Taphonomy of the late Miocene mammal locality of Akkaşdağı, Turkey

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ABSTRACT
The taphonomy of the late Miocene fossiliferous deposit of Akkaşdağı (Anatolia, Turkey) is presented. The study of bone surface shows few occurrences of weathering and carnivore action. Dissolution marks (roots, fungi and micro-organisms) are the most abundant traces found on the bone surface. The study of bone orientation and some field observations testify to the existence of a predominant direction. Water is considered the main accumulating agent. Nevertheless, the study of surface abrasion shows that bones did not travel from a long distance. The events that contributed to the formation of the fossiliferous site are reconstructed: the hypothesis of catastrophic mortality causes is held as the most probable. Animals would have been killed by toxic emanations of volcanic origins. Their remains were subjected to the action of disarticulating agents, especially carnivores. Finally, they would have been transported by the water to some holes in the ground and covered quickly by tufaceous sediments.

KEY WORDS
Mammalia,
large mammals,
taphonomy,
weathering,
late Miocene,
Akkaşdağı,
Central Anatolia,
Turkey.

RÉSUMÉ
Taphonomie du gisement de mammifères du Miocène supérieur d'Akkaşdağı, Turquie.
La taphonomie du gisement miocène supérieur d'Akkaşdağı (Anatolie, Turquie) est présentée. L'étude de la surface osseuse montre une faible incidence de l'altération due aux agents météorologiques et des attaques des carnivores. Les empreintes de dissolution (radicules, champignons et micro-organismes) sont les traces les plus abondantes. L'étude de l'orientation des os et quelques observations de terrain témoignent de la présence d'une direction privilégiée et de l'eau comme agent d'accumulation. Cependant

l'étude de l'abrasion des surfaces osseuses indique que les os n'ont pas été transportés sur une longue distance. Les événements ayant contribué à la formation du site fossilifère sont reconstruits : l'hypothèse des causes de mortalité catastrophiques est privilégiée. Les animaux auraient été victimes d'émanations toxiques d'origine volcanique. Leurs restes sont restés à la merci des agents de désarticulation, notamment les carnivores. Enfin, ils auraient été entraînés par l'eau dans des dépressions du terrain et recouverts rapidement par les sédiments volcaniques qui ont contribué à leur préservation.

MOTS CLÉS
Mammalia,
grands mammifères,
taphonomie,
altération osseuse,
Miocène supérieur,
Akkaşdağı,
Anatolie Centrale,
Turquie.

INTRODUCTION

Taphonomy is the science which studies the embedding laws of animal and vegetal remains, i.e. their transaction from the biosphere to the lithosphere (Efremov 1940; Behrensmeyer *et al.* 2000). Its main aim is to contribute to the reconstruction of paleoenvironment and to understand the processes converging to the formation of the fossiliferous assemblage (Behrensmeyer 1975, 1982).

The power of taphonomy depends upon how the first phases of the excavation are led: the more accurate the latter the more powerful the former. An attentive collection of each specimen, including the smallest fragment of bone, and the attribution of coordinates to each remains form its basis (Shipman 1981; Lyman 1994). Such methods are typical of archaeological or prehistoric excavations, where the exact position and orientation of each specimen have a capital importance. However, the results supplied by taphonomy are more and more appreciated by palaeontologists, even for sites where the anthropical absence during their formation is undoubtful. This involves the utilisation of archaeological techniques for more and more palaeontological excavations (Pereda-Suberbiola *et al.* 2000; Alberdi *et al.* 2001).

For palaeontological expeditions, time and finances might represent a constraint for very careful-done collections in the field. This leads to continue using the classical methods of palaeontological excavations. However, even in such situations, the examination of the remains on the field and the attentive study of their surface allow us to work out some hypotheses about the origins and the agents involved in the fossil accumulation. It is then possible (with the help of other disciplines) to point out the sequence of the events which allowed the formation of the fossiliferous assemblage (e.g., see Palmqvist & Arribas 2001a).

The material concerned by the taphonomical analysis comes from the excavations at Akkaşdağı between 1997 and 2001. The bone pockets, all at the same stratigraphic horizon, are numbered as AK2, AK3... (2000-2001 excavations) or AKA and AKB (1997 excavations). Material is presented at the Natural History Museum in Ankara (MTA).

MATERIALS AND METHODS

Akkaşdağı site, inside the Çankırı basin (Central Anatolia, Turkey), is formed by several fossiliferous pockets which yielded a large number of taxa (Appendix: Table 1; for the description of Akkaşdağı site and its fossiliferous pockets see Kazancı *et al.* [1999] and Seyitoğlu *et al.* [2005]). The taphonomic study is founded on the observation of 75% of materials dug during the field season of 2000 and on all the fossils collected during 2001, i.e. 81% of all the specimens from the site. Other 354 bones, collected before 2000, are not considered because they lack a precise stratigraphical position. At present the whole collection is housed in MTA.

