

Plio-Pleistocene Carnivora of North-western Africa : a short review

Brève revue des Carnivora du Plio-Pléistocène du Maghreb

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Abstract

The fossil record of North-Western African carnivores is very patchy. The richest assemblage is that of the Late Pliocene of Ahl al Oughlam, with more than 20 species belonging to the main modern families. Some additions to its study [11] are made here. The rather poor Early Pleistocene faunas are mainly marked by the arrival of a large *Canis*. A fauna of modern type, with e.g., the duo *Hyaena - Crocuta*, settles in the earliest Pleistocene site of Tighenif, where some older elements linger on (*Homotherium*), beside some taxa of doubtful affinities, like a large *Panthera*, and a strange canid close to *Nyctereutes*, dominant at this site as well as at the slightly younger ones of Thomas and Oulad Hamida Quarries in Casablanca. All these faunas consist mostly of African taxa, together with a Palearctic component whose importance increases towards the end of the Pleistocene.

Résumé

Brève revue des carnivores du Plio-Pléistocène du Maghreb. La documentation concernant les carnivores du Plio-Pléistocène du Maghreb est très discontinuée. L'assemblage le plus riche est celui du Pliocène supérieur d'Ahl al Oughlam, avec plus de 20 espèces appartenant aux principales familles modernes; quelques compléments à son étude [11] sont apportés ici. Les faunes du Pléistocène inférieur, assez pauvres, sont surtout marquées par l'arrivée des grands *Canis*. Tighenif, au tout début du Pléistocène moyen, voit se mettre en place des éléments d'une faune de type moderne, avec en particulier le duo *Hyaena - Crocuta*, tout en conservant des survivants anciens (*Homotherium*). S'y ajoutent quelques taxons mystérieux, comme un grand *Panthera*, et un étrange canidé voisin de *Nyctereutes*, dominant dans ce site comme dans ceux un peu plus récents des carrières Thomas et Oulad Hamida à Casablanca. Toutes ces faunes comportent toujours une majorité de taxons africains, avec néanmoins une composante paléarctique qui s'accroît à la fin du Pléistocène.

Keywords : North-western Africa, Carnivora, Mammalia, Pliocene, Pleistocene

Mots clés : Afrique du Nord-ouest, Carnivora, Mammalia, Pliocène, Pléistocène

1. Introduction

Our knowledge of North-Western African Plio-Pleistocene mammal localities owes much to Camille Arambourg, who conducted numerous excavations in what was then France or French dependencies. The main ones are Lake Ichkeul and Aïn Brimba in Tunisia, of Early / Middle Pliocene age, and Aïn Boucherit and the overlying Aïn Hanech layers in Algeria, of Early Pleistocene age. His study of the "Villafranchian" carnivores was published after his death [2]. His

richest collection, from the Early / Middle Pleistocene of Tighenif (= Ternifine) in Algeria, remains unpublished but, thanks to the kind help of C. Sagne, I was able to study it in Paris.

During the last 20 years, important new sites have been excavated in Morocco under a Franco-Moroccan program. Ahl al Oughlam, dated to about 2.5 Ma. [11,13] is the richest, with more than 100 species of vertebrates, of which more than 20 are carnivores. The fossiliferous level consist of loose sands or breccias, filling gaps and fissures between collapsed blocks of calcareous sandstone, providing shelter for carnivores which certainly used them as dens, hence their high abundance and diversity. Unfortunately, excavations are no longer possible because of the present use of this former quarry as a garbage dump. Thomas Quarry (formerly Thomas Quarry 1) and "Grotte des Rhinocéros" in Oulad Hamida 1 Quarry (formerly Thomas Quarry 3), also near Casablanca, which probably date from the beginning of the Middle Pleistocene [37,39,40] have also yielded large carnivore collections, mostly unpublished [4]. Good collections have also been made in the Late Middle and Late Pleistocene, but many of them, especially the older ones, suffer from a lack of stratigraphic control. I shall below review the carnivores of these sites in taxonomic order.

