemblages should control overprinted taphonomic processes, which, instead, may provide climatic information (e.g. re-sedimentation or reworking). Ecological conditions and global climate changes have frequently been linked to human evolution (as well as other animal and botanical species). If so, the interpretation of palaeoclimates is based on a wide range of evidence from marine and terrestrial records that need correlation. Terrestrial palaeoclimatic evidence includes faunal and botanical records, as well as geological and isotopic records and fine radiometric dating, but palaeoclimatic evidences are especially hard to interpret in terrestrial ecosystems (Behrensmeyer, 2006). Correlation between the climatic signal and the actual evolutionary event remains frequently uncertain, but increasing the number of reliable database available may result in higher confidence of correlation.

In this respect, taphonomy plays an important role. The first step is to be aware that what we have today as fossils do not have any metabolic actions, and neither are they past organisms (Shipman, 1981; Fernández López, 1991). A fossil bears preserved/transformed original palaeobiological information (i.e. macro-, micro- or nanomorphology of a recognizable past organism skeleton trait), but superimposed on their surface or in their histology or geo- and biochemical composition, there is a new record of information of the past environments and activity of contemporaneous living organisms. Secondly, fossils are found in sites that may or may not correspond with their past optimal habitat. Thirdly, time-averaging and pre- or post-burial mixtures need to be considered to establish synchrony and contemporary climatic and evolutionary events. Fossil-site relationship is basic information to document climate-driven environmental shifts which document global scale signals. For all this the study of mechanisms that generate fossils (taphonomy) cannot be simplistically seen as the evidence of bias, but as the science to describe the natural “life” of a fossil to retrieve the original palaeobiological-palaeoecological- and other palaeontological information to reconstitute the past in all details.

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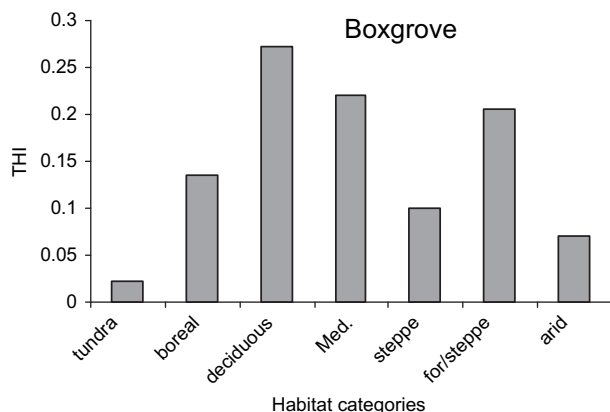


Fig. 5. Taxonomic Habitat spectrum from Boxgrove (Middle Pleistocene, UK).

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