All my field observations were made during the field season of 2001 when I particularly worked in a fossiliferous pocket, the AK-11. I measured the orientation of bones from this pocket with the aid of a field-compass. To these data, I added the measures obtained by S. Sen and his collaborators from the pocket AK-2, in 2000.

The orientation study has been made with a rose diagram of nine sectors, each 20° wide (for the method see Shipman 1981; Valli 2001). I did not consider the third dimension because of the kind of deposit and the position of bones. They were basically horizontal or just slightly tilted: out of 71 measures of bone slope, made in 2000, only 12 exceed 10°, and among these, only two exceed 18°. On the basis of observations the oblique position of bones can be explained by the overlapping of other fossils or by the uneven bottom of the pockets. The study of weathering and abrasion has been done by direct observation of the bone surface, using the method and the characters established by Behrensmeyer (1978) and Fiorillo (1988), respectively. The direct observation was also useful for detecting all kinds of marks on the bone surface.

DISCUSSION

Number of specimens and minimum number of individuals (MNI)

Determined specimens are listed in Appendix (Table 1). The MNI (Shipman 1981; Lyman 1994) is valued on the basis of the most common recognizable anatomical remains for each taxon (e.g., MNI of *Hipparion* Christol, 1832 species was valued by anterior cannon bone; MNI of gazelles by horn-cores). Young individuals have been distinguished from adults. However, few taxa present taxonomic problems: for example, it was not possible to assign milk teeth to the different *Hipparion* species. Therefore all the juvenile individuals of those taxa have been grouped together. At least six species of carnivores are present, but many specimens are not identifiable. For this reason they have been grouped together, as in the case of hipparions.

Perissodactyl ungulates dominate the fauna by both number of taxa and specimens. Juveniles never exceed more than half of the total number of individuals. This is true for *Ancylotherium pentelicum* (Gaudry & Lartet, 1856), *Choerolophodon pentelici* (Gaudry & Lartet, 1856), *Helladotherium* sp. and *Miotragocerus valenciennesi* (Gaudry, 1865). For these taxa the ratio juveniles/adults is 50% (but only for *M. valenciennesi* we have found more than two individuals). For all the other taxa the ratio is lower: e.g., for *Microstonyx major* (Gervais, 1848) it reaches 22% and for *Protoryx laticeps* (Andree, 1926) only 12%. Finally, the more important is the number of specimens and the MNI for the same taxon (carnivores are an exception because of identification problems). This means that the number of specimens and the MNI are fairly equivalent in drawing up taxon abundance.

Body mass

Body mass for ungulate taxa (with the exception of *Zygolophodon* sp.) is estimated (Appendix: Table 1). Most of the data are from Fortelius's NOW database (NOW database 2003; see also Fortelius *et al.* 1996a). Fortelius also calculated and provided me estimates of body mass for suids. He used the M2 length and the equation of Fortelius *et al.* (1996b), which was specifically devised for suids. *Microstonyx major* from Akkaşdağı is thought to have a body mass of about 210 kg. *Palaeoryx majori* Schlosser, 1904 has the skull of the same size as *P. pallasi* (Wagner, 1857) and *Miotragocerus valenciennesi* is a senior synonym of *Tragoportax gaudryi* (Kretzoi, 1941) (Kostopoulos pers. comm.), so I used the body mass of these two species. *Gazella* aff. *pilgrimi* (Bohlin, 1935) is similarly-sized to other species found in Akkaşdağı site, so I gave both the same body mass. The body mass of *Protoryx laticeps* was evaluated by the size of m1 according to Legendre's method (1989). *Choerolophodon pentelici* and *Ancylotherium pentelicum* body masses were estimated about 3000 kg (from data in Bonis *et al.* 1994) and 1000 kg respectively. Akkaşdağı *Orycteropus* Cuvier, 1798 is almost mean-sized between *O. gaudryi* Major, 1893 and the recent species, so its body mass was inferred by them. It has also been checked with

Martinez & Sudre's method (1995), using the length and the width of the astragalus: the two results matched fairly well. *Hipparion moldavicum* Gromova, 1952 and *H. brachypus* Hensel, 1862 body masses were estimated from their metapodials, as in Eisenmann & Sondaar (1998). Hipparions measures were taken from Geraads *et al.* (2001) and Eisenmann (1995).

Abundance of anatomical elements and patterns of differential breakage

The best conserved bones are the strongest ones. Among the girdle and the limb bones (pelvis, scapulae, humeri, radii, metapodials, femora, tibiae, calcanei and astragali), the vertebrae and the ribs, the cheek teeth, the skull and the cranial appendages (a total of 1756 specimens), teeth are the most numerous, preserved as isolated tooth or ranging in toothrow, followed by metapodials. Among the long bones, tibiae and humeri are well represented. On the contrary, vertebrae and ribs (especially the last) are relatively rare. Number and percentage of each skeletal element are given in Appendix (Table 2).

