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Biogeographic relationships of Pliocene and Pleistocene North-western African Mammals

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Abstract

North-western Africa, today included in the Palaearctic realm, is well separated from the Ethiopian province by the Sahara, but the distribution of large mammals shows that these biogeographic domains cannot simply be extrapolated to the late Cenozoic. In the latest Miocene and earliest Pliocene, there were close connections with central Africa, but also remarkable similarities with East Africa, in some instances reaching the species level. There is no evidence of northern influence among large mammals, although several small mammals had a wide range in the Mediterranean. East African or pan-African forms are also largely predominant in the well sampled Late Pliocene, their low diversity resulting probably from local environmental conditions. There are but a few immigrants from Eurasia, mostly carnivores. During the Early Pleistocene, limited exchanges occur with the Middle East, but many more with the rest of Africa. By the Middle Pleistocene similarities with East Africa reach their climax, and it is only with the latest part of this period that some northern immigrants put a Palaearctic stamp on this fauna, the “Ethiopian” character of which decreases by extinction of many of its elements.

Keywords – North Africa – Pliocene – Pleistocene – Mammalia – biogeography

1. Introduction

The present-day Sahara, the largest dry desert in the World, is the main geographic feature of Africa, establishing between areas at higher and lower attitudes a biogeographic barrier far more efficient than, e.g., the East African rift. It separates a southern, so-called Ethiopian faunal realm from the Palaearctic one, which incorporates the areas south of the Mediterranean. I believe that looking at such a formidable barrier today has influenced many conceptions about the past biogeographic relationships of North African mammals. In spite of the abundant evidence showing that, as recently as the Holocene, the Sahara was wet and inhabited by a variety of large mammals, the groundless idea that there must have been a proto-

Sahara barrier perhaps as early as the Miocene has long been admitted (Thomas, 1979; Thomas et al., 1982). However, no detailed comparison of North-African mammalian faunas with European and Ethiopian ones, supporting a North-South distinction, has ever been undertaken. It is likely that the fact that late Cainozoic North African mammalian faunas were mostly studied by French palaeontologists (the first of whom being Camille Arambourg), more acquainted with European faunas than with East African ones, and more prone to compare the North African ones with the ones they knew best, contributed to increase their apparent Palaearctic aspect.

I shall review below the Late Miocene to Late Pleistocene mammalian faunas of North-western Africa, roughly in chronological order. There is virtually no absolute dating for the sites of this area, and all ages are estimated by biochronology but, except for some uncertainties mentioned below, these estimates are rather satisfactory.

2. – Biogeographic affinities of mammalian faunas

2.1 - Late Miocene and Early Pliocene

This period is poorly documented in North Africa. The main site is Sahabi in Libya, referred by Bernor and Pavlakis (1987) to the Early Pliocene, but now usually referred to the Late Miocene (Howell, 1987; Geraads, 1989), although probably encompassing more than a short time slice. Its African affinities are numerous (Geraads, 1989), with for instance *Redunca*, *Damalacra*, *Stegotrabelodon*, and *Brachypotherium*, all unknown outside this continent at that time. An antelope assigned to a Eurasian genus (*Prostrepsiceros* for Lehmann and Thomas, 1987, *Dytikodorcas* for Bouvrain and Bonis, 2007) could well be close instead to the African impala (*Aepyceros*), thus removing one of the very few northern affinities of the fauna. The Sahabi boselaphine, *Tragoportax cyrenaicus*, could be closer to the Lothagam one in Kenya (Harris, 2003) than to European forms. Sahabi shares some specific similarities with the fauna of Toros Menalla, in the Late Miocene of Chad. It has an anthracothere (Lihoreau et al., 2006), probably the same species of *Machairodus* (Peigné et al., 2005), and a primitive hippotragine, *Tchadotragus* (Geraads et al., 2008). This speaks in favour of a Chado-Libyan sub-province within a larger African one, because hippotragines are unknown outside Africa at that time, and anthracotheres went extinct in Europe much earlier. This is confirmed by the discovery of late Miocene paleo-rivers flowing north into the Mediterranean from paleo-lake Chad (Griffin, 2006), thus providing easy connection for a variety of mammals.

In the Maghreb, no fauna comparable in richness to that of Sahabi is known. Douaria in Tunisia, the age of which is imprecise but certainly in the 5-8 Ma range, yielded an anthracothere (Pickford, 1991) and two species of rhinos, one of which (Guérin, 1966, and pers. obs.) is close

to brachytheres, a group which also went extinct in Europe much earlier. In East Africa instead, it survives until the Late Miocene at Lothagam (Harris and Leakey, 2003), and the fauna of Douaria is thus clearly of African character, showing no definite northern influence.

Such northern forms are also absent from the later site of Hamada Damous, in the same country, which yield a suid intermediate between *Nyanzachoerus* and *Notochoerus* (Coppens, 1971); both genera are best known in Early and Middle Pliocene East African sites, but unknown in Europe.

Further West, at Lissasfa in Morocco, close to the Miocene-Pliocene boundary, we (Raynal et al., 1999) discovered a bovine skull close to *Ugandax* from Central and Eastern Africa, and a canid with upper molars large relative to the carnassial, thus quite distinct from the contemporaneous Spanish form, *Canis cipio* (Pons-Moyá et al., 1978).