2. Systematic overview

Small carnivores are rare in the Plio-Pleistocene of North Africa, because the sediment has seldom been screened. The best sample is from Ahl al Oughlam, but no significant new discovery has been made recently.

Among the Herpestidae, *Herpestes abdelalii* is a rather common form at Ahl al Oughlam. It is about the same size as *Herpestes paleoserengensis* from Laetoli [31], but p2 is narrow, without a posterior cuspid, and with an anteriorly placed main cuspid, P3 is longer, the parastyle of P4 is smaller. It is slightly smaller than *Galerella primitivus* from Olduvai [30], which is mostly known from milk-teeth. *Herpestes ichneumon* has been reported from the Middle Pleistocene onwards. Its earliest occurrence is at Thomas Quarry [4].

A single lower carnassial from Ahl al Oughlam has been referred to *Ichneumia* [11], a genus which is very rare as a fossil, as it has been reported only from Olduvai [30] and more recently from Lemudong'o [18]. The large talonid with a high hypoconid, and high, almost equilateral trigonid with sub-equal cuspids better match the carnassial of this genus than that of any other modern form, but the cuspids are more isolated than in modern *I. albicauda*, and the talonid is broader, so that the inclusion in *Ichneumia* now appears questionable, and this tooth might in fact belong to a new genus.

The Viverridae have a very sparse record in North-West Africa. From Ahl al Oughlam [11], a single m1 of large size has a rather open trigonid, with low cuspids, a large metaconid, and a

broad talonid with a large central basin circled by a ridge consisting of several cuspids with the entoconid rather posterior. This tooth is almost identical to a specimen of "*Viverra*" *leakeyi* from Omo Shungura E3, and there is no doubt about its specific identity, although it is a bit larger. This species is known from Olduvai bed I [29], Omo Shungura member C to member G [32], and Laetoli [31]; it is clearly distinct from both *Megaviverra* and from earlier large African *Viverra*. The occurrence of "*Viverra*" (or *Civettictis*) *leakeyi* at Ahl al Oughlam is clear evidence of a biogeographic connection between Morocco and East Africa.

In North-western Africa, the earliest occurrence of *Genetta*, a genus which is rather rare in the fossil record, is from the Middle Miocene of Beni Mellal [15], but there is no carnassial. A single m1 from Ahl al Oughlam [11], belongs to a *Genetta* sp. that is slightly different from the Kanapoi form [48] in that the talonid is larger, the notch between the metaconid and protoconid is deeper, and the tooth as a whole is slightly smaller. It is more different from the Lothagam [49] and Lukeino specimens [27], which have a lower protoconid and larger metaconid.

The genus has also been reported from the late Middle Pleistocene [24].

There are 4 species of *Hyaenidae* at Ahl al Oughlam. The smallest was referred with some doubts [11] to *Hyaenictitherium*, which is mostly a Late Miocene genus, of which it would be the latest representative. ([46], fig. 3). Its main primitive features are the relatively small size, a very large M1, and the presence of an m2, known only by its alveolus. The anterior accessory cusps of the premolars are quite small, as in *H. minimum* from the Late Miocene of Chad [5]. However, it differs from upper Miocene forms by the loss of M2 and p1, and by some broadening of the premolars (more so than in the Mio-Pliocene *Hyaenictitherium*). These are similarities with more derived forms, like *Hyaena* and especially *Ikelohyaena* and it is indeed close to this form in a cladogram based upon the matrix published by Werdelin and Solounias [52].

Crocota is the most common hyaenid in North-western Africa. The earliest is the species from Ahl al Oughlam, *Crocota dbaa*, which, like the modern spotted hyena, has large p3 and P3, a p3 inserted lower than the small p2, and a small talonid on m1, but it is more primitive than *C. crocuta* in its lower p3, and a lower carnassial with less reduced talonid, metaconid always present, and narrow paraconid. It also differs in its strong external cingulum on p4 and m1. On the upper P3, the accessory cusps are larger, and on the carnassial the metastyle is shorter than in the extant species. It is certainly close to *Crocota dietrichi* from Laetoli [34], but the latter has no strong cingulum on p4, and p3 is very low.