The percentage of breaking-down of the main limb bones is showed in Appendix (Table 3). Humeri, femora and tibiae are mainly composed by their distal end (87%, 46% and 81% respectively), alone or with a part of diaphysis. This result shows that the less resistant parts of the bone were the easier to be destroyed. The frequences for specimens of humerus and tibia agree with proximodistal patterns of bone consumption by hyenas described by Palmqvist & Arribas (2001b). So, among the different causes producing the breakage of weaker elements of the bones (and of the whole skeleton) the action of the carnivores has to be considered (Shipman 1981; Lyman 1994 and references therein). The relative number of complete metapodials (36%) also agrees with this last hypothesis (Haynes 1982; Fosse 1996): the number of complete metapodials (125) is the highest of the postcranial bones. Trampling can also be involved (Behrensmeyer *et al.* 1986) in the breakage of the bones.

The shape of the broken fossils fits well with the one produced by trampling or carnivores action (Miller 1969; Binford 1981; Shipman 1981; Haynes 1983).

Weathering

Weathering mainly depends on the atmospheric agents. If it acts for a short time, the effect is limited to the bone surface, but the whole tissue of the bone can be affected, after enough time (Lyman 1994). The remains were studied according to the criteria outlined by Behrensmeyer (1978). I considered the long bones and the metapodials, the skull, the mandibles, the ribs and also studied the flat bones. I examined diaphysis surfaces, far from the bone extremities, on which the carnivore action is generally concentrated. In some extremities (e.g., the proximal end of humerus or tibia, the distal end of metapodials; see Lyman 1994) the bone tissue is less thick and easier to be chewed. On such parts the weathering can be hidden by the tooth marks. For the vertebrae, I focused my attention on their body, because the apophyses often are lacking or damaged. Concerning the cheek toothrow, I only considered the bone where they were installed, the maxillar or the dental bone. I neglected isolated teeth, phalanges, carpal and tarsal bones, as indicated by Behrensmeyer (1978). In addition, I was careful that weathering marks were not covered by other kind of traces.

The 845 bones available for the study are from all the fossiliferous pockets (Appendix: Table 4). Stage "0" (no weathering) is the most common with 798 specimens (93% of total). Stage "1" (surface only weakly weathered) is by far less common: 51 specimens. Stages "2" and "3" (surface medially weathered) are very rare: four specimens for the first case (they only come from three pockets: AK-4, AK-5 et AK-11/12) and only one for the latter, coming from AK-5, which is the richest pocket of the whole site. Stages "4" and "5" (the whole tissue of the bone is affected by weathering) are absent. No correlation was found between the weathering stage and the position of the bone inside the sediments, so weathering worked before the accumulation of bones took place.

Weathering was generally used to estimate the time elapsed between the loss of the flesh and the definitive burial of the bones into the sediments (Behrensmeyer 1978; Culter *et al.* 1999). However, other studies showed that weathering depends on a series of parameters, the most important of which would be the vegetable cover of the deposit place (Tappen 1994), the density of the different parts of the bones, and the climate (Andrews & Armour-Chelu 1998). At present, the relation between the weathering and the burial time seems well established only in the African tropical savannah, where it was studied for the first time. At Akkaşdağı, lacking precise data about the vegetation cover during the Miocene, it is not possible to estimate the time of the bone burial. Nevertheless our data are not incompatible with a relatively fast burial of the fossils into the sediments.

ABRASION

Aside from weathering, I carried out the study of the abrasion of the bone surface in order to highlight a possible hydraulic transport. The number of fossils showing traces of abrasion (see Fiorillo [1988] for examples of such kind of mark) is only 96 out of 1630 (only 6% of the total). All these fossils are only slightly abraded (stage "1" according to Fiorillo 1988). The most common specimens bearing abrasion marks are teeth (27) and the cranial appendages of bovids (15). The third most common abraded bone is the astragalus (nine specimens). They are all relatively strong remains which can support a long transport better than other kinds of bones, such as vertebrae or ribs (only 12 specimens belong to these).

The lack of abrasion does not necessarily mean that the remains were not affected by the transport. Actually, it could depend on other factors, like the composition and the texture of the sediment in which the transport took place, the quality of the bone (its physical and chemical features) and the presence of flesh or other tissue around the bone (Lyman 1994).

In order to check a possible action of the water, a test using the Voorhies's categories was performed. All the fossils listed in Appendix (Table 2) were divided in three groups, on the basis of their density, according to Voorhies (1969), Behrensmeyer (1975) and Hunt (1978). Group I, which includes vertebrae and ribs, consists of 120 specimens; group II (girdle and limb bones except the broken distal ends of humerus, femur and tibia) comprises 718 specimens; group III (including the most dense elements of the skeleton, like teeth, skull and broken distal ends of humerus, femur and tibia) 918 items. A χ^2 test (Sokal & Rohlf 2001) points out that this distribution is different from the random one, consisting of the same number of total items (1756), at a very high significative level of statistical confidence ($p < 0.001$). So, a sorting of bones by density cannot be rejected.