Lissasfa yielded an interesting rich fauna of rodents (Geraads, 1998b) which allowed its precise dating, but also show that they do not follow the same biogeographic pattern as large mammals. We will see that this difference is a steady feature for the whole late Cainozoic. Lissasfa yielded one of the earliest *Mus* of the western part of the Old World, probably originating from the Siwalik *Mus*, but this microfauna also includes several taxa that are also present in Western Europe, especially in Spain, or elsewhere in the Mediterranean basin, but are wholly unknown in East or South Africa at that time. These are *Paraethomys*, *Ruscinomys*, *Myocricetodon*, and *Protatera*. *Myocricetodon* had a much larger range earlier in the Miocene, but the other three genera were definitely involved in a latitudinal dispersal phase in the latest Miocene. Several other rodents, absent from Lissasfa but present in other North African localities, *Apodemus*, *Castillomys*, *Eliomys*, and *Stephanomys* (Coiffait-Martin, 1991) confirm the existence of rodent exchanges between North-western Africa and Spain (Geraads, 1998a).

Remarkably, very few large mammals were involved in these exchanges. The earliest North African records of the Cercopithecinae *Macaca* are at Sahabi and at Menacer, a Turolian site in Algeria (Thomas and Petter, 1986); Delson (1975) surmised that it could be the vicariant sister-taxon of the Papionini, known further south, but this genus has also been reported from the earliest Pliocene of the Middle Awash in Ethiopia. Its occurrence in the latest Miocene of Casablanca-M in Spain (Fortelius, 2007) shows that it certainly crossed the Gibraltar straits. Hippos followed the same route, as they probably originated in Africa from a form close to the Middle and Late Miocene *Kenyapotamus* (Pickford, 1983), and are present in Spain by the Late Miocene (Venta del Moro, El Arquillo). *Camelus* (or *Paracamelus*) is also sometimes cited as an example of trans-Gibraltar connection, but its fossil record in the western part of the Old World is far too incomplete to reconstruct its history. It suddenly appears as early as the latest Miocene

in Spain (Morales et al., 1980), so that whatever route it followed left no track, which is not surprising, as this group is always quite rare in any site. Subsequent records in the Early Pliocene of Chad (Likies et al., 2003), and Middle Pliocene of North Africa (Arambourg, 1979), could well be the result of a more southern east-west migration. A seemingly Palaeartic element in Pliocene North African faunas is the Caprini of Aïn Brimba in Tunisia (Arambourg, 1979). Caprini have a very sparse record in Africa, but it should be noted that the modern Barbary “sheep”, *Ammotragus*, has been shown to be more distant from goats than previously thought, so that this group could have a long history in Africa (but see below).

2.2 - Late Pliocene

Ahl al Oughlam, a fissure filling near Casablanca, is by far the richest site of this period in North Africa, and one of the richest in the Old World, with over 100 vertebrate species, of which 58 are mammals (Geraads, 2006, and refs therein). The large mammals can be divided into 4 groups, according to their biogeographic affinities.

1) Those which already had a very wide distribution before the Late Pliocene, so that it is hard to say if they originate from African forms, or immigrated from elsewhere. Uncertainties may be increased by doubts about the monophyly of some of these genera, which are: *Elephas*, *Anancus*, *Hystrix*, and several carnivores: *Hyaenictitherium*, *Chasmaporthetes*, *Dinofelis*, *Felis*, *Homotherium*.

2) Those which are certainly of African origin, as they are known in this continent before the time of Ahl al Oughlam, while they are unknown elsewhere. These include a number of carnivores (Geraads, 1997; see also Hendeby, 1974; Petter and Howell, 1977; Barry, 1987; Petter, 1987 for the other localities): *Herpestes*, *Ichneumia* and *Genetta* (known as early as the Late Miocene), *Civettictis* (known from Omo as *Viverra leakeyi*), *Crocuta*, *Panthera*, *Acinonyx* (all known at Laetoli), *Vulpes* (known from the Late Miocene of Chad: Bonis et al., 2007), *Prepoecilogale* (known at Laetoli), *Mellivora* (known in the Early Pliocene of Langebaanweg in South Africa) and probably *Ictonyx* (*Poecilictis*), unknown in the Pliocene, but with no extra-African record. Other definitely African forms are: *Theropithecus* (mostly represented earlier by *Th. darti* both in East and South Africa: Alemseged and Geraads, 1998), *Lepus* (reported from Kanapoi: Harris et al., 2003), *Hipparion pomeli* (which belongs to the *H. hasumense* group, known at Hadar: Eisenmann and Geraads, 2007), *Kolpochoerus* (with no Pliocene extra-African record), *Sivatherium* (definitely known at Langebaanweg), and several bovids (Geraads and Amani, 1997): *Tragelaphus* and *Kobus* (two African genera first documented at Langebaanweg), and *Beatragus* (unknown outside Africa). The North African Late Miocene and Early Pliocene

record is too patchy to rule out the hypothesis that some of these taxa had a North African origin, but it is likely that most of them arose instead in East or South Africa, later to expand northwards across the present-day Sahara. Non-mammalian Ahl al Oughlam taxa with East African close relatives are the viper *Bitis* (Bailón, 2000), and the love-birds *Agapornis*, a genus known only in Africa (C. Mourer-Chauviré, pers. comm.).

