What Taphonomy can and cannot tell as

Qué puede y qué no puede aportarnos la Tafonomía

Peter ANDREWS
Natural History Museum. London SW7 5BD. U.K.

ABSTRACT

The fossil record is generally incomplete and does not provide a true representation of past faunas. The study of taphonomy is aimed at understanding the processes by which the fossil record is altered both to provide direct information on the environment and to attempt to minimize the potential biases so as to arrive at a better representation of the source faunas. The description of alterations to animal bones provides a basis for assessing loss of material from faunas, and this is referred to here as the destructive effects of taphonomic modification. In addition, however, there are constructive aspects of taphonomy, whereby animal remains that are buried quickly or are preserved in sheltered environments can be seen to be little altered from their original state. In the latter case it may be said that study of taphonomy provides evidence of lack of change and lack of bias, and this is perhaps even more important than showing the presence of change. Two examples of these two aspects of taphonomy are given for fossil faunas from the Miocene site at Pasalar, Turkey, and the middle Pleistocene fauna at the Sima de los Huesos, Atapuerca, Spain.

Key words: Taphonomic gain, Taphonomic loss, Atapuerca, Pasalar, fossil record.

Cuadernos de Geología Ibérica, n.º 23, 53-72.
Servicio de Publicaciones. Universidad Complutense, Madrid, 1997.

RESUMEN

El registro fósil es por lo general incompleto y no nos aporta una verdadera representación de las faunas del pasado. Los estudios de Tafonomía tienen como finalidad la comprensión de los procesos de alteración experimentados por el registro fósil con objeto tanto de aportar una información directa sobre el medio ambiente, como de intentar minimizar los potenciales sesgos y obtener así una mejor representación de las faunas originales. La descripción de los procesos de alteración experimentados por los huesos de animales nos aporta una base para calcular la pérdida de material a partir de la fauna original. Esto es lo que aquí denominamos los efectos destructivos de la modificación. Sin embargo, existen también efectos constructivos de la tafonomía cuando los restos de animales son enterrados rápidamente o conservados en ambientes protegidos, mostrando alteraciones mínimas de su estado original. En este último caso puede decirse que los estudios tafonómicos aportan una evidencia de falta de cambio y de sesgo, y esto es quizás más importante aún que mostrar la existencia de cambios o alteraciones. Aquí se presentan dos ejemplos de estos dos aspectos de la tafonomía para el caso de las faunas fósiles de los depósitos miocenos de Pasalar en Turquía y de las faunas del Pleistoceno Medio de la Sima de los Huesos en Atapuerca, España.

Palabras clave: Ganancia tafonómica, pérdida tafonómica, Atapuerca, Pasalar, registro fósil.

INTRODUCTION

One of the main justifications of the subject of taphonomy has traditionally been the need to take account of perceived bias in the fossil record. It is taken for granted that the fossil record is either incomplete in some way, or it does not provide a true representation of the animals living at the time and place of origin of the fossil assemblage (Lyman 1994). Such fears are all too often justified, and examination of the taphonomy of fossil assemblages is necessary to allay them, but it should not be assumed that fossil assemblages are *always* greatly changed by taphonomic modifications. In many cases, the fossil assemblages that are best represented in the fossil record are those that *lack* taphonomic modifications simply because these processes, where they occur, are essentially destructive and render bones less likely to survive.

Taphonomy should perhaps be regarded as a cautionary discipline, necessary to demonstrate either the lack of taphnomic bias or, if present, its nature. If totally absent from a fossil assemblage, it may be that the structure of the assemblage matches that of the death assemblage from which it was derived. If present, however, examination of the taphonomic modifications preserved on the fossils may provide evidence of the history of preservation so that the nature of the bias can be determined and some allowance be made for the various processes involved (Brain 1981; Andrews 1990a & b).

Taphonomy was first defined by Efremov (1940) as the science of burial. Most recently this has been extended to «the study of the transition, in all its details, of organics from the biosphere to the lithosphere» (Lyman 1994). These definitions include the implication that there may be positive as well as negative aspects to its effects, also expressed obliquely in Fernandez Lopez (1991) who states «Fossilization... means an increase in taphonomic information... which does not necessarily involve loss or decrease of palaeobiological information». The positive effects concern the actual burial process, for it is known that animal bones that are buried rapidly in the right sort of environment survive for long periods of time with little modification. Animal remains that are not buried rapidly, or are buried in active environments, are subject to the negative forces of taphonomy and are modified accordingly. It is possible, therefore, to distinguish these two aspects of taphonomy in order to gain a more realistic vision of the significance of the subject to palaeontology and archaeology. I have done this by distinguishing its **constructive** effects from its **destructive** ones (figure 1).

The flow diagram in figure 1 derives from one that I have used previously (Andrews 1990). It shows the 'flow' downwards from living animals at the top centre through to a fossil (or archaeological) assemblage at the bottom centre. On the left of the figure are the constructive effects, and on the right the destructive ones. These will be considered in turn.

CONSTRUCTIVE EFFECTS

Animals die from a variety of causes, not all of them destructive (except of course for the animals concerned). Animals may die by themselves and their remains stay isolated through burial and fossilization, resulting in their recovery as isolated fossils. A good example from the anthropological record is the *Dryopithecus* skeleton found by Moya Sola and Kohler (1993) at Can Llobateres, Spain. This specimen has well preserved cranial and postcranial remains scattered over a few square metres of horizontal