BIOLOGICAL MARKS

Recognising the nature of the different marks on the bone surface is a very old and difficult problem. Nowadays, among numerous scientific works presenting a good selection of non anthropical bone marks, the paper by Pei (1938) is worth to be mentioned. I got benefit from this paper together with those by Miller (1969), by Haynes (1980, 1983, 1985) and by Saunders & Dawson (1998) to recognise each kind of mark on the bones from Akkaşdağı.

2196 remains were available for this analysis, but on 393 (almost 18%), the marks were not detectable because they were hidden by other kind of traces or because the bones were damaged. Biological marks detected on fossils for each fossiliferous pocket are given in Appendix (Table 5). Carnivore marks are named following Binford (1981). The traces made by roots, microorganisms and fungi are grouped together under the term of "dissolution marks" (Valli 2001).

During the field season of 2000, a few tooth marks attributed to a large rodent, perhaps a porcupine, were found on a bone. Actually, I could not see any trace that could be surely attributed to such or other type of rodent. If this kind of marks is present, they are on bones that I was not able to survey (see Materials and methods).

Appendix (Table 5) shows that most of the fossils do not present any biological mark. The most common marks are due to the action of plants

FIG. 1. — Punctures (arrow) on the distal part of a *Hipparion*'s radio-cubitus. Scale bar: 5 cm.

and/or micro-organisms. They are particularly abundant on the bones coming from the fossiliferous pockets AK-11 to AK-14. In them, the bone bearing such marks outnumbers that of fossils without any kind of traces (except in AK-11/12, where, nevertheless, the number of dissolution marks is almost equal to the other; six and seven respectively). The pockets from AK-11 to AK-14 were dug during the field season of 2001. They yielded bones which laid close to the ground surface, closer than all the other remains from anywhere. The surface of such fossils has been deeply dug by dissolution marks, probably caused by the action of recent plant roofs, because of the proximity of the modern surface. Although we found some recent roots reaching important depth, their action was rarer and rarer towards the bottom. There is probably a correlation between the depth and the number of bones affected by root marks. Moreover, several fossils may have been preserved against the root action by other bone laying just above them.

I specify that all the dissolution marks found on the fossils collected few centimetres far from the surface are interpreted as caused by modern plants.

Carnivore tooth marks are by far less common; "punctures" predominate among them. Figure 1 shows an example of puncture on the distal end of a *Hipparion* radio-cubitus (specimen AK3-215). This kind of traces proves that carnivores affected the remains, but by the fact they are scarce I argue that carnivores were not the main responsible agents of the bone accumulation process.

Spiral fractures on long bones or metapodials are also rare: I only found 10, six of which in the fossiliferous pocket AK-2. The others come from AK-5, 7, 11, 12. This kind of breaking-down (helicoidal, oblique with regard to the longitudinal axis of the bone and not affecting the extremities; Haynes 1986) is due to several causes, either anthropical or not (Valli 2001 and references therein). When they are found in non anthropic fossiliferous deposits, they are generally interpreted as made by the carnivores or caused by the trampling.

Except the dissolution marks which affect the bones collected near the surface, all the other traces detected on the fossils are ancient, no recent ones were recognized.

Finally, I did not find any trace of gastric juices on the bones.

ORIENTATION OF BONES

Studying the spatial position of the fossils in a site allows us to put in evidence whether there is any preferential orientation of the remains and, then, to infer the accumulation agents.

In Akkaşdağı site, measuring the spatial disposition of all bones would have needed too much time. So I limited the survey to two pockets, as explained in Materials and methods. However, other field observations can reinforce the results.

The fossiliferous pocket AK-11 yielded 184 fossils, 91 of which were used for the study of bone orientation. The bone distribution inside the 20° sectors is shown in Figure 2: in the picture, each

sector is converted in a column. A χ^2 test (Sokal & Rohlf 2001) points out that the random orientation of fossils cannot be rejected at a significative level of statistical confidence ($p < 0.5$; $\chi^2 = 7.60$, with 8 degrees of freedom).
In opposition, the measures taken on 71 bones from AK-2 during the field season 2000 indicate that the fossils had a feeble orientation ($p < 0.1$; $\chi^2 = 14.31$, with 8 d.f.). The bone distribution is showed in Figure 3. A peak is present between 120° and 140°.
The following observations confirm such result:
1) A rhinoceros skull (AK4-212, *Ceratotherium neumayri* (Osborn, 1900), determined by P.-O. Antoine) was found stuck inside the pocket AK-4. It was roughly oriented along the North-South axis, making barrage against the other bones. Those are all placed at the western side of this skull, as if they were coming from a source far on the West.
2) Another skull, of a Suidae (AK5-501, *Microstonyx major*, determinated by M. Fortelius), was found with two vertebrae fitted in its orbits. It was turned towards an axis comprised between West and North-West.
3) In the pocket AK-3, 10 long bones are clearly disposed along the same direction, roughly 110° (Fig. 4). Close to these remains, three other bones are almost perpendicular to the first: they are placed at the oriental extremity of the cluster, near the bank of the pocket.
But if bones in other pockets mainly show a preferred orientation, even if feeble, why those from AK-11 seem to be randomly oriented? The fossiliferous pocket AK-11 is particular for one reason: 66 specimens, more than 33% of the fossils retrieved there were found in anatomical connection (mainly *Hipparion* cannon bones with splint bones [42.8%], but also vertebrae [21.4%] and the complex tibia + tarsus + metatarsal [21.4%]). That percentage is much larger than in other pockets, revealing that several specimens were still covered by soft tissues when they reached their final position.
It is known that articulated limb bones or elements of the axial skeleton are more easily transported by water than their isolated elements