At Ain Hanech, a single mandible described by Arambourg as *Crocota* plots in the PCA among Middle and Late Pleistocene forms and the modern species, far from the Ahl al Oughlam *Crocota* and even far from early Pleistocene forms ([14], Fig. 1). It provides strong, if not definite, evidence against an earliest Pleistocene age for this locality.

After that time, *Crocota* is present in almost all Pleistocene sites. It is the most common hyaenid at Tighenif, and it is at about that time that it appears in Europe.

The second hyaenid from Ahl al Oughlam, *Pliocrocota perrieri*, is somewhat larger than the *Crocota*, its teeth are broad, and the carnassial is short, with a long paraconid and no metaconid. It clearly belongs to this species (perhaps ancestral to *Pachycrocota brevirostris*), which is widespread in Eurasia but has not been reported from East or South Africa. The form from Ahl al Oughlam has broad teeth for its size, warranting subspecific distinction from Eurasian forms, as *P. perrieri latidens* [11].

The set of teeth from the (Middle ?) Pliocene of Aïn Brimba that Arambourg [2] had called *Hyaena striata praecursor*, but that has been referred to *Pachycrocota* [19], should perhaps also be assigned to *P. perrieri*, but they are narrower. They could instead be closer to some more primitive form, like *Hyaenictitherium "arkesilai"* from Sahabi [52], although the teeth are broader and p2 is smaller at Aïn Brimba.

It is worth noting that at Ahl al Oughlam the morphospace (represented by the length and width of lower teeth) is equally partitioned between the 3 species of bone-cracking hyenas, with *Crocota* at about mid-distance between *Hyaenictitherium ? barbarum* and *Pliocrocota perrieri*, but that after the extinction of these species, *Crocota* seems to fill the niche that was previously occupied by *P. perrieri*.

Ahl al Oughlam is the only site in North Africa with *Chasmaporthetes*, but there are only mandibular remains. The teeth are small, the premolars have strong anterior accessory cuspids, as at Sterkfontein and Swartkrans, but the p3 is longer relative to p4 than in most other forms from Africa and Eurasia, except the Mio-Pliocene forms from Chad [6] and Langebaanweg, and *Ch. melei* from Sardinia [42], because the anterior cuspid of p3 is stronger than in *Chasmaporthetes lunensis* from Eurasia. Thus, North-African *Chasmaporthetes* is more like the African than the Eurasian forms.

From Ternifine onwards, there is a true *Hyaena*, coexisting with *Crocota*, and the hyaenid assemblage becomes similar to that of modern faunas.

The Felidae include both Felinae and Machairodontinae, but no definite *Megantereon*. Among machairodonts, the earliest and most complete specimen is the skull from Aïn Brimba that was referred to *Machairodus* by both Arambourg [2] and Petter and Howell [33]. The main difference with *Homotherium* is the large size of the bi-rooted upper P3 (Fig. 1). This is not unexpected for an early form of this genus, but even in the early *Homotherium* from Hadar the P3 is strikingly smaller. Arambourg also referred a 3rd metatarsal to this species. It is more curved, and the facet for the 4th metatarsal is more concave and less vertical than in the *Homotherium* from

Senèze or than in the specimen from Ahl al Oughlam, and it looks more like that of the Pikermi *Machairodus* (BMNH), which is more similar to that of a lion.

At Ahl al Oughlam there are some postcranial and dental remains, including a few isolated teeth, but the best specimen is a fragment of muzzle (Fig. 2). The canine is rather small, with an almost straight distal edge (even less concave than in *H. nestianus*), finely serrated mesial and distal edges without any wear facet, and a short root, but these latter two features might owe to the young age of the animal, as the canine is not fully erupted. The P3 is quite small (Fig. 1). P4 has no preparastyle, and its protocone is virtually lost.

At Ternifine there are three very compressed, incomplete upper canines, similar to those of *Homotherium*, and associated lower premolars showing that p3 is also much reduced.