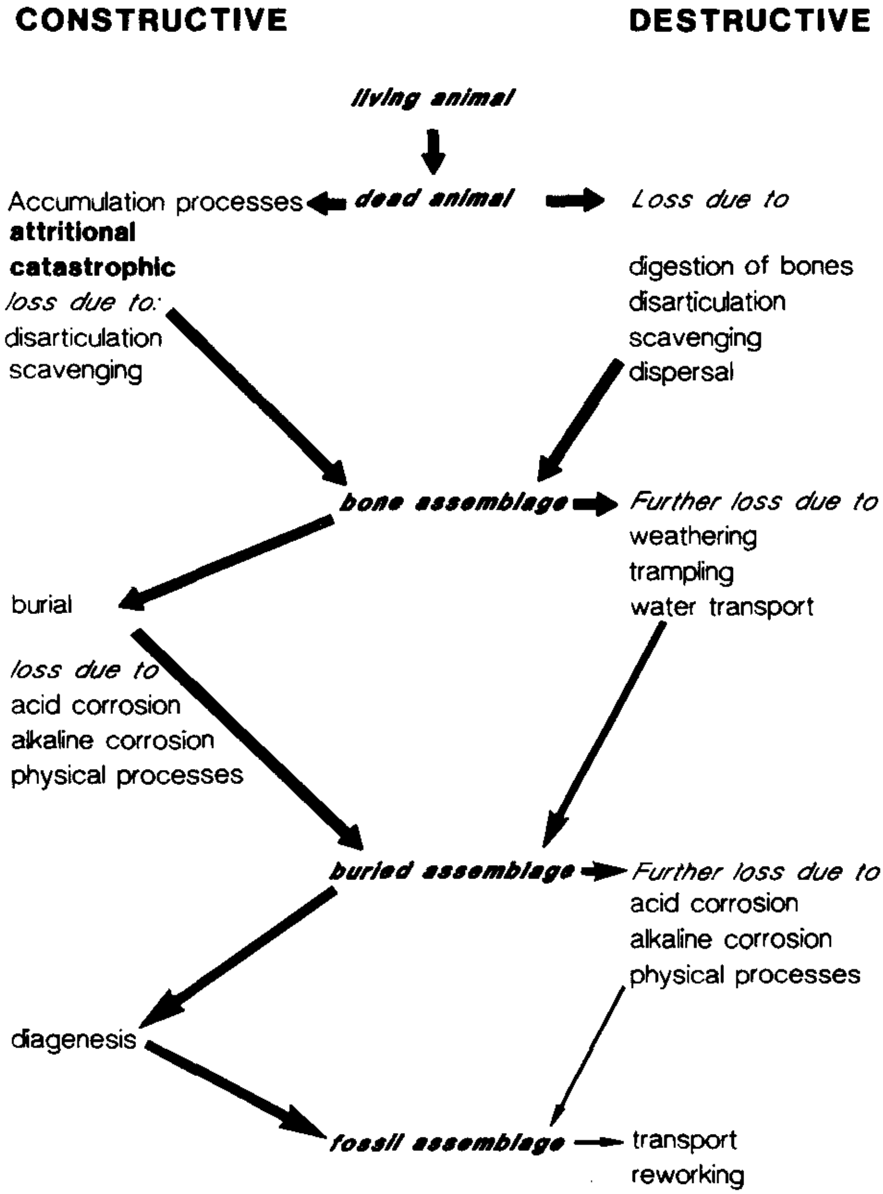


Fig. 1.–Flow chart of taphonomic modifications distinguishing between constructive sequences of accumulation and burial and destructive sequences involving bone loss.

Fig. 1.–Diagrama de flujo de las modificaciones tafonómicas en el que se muestra la distinción entre secuencias constructivas de acumulación y enterramiento y secuencias destructivas, que implican pérdida de material oseo.

area but from a single stratigraphic horizon lacking any other fossils. Alternatively, an animal population may be subject to predation by a bone-accumulating carnivore, and parts of the population may then end up in a carnivore or under an owl roost (Brain 1981). Very often such prey populations have attritional mortality patterns because predators tend to select the weaker members of the population, particularly the very old and young (Klein 1989). When these bone assemblages are buried rapidly, the attritional mortality patterns may be preserved (Klein 1982). Scavenged bone assemblages may lack this pattern because there may be many different sources for the bones, and other taphonomic processes may similarly modify the original mortality pattern.

Catastrophic assemblages may arise from a variety of natural causes. For example, sudden floods may kill an entire community, and the age structure of the dead animals therefore reflects the age structure of the living populations, i.e. with abundance of young individuals. In some years the wildebeest migration in East Africa results in many deaths as the animals cross the rivers that lie across the migration route, and when they are trapped by the high river banks and drown. The bodies are washed on to sand banks and accumulate in great numbers, with juvenile individuals predominating in a catastrophic mortality pattern. This pattern may be preserved through subsequent taphonomic processes, but if the modifications are extreme, for example if all the juvenile individuals are destroyed by scavenging hyaenas, or if reworking of the bones occurs through water transport, the original pattern may be irretrievably lost.

The common pattern to these accumulations and the preservation of the death assemblage mortality profiles is rapid burial. Without this, scavenging and secondary transport would soon obliterate the primary pattern that produced the assemblage, whether it be attritional or catastrophic. As a first generalization, it may be said that most fossil assemblages of any quality represent animal bone accumulations which were buried rapidly and which therefore were subjected to only the first stages of destructive taphonomic processes. Animal bones that were not buried rapidly simply became dispersed and destroyed by these processes (see below).

Even after burial, bones are subject to a number of processes depending on the nature of the burial substrate. Caves are a special environment that will be considered below, but in active terrestrial environments a number of physical and chemical processes operate, producing bone degradation. I made a first attempt at analysing these in La Reunion de Tafonomia y Fosilizacion held in Madrid in 1990. I divided taphonomic processes into physical, chemical and biological activity patterns (Andrews 1990b, table 1), but it was not clear from this how the different processes operated and at what stage. In fact, all three processes operate after burial and are shown here on the left hand side of the flow diagram (figure 1).

Physical damage occurs in all environments after burial due to soil movements, pressure of the weight of the soil or sediments, and compaction. All of these can result in the crushing or breakage of bones, and in more extreme cases in their complete destruction.