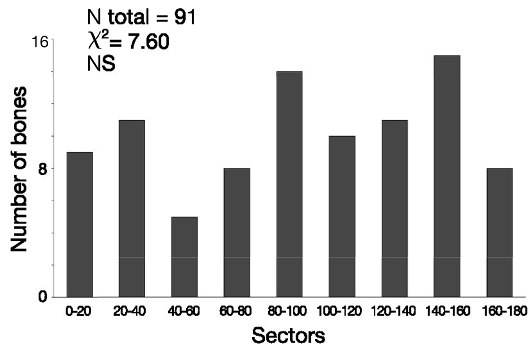

FIG. 2. — Orientation diagram of long specimens from AK-11: each column represents a 20° sector.

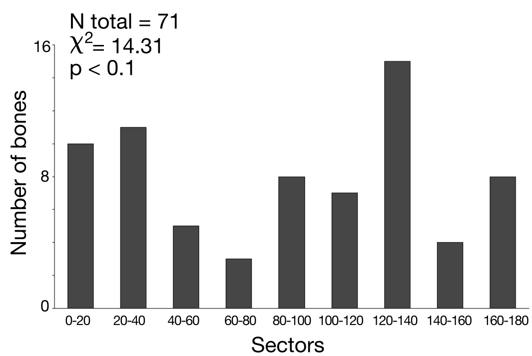

FIG. 3. — Orientation diagram of long specimens from AK-2 (only specimens collected in 2000): legend as Figure 2.

(Coard 1999). However, articulated elements, like part of a leg, suffer different coercion than the isolated ones, which are more rigid. Then, their disposition inside a bone accumulation could be different than that of isolated remains or fragments. If their proportion is significative, they could hide the effects of the orientation.
Finally, all the observations agree with the probable existence of a main current direction with axis NW-SE. Bone source would have been placed toward NW from the fossiliferous site (as inferred by the accumulation of the bones close to the rhinoceros skull AK4-212).

FIG. 4. — Detail of the fossiliferous pocket AK-3, during the excavation; 10 bones are oriented to 110°.

MORTALITY CAUSES

The study of populations, made with the aid of the mortality profiles, allows us to understand the causes of animals' mortality from the type of profile obtained: attritional (i.e. "U"-shaped), or catastrophic (i.e. "L"-shaped; see Shipman 1981; Lyman 1994). In order to construct such profiles it is necessary to assign an age to each individual of the species considered. The most common method is to evaluate it from the teeth wear of the most abundant taxon (Klein & Cruz-Uribe 1984). In particular, in Akkaşdağı site the most common species are those of the genus *Hipparion*.

However, in establishing such a profile a few problems emerge, mainly the one derived from the fact that isolated teeth cannot be determined exactly. Moreover, the number of juveniles is only known for the whole genus *Hipparion*, not for each species (a method to evaluate the number of juveniles for each species would be to calculate the percentage from the total value using the percentages of the adults from the Appendix [Table 1]; anyway, it is not sufficient to establish the age classes for the taxa).

In addition, in order to assign the correct age we have to compare our individuals with a well chosen reference. Of course the reference for vanished animals is the closest extant species. The closest relatives to *Hipparion* are horses, asses and zebras.

For horses belonging to the genus *Equus* several references have been performed (see among others, Levine 1983; Fernandez & Legendre 2003). However, their use for a *Hipparion* population is tricky. *Hipparion* are hypsodont equids, like horses, but with a different degree of hypsodonty. The usage of a horse reference could bring some distortion. In addition, zebras and horses are grazers but the diet of the different species of *Hipparion* and related genera, which can differ from one another, is not known exactly (Hayek *et al.* 1992; Eisenmann 1996; MacFadden *et al.* 1999; Fortelius & Solounias 2000; Kaiser *et al.* 2000). So I prefer to perform a simpler analysis.