3) Those, mostly carnivores, which are probably of northern (European) origin. They include *Pliocrocuta*, a widespread taxon in Eurasia, but with no record in Africa besides Ahl al Oughlam, *Lynx*, doubtfully present at Ahl al Oughlam, and known at Çalta and Perpignan (Ginsburg, 1998, but the systematics of this genus is debated: Morales et al., 2003), *Nyctereutes*, a mainly Eurasian genus, known since the Early Pliocene in Europe before its first (uncertain) record in Africa at Laetoli (Barry, 1987), and *Ursus*, well known in Europe (Werdelin and Lewis, 2005, mentioned also an ursine bear from East Africa, but this report is so unexpected that it has to be confirmed). The latter taxon provides the best evidence of crossing of the Gibraltar straits, certainly easy for such a good swimmer. *Nyctereutes* could have followed the same route, as the species from Ahl al Oughlam bears special resemblance to Spanish forms. *Pliocrocuta* could be of Asiatic origin, but systematics of this group is still imperfectly understood. African otters display a clear disjunction in two groups: all North African ones belong to *Lutra*, a Eurasian genus unknown at that time south of the present-day Sahara, where it is replaced by *Aonyx* and *Enhydriodon*, two genera absent from North Africa; needless to say that *Lutra* is also a good swimmer.

4) Those whose origin is still debatable. There is a medium size canid whose affinities with *Canis* and “*Eucyon*” have not yet been fully worked out. Leporids other than *Lepus* belong either to *Serengetilagus* (an East African genus) or to *Trischizolagus* (a Mediterranean one), while *Prolagus* is a Mediterranean genus. An alcelaphine antelope, referred to *Parmularius*, a purely African genus, by Geraads and Amani (1998) might belong instead to *Damalops*, a genus also known in the latest Pliocene of the Siwaliks (Pilgrim, 1939) and Tajikistan (Dmitrieva, 1977), but still almost certainly of African origin. The affinities of the Bovini from Ahl al Oughlam are still unclear because no reasonably complete horn-core has been found, but its primitive premolars suggest that they might lie with the “*Leptobos*” from Eurasia.

In spite of the clear similarities of Ahl al Oughlam with East African faunas, some significant elements of the latter are missing in the Moroccan site. These are first the Hominidae, as there is no evidence whatsoever of human presence at Ahl al Oughlam, all Cercopithecidae other than *Theropithecus*, *Deinotherium*, all Suidae except *Kolpochoerus*, *Giraffa*, and *Aepyceros*. Remarkably, most of these taxa, if not all of them, are ecologically linked to at least

some kind of wood cover. This is in agreement with the high proportion of alcelaphine and antilopine bovids at Ahl al Oughlam, a definite indicator of dry open landscape, so that their absence in Morocco might be due to local ecological conditions.

The list of genera that are present in Europe and Western Asia in the Late Pliocene, but absent from North Africa, is much longer. It includes many carnivores: the viverrids *Viverra* and *Megaviverra*, the felid *Puma* (or *Jansofelis*), the canid *Cuon* (to which can be added *Vulpes* of *alopecoides* type, with long carnassials), and the mustelids *Baranogale*, *Martes*, *Mustela*, and *Meles*. There are also some large ungulates, such as the rhino *Stephanorhinus*, the proboscidean *Mammot* (= *Zygodon*), *Tapirus*, and a cercopithecoid primate, *Paradolichopithecus*. But the main differences lie in the composition of the artiodactyl faunas, whose northern representatives unknown in the Maghreb at this time include the wild boar *Sus*, perhaps a palaeotragine giraffid (*Mitilanotherium*), the various members of the family Cervidae, with at least four genera, *Cervus*, *Croizetoceros*, *Eucladoceros* and *Alces* s.l., of which there is not a single tooth or bone in Africa, and several bovids whose systematic position is not always clear, but which are definitely not members of the dominant African tribes (Tragelaphini, Reduncini, Hippotragini and Alcelaphini): *Gazellospira*, *Procamptoceras*, *Pliotragus*, *Gallogoral*, *Hemitragus*, *Megalovis*, *Ovis*.

To express more objectively the similarities between Ahl al Oughlam and other sites of comparable age, I have computed some indices from their faunal lists of large mammals. There are many such indices, based upon the number of taxa shared by the two faunal lists (*A*), and the numbers of taxa peculiar to each of them (*B* and *C*). I chose Simpson index of similarity, $A / (A + B)$ if $B < C$ or $A / (A + C)$ if $C < B$, and Pickford index of distance, transformed to 1-(Pickford index) for homogeneity, thus becoming $A(A + B + C) / (A + B)(A + C)$. They are less sensitive to unequal sampling than some other commonly used indices. Results, at generic level, are provided in Table 1: they clearly show that it is with East African that the similarities are greater, in spite of the difference in latitude. Compared with European sites, even those of closely similar age, the indices are much smaller. Thus, the difference in faunal composition is quite clear, and so sharp that it cannot merely be explained by differences in ecological conditions.

By contrast, the rodents tell again a very different story (Geraads, 1995). In spite of the great number of rodent teeth that have been collected by screening, only five species have been found, besides the widespread *Hystrix*. They mainly belong to lineages already present in earlier sites, such as *Mus*, also known in East Africa and the Siwaliks, but totally absent from Europe, and *Paraethomys*, a genus now extinct in Europe, but which will continue in North Africa, as an endemic lineage, until the end of the Middle Pleistocene. *Gerbillus* also appears there, at about

the same time as at Omo in Ethiopia (Wesselman, 1984), and will also have a long history in the Maghreb. Ahl al Oughlam lacks the diversity of murids found in East African sites of this age, but also fully lacks any arvicolid, the dominant group in Europe at that time. Remarkably, this original composition of North African rodent faunas will remain virtually unchanged until the end of the Pleistocene (Jaeger, 1975). Other small mammals show less endemism. *Asoriculus*, also known in Morocco at Irhoud Ocre, is present in Europe, while *Suncus* has been described from East Africa (Wesselman, 1984).