Acid corrosion of animal bone can occur in a number of different ways. Bones buried in acid soils suffer extensive corrosion over the whole surface (the source of the acidity may be from the mineral content of the soil or from organic sources such as urine or organic decay); more localized damage is caused by acid solution at the tips of growing roots, producing characteristic grooving along the bone surfaces. These modifications can readily be distinguished from the localized corrosion produced by digestion of bones (Andrews 1990a, figures 1,11-1,12). Alkaline corrosion appears to occur in cave environments, although the process has yet to be duplicated in any naturalistic experiment (Fernandez-Jalvo 1994). It is mainly characterized by the formation of solution pits in the surfaces of bones, with preferential damage to bone and dentine as opposed to tooth enamel. It is likely that alkaline corrosion also occurs in alkaline soils, but this has yet to be demonstrated.

Biological activity after burial can produce dispersal of bones and some degree of damage. Earthworm activity can both disperse small bones, with the smaller the bone the greater the dispersal, and cause superficial damage (Armour-Chelu & Andrews 1994) similar to acid corrosion. Extensive damage can be done by invertebrate action, for example termites appear to eat bone on occasion and certainly produce extensive damage. The acidity in soils due to urine or decay products could also be considered the result of biological activity, and it must be considered also that some biological/chemical change in soils or sediments derives from the animal remains themselves. Organic acids from the decay of animal bodies produce a locally acid environment that may cause extensive damage to the bones from the same animals (Bell et al. 1996).

All of these processes are subject to fluctuations in time and space. The chemical characteristics of the fossilization environment may be summarized in terms of acidity, organic content, mineral content and aeration/wetness (e.g. in terms of available oxygen). Some of these are local in extent and some may be more widespread. For example, the effects of organic acidity from the decay products of animal remains are both local in space - in the immediate vicinity of the animal —and are short-lived in time— the organic acidity is soon used up. In sealed environments, the available oxygen may soon be depleted, so that once this stage is passed the decay processes may be nearly halted. Similarly, exhaustion of available nutrients may have far reaching effects on the micro-organisms associated with break-down of animal remains. On the other hand, the minerals from the substrate may be more extensive in both space and time, although once again their eventual depletion will change the break-down environment of the fossils. Extremes of wetness and drying are extremely destructive, with the former producing surface decay and the latter the rapid destruction of organic content of bones, so that in variable environments with alternating wet-dry periods bone is not preserved for long. These variations may be the product of climatic variations on a daily, seasonal or long term basis.

Preservation factors after burial

The factors leading to the preservation of bones can be summarized from the above discussion. Their common property is protection from all but early stages of taphonomic modification through the rapid burial of animal (or plant) remains, the presence of thick vegetation, or the existence of shelter such as is provided by caves. Protection from weathering, trampling and scavenging is provided by this means, and protection from transport is also afforded unless of course the substrate in which the bones are buried is itself transported. No protection is provided against chemical and physical modification in the burial environment.

Bones covered over by thick ground vegetation are protected almost to the same extent as buried bones, and they are subject to similar degrees of corrosion. Conditions of high humidity may prevail under close and thick vegetation in open conditions, *i.e.* where ground vegetation is very thick, while in wooded conditions there may be heavy shade from trees but less humid conditions if the ground vegetation is not so thick. Protection is provided against surface weathering, transport and to a lesser extent against scavenging, but being on the surface still there may be damage from trampling in addition to the corrosion resulting from chemical changes in the high-humidity environment.

Another and quite separate factor leading to the preservation of bones for fossilization results from any situation where there is a super-abundance of animal remains. During a drought or any form of catastrophic animal mortality, there may be such a glut of animal remains that scavengers are not able to process all of them. This happened, for example, in the 1973/74 drought in East Africa, when so many animals died in certain regions that their mummified carcasses remained untouched for long periods of time without any damage from scavengers. They were thus protected from scavenging and surface weathering for a considerable period.

Extreme weather conditions can also provide short term protection from damage. Extreme cold may inhibit surface weathering, so that bones from the Arctic, for example, may persist on the surface for hundreds of years without any great degree of weathering. Extreme arid conditions also may protect bone since mummification of carcasses results in retention of skin on carcasses and therefore protection from weathering. No protection is afforded in these situations against insect attack, trampling and scavenging.

Caves have been mentioned as a special case, and they may be seen as a sort of half-way stage to burial. Bones deposited in or transported into caves are protected from most effects of surface weathering even if they remain for long periods on the floor of the cave. Further protection is afforded if the bones are buried in the cave sediments in the same way as seen above for surface specimens, and the same degree of protection is provided as for surface burials. If they remain long on the surface of the cave floor, the bones are exposed to more concentrated trampling and scavenging than those in open conditions because of the concentrating effects of the cave chamber. On the other hand, protection against some climatic and other fluctuations may be provided in cave environments, for example the effects of diurnal/nocturnal fluctuations, seasonal or long term climatic changes, and the extreme effects of wetting and drying.

DESTRUCTIVE EFFECTS

The destructive effects of taphonomic modifications are generally better documented than the constructive ones (Behrensmeyer 1975, 1978; Hill 1979; Shipman 1981; Brain 1981; Andrews 1990a; Lyman 1994). They are shown on the right hand side of figure 1 listing the major losses from bone assemblages at successive stages in the transition from biosphere to lithosphere. Some examples from these stages will suffice to illustrate the destructive effects, although degrees of destruction range from slight to total.

Many animals die as a result of predation, and their bones may preserve the marks left by the predators. These may take the form of chewing punctures or scratches (Haynes 1980) or etching by digestive acids and enzymes if the bones are ingested (Andrews 1990a). In both cases there may be preferential loss of certain bone types, so that some skeletal elements are under-represented in the assemblage, and species representation in the prey assemblage is also biased by the hunting preferences of the predator, for example size limitations in capturing prey, prey availability in the preferred habitat of the predator, the effects of daily activity on the part of both predator and prey, and many others. All these amount to a considerable selection of available fauna to produce the prey assemblage, which may therefore be unrepresentative of the fauna as a whole. Some allowance can be made for this selection if the predator can be identified, and this has been achieved in some detail for sequences of cave faunas in England (Westbury cave-Andrews 1990a) and in Spain (Atapuerca cave-Fernandez-Jalvo 1994; Fernandez-Jalvo & Andrews 1992). An example of a bone that has been modified by spotted hyaena (*Crocuta crocuta*) is shown in figure 2: there is a puncture in the centre of the picture 2.4mm minimum diameter, and this and the whole surface of the bone has been polished and smoothed by stomach acids following ingestion and regurgitation.