Considering the genus *Hipparion* as a whole, and counting the number of juveniles (animals still having milk teeth), of adults and old individuals (animal with teeth strongly worn, more than half of the crown height), I obtain 16 juveniles, 29 adults and six old individuals. The number of adults, in this case, was established by counting teeth, so, it is lower than the value shown in Appendix (Table 1). Nevertheless, in order to be compared with the other classes of age, the number of adults has to be obtained by their teeth.

I used the Blumenschine's method (1991) which consists in grouping the age classes in four clusters (two classes of juveniles, one of adults and one of old individuals). Then, the two last classes are compared: if the number of individuals of the last one is higher than the other, the mortality profile is attritional. It is catastrophic in the opposite case.

I performed a χ^2 test in order to compare the number of adults and old individuals of my mortality profile with those from other authors (Appendix: Table 6). The results are consistent with a catastrophic profile. Attritional causes of mortality can be rejected.

Anyway, in order to perform a more accurate test, it would be necessary to draw up the

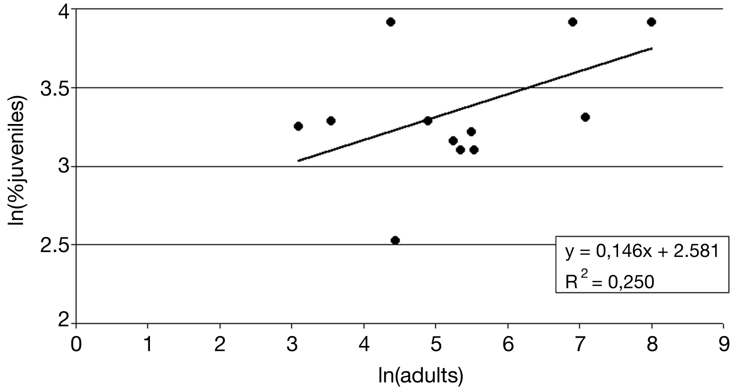

FIG. 5. — Regression analysis (minimum squares method) of the proportion of juveniles on estimated adult body mass (in kg) for herbivore taxa of the Akkaşdağı fossiliferous deposit (data from Appendix: Table 1).

mortality profiles of the different species of the genus *Hipparion*, which is not possible in our case. Nevertheless, with a more accurate analysis of teeth more adults would be identified, but no more young nor old individuals would come out, so the result would not change.

Another type of method can be used to test the causes of mortality. A new approach establishes a relation between the relative abundance of remains of juveniles among ungulates and the average adult body mass estimated for each species. Palmqvist *et al.* (1996) found that for 19 African ungulate species hunted by five large predators, the relationship between the natural logarithms of such measures is:

ln(% juveniles) = 2.966 (± 0.201) + 0.203 (± 0.201) × ln(W adultes).

In Palmqvist's test n = 19, r_1 = 0.841. Data for Akkaşdağı site are plotted in Figure 5. The relationship is given by:

ln(% juveniles) = 2.581 (± 0.428) + 0.146 (± 0.076) × ln(W adultes)

with n = 13 and r_2 = 0.500. The two correlation coefficients can be considered different with $p < 0.1$ but not with $p < 0.05$, so the attritional component cannot completely be discarded. The relationship is positive, but the data are very scattered. In addition, among the heaviest mammals, which are the principal responsibles for the positive relationship of the regression, *A. pentelicum*, *C. pentelici* and *Helladotherium* sp. are each known only by two individuals. An accurate analysis would need more specimens belonging to these taxa.

DISCUSSION OF THE RESULTS

The results from the taphonomic analysis allow several considerations.

The indications of a preferential direction, at least as measured in one pocket and inferred by field observations in other three, raise the problem of the bone accumulating agent. Both bone breakage-patterns and the presence of tooth marks clearly prove that the bones were affected by carnivores, but the small number of traces indicates that their activity was quite limited. Among the taxa recognised there are some hyenas (Bonis 2005). It is known that these carnivores can do bone accumulation near and/or inside their dens (Brain 1981; Fosse 1996). The breaking-down from Akkaşdağı differs both qualitatively and quantitatively from that found in a bone assemblage made by the giant, short-faced hyenas *Pachycrocuta brevirostris* (Aymar, 1856) (Saunders & Dawson 1998). In addition, the hyenid from Akkaşdağı are taxonomically different from the recent ones as well as from the fossil species known to accumulate bones (Fosse 1996; Arribas & Palmqvist 1998), so, it is difficult to make speculations about their habits.

However, it is unlikely that an accumulation made by a carnivore is oriented. It is most likely that such an assemblage have been piled up by water. During the field season of 2001, some clay remains, which seem to be carried by water, were found inside the pocket AK-3. In addition, in AK-2, during 2000, a giraffid tibia with a partial humerus of an *Hipparion* driven into its proximal end was collected. Clearly an agent like a water stream could have inserted the humerus into the giraffid bone; it is much harder to attribute such an action to a carnivore.