2.3 - Early Pleistocene

Faunas of this period are much less rich than that of Ahl al Oughlam. The stratigraphic succession at Aïn Jourdel in Algeria (Thomas, 1884) includes several levels, the lowest being probably of Late Pliocene age, with a new alcelaphine, likely of East African origin, *Oreonagor*, and an upper level with *Tragelaphus gaudryi*, a species well-known at Omo (Gentry, 1985) in Ethiopia. Aïn Boucherit has one more alcelaphine genus, certainly immigrated from East Africa, *Parmularius* (described as *Redunca eulmensis* by Arambourg, 1979), together with a more derived species of *Oreonagor*. *Parantidorcas* is certainly an antelope, but its affinities remain unclear; it could be related to African *Antidorcas*, although the strong homonymous torsion of its horn-cores reminds of the Late Miocene Eurasian *Oioceros*. In any case, there are thus at least two more East African immigrant bovids near the Plio-Pleistocene boundary. However, the best evidence for connections between equatorial Africa and the Maghreb at that time is the arrival of hippos of modern type (tetraprotodont *Hippopotamus*). They are recorded only slightly later, at perhaps 1.4 Ma, in Western Europe (Atapuerca faunal unit 1: Cuenca-Bescós and García, 2007), where they probably arrived from the East, as they are known in the Early Pleistocene of Ubeidiya in Israel (Faure, 1986) and at Kapetanios in Greece (Koufos and Kostopoulos, 1997). Indices of similarity (Table 2) are again much greater when compared with East Africa than with Eurasia.

The site of Aïn Hanech, stratigraphically above that of Aïn Boucherit, yielded a fauna ecologically similar to that of the latter level, but rather sharply distinct in its faunal composition, suggesting that they are separated by a significant amount of time, and the fauna of Aïn Hanech, probably the earliest North African site documenting human presence, points to an age of perhaps 1.2 to 1.4 Ma. (Geraads et al., 2004, contra Sahnouni et al., 2002). It attests the first immigration of a large canid, considered as closed to *Lycaon* by Martínez-Navarro and Rook (2003) but lacking the derived features of this genus, and probably closer to *Canis atrox* from South Africa, to which it was first referred by Arambourg (1979). Other definite immigrants

from the south are *Oryx*, also known in the roughly contemporaneous site of Mansourah (Chaid-Saoudi et al., 2006) and the large alcelaphine *Numidocapra*, of which Aïn Hanech is the type-locality of the type-species, but which is also present in Djibouti (Bonis et al., 1988) and the Middle Awash (Vrba, 1997).

There are, however, some possible connections with Eurasia, and especially with the Near East. The bovine described under two different names, *Bos bubaloides* and *B. praeaffricanus*, by Arambourg (1979) is probably closer to Eurasian *Leptobos* than to African *Pelorovis*, in spite of a similar course of its horn-cores. In any case, *Pelorovis* is also present at Ubeidiya (Geraads, 1986). A very poorly known giraffid, described as *Giraffa pomeli* by Arambourg but definitely not of this genus, might be close to the *Giraffa* sp. of Ubeidiya but certainly distinct from East African forms. Giraffids are extinct in Europe at that time. North African representatives of the suid *Kolpochoerus* seem to belong to a local lineage (*Kolpochoerus maroccanus*), distinct from the East African ones (Geraads, 2004), but its possible connection with the poorly documented Ubeidiya form remains conjectural. The asinian equid *Equus tabeti* has been described from both Aïn Hanech (Arambourg, 1970) and Ubeidiya (Eisenmann, 1986).

However, these similarities should not be overestimated, as the Aïn Boucherit and Aïn Hanech faunas remain very different from the Dmanisi (Lordkipanidze et al., 2007) and Ubeidiya ones, which are almost fully Eurasian in character, with especially an overwhelming majority of cervids among ruminants. Indices of similarity (Table 3) show that these latter sites are still much less similar to Aïn Hanech than are the East African ones.

2.4 - Middle Pleistocene

The site of Tighenif (= Ternifine) is still the earliest with fossil hominid remains in North Africa, dated to close to the Early / Middle Pleistocene boundary (Geraads et al., 1985). Ecologically, the fauna reminds of those of the earlier sites, with a majority of dry open country forms, oryx, gazelles and Alcelaphini. Most of its genera are also found in East and South Africa, the most characteristic ones being: *Lycaon*, *Theropithecus*, *Ceratotherium*, *Loxodonta*, *Metridiochoerus*, and most bovids (*Tragelaphus*, *Oryx*, *Hippotragus*, *Parmularius*, *Connochaetes*: Geraads, 1981), although its bovine could be a descendant of the one found at Aïn Hanech, perhaps more closely related to European *Leptobos* than to the African *Pelorovis*, and its dominant gazelle, *G. dracula*, could be related to the earlier European *G. borbonica* (Gentry, 1990). Trans-African connections far outweigh this only possible evidence of migration from the north, and Tighenif is perhaps the most “East African” of all sites in the Maghreb: the

first Eurasian site in Table 4, Ubeidiya, has a far lower similarity index with Tighenif than many East African sites.