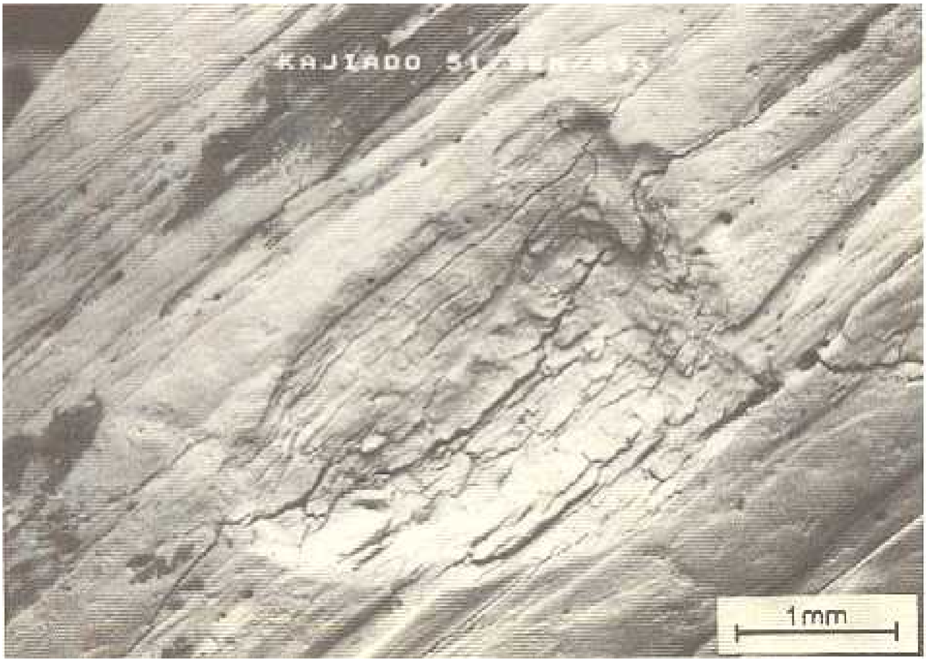


Fig. 2.–Surface polishing of a recent bone ingested by a spotted hyaena in Kenya with a puncture mark made before digestion.

Fig. 2.–Pulimiento superficial en un hueso actual ingerido por una hiena manchada en Kenya con una marca de mordedura realizada antes de la digestión.

Disarticulation patterns of animal skeletons influence the preservation of bones whether the agent of disarticulation is a predator or other taphonomic process. For example, skulls and forelimbs are less tightly attached to the rest of the skeleton than hindlimbs and vertebrae, and having become detached early on these elements are more likely to be dispersed or carried off by scavengers than are more firmly attached elements (Hill 1979). Scavenging is a major factor in dispersal, but its effects cannot easily be distinguished from other dispersal agents such as predation and trampling. Scavenged assemblages lack the selectivity of predated assemblages noted above, but the damage to the bones is very similar. One example of a fossil site in Spain with good evidence of scavenging is seen in the human remains in the Sima de los Huesos, more than half of which have punctures and scratches from a small canid which gained entry to the cave and scavenged the large numbers of bones after the bodies had rea-

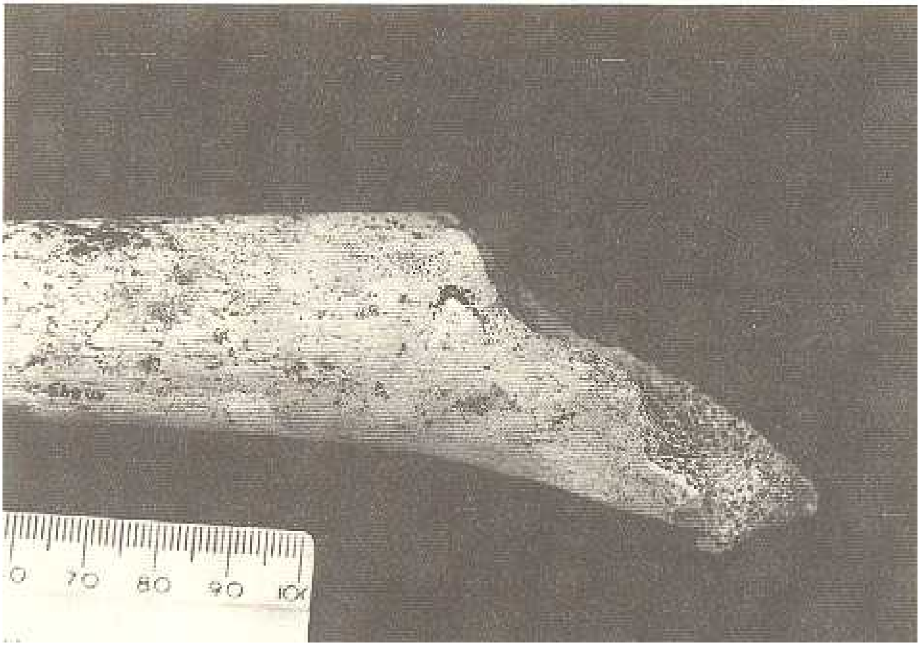


Fig. 3.–Specimen AT-843 from middle Pleistocene deposits at the Sima de los Huesos, Atapuerca, showing surface punctures made by a small canid and edge punctures along a spiral break made by a larger carnivore.
Fig. 3.–Ejemplar AT-843, procedente de los depósitos del Pleistoceno Medio de la Sima de los huesos, Atapuerca, que muestra mordeduras superficiales hechas por un cánido de pequeño tamaño y una serie de mordeduras marginales realizadas a lo largo de una rotura espiral hechas por un carnívoro de mayor talla.

ched their final resting place by other means (Andrews & Fernandez-Jalvo, in press). The sizes of the carnivore punctures (figure 3), their distribution and their numbers are all consistent with a recent assemblage of sheep bones which I have been studying for many years and which are known to have been scavenged by foxes (*Vulpes vulpes*).

