

The late Pliocene locality of Ahl al Oughlam, Morocco: vertebrate fauna and interpretation

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The late Pliocene site of Ahl al Oughlam near Casablanca, Morocco, dated to *ca.* 2.5 Ma, yielded the richest vertebrate fauna of the North African late Cainozoic. It includes more than 55 species of mammals, and a variety of birds and reptiles, probably accumulated by carnivores. The faunal assemblage, and its poor diversity, point to a quite open and not very favourable environment, perhaps markedly seasonal. Overall similarity of the ungulate fauna with the rest of Africa definitely shows that the Sahara did not yet act as a major geographical barrier for large mammals, but there is no evidence of human presence.

INTRODUCTION

The site of Ahl al Oughlam (AaO) is an abandoned sandstone quarry located at the southeastern fringe of the city of Casablanca, which will probably surround it in the near future (Figure 1). It was first mentioned by Biberson (1961) as *carrière Déprez*. A high marine level, about 105 m above the present sea level, referred to the Messaoudian of the local terminology, provided some broken pebbles that Biberson took as representatives of the first stage of the North African pebble culture, but it has been shown that they are not man-made (Raynal *et al.*, 1990). In 1985, J-P. Raynal and J-P. Texier discovered some fossils in a complex of karst and fissure fillings within a consolidated dune (calcarenite) above this marine level. Systematic excavations were undertaken from 1989 onwards, as part of the *Programme Casablanca*, led by J-P. Raynal and F-Z. Sbihi-Alaoui, of the Institut National des Sciences de l'Archéologie et du Patrimoine (Raynal *et al.*, 1990; Geraads *et al.*, 1998). About 3–4 cubic metres of sediment were excavated and screened, mostly from a small cave, about 1 m high after removal of the sediment and only accessible by crawling. All easily accessible fillings have now been removed, and extension of the excavation would require further blasting of the quarry, and house destruction, an unlikely procedure. Although the quarry is officially scheduled as a protected site, it is to be feared that it will soon be fully filled with rubbish and lost to science.

The highly calcareous sediments consist of loose clays with very friable bones and teeth, and concrete-hard calcified breccias, from which bones and teeth were extracted by acid cleaning. Most bones, except the most robust ones, are crushed. The concentration of fossils varies, but is always high, and the volume of fossils sometimes exceeds that of the sediment itself.

The fillings are not stratified, and as the populations of the various rodent species from the different interconnected fissures do not significantly differ in tooth measurements, they can be considered as instantaneous at the geological scale.

The faunal collection consists of more than 4000 identified remains of large mammals, plus thousands of rodents, insectivores and bats, to which should be added a remarkable collection of birds, as well as reptiles, amphibians and fishes. The faunal list includes more than 100 species of vertebrates, of which about 55 are mammals, making it by far the richest site of the late Neogene of North Africa, only matched by Fayum for the whole Cenozoic. Although no absolute dating is possible, the mammalian fauna unambiguously points to an age close to 2.5 Ma, thus roughly contemporaneous with Bouri-Hata, Wilti

Dora or Gamedah in the Middle Awash and Omo-Shungura member D-E in Ethiopia, the Lokalalei member of the Nachukui Formation and the gap in the Burgi member of the Koobi Fora Formation in Kenya, upper Ndolanya beds of Laetoli in Tanzania, and perhaps Sterkfontein Member 4 in South Africa. In North Africa, it is certainly contemporaneous with some levels of Aïn Jourdel in Algeria, with which it shares some species, but Arambourg's localities of Aïn Boucherit and Aïn Hanech are significantly younger, by about 0.5 Ma and 1 Ma, respectively (Arambourg, 1970, 1979; Geraads, 2002; Geraads *et al.*, 2004). Incidentally, the fauna from Ahl al Oughlam demonstrates that the Messaoudian, previously taken as the basal stage of the Quaternary, is in fact of Pliocene age.

FAUNAL CONTENT

Ahl al Oughlam is the only North African Late Neogene site rich both in micro- and macro-mammals. A short summary of the fauna is given below. Taxa from AaO that were described as new are marked *.

Primates: *Theropithecus atlanticus* was first defined upon a single molar from the Algerian site of Aïn Jourdel. The AaO sample, although consisting mostly of isolated teeth, helps clarify its differences from the East and South African *T. darti* (Alemseged & Geraads, 1998). *Macaca* sp. is here shown, for the first time, to coexist with the former genus.