Another possibility is that the water carried some animal remains into a hyena den and that the fossiliferous accumulations are the result of the effort of the water and such a carnivore. However, the low number of carnivore marks makes this hypothesis little probable. In addition, no coprolithes or traces of gastric juices on the fossils were found. Most likely the accumulations are mainly due to the action of water, even if the action of the carnivores cannot completely be rejected. The bones might have been carried by a stream and dumped into the pockets. In any case, bones did not travel from very far because the abrasion marks on bone surface are scanty. The distribution of the elements of the skeleton into the Voorhies's groups is consistent with the proximity between the fossiliferous pockets and the locality where the bones were removed from.

Inside AK-11, where the bones are mainly randomly oriented, a part of the fossils might have arrived in anatomical connection and still covered by soft tissues (the abrasion in such a pocket is almost non-present, less than 2%). Coercion on the articulated remains and the bank-effect (when a bone comes against a barrier, e.g., the bank of a pocket, and stops close to it, it takes an orientation that will be parallel to the line bank despite the stream carrying them) might explain the position of some fossils inside AK-11 or elsewhere.

The carnivore action might not have been the only responsible of the bone breaking-down: other physico-chemical factors could contribute, as the corrosion led by plant roots and by fungi (Lyman 1994; Cilli *et al.* 2000). For example, roots are able to perforate the bone (Behrensmeyer 1978). Dissolution marks (roots, fungi, and micro-organisms) are the most common kind of traces on the bone surface, especially in the uppermost fossil-bearing layers, where the bones were the most damaged. Root action on these bones, in superficial levels, is performed by the recent plants. In the same pockets, but in lower levels, we generally found fossils without dissolution marks.

The destruction caused by the Tertiary plants is more difficult to quantify. Even if the dissolution caused by the roots of plants is not longer matter of doubt, to my knowledge, no one has yet carried out tests to analyse the time and the patterns of their action on the buried bones.

On the basis of the geological context (traces of chimneys for the passage of volcanic gas; Karadenizli *et al.* 2005; Kazancı *et al.* 2005) a catastrophic death for the animals, owing to toxic emanations of volcanic origin, is justified. The results from the study of the populations and the relationship between the percentages of juvenile versus adult body mass do not give clear results: the analysis performed using the Blumenschine's method grants a privilege to a catastrophic mortality, but the other, based on the percentage of juveniles, seems not to exclude attritional causes. Both methods bear some defects: the first, the lack of precision in making the age classes, the second, the number of data of the heaviest mammals, which are too few.

The taphonomic data are inadequate to point out between the two possibilities: probably the catastrophic event added its effects on the ones due to attritional causes. The whole fauna could have suffered the volcanic emanations and the body of the mammals killed by that poisonous gas have been mixed to the remains of the carnivores' killings.

The bones have been covered quite fast by sediments. In fact, even if the presence of a vegetable cover can slow down the weathering effects (Kerbis Peterhans *et al.* 1993; Tappen 1994) or scavenger attacks (Domínguez-Rodrigo 1999), the quantity and the quality of the weathering detected on the fossil surface is compatible with a fast burial of the remains.

Finally, the preservation effects of the tuffaceous sediment must be recognised. Actually volcanic sediments are known to favour fossil conservation (Pickford 1986). The bones, buried in such sediments were safe from damaging phenomena, except from diagenesis and the dissolution action of plant roots, fungi and micro-organisms, and erosion.

CONCLUSIONS

The late Miocene site (MN 12, middle Turolian) of Akkaşdağı represents a good example of fossiliferous site where different sciences (taxonomy, geology, geochechimistry, and taphonomy) give their contribution to the understanding of the phenomena producing the fossiliferous accumulations.

The environment of the area, as it can be deduced from the mammal fauna (more than 23 species of large mammals, belonging to five different orders, are known from the site; Appendix: Table 1), was more humid and luxuriant than now. Taxa well adapted to a woodland country (chalicotheres, giraffids) have been found as well as others, more common, open habitat dwellers (gazelles and hipparionine horses).

The event reconstruction grants a privilege to a catastrophe (emanation of toxic gas of volcanic origin) which killed the animals living in the vicinities. Their carcasses were available for the carnivores and other agents which dismembered them. Such rests were mixed to the others produced directly from the carnivores's hunts. Hyenas, probably the main scavenger, are well represented: it is likely that they were attracted by the meat and died due to the toxic gas.

Water is considered the main accumulating agent: a stream might have carried all the remains into some depression of the ground, acting like traps. Fossil source should be placed somewhere at Northwest from the site, but not too far. The bones, after their deposition, were buried quite fast, as indicated by the weak degree of weathering. Under the ground they were safe from weathering agents and carnivores, but they were exposed to the attack of roots, buried microorganisms and fungal hyphens. All these agents as well as those which acted out of the sediments corroded the bone surface. Alkaline nature of the sediments (tuff of volcanic origin) allowed fossil preservation inside the pockets. Finally, the erosion released some remains which permitted the fossiliferous site to be discovered.