An upper carnassial from Aïn Brimba was referred to *Megantereon* [28], but the long metastyle and relatively small protocone suggest *Dinofelis* instead. Still, the most conclusive evidence of *Dinofelis* in North Africa is at Ahl al Oughlam, where it is represented by poorly preserved remains [12]. Their most remarkable features are the bizarre morphology of the auditory area, with a paroccipital process distant from a forwardly stretched mastoid, the large size of the upper canine, the presence of a P2, and the short P3 and p4. The upper carnassial has a small protocone, a conspicuous preparastyle (stronger than at Aïn Brimba), and the maximum width of the blade lies in the middle of the tooth. Tooth proportions are close to *D. aronoki* from Koobi Fora and *D. darti* from Makapansgat [50] but m1 is thicker.

The Felinae are most diverse at Ahl al Oughlam, with probably five species. A single mandible of *Felis* is similar to modern cats, but the accessory cuspids of p3, especially the posterior one, are weak, and the main cuspid of p4 is high. The same differences hold when compared to the Laetoli form, or to the Late Miocene *Felis attica*, but similar features were noted [23] in *Felis lunensis* from the Pliocene of Europe, and it could be the same species.

A small *Felis* is also present at Tighenif (where there are no lower premolars), and at the Grotte des Rhinocéros (where the accessory cuspids of p3 are stronger, as in modern forms). Both can be referred to *Felis silvestris* cf. *libyca*.

The most common felid at Tighenif matches *Caracal caracal* in the proportions of its teeth, with a p3 smaller than in lynxes, but the accessory cuspids are strong and the main cuspid of p3 is higher than in the caracal.

A distal humerus from Ahl al Oughlam, with two well marked stop facets for the radius and ulna, is relatively broader than in *Panthera* and the susepitrochlear foramen is less slit-like. It can be referred to a lynx, as it is almost identical in size and morphology to that of *Lynx lynx*.

Still, the most definite record of a lynx in North Africa is from Oulad Hamida 1 Quarry, in deposits equivalent in age to Grotte des Rhinocéros (early Middle Pleistocene). Called *Lynx thomasi*, it is remarkable in its very long m1, and is probably descended from a form close to the

Spanish *Lynx pardina*. This is one of the very few definite examples of immigration of a large mammal from the North [10].

Panthera pardus is the most common felid at Ahl al Oughlam, and it is therefore much more common than in East Africa. It the size of a small leopard, but some tooth proportions, especially the small lower p4 are different from *Panthera pardus* and reminiscent of the European puma, *Puma pardoides*, first identified at Saint Vallier, a French site dated to about 2 Ma., where it was called *Panthera schaubi* [47]. Indeed, it has recently been suggested [17] that the small African Plio-Pleistocene leopards usually referred to *P. pardus* belong in fact to this Eurasian species. However, at Ahl al Oughlam, the anterior border of the muzzle and the chin are less steep than in *Puma pardoides*, the palatal notches are different, the M1 is larger, the p4 not particularly broad, and all canines are grooved. I believe that we are definitely dealing with a true leopard here, and the same is probably true of other African sites; perhaps the characters by which these Pliocene African forms differ from modern panthers are simply primitive.

There is no dental evidence of a large *Panthera* at Ahl al Oughlam, but a lion-sized feline complete humerus is much too large to belong to *Panthera pardus*. It differs from modern *P. leo* or *P. tigris* in that the distal end is broad compared to its thickness, and the susepitrochlear foramen is high. This is the earliest evidence of a large *Panthera* in North Africa, but it probably does not belong to the *P. leo* lineage. A few specimens from Tighenif are also lion-sized. The remarkable features of the most complete mandible are the large anterior accessory cuspid of p4, and the narrow teeth; the precise length of m1 is unknown, but in any case it is somewhat of an outlier on the PCA of lower teeth measurements. Thus, there is some evidence, albeit slender, that we have in the Plio-Pleistocene of North Africa some lion-sized *Panthera*, perhaps of a single lineage that is not *P. leo*.