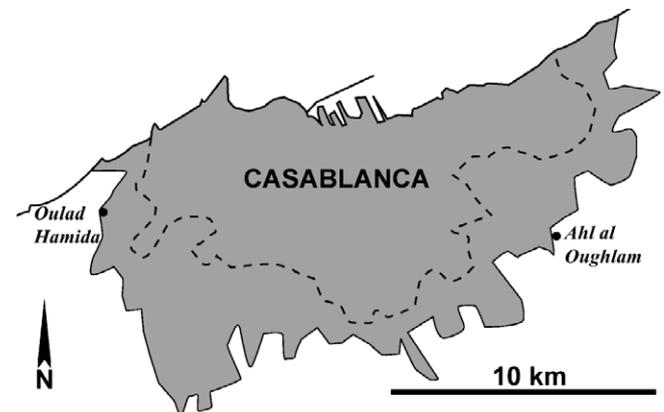


Figure 1. Sketch map of the Casablanca urbanized area (from Google Earth, 2006), with the location of Ahl al Oughlam (33°34'11"N, 07°30'44"W), and Thomas-Oulad Hamida quarries (33°34'06"N, 07°42'00"W). Dashed line = outline of Casablanca around 1985.

Carnivores are extremely diverse (Geraads, 1997). The carnivore fauna of this time period in North Africa was virtually unknown, which explains the abundance of new taxa.

Herpestidae: *Herpestes abdelalii** is more primitive than the living mongoose *H. pulverulentus*. *Ichneumia nims** belongs to a genus quite rare as a fossil, and formerly known only in East Africa.

Viverridae: *Viverra leakeyi* was formerly known from Omo, Laetoli, and Langebaanweg, but the morphology of the AaO carnassial best matches that of a tooth from Omo E3. *Genetta* sp. is also illustrated by a carnassial.

Hyaenidae: this is the dominant carnivore family, with almost 200 specimens belonging to four species. *Crocota dbaa** is close to the ancestry of the spotted hyaena *C. crocuta*, but is more primitive, especially by its smaller p3 and the presence of a metaconid on m1. It is close to *C. dietrichi* from Laetoli. *Pliocrocota perrieri latidens** differs from the contemporaneous European *P. perrieri* by its very broad teeth. *Hyaenictitherium ?barbarum** is a late survivor of a Miocene group of primitive hyaenas, with a long p2 and a persisting m2. Such a primitive form is unknown elsewhere at that time. *Chasmaporthetes nitidula darelbeidae** is a hunting hyaena close to the Eurasiatic and South African one.

Felidae: *Acinonyx aicha** is a primitive cheetah, with a skull morphology reminiscent of that of a panther, but with a dentition close to that of the European *A. pardinensis*. *Dinofelis* sp. is represented by few specimens (Geraads, 2004b), but is remarkable for the large canine and persistence of P2; it may be close to the Siwalik *D. cristata*. *Panthera pardus* is rather common, and similar to the living panthers. *Lynx ?* sp. is identified on the basis of the size of a single humerus. *Felis* cf. *silvestris*, close to the living wild cat, is a rare form at that time. *Homotherium* sp. is represented by a few teeth and limb-bones that cannot be more precisely identified.

Canidae: *Nyctereutes abdeslami** is the most common medium-sized carnivore, whereas the genus is quite rare elsewhere in Africa. The premolars are small, and the crushing part of the dentition, with a large m1 entoconid and a long m2, is still more developed than in other species of the genus. A larger canid, of which a skull has recently been found, was cited (Geraads, 1997) as *Canis* aff. *aureus*, but could be related to the widespread primitive canid *Eucyon*. *Vulpes* aff. *rueppelli* is undoubtedly related to the African desert foxes rather than to the Eurasiatic forms, which have longer carnassials.

Mustelidae: *Prepoecilogale* cf. *bolti* is a small mustelid perhaps identical to the one first described by Cooke (1985) from Bolt's Farm, and later reported from Laetoli. *Poecilictis libyca minor** is a smaller subspecies of another zorilla living today in the northern part of Africa. *Mellivora* cf. *capensis*, the honey badger, is a widespread species, perhaps already present at Langebaanweg. *Lutra fatimazahrae** differs in several features from both European (*L. simplicidens*) and African (living *Lutra* and Pliocene '*Torolutra*') otters.