Weathering is a major source of damage to bones, and unless special conditions of rapid burial prevail the great majority of bones that remain any time on the surface of the ground are totally destroyed by weathering. Bones accumulating on a land surface have an attritional weathering distribution as new bones come on to the surface through the death of animals and old bones are lost due to weathering, with all stages of weathering being more or less evenly represented (Behrensmeyer 1978; Potts 1986; Andrews 1995). Smaller and weaker bones are preferentially lost as they are destroyed more quickly by weathering, and the process is both quicker and the stages are different in small mammals like rodents compared with large mammals (Andrews 1990a). Teeth normally persist for longest, and so the taxonomic composition of an attritional weathering assemblage may be representative of the source fauna, since most taxonomic identifications are based on the teeth, so that even heavily modified weathered assemblages may not have a strong taxonomic bias. I have recently described an example of an attritional weathered faunal assemblage from Miocene deposits at Pasalar, Turkey (Andrews 1995), where it was inferred that the bones accumulated over a period of some tens of years, based on the pattern of weathering (figure 4), and on this basis it was suggested that the taxonomic composition based on the large numbers of isolated teeth was not strongly affected by these early taphonomic modifications such as weathering. The assemblage was subsequently transported to the present fossil locality, superimposing a further set of modifications (see below).

Trampling has been mentioned above as a dispersal agent, and it is also a cause of breakage of bones and of its eventual loss. Where there are concentrations of animals for any reason, for example near shade trees or animal trails, the effects of trampling may be extreme, with bones being moved large distances relatively quickly, but where bones are protected by vegetation or some other cause, the effects of trampling are much less. These effects are similar to those produced by weathering, with preferential loss of weak and small bones, but usually there is little evidence for the occurrence of trampling unless the bones are on a rocky substrate so that scratches (cut-mark mimics) develop on their surfaces (Andrews & Cook 1985; Olsen & Shipman 1988). An example from a fossil site that is of particular interest is the Nean-

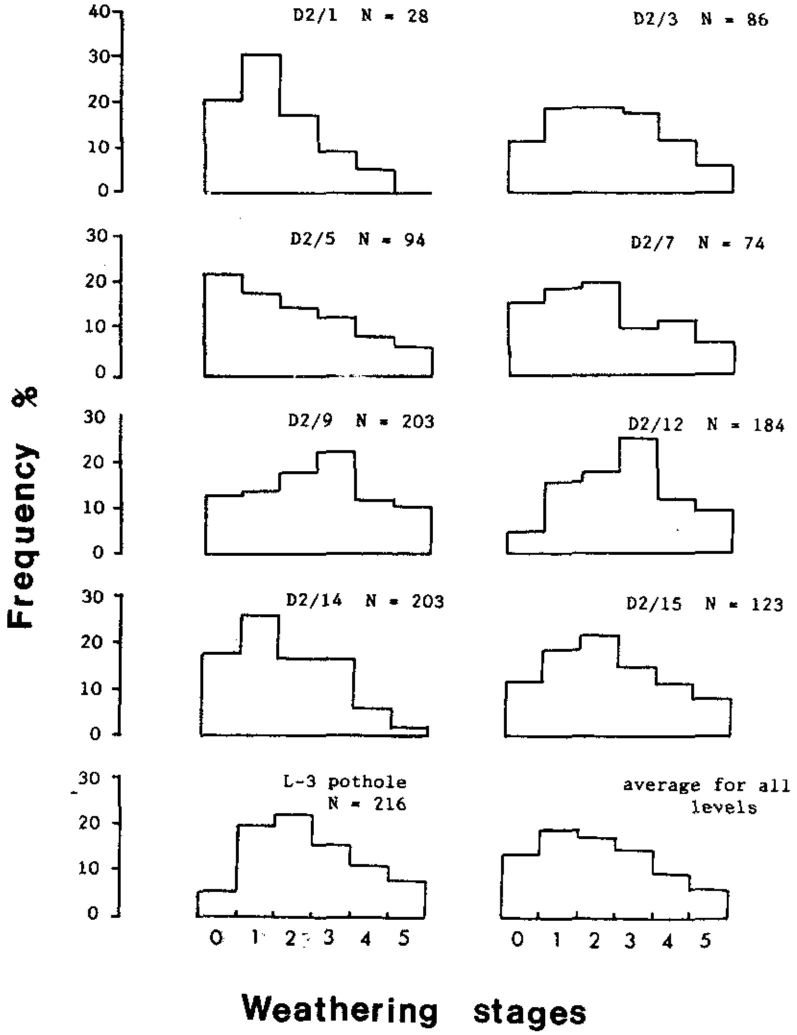
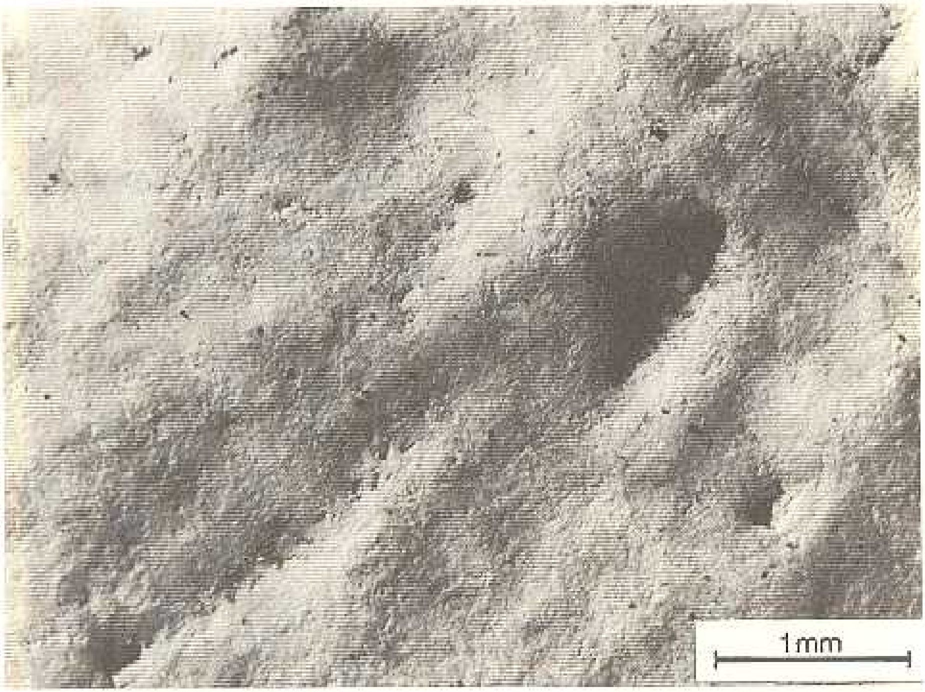