Rodents (Jaeger, 1975; Geraads et al., 1986) mostly include North African endemic lineages (*Paraethomys*, gerbillids) plus an East African murid (*Arvicanthis*) and the only arvicolid of North Africa, *Ellobius*, definitely of Central Asiatic origin.

Aïn Maarouf near El Hajeb in Morocco yielded a small fauna (Geraads and Amani, 1997) similar to that of Tighenif, but with the addition of a new alcelaphine, *Rabaticeras*, also reported from a few earlier East and South African sites, testifying to a new immigration from the South.

Recent excavations in the former “Thomas Quarries” near Casablanca allowed refining of the stratigraphy and biochronology of the various archaeological levels in these quarries, now referred to as “Thomas Quarry” (= former Thomas Quarry 1), and “Oulad Hamida 1”, (= former Thomas Quarry 3), the latter including mainly the “Grotte des Rhinocéros” (Raynal et al., 1993; Rhodes et al., 2006). Although definitely of various ages, all these levels are younger than Tighenif, from which they can be distinguished by a significant, but not major, turnover: *Metridiochoerus* is replaced by *Phacochoerus*, the origin of which is certainly to be sought close to the East African *M. hopwoodi*, while *Kolpochoerus* survives; the most common alcelaphine looks close to a strange form from the Okote member of Koobi Fora, referred to ? *Damaliscus* by Harris (1991). The strongest evidence of a European immigration is a lynx (Geraads, 1980) which might share a relatively recent common ancestry with the modern Spanish *Lynx pardina*. Despite recent claims to the contrary (Martínez-Navarro et al., 2007) I do not believe that the origin of *Bos* is to be sought in Africa, the Middle Pleistocene East African *Bos* (Geraads et al., 2004) being probably of Asiatic origin, while North African late Middle Pleistocene *Bos primigenius* probably came from Eurasia.

Among rodents, *Eliomys* re-appears for the first time since the earliest Pliocene, but its similarities with the garden dormouse of the Balearic Islands suggest a new immigration.

2. 5 - Late Pleistocene

Several new taxa appear during this period, but the documentation during the latter part of the Middle Pleistocene is relatively poor, and they might in fact have arrived earlier. Among bovids, the giant buffalo *Pelorovis* (or *Syncerus*) *antiquus*, and the hartebeest *Alcelaphus* definitely came from East Africa, where they are known much earlier (Gentry and Gentry, 1978; Vrba, 1997). *Ammotragus* could be the end product of a North African caprine lineage, or alternatively could be of European origin, as the genus has recently been reported from Le Vallonnet, a ca. 1 Ma site in Southern France (Moullé et al., 2004). Two deer, a small variety of

the red deer *Cervus elaphus*, and a megacerine, *Megaceroides algericus*, also appear during this period, although the precise date of their arrival is unknown. Deer are good swimmers, and the Gibraltar straits, only about 15 km wide at its narrowest stage, was certainly not impassable, neither for them, nor for *Sus*, which has been reported from the late Middle Pleistocene (Michel, 1989), and persists until the present-day. This crossing is much less likely for the rhino *Stephanorhinus*, certainly present during the first half of the Late Pleistocene, and its occurrence at Haua Fteah (Klein and Scott, 1986) in Eastern Libya suggests that it came from the east, following the southern Mediterranean shore. These new immigrants increase the Palaeartic component in North-western African faunas, while the “Ethiopian” component decreases because of the extinction of several of its elements in the course of the Late Pleistocene: Tragelaphini, *Hippotragus*, Reduncini, *Camelus* (later re-introduced as a domestic form), *Phacochoerus*, hippos, *Ceratotherium*, all disappear before historic times. So, although there is no definite new evidence of immigration from the south during this period, it might well be that this faunal turnover was more related to climatic change in the area itself than to the establishment of the Sahara barrier, the loss of diversity experienced by both the large and small mammals being a clear indicator of environmental stress.

3. - Conclusion

From the Late Miocene to the Middle Pleistocene, many new lineages of large mammals arose throughout Africa, but most of the centers of origins were probably located in the eastern part of the continent. Then, they expanded their ranges within Africa, as far as no geographical or ecological barrier stopped them. The regular immigration of these new taxa of southern origin in the north-western part of the continent demonstrates that no such efficient barrier can have existed for any long period. This does not mean that there was no desert in the Sahara area: indeed, recent finds have demonstrated the occurrence of desertification as early as the Miocene (Schuster et al., 2006) but the mammalian evidence demonstrates that these desert zones were either not large or not permanent enough to set a barrier preventing migration across it. Our present-day conception of the Sahara is clearly not applicable to this period.

Surprisingly, the human fossil evidence in North-western Africa does not seem to conform to this biogeographic history based upon regular latitudinal exchanges. The complete absence of Hominids at Ahl al Oughlam is most unexpected, given the strong East African aspect of the fauna of this site, which is so rich that this can probably be taken as an evidence of absence of hominids in North Africa at that time. As noted above, other eastern African taxa that are lacking at Ahl al Oughlam are those that require some amount of tree cover, and this suggests

that the dominant physiognomy of the landscape in North-western Africa in the late Pliocene / early Pleistocene was very open. By contrast, the abundance of cervids in early Eurasian hominid-bearing sites such as Dmanisi or Ubeidiyeh testifies to the preference of early *Homo* for some wood cover, and their immediate ancestors by the time of Ahl al Oughlam may have had similar requirements, although the presence of *Australopithecus* in Chad in sites wholly lacking woodland bovids (Geraads et al., 2001) precludes any simple interpretation.