Ursidae: *Ursus* cf. *etruscus* is the earliest true bear of North Africa, obviously an immigrant from Europe.

Odobenidae: *Alachtherium africanum**, a walrus, is doubtless the most unexpected find from AaO, as, in the Eastern Atlantic, no living or fossil walrus was previously known south of Belgium.

Rodents (Geraads, 1995): the Muridae is by far the most abundant family. *Paraethomys chikeri* is a large species of a genus known on both sides of Gibraltar since the late Miocene, and persisting until the late Pleistocene in Morocco. *Praomys skouri oughlamensis** belongs to a group whose systematics is complex, but their North African representatives may in fact be endemic

and deserve generic distinction. *Mus haouzi*, the most common rodent, also belongs to a genus known in North Africa since the late Miocene. It is not much different from the modern *M. musculus*. The gerbillid *Gerbillus bibersoni* is one of the earliest members of this genus. Other rodents, including the ctenodactylid *Irhoudia* aff. *bohlini* and *Hystrix* sp., are quite rare.

Lagomorphs have not been studied yet, but include a true hare, *Lepus* sp., an ochotonid common in the Mediterranean basin, *Prolagus* n. sp., and a member of the *Serengetilagus-Trischizolagus* group, best known in the Pliocene of the Mediterranean basin and in East Africa, but which survived until the Middle Pleistocene in Morocco (Geraads, 1994).

Insectivores (Geraads, 1995) consist mostly of soricids, although *Crociodura* is absent. *Suncus barbarus**, a genus not previously reported from North Africa, is the most common shrew. '*Episoriculus*' *maghrebiensis* is close to European forms, whose systematics is difficult. There is also a hedgehog, *Erinaceus (Atelerix)* sp.

Bats: there are at least six species, now under study (Eiting *et al.*, in press).

Proboscideans (Geraads & Metz-Muller, 1999) are represented by limb bones and juvenile teeth only, making precise identification difficult. An *Elephas* cannot be distinguished from *E. recki*, which might be represented in the Maghreb by successive subspecies, as in East Africa. *Anancus* looks closer to *A. osiris* from Egypt than to European forms.

Cetaceans were probably stranded individuals of small species brought into the caves by carnivores. The most common one is a dolphin, *Delphinus* or *Stenella* sp., but there is also a pigmy toothed whale, *Kogia* sp., represented by a single petrosal. In contrast to the walrus, both live today in warm or temperate waters.

Rhinoceros: there are some milk teeth, and many distal limb elements of *Ceratotherium mauritanicum*, a forerunner of the living white rhinoceros.

Equids: *Equus* is definitely absent, implying that the site is certainly older than about 2.3 Ma., as it is present at that time in Europe (Roccaneyra), East Africa (lower Omo G), and perhaps South Africa (Sterkfontein 4). A new species of *Hipparion* (Eisenmann & Geraads, submitted) is well represented by numerous limb bones and a skull.

Suids are represented by a single species, *Kolpochoerus phaccochoeroides*, endemic to North Africa and clearly distinct from the East and South African *K. heseloni* (Cooke, 1997). Tooth and skull morphology (Geraads, 1993, 2004a) suggest that it might be the sister taxon of *Hylochoerus*.

Camels, *Camelus* sp., are extremely rare, as elsewhere in Africa at that time.

Giraffids (Geraads, 1996) are also represented by a single species, *Sivatherium maurusium*, which is very common; the postcranial sample is probably the best in Africa, but dental remains are rare.

Bovids (Geraads & Amani, 1998) are, as usual, the most common group. Some teeth of *Tragelaphus* sp. could belong to *T. gaudryi*, defined in Algeria, but best known from Omo (Gentry, 1985). An unidentified Bovini is common and probably identical to one of the species described by Arambourg (1970) but cranial remains are too fragmentary to decide whether it is closer to *Pelorovis* or to European forms. *Kobus barbarus** is a waterbuck slightly larger than *K. kob*. *Beatragus antiquus remotus**, an alcelaphine with long slender horn-cores, belongs to a genus previously known only in East Africa. *Parmularius atlanticus** confirms that this genus, known by a few other remains in North Africa, has a Pan-African range. *Gazella (Deprezia) psolea**, the most common large mammal, is remark-

Table 1. Relative abundance of the main groups of ungulates and *Theropithecus*, and of some anatomical parts. MNI juvenile is calculated from the most common deciduous premolar, MNI adult from the number of m3s or M3s. No matching was possible because some of the material is in Paris, some in Rabat.