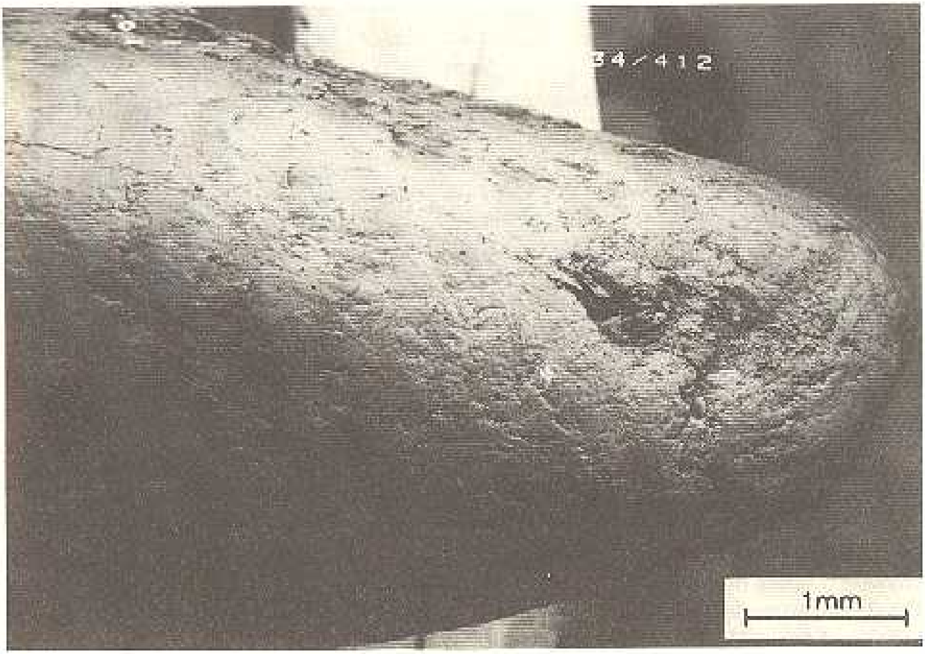
Fig. 4.–Weathering profiles of nine stratigraphic horizons in Miocene deposits at Pasalar, Turkey. The weathering stages follow Behrensmeyer (1978), with 0 = no weathering and 5 = heavy weathering just prior to collapse of the bone. The level identifications are for a single stratigraphic column with samples taken at 6 cm intervals except for the L-3 pothole, and the average for all levels is shown bottom right. N signifies the numbers of specimens in each sample.

Fig. 4.–Perfiles de meteorización de nueve horizontes estratigráficos en los depósitos miocenos de Pasalar, Tuquía. Los estadios de meteorización son los establecidos por Behrensmeyer (1978), en donde 0 = meteorización nula, y 5 = fuerte meteorización, estadio inmediatamente anterior al colapso del hueso. Las identificaciones de los niveles se han realizado en una única columna estratigráfica tomando las muestras a intervalos de 6 cm excepto en el punto de muestreo L-3, y el valor medio para todos los niveles se muestra en la parte inferior derecha. N indica el valor del número de ejemplares en cada muestra.

Fig. 5.–Shaft of fossil bone from late Pleistocene deposits at Krapina. Croatia. showing multiple parallel grooving resulting from trampling.

Fig. 5.–Fragmento de hueso fósil de los depósitos del Pleistoceno Superior de Krapina, Croacia, que muestra los múltiples surcos paralelos resultantes del pisoteo.


1mm


34/412
1mm

dertal site at Krapina in Croatia, where numerous marks on the Neandertal bones were interpreted as cut marks but in fact should be identified for the most part as trampling marks (figure 5; see also figure 6). The large numbers of shallow parallel marks along the shafts of limb bones are clear evidence of trampling as opposed to human action as the source for most of the marks (there are of course some genuine cut marks on the Krapina material).

Transport by wind, water or simply gravity is another major dispersal agent, and it is one that commonly leaves its mark on the bones. Polishing of surfaces and rounding of ends of bones are characteristic of transported bone, and similar modifications occur on bone that is reworked in sediment or on bone that is stationary but has sediment moved over or around it This form of abrasion does not necessarily indicate movement of the bone, and in fact transport of bone over limited distances may occur without any abrasion at all. The polished surface of a bone eroded by wind-blown sand is shown in figure 6 compared with a bone rounded and polished by trampling in a hyaena den, both cases of abrasion by sediment movement around a bone rather than movement of the bone itself. My analysis of the Pasalar fossils indicated the superimposition of rounding on weathered bones resulting from transport of the bones from their original place of accumulation to the present fossil site, with some bones extremely rounded (figure 7 right) and some only moderately so and with the evidence of weathering still apparent on the surface (figure 7 left).

For the most part, fossil assemblages show evidence of just two or three stages of taphonomic modification. More than that would result usually in the destruction of the bones and consequent loss of the assemblage, and it may happen also that the later modifications obliterate all sign of the earlier ones. It would also seem to be the case that rapid burial is important in preserving bones that have been subjected to destructive processes, so that, for example, a predator assemblage with evidence of gnawing and digestion would only be preserved with this evidence intact if the modified bones were buried rapidly after deposition by the predator. Their subsequent history after burial is subject to the same processes of chemical, physical and biological change already described in the previous section.