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APPENDIX

TABLE 1. — Fossil macromammals collected in the paleontological deposit of Akkaşdağı: number of identifiable specimens (**NISP**), minimum number of individuals (**MNI**, juveniles in brackets) and estimated adult body mass (in kg). *, specimens identified at genus level.

Taxon	NISP	MNI	Adult body mass
Carnivora	49	6(2)	
Tubulidentata			
Orycteropus	7	2	35
Artiodactyla			
Microstonyx major	56	9(2)	210
Palaetragus rouenii	8	1	230
Helladotherium sp.	13	2(1)	1000
Samotherium sp.	6	1	600
Gazella cf. *capricornis*	88	31(8)	22
Gazella aff. *pilgrimi*	9	3	22
Prostrepsiceros rotundicornis	45	15(4)	35
Protoryx laticeps	41	16(2)	85
Miotragoceros valenciennesi	7	4(2)	80
Tragoportax aff. *gaudryi*	3	2	80
Palaeoryx majori	7	1	200
Perissodactyla			
Ancylotherium pentelicum	5	2(1)	1000
Ceratotherium neumayri	95	11(3)	1200
Stephanorhinus pikermiensis	5	2	1100
Chilotherium sp.	1	1	700
Acerhorhinus sp.	6	1	700
Hipparion brachypus	94	9	245
Hipparion cf. *longipes*	154	14	255
Hipparion dietrichi	191	13	190
Hipparion moldavicum	216	19	133
Total *Hipparion* species	2048*	71(16)	
Proboscidea			
Choerolophodon pentelici	8	2(1)	3000
Zygolophodon sp.	1	1	

TABLE 2. — Number and percentage of anatomical elements.

Anatomical element	Number	%
Skull and cranial appendages	55	3.1
Cheek teeth	664	37.8
Vertebrae	109	6.2
Ribs	11	0.6
Pelvis and scapula	82	4.7
Humerus	78	4.5
Radio-cubitus	57	3.2
Femur	65	3.7
Tibia	125	7.1
Metapodials	348	19.8
Astragalus	102	5.8
Calcaneus	60	3.5
Total	1756	100

TABLE 3. — Breaking-down of the main limb bones; in bracket, the total number for the anatomical element; "fragment" the smallest part still recognizable of the bone.

Bone	Complete	Proximal end	Diaphysis	Distal end	Fragment
Humerus (78)	0%	4%	5%	87%	4%
Radius (57)	11%	50%	2%	33%	4%
Femur (65)	5%	20%	23%	46%	6%
Tibia (125)	8%	6%	3%	81%	2%
Metapodials (348)	36%	34%	1%	26%	3%

TABLE 4. — Weathering marks on fossil bones per fossiliferous pocket (following Behrensmeyer 1978); percentages in bracket.

Fossiliferous pocket	Stage "0"	Stage "1"	Stage "2"	Stage "3"
AK-2	179	10	0	0
AK-3	50	4	0	0
AK-4	69	8	1	0
AK-5	189	14	2	1
AK-6	107	4	0	0
AK-7	43	3	0	0
AK-10	2	0	0	0
AK-11	82	1	0	0
AK-11/12	8	3	1	0
AK-12	61	3	0	0
AK-13	3	0	0	0
AK-14	5	1	0	0
Total	789 (93.4)	51 (6.0)	4 (0.5)	1 (0.1)

TABLE 5. — Detected marks on fossil bones per fossiliferous pocket; naming of carnivore marks (punctures, scares, pits and furrows) follows Binford (1981); "dissolution marks" lumps together marks made by roots, fungi and micro-organisms; percentages in bracket.

Fossiliferous pocket	Dissolution marks	Punctures	Scares	Pits	Furrows	Without marks
AK-2	106	14	0	4	4	292
AK-3	43	5	1	0	0	46
AK-4	66	3	1	1	0	125
AK-5	172	15	6	10	1	273
AK-6	50	4	0	2	0	158
AK-7	20	2	0	0	0	90
AK-10	1	0	0	0	0	14
AK-11	107	5	0	0	0	39
AK-11/12	6	0	0	0	0	7
AK-12	49	2	0	0	1	30
AK-13	7	0	0	0	0	7
AK-14	13	0	0	0	0	1
Total	640 (35.5)	50 (2.8)	8 (0.4)	17 (0.9)	6 (0.3)	1082 (60.1)

TABLE 6. — Comparison between the number of adult and old individuals for Akkaşdağı Hipparion (first line) and those of other mortality profiles; the total numbers (adults + old individuals) are normalised to 35, as that of Akkaşdağı profile; *, data from Klein & Cruz-Uribe (1984).

	Adults	Old individuals	χ^2	
Akkaşdağı *Hipparion*	29	6		
Catastrophic profile*	23	12	2.69	$p > 0.1$
Attritional profile*	13	22	15.24	$p < 0.001$