	Adult weight (kg)	MNI juv. (based on teeth)	MNI adult (based on teeth)	No. horn-cores	No. tali	No. distal humeri
Gazelles	30	3	34	135	25	22
<i>Theropithecus</i>	30	4	4		1	0
Bovoid size class III	110	6	17	26	12	40
<i>Kolpochoerus</i>	150	6	26		3	9
<i>Hipparion</i>	200	8	8		43	10
Bovini	1000	6	4	1	62	43
<i>Sivatherium</i>	2000	4	3	0	33	3
Proboscideans	4000	3	0		3	1
<i>Ceratherium</i>	4000	3	0		5	0

able for the shortening of its nasal bones, reminiscent of the saiga, *Saiga tatarica*, and dik-dik, *Madoqua* sp. *Gazella thomasi* is a smaller, less common species.

Non-mammalian fauna: this is also quite diverse. The **amphibians**, *Bufo viridis*; *Bufo* sp. and *Hyla* cf. *meridionalis*, have been studied by Bailon (2000), together with the **reptiles**. These include tortoises (*Testudo* sp.; *Geochelone* sp.), *Crocodylus* sp., the rare Amphisbaenidae (*Trogonophis darelbeidae**; *Balnus* sp.), several lizards (Gekkonidae indet., *Eumeces algeriensis*, *Chalcides* sp., cf. *Acanthodactylus* sp., *Ophisaurus koellikeri*) and snakes (*Coluber hippocrepis*, *Malpolon* sp., cf. *Macroprotodon* sp., *Macrovipera* sp., *Bitis* sp.). Many of these genera had not been reported previously as fossils from Morocco, from Africa, or even elsewhere.

Birds: there are about 25 species, under study by C. Mourer-Chauviré. Sea birds predominate (albatrosses Diomedidae, gannets Sulidae, petrels and shearwaters Procellariidae, auks Alcidae); several of them are now found at high latitudes. There are also some ground dwellers (ostriches Struthionidae, bustards Otidae, pheasants Phasianidae) and owls, but the presence of a parrot is more unexpected. Still, the greatest surprise came from the discovery of large soaring birds with pseudo-teeth, of the family Pelagornithidae, of which they are the most recent representatives (Mourer-Chauviré & Geraads, in press).

Fish: there are a few remains of Sparidae (bream) and sharks (Plagiostomi).

The most noteworthy absence is that of any human remains, or trace of human presence whatsoever. Although absence of evidence is not evidence of absence, the large number of fossils collected, and of species belonging to all size groups and trophic categories, precludes a taphonomic or collecting bias against hominids. It is much more likely that hominids had not yet reached the northwestern Atlantic coast at that time.

COMPOSITION OF THE BONE ASSEMBLAGE

Most of the rodents and insectivores, which were found in different parts of the cave system from the macromammals, were probably the prey of owls. One of the most striking features of the large mammal assemblage is the high proportion of carnivores, both in number of species and in number of specimens: the ratio (carnivore NISP)/(NISP of other mammals) is about 1/6, but carnivore postcranial remains are rare. Similar characteristics were found by Brain (1981) in hyaena lairs, and show that the fissures did not merely act as a natural trap, but that most of the bones (including probably some of the carnivores themselves) were brought in by carnivores. Still, the topography of the main cave, where many bones were found

below a vertical chimney, strongly suggests that some animals fell into a pit. They may have attracted carnivores, which later became trapped as well. Despite this, few bones bear definite carnivore tooth marks, but many are broken, and there are numerous long bones splinters, especially of medium or large size. Only a few bones bear definite porcupine gnawing marks, and *Hystrix* certainly did not bring more than a small part of the collection into the cave.

The assemblage includes the full range of ungulate sizes, except the very small ones (dik-dik size); as most of the sediment was carefully screened (at 0.8 mm) and not a single tooth was found, they were certainly absent. Other ungulates, and *Theropithecus*, are very unevenly represented in terms of anatomical elements and ontogenic age (Table 1).