Based upon present knowledge, it is only in the middle part of the Early Pleistocene that hominids appear in North Africa, at Ain Hanech and Mansourah but, since the environment of these sites was not significantly more wooded than that of Ahl al Oughlam, this can perhaps be seen as an evidence of their increasing adaptability. Later, North African *Homo mauritanicus* may have followed his own local evolution, without any further connection with African and Eurasian members of the genus. Obviously, environmental conditions were no longer the main determinant of the geographic distribution of these hominids.

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Figure captions

Fig. 1. Situation of the localities mentioned in Tables 1-4.

Fig. 2. Range of some North-African mammalian taxa, together with their range (when larger) in the rest of Africa (dotted line) and in Eurasia (dashed line). The main sites are listed at left at their approximate chronological position, but they may not sample all contemporaneous taxa. Chronological scale is logarithmic.

Table 1. Simpson index of similarity and 1-(Pickford index of distance) of Ahl al Oughlam compared with some North African (AFN), Central African (AFC), East African (AFE), South African (AFS), Western European (EURW), Eastern European (EURE), and Central Asian (ASC) sites of comparable age. Faunal lists have been updated from a variety of sources.

| AHL AL OUGHLAM | | | | | |
|---------------------------|------|-------|---------------------------|------|-------|
| SIMPSON INDEX | | | 1-PICKFORD INDEX | | |
| Turkana Late Plioc. | AFE | 0.737 | Turkana Late Plioc. | AFE | 0.825 |
| Turkana Early Pleisto. | AFE | 0.632 | Peninj | AFE | 0.799 |
| Aïn Boucherit | AFN | 0.615 | Ichkeul+Brimba | AFN | 0.789 |
| Ichkeul+Brimba | AFN | 0.6 | Aïn Boucherit | AFN | 0.777 |
| Bouri-Hata | AFE | 0.579 | Hadar-KH | AFE | 0.776 |
| Konso Gardula 1 2 | AFE | 0.579 | Tighenif | AFN | 0.776 |
| Peninj | AFE | 0.579 | Turkana Early Pleisto. | AFE | 0.754 |
| Hadar-KH | AFE | 0.526 | Bouri-Hata | AFE | 0.744 |
| Tighenif | AFN | 0.526 | Konso Gardula 1 2 | AFE | 0.744 |
| Chiwondo3A | AFS | 0.474 | Olduvai up. + mid. bed II | AFE | 0.699 |
| Hadar-DD | AFE | 0.474 | Hadar-SH | AFE | 0.689 |
| Hadar-SH | AFE | 0.474 | Hadar-DD | AFE | 0.671 |
| Laetoli upper bed | AFE | 0.474 | Chiwondo3A | AFS | 0.637 |
| Olduvai up. + mid. bed II | AFE | 0.474 | Laetoli upper bed | AFE | 0.637 |
| Aïn Hanech | AFN | 0.462 | Aïn Hanech | AFN | 0.632 |
| Koro-Toro | AFC | 0.429 | Koro-Toro | AFC | 0.609 |
| Olduvai bed I | AFE | 0.368 | Olduvai bed I | AFE | 0.601 |
| Ubeidiya | EURE | 0.333 | Ubeidiya | EURE | 0.544 |
| Makapan 3-4 | AFS | 0.263 | Makapan 3-4 | AFS | 0.417 |
| St Vallier | EURW | 0.214 | Sterkfontein 4 | AFS | 0.368 |
| Sterkfontein 4 | AFS | 0.211 | St Vallier | EURW | 0.338 |
| Atapuerca FU1 | EURW | 0.2 | Atapuerca FU1 | EURW | 0.284 |
| La Puebla | EURW | 0.182 | La Puebla | EURW | 0.268 |
| Almenara | EURW | 0.167 | Kromdraai A | AFS | 0.254 |
| Kromdraai A | AFS | 0.167 | Sesklon | EURE | 0.254 |
| Sesklon | EURE | 0.167 | Kuruksai | ASC | 0.225 |
| Kuruksai | ASC | 0.133 | Almenara | EURW | 0.211 |
| Kopala 2 | ASC | 0.111 | Kopala 2 | ASC | 0.158 |
| Tegelen | EURW | 0.111 | Tegelen | EURW | 0.158 |
| Chilhac | EURW | 0.1 | Gerakarou | EURE | 0.147 |
| Gerakarou | EURE | 0.1 | Podpusk-Lebyazhje | ASC | 0.147 |
| Podpusk-Lebyazhje | ASC | 0.1 | Chilhac | EURW | 0.147 |
| Senèze | EURW | 0.059 | Senèze | EURW | 0.108 |
| Dmanisi | EURE | 0 | Dmanisi | EURE | 0 |
| Livakos | EURE | 0 | Livakos | EURE | 0 |
| Varshets | EURE | 0 | Varshets | EURE | 0 |

Table 2. Same as for Table 1, but for Aïn Boucherit.