Fig. 6.–Rounding and polishing produced by three different processes. Top, the surface of a recent bone abraded by wind-blown sand; bottom, the broken end of a recent limb bone found buried in a hyaena den and abraded by trampling.

Fig. 6.–Redondeamiento y pulimiento producido por tres procesos distintos. Arriba, la superficie de un hueso actual con señales de abrasión producidas por la arena y el viento. Abajo, el extremo fragmentado de un hueso largo actual encontrado enterrado en una guarida de hiena y que muestra señales de abrasión por efecto del pisoteo.

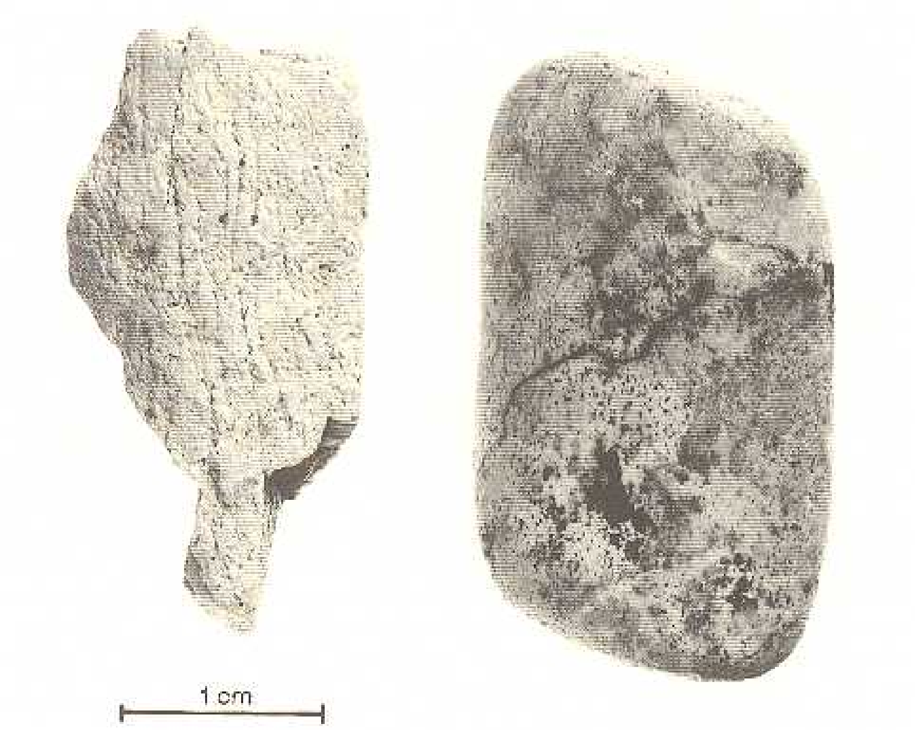


Fig. 7.–Two fossil bones from the Miocene site at Pasalar rounded by transport abrasion, with the left hand bone still showing evidence of weathering prior to abrasion. See also figure 2 for surface polishing by digestion.

Fig.7.–Dos huesos fósiles del yacimiento Mioceno de Pasalar redondeados por la abrasión durante el transporte y el de la izquierda mostrando aún señales de meteorización anteriores a la abrasión. Véase también la figura 2 como ejemplo de pulimiento por digestión.

DISCUSSION

It is evident that taphonomy operates as a process-driven subject, so that the investigation of taphonomy is primarily an investigation into process. The range of processes has already been outlined, and the evidence for process can be found in the objects in the fossil record. It should be noted that these objects come in several different types, only one of which has been discussed here, namely the bones from vertebrates. The examples given here are also restricted to processes linked with surface modifications of bone, but analysis of trace elements and isotopes in fossils, chemical and physiological change, and alterations in the biomolecular structure of the fossils are all equally important subjects. In concentrating on the surface modifications of the fossils I do not mean to imply that this is the only source of taphonomic data. It happens to be the one I am most familiar with, and it also serves to demonstrate the main point of this paper, namely that there is a positive side to taphonomy that needs to be recognized distinct from its more negative aspects, which all too often are the ones given most emphasis. It is probably not too much of an exaggeration to say that the fossil assemblages that best survive are the ones that have *not* been greatly modified by destructive processes, and this point can be illustrated by means of two fossil sites mentioned earlier where the presence of some degree of modification has been demonstrated.

The first example is from middle Pleistocene deposits in the Sima de los Huesos, in the Sierra de Atapuerca, near Burgos, Spain. This site contains an estimated 32 individuals of fossil humans, with all body parts represented and for the most part well preserved. It is evident that the source of the fossils was relatively complete bodies, and the lack of weathering and abrasion indicates lack of surface exposure and transport, so that the bones must have been preserved early on within the cave system. Two types of carnivore damage have been observed (Andrews & Fernandez-Jalvo, in press), one caused by a large carnivore and the other by a small canid. The large carnivore marks are not common, and they are most similar to the marks made on present-day lion kills. Some of the evidence for large carnivore has probably been obscured by the later marks which were made by small canids the size of foxes and which are very abundant. Fossils of foxes are the most abundant small carnivore remains found in the cave, and more than half the human fossils in the cave show signs of small canid chewing marks. The relatively low proportions of bones such as ribs, vertebrae and foot bones are probably the result of the scavenging, these bones either having been eaten and digested or were carried out of the cave by the small canids. The carnivores caused some breakage of the bones, and there was also considerable post-depositional breakage probably caused by falling blocks of limestone or trampling. These modifications caused disproportions in skeletal element preservation but probably little loss of human individuals. There is no evidence of modification by human action, for example in the form of cut marks on the bones, and the primary collecting agent which resulted in such a large accumulation of human remains is still unknown, but it has been proposed that the accumulation of such a large sample of humans, in the absence of any herbivorous mammals, may be the result of human activity (Andrews & Fernandez-Jalvo, in press), and that the evidence of carnivore damage is the result of scavenging.