Perhaps the most obvious difference is that all very large animals, Bovini, *Sivatherium*, rhinoceroses, proboscideans, are better represented by milk teeth than by third molars, and the proportion of milk teeth increases with size (there is not even a fragment of proboscidean permanent tooth). By contrast, the sample of medium-sized animals includes significant, and sometimes very high, numbers of permanent teeth. It is likely that some of the milk-teeth of the small to medium-sized bovinds, especially the worn ones, which are more breakable, were broken and discarded as useless, without significantly altering the proportions. The differential destruction of gazelle teeth is confirmed by the great number of the robust horn-cores, about twice higher than expected from the number of m3s.

A second obvious difference is that the numbers of the best preserved postcranial remains, such as tali (mostly of adult individuals) and adult distal humeri, do not follow those of teeth. The most common ones are those of medium size; small gazelle bones are less common than expected, as are the very large long bones, but the tali of rhinoceroses and proboscideans, all of adult size, are relatively quite numerous. The discrepancy between *Sivatherium* tali and distal humeri is especially noticeable. A similar bias affects *Hipparion*, whereas bovid size class III displays the opposite difference. *Kolpochoerus* (and *Theropithecus*) postcranials are remarkably rare.

Several factors certainly account for this uneven representation of the various anatomical elements. Some of the smaller bones may have been broken and discarded during the course of the difficult excavations, but it is more likely that many were chewed and eaten or reduced to unidentifiable fragments by carnivores. The low proportion of suid postcranials is also found in East African open-air sites; this may be partly due to the very good preservation of their teeth (especially those which are unworn or little worn). The virtual absence of long

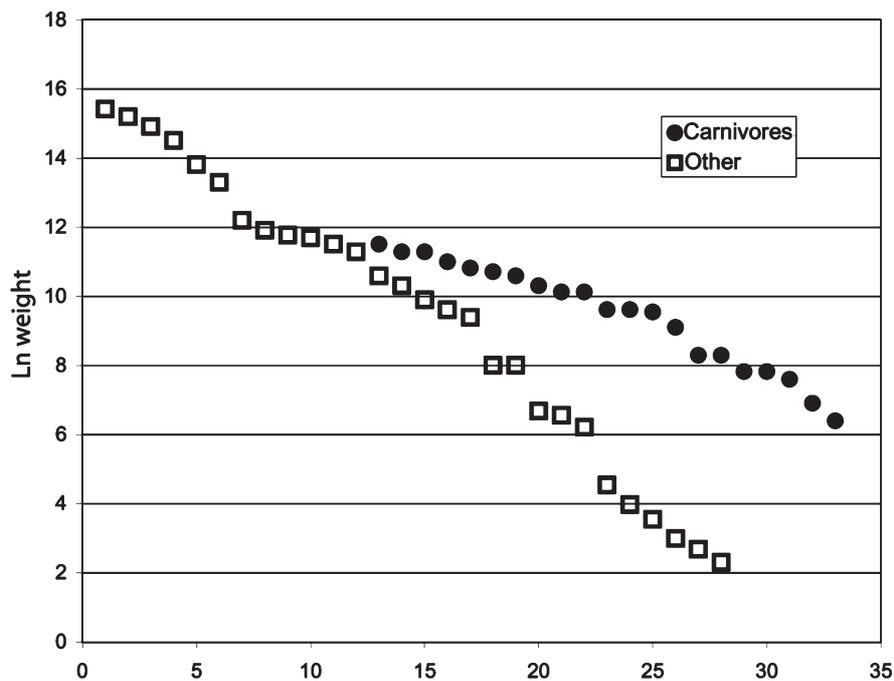


Figure 2. Cenogram of Ahl al Oughlam.

bones, cranial remains, and teeth of very large adult animals, suggests that the carnivores (the largest one, *Homootherium*, is lion-sized) were unable to carry heavy elements such as heads or large elements of the limbs, as also assumed by Klein *et al.* (1999). Klein (1989) also assumed that large long bones, first broken for marrow, become more heavily fragmented during the depositional process.

Some of the numbers remain hard to explain. Such is the low number of *Hipparion* distal humeri (definitely not confused with those of bovids!), or of bovid size III tali, which are of similar size and robustness to the distal humeri but more common. These differences cannot be wholly explained by differential mechanical preservation, and imply selective sorting by the carnivores. Perhaps the distal limbs of the smaller animals were not considered by the carnivores as worth being carried, but it is difficult to understand how any kind of selection can have differentially affected the Bovini on the one side, and *Hipparion* and *Sivatherium* on the other.