| AÏN BOUCHERIT | | | | | |
|---------------------------|------|-------|---------------------------|------|-------|
| SIMPSON INDEX | | | 1-PICKFORD INDEX | | |
| Bouri Daka | AFE | 0.692 | Aïn Hanech | AFN | 0.852 |
| Konso Gardula 1 2 | AFE | 0.692 | Peninj | AFE | 0.824 |
| Peninj | AFE | 0.692 | Bouri Daka | AFE | 0.808 |
| Turkana Early Pleisto. | AFE | 0.692 | Konso Gardula 1 2 | AFE | 0.791 |
| Ahl al Oughlam | AFN | 0.615 | Ahl al Oughlam | AFN | 0.777 |
| Aïn Hanech | AFN | 0.615 | Turkana Early Pleisto. | AFE | 0.769 |
| Elandsfontein | AFS | 0.615 | Elandsfontein | AFS | 0.744 |
| Konso Gardula 3 4 | AFE | 0.615 | Olduvai bed IV | AFE | 0.744 |
| Olduvai bed IV | AFE | 0.615 | MK-GarbaIV | AFE | 0.74 |
| Turkana Late Plioc. | AFE | 0.615 | Konso Gardula 3 4 | AFE | 0.734 |
| MK-Garba IV | AFE | 0.538 | Turkana Late Plioc. | AFE | 0.689 |
| Bouri-Hata | AFE | 0.462 | Ichkeul+Brimba | AFN | 0.677 |
| Ichkeul+Brimba | AFN | 0.462 | Ubeidiya | EURE | 0.641 |
| Tighenif | AFN | 0.462 | Tighenif | AFN | 0.632 |
| Ubeidiya | EURE | 0.462 | Bouri-Hata | AFE | 0.577 |
| Bou Knadel | AFN | 0.385 | Bou Knadel | AFN | 0.556 |
| Hadar-KH | AFE | 0.385 | Hadar-KH | AFE | 0.547 |
| Olduvai up. + mid. bed II | AFE | 0.385 | Sesklon | EURE | 0.538 |
| Kopala 2 | ASC | 0.333 | Olduvai up. + mid. bed II | AFE | 0.531 |
| Livakos | EURE | 0.333 | St Vallier | EURW | 0.505 |
| Sesklon | EURE | 0.333 | Kopala 2 | ASC | 0.487 |
| Makapan 3-4 | AFS | 0.308 | Livakos | EURE | 0.487 |
| Olduvai bed I | AFE | 0.308 | Chilhac | EURW | 0.462 |
| St Vallier | EURW | 0.308 | Gerakarou | EURE | 0.462 |
| Chilhac | EURW | 0.3 | Podpusk-Lebyazhje | ASC | 0.462 |
| Gerakarou | EURE | 0.3 | Olduvai bed I | AFE | 0.453 |
| Podpusk-Lebyazhje | ASC | 0.3 | La Puebla | EURW | 0.441 |
| La Puebla | EURW | 0.273 | Makapan 3-4 | AFS | 0.423 |
| Sterkfontein 4 | AFS | 0.231 | France MNQ20 | EURW | 0.385 |
| France MNQ 20 | EURW | 0.231 | Sterkfontein 4 | AFS | 0.346 |
| Tegelen | EURW | 0.222 | Tegelen | EURW | 0.342 |
| Atapuerca FU1 | EURW | 0.2 | Atapuerca FU1 | EURW | 0.323 |
| Kromdraai A | AFS | 0.167 | Kromdraai A | AFS | 0.295 |
| Varshets | EURE | 0.167 | Dmanisi | EURE | 0.275 |
| Dmanisi | EURE | 0.154 | Senèze | EURW | 0.253 |
| Senèze | EURW | 0.154 | Varshets | EURE | 0.231 |

Table 3. Same as for Table 1, but for Aïn Hanech.

| AÏN HANECH | | | | | |
|---------------------------|------|-------|---------------------------|------|-------|
| SIMPSON INDEX | | | 1-PICKFORD INDEX | | |
| Bouri Daka | AFE | 0.846 | Bouri Daka | AFE | 0.917 |
| Turkana Early Pleisto. | AFE | 0.846 | Turkana Early Pleisto. | AFE | 0.893 |
| Turkana Late Plioc. | AFE | 0.846 | Turkana Late Plioc. | AFE | 0.886 |
| Konso Gardula 1 2 | AFE | 0.769 | Aïn Boucherit | AFN | 0.852 |
| Elandsfontein | AFS | 0.692 | Konso Gardula 1 2 | AFE | 0.852 |
| Konso Gardula 3 4 | AFE | 0.692 | Peninj | AFE | 0.824 |
| Olduvai bed IV | AFE | 0.692 | Elandsfontein | AFS | 0.808 |
| Peninj | AFE | 0.692 | MK-Garba IV | AFE | 0.808 |
| Aïn Boucherit | AFN | 0.615 | Olduvai bed IV | AFE | 0.808 |
| MK-Garba IV | AFE | 0.615 | Konso Gardula 3 4 | AFE | 0.799 |
| Tighenif | AFN | 0.615 | Ubeidiya | EURE | 0.786 |
| Ubeidiya | EURE | 0.615 | Tighenif | AFN | 0.777 |
| Asbole | AFE | 0.538 | Asbole | AFE | 0.692 |
| Olduvai up. + mid. bed II | AFE | 0.538 | Olduvai up. + mid. bed II | AFE | 0.692 |
| Ahl al Oughlam | AFN | 0.462 | Isenya | AFE | 0.677 |
| Isenya | AFE | 0.462 | Ahl al Oughlam | AFN | 0.632 |
| Mosbach 5 | EURW | 0.4 | Olduvai lower bed II | AFE | 0.59 |
| Bou Knadel | AFN | 0.385 | Mosbach 5 | EURW | 0.585 |
| Olduvai I | AFE | 0.385 | Bou Knadel | AFN | 0.556 |
| Olduvai lower bed II | AFE | 0.385 | Olduvai I | AFE | 0.547 |
| Atapuerca FU4 5 | EURW | 0.333 | France MNQ20 | EURW | 0.492 |
| Kopala 2 | ASC | 0.333 | Atapuerca FU4 5 | EURW | 0.487 |
| Livakos | EURE | 0.333 | Kopala 2 | ASC | 0.487 |
| France MNQ20 | EURW | 0.308 | Livakos | EURE | 0.487 |
| Gerakarou | EURE | 0.3 | Gerakarou | EURE | 0.462 |
| Untermassfeld | EURW | 0.25 | Untermassfeld | EURW | 0.423 |
| Dmanisi | EURE | 0.231 | Dmanisi | EURE | 0.396 |
| Ichkeul+Brimba | AFN | 0.231 | St Vallier | EURW | 0.396 |
| St Vallier | EURW | 0.231 | Ichkeul+Brimba | AFN | 0.385 |
| Sterkfontein 4 | AFS | 0.231 | Sterkfontein 4 | AFS | 0.346 |
| Tegelen | EURW | 0.222 | Tegelen | EURW | 0.342 |
| Atapuerca FU1 | EURW | 0.2 | Atapuerca FU1 | EURW | 0.323 |
| Chilhac | EURW | 0.2 | Chilhac | EURW | 0.323 |
| Varshets | EURE | 0.167 | Senèze | EURW | 0.253 |
| Makapan3-4 | AFS | 0.154 | Varshets | EURE | 0.231 |
| Senèze | EURW | 0.154 | Makapan 3-4 | AFS | 0.224 |
| Apollonia | EURE | 0.143 | Apollonia | EURE | 0.209 |