The other example is the terrestrial Miocene site at Pasalar, Turkey. Extremely abundant fossil remains from over 50 species are present at this site, mainly represented by isolated teeth and lesser numbers of jaws and postcrania. Breakage is extreme, and several sequential taphonomic stages can be recognized. First, the bones were accumulated at a place away from the present site, partly by carnivore action and partly as an attritional weathered assemblage. Some of the bones were buried or part-buried and so were protected from weathering. Destruction of bone tissue by weathering resulted in accumulations of teeth, some of which were marked by plant roots. This bone and tooth assemblage was transported from the initial place of deposition to the present fossil site, with differential abrasion affecting the weathered bone more than the unweathered or buried bone. Further sediment movement resulting from spring action produced further abrasion and winnowing of the deposits, concentrating the bone in areas of coarse sediment and further removing bone tissue through chemical solution, for example leaving tooth rows in anatomical position but with little of the jaws remaining. These extensive taphonomic modifications resulted in great bone loss but little taxonomic bias because of the good preservation of the teeth.

CONCLUSIONS

In the two case studies, the analysis of taphonomic modifications has added greatly to knowledge of the environment and the nature of the fossil assemblages. In doing this they demonstrate the constructive aspect of taphonomy, where knowledge is added to the interpretation of a fossil site rather than being lost through the destructive effects of taphonomic modification. This is particularly the case for the Miocene deposits at Pasalar, for the sequence of events illustrated by the fossil bone preservation provides a picture of a dynamic environment, with bones accumulating on hill slopes, weathering and being modified by carnivores, then transport by flood action to the valley bottom where spring action and seasonal change in water regime continued the modification processes. This evidence alone suffices to indicate an environment of high topograpic relief in a seasonal climate but with high rainfall, and this contributes greatly to the final assessment of palaeoecology. In the case of the middle Pleistocene human fossils from Atapuerca, the lack of modifications indicates early preservation in the cave system, and combined with the high selectivity of human remains may further indicate human agency in the accumulation of the assemblage. The later scavenging of the assemblage provides a picture of quantities of human carcasses and/or bones being ravaged in the cave, loss of parts of the skeleton, with burial in the sediment following afterwards.

ACKNOWLEGEMENTS

I am most grateful to Guillermo Meléndez for inviting me to take part in the Taphonomy meeting at Zaragoza, and to Yolanda Fernandez-Jalvo for comments on the text.

REFERENCES

ANDREWS, P. (1990a): *Owls, Caves and Fossils*, University of Chicago Press.

—(1990b): «The basis for taphonomic research on vertebrate fossils». In: S. FERNÁNDEZ LÓPEZ (ed.), *Conferencias de la Reunión de Tafonomía y Fossilización*, Editorial Complutense, Madrid: 33-43.

—(1995): «Time resolution of the Miocene fauna from Pasalar», *J. Hum. Evol.*, 28: 343-358.

—& COOK, J. (1985): «Natural modifications to bones in a temperate setting», *Man*, 20: 675-691.

—& FERNÁNDEZ-JALVO, Y. (in press), «Surface modifications of the Sima de los Huesos fossil humans», *J. Hum. Evol.*

ARMOUR-CHELU, M. & ANDREWS, P. (1994): «Some effects of bioturbation by earthworms (Oligochaeta) on archaeological sites», *J. Arch. Sci.*, 21: 433-443.

BHRENSMEYER, A. K. (1975): «Taphonomy and palaeoecology of the Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya», *Mus. Comp. Zool. Bull.*, 146: 473-578.

—(1978): «Taphonomic and ecologic information from bone weathering», *Paleobiology*, 4: 150-162.

BELL, L; SKINNER, M. F. & JONES, S. J. (1996): «The speed of post-mortem change to the human skeleton and its taphonomic significance», *For. Sci. Int.*, 82: 129-140.

BRAIN, C. K. (1981): «The Hunters or the Hunted», University of Chicago Press.

EFREMOV, J. A. (1940): «Taphonomy: a new branch of palaeontology», *Pan-Am. Geol.*, 74: 81-93.

FERNÁNDEZ-JALVO, Y. (1994): «Small mammal taphonomy at La Trinchera de Atapuerca (Burgos, Spain)», *Palaeogeog., Palaeoclimat., Palaeoecol.*, 114: 167-195.

—& ANDREWS, P. (1992): «Small mammal taphonomy of Gran Dolina, Atapuerca, Burgos, Spain», *J. Arch. Sci.*, 19: 407-428.

FERNÁNDEZ LÓPEZ, S. (1991): «Taphonomic concepts for a theoretical biochronology», *Rev. Esp. Pal.*, 6: 37-49.

HAYNES, G. (1980): «Evidence of carnivore gnawing on Pleistocene and recent mammalian bones», *Paleobiology*, 6: 341-351.

HILL, A. (1979): «Disarticulation and scattering of mammal skeletons», *Paleobiology*, 5: 261-274.

KLEIN, R. G. (1982): «Age (mortality) profiles as a means of distinguishing hunted species from scavenged ones in Stone Age archaeological sites», *Paleobiology*, 8: 151-158.

—(1989): «Biological and behavioural perspectives on modern human origins in Southern Africa». In: P. MELLARS & C. STRINGER (eds.), *The Human Revolution*, Edinburgh University Press, Edinburgh: 529-546.

LYMAN, R. L. (1994): *Vertebrate Taphonomy*, Cambridge University Press, Cambridge.

MOYA-SOLA, S. & KOHLER, M. (1993): «Recent discoveries of *Dryopithecus* shed new light on the evolution of great apes», *Nature*, 365: 543-545.

OLSEN, S. L. & SHIPMAN, P. (1988): «Surface modification on bone: trampling versus butchery», *J. Arch. Sci.*, 15: 535-553.

POTTS, R.: «Temporal span of bone accumulation of Olduvai Gorge and implications for early hominid foraging behaviour», *Paleobiology*, 12: 25-31.

Manuscrito recibido: 13-06-96
Manuscrito aceptado: 18-06-97