ECOLOGY

Contrasting with the diversity of carnivores, which depend on the availability of prey, the poor diversity of other mammals is the most noticeable feature of the Ahl al Oughlam mammalian assemblage. This is also in sharp contrast with most East or South African sites of similar age. A single species of primate dominates, instead of three to five commonly found elsewhere. Given the thousands of collected teeth, the number of rodent and insectivore species (respectively six and three) is also low. Rhinocerotidae, Equidae, Suidae, and Giraffidae are all represented by a single species, whereas two or three are usual in East Africa. Even the bovids, with seven species, are less diverse than they are further south, where well-sampled sites often yield 10 species or more. Even though Ahl al Oughlam probably samples only alpha-diversity, whereas open-air sites may combine faunal remains from several habitats, its fauna is also clearly less diverse than those of the South-African cave sites.

Thus, although diversity (or, more correctly, richness) has probably no straightforward ecological meaning, it is clear that Ahl al Oughlam is not a sample from a very favourable environment. Several indicators point to an open landscape.

Such are the absence of tree-dwelling monkeys, the virtual absence of forest or even woodland antelopes (Cephalophinae, Tragelaphinae, *Hippotragus*, *Aepyceros*), and the abundance of gerbillids. All bovid tali are low relative to their width: the ratio minimum height *vs* median width (LI/WI of DeGusta & Vrba, 2003) never exceeds 1.4, while it often exceeds this value in forest dwellers (DeGusta & Vrba, 2003, Fig. 2). Some of these absences may have a biogeographic origin (e.g. *Aepyceros* is not definitely known in North Africa), but the overall picture is consistent with a sparse wood cover. In this context, the abundance of *Sivatherium maurusium* shows that it was mostly a grazer.

Cenograms are frequently used for palaeoecological reconstruction, but their validity has been seriously questioned by Rodríguez (1999), who found that only the number of species between 0.5 and 8.0 kg, and, to a lesser extent, between 0.5 and 25 kg can provide some indication on the vegetation physiognomy. These numbers at AaO (respectively 5 and 8; Fig. 2) are compatible with any environment except forest and desert, but best fit shrubland and bushland.

The presence of some species that indicate a cold climate is unexpected, as it is generally agreed that the climate at that time was warmer than today, although the difference was not great at this latitude. Even if the walrus was not a permanent resident there, it certainly lived in cool sea waters. Several of the birds are also found today only at northern latitudes, but evidence provided by this group is ambiguous, as there is also a parrot. Perhaps high seasonality could explain these apparent inconsistencies and the stress on the mammalian fauna.

BIOGEOGRAPHY

Table 2 gives the number of terrestrial mammalian genera shared by Ahl Oughlam and other areas of the Old World in the Late Pliocene and early Pleistocene. The low number obtained for North Africa apparently stems from the poor sampling of this province before the discovery of Ahl al Oughlam. The total for the three main regions of Africa is comparable, and higher than for other regions, but this masks differences between mammalian groups. Carnivores are very loosely linked to their habitat, and are therefore widespread: many of the genera

Table 2. Number of genera in common between AaO and the main regions of the Old World.

	Africa			Europe			Asia	
	N *	E	S	W	C + E	SE	SW	E
Carnivores	11	16	16	15	12	12	14	16
Microfauna	11	8	6	6	7	8	5	6
Primates	2	1	1	2	1	1	1	1
Ungulates	12	13	11	4	6	6	8	7
Total	36	38	34	27	26	27	28	30

*Excluding Ahl al Oughlam.

present at Ahl al Oughlam are present as far east as China or the Siwaliks, while they may be absent from Europe. The microfauna includes some ubiquitous forms, several Afro-Indian genera, a Mediterranean form (*Paraethomys*), and a single endemic genus (*Irhoudia*). *Episorculus* is the only genus of definitely European affinities.

It is with the ungulates that the differences between provinces are most marked. Only a few widespread taxa are known on both sides of the Mediterranean; some ventured into the Near East (like *Homo* did), and some have a latitudinal extension into the Siwaliks (like *Kobus* or *Sivatherium*), but almost all genera from Ahl al Oughlam are also known in East and/or South Africa. In some instances, even the species are identical, in spite of a distance of up to 8000 km. Such a faunal similarity demonstrates that, as for earlier periods, there was no continuous barrier to hinder free faunal exchanges between North Africa and the rest of the continent, even though desertification of the Sahara was already under way.

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