Table 4. Same as for Table 1, but for Tighenif.

| TIGHENIF | | | | | |
|---------------------------|------|-------|---------------------------|------|-------|
| SIMPSON INDEX | | | 1-PICKFORD INDEX | | |
| Turkana Late Plioc. | AFE | 0.947 | Turkana Late Plioc. | AFE | 0.97 |
| Turkana Early Pleisto. | AFE | 0.842 | Elandsfontein | AFS | 0.921 |
| Elandsfontein | AFS | 0.789 | Turkana Early Pleisto. | AFE | 0.912 |
| Bouri Daka | AFE | 0.684 | Bouri Daka | AFE | 0.855 |
| Konso Gardula 3 4 | AFE | 0.684 | Konso Gardula 3 4 | AFE | 0.842 |
| Peninj | AFE | 0.632 | Peninj | AFE | 0.842 |
| MK-GarbaIV | AFE | 0.625 | MK-GarbaIV | AFE | 0.822 |
| Aïn Hanech | AFN | 0.615 | Aïn Hanech | AFN | 0.777 |
| Olduvai bed IV | AFE | 0.579 | Ahl al Oughlam | AFN | 0.776 |
| Isenya | AFE | 0.533 | Olduvai bed IV | AFE | 0.772 |
| Ahl al Oughlam | AFN | 0.526 | Olduvai up. + mid. bed II | AFE | 0.752 |
| Lainyamok | AFE | 0.526 | Bou Knadel | AFN | 0.737 |
| Olduvai up. + mid. bed II | AFE | 0.526 | Lainyamok | AFE | 0.732 |
| Bou Knadel | AFN | 0.5 | Isenya | AFE | 0.73 |
| Olduvai I | AFE | 0.474 | Olduvai I | AFE | 0.723 |
| Aïn Boucherit | AFN | 0.462 | Ubeidiya | EURE | 0.678 |
| Ubeidiya | EURE | 0.444 | Asbole | AFE | 0.642 |
| Asbole | AFE | 0.421 | Aïn Boucherit | AFN | 0.632 |
| Olduvai lower bed II | AFE | 0.4 | Olduvai lower bed II | AFE | 0.589 |
| Atapuerca FU4 5 | EURW | 0.333 | Sterkfontein 4 | AFS | 0.521 |
| Ichkeul+Brimba | AFN | 0.333 | Ichkeul+Brimba | AFN | 0.509 |
| Makapan 3-4 | AFS | 0.316 | Makapan 3-4 | AFS | 0.487 |
| Sterkfontein 4 | AFS | 0.316 | Atapuerca FU4 5 | EURW | 0.439 |
| Atapuerca FU1 | EURW | 0.3 | Atapuerca FU1 | EURW | 0.411 |
| Kromdraai A | AFS | 0.25 | Kromdraai A | AFS | 0.368 |
| Untermassfeld | EURW | 0.25 | Untermassfeld | EURW | 0.368 |
| Kopala 2 | ASC | 0.222 | Kopala 2 | ASC | 0.304 |
| Livakos | EURE | 0.222 | Livakos | EURE | 0.304 |
| Gerakarou | EURE | 0.2 | Gerakarou | EURE | 0.284 |
| Mosbach 5 | EURW | 0.2 | Mosbach 5 | EURW | 0.284 |
| Apollonia | EURE | 0.143 | Dmanisi | EURE | 0.233 |
| Dmanisi | EURE | 0.143 | St Vallier | EURW | 0.233 |
| St Vallier | EURW | 0.143 | France MNQ20 | EURW | 0.225 |
| Vergranne | EURW | 0.143 | Apollonia | EURE | 0.188 |
| France MNQ20 | EURW | 0.133 | Vergranne | EURW | 0.188 |
| Chilhac | EURW | 0.1 | Chilhac | EURW | 0.112 |
| Senèze | EURW | 0.059 | Senèze | EURW | 0.108 |