Two lower carnassials from the Grotte des Rhinocéros are intermediate in size between lions and panthers. They are too broad for *Acinonyx*, and could belong to the European *P. gombaszoegensis*, but such an identification would be premature, and I would not conclude that there was a migration of this species from the North.

The earliest true *P. leo* is probably the one from late Middle Pleistocene of Doukkala [26].

Acinonyx aicha is represented at Ahl al Oughlam by a complete skull, unfortunately completely crushed, a maxilla and some teeth. It is less abundant than *Panthera*, but this is the only African site where the cheetah is not rare, and the only Plio-Pleistocene site with *Acinonyx* in North Africa. The skull lacks the characteristic bending and shortening of the temporal fossa of the modern cheetah. There is no P2, and P3 is close to the canine, very large, with a main cusp that is high but lower than in the modern cheetah, and with strong accessory cusps. This tooth also differs from that of the modern form in that the anterior cusp is not in line with the main axis, and in its broad posterior part. M1 is broad and two-rooted. *Acinonyx aicha* differs from *A. pardinensis* from

Saint-Vallier in its longer P3. Viret [47] illustrated a skull much like that of the modern *Acinonyx*, but this skull is heavily reconstructed, and a second skull from Saint-Vallier (CCEC QSV-115), crushed but unreconstructed, is much more like those of *Panthera* or *A. aicha*, and it is likely that this was the usual morphology of late Pliocene *Acinonyx*.

The earliest representative of the Canidae in North Africa is a fragment of maxilla from Lissasfa, a site near Casablanca dated by rodents to about 5.5 to 6 Ma. [38]. The M1 is long for its width, and the P4 is much shorter than in European *Canis* of similar age such as *C. cipio* from Concu [36]. It is probably also different from the *Vulpes* from the Late Miocene of Toros Menalla in Chad, which does not have very large posterior teeth [7]. Among modern canids, only *C. adustus* may have such a short carnassial, but at Lissasfa the muzzle is quite short, in sharp contrast to the side-striped jackal. The carnassial is also short in the "aff. *Canis brevirostris*" from Laetoli [3], referred to *Nyctereutes* [51], and in some other *Nyctereutes*, and this is the most likely identification.

At Ahl al Oughlam there is a true *Nyctereutes*, with a subangular lobe, very large m2 and m3, and an m1 entoconid that is as large as the hypoconid, unlike in most other *Nyctereutes*. I have referred it to a new species, *N. abdeslami* [11]. Although some specimens have an outlier position on the PCA, it is close to some Spanish forms, but I refrain from concluding from this an immigration from the north, pending revision of *Nyctereutes*-like African forms.

In the Middle Pleistocene, the most common form of canid, which is abundant both at Tighenif and the Thomas and Oulad Hamida quarries, is mostly known from isolated teeth, plus some maxillae and mandibles. The upper molars are long relative to their width, the metaconid is large and the talonid is wide on m1. Again, the muzzle is very short and thus very different from that of *Canis adustus*. These teeth are much more like those of *Nyctereutes*, but the mandible lacks the subangular lobe. I tentatively refer this canid to *Nyctereutes* sp., assuming that it must be descended from some *N. donnezani*-like form without a subangular lobe, rather than from the Ahl al Oughlam form. It may be that the importance of this latter feature has been overestimated.

The small *Vulpes* from Ahl al Oughlam shares some morphological characters with the fennec, such as the rather short trigonid on m1, but the talonid cuspids are less widely spaced, and it is of larger size. One of the four m1s has an incipient crest between hypoconid and entoconid, and the other three do not. The lower premolars are unknown, but are closely packed, in contrast to *V. riffautae* from the late Miocene of Chad [7]. Other differences from this species, which is of the same size, are that lower m1s have a small pre-entoconid, that the talonid of m2 is shorter than the trigonid, and that the entoconid of this tooth is at least as large as the hypoconid. Still, there are some similarities with the Chadian form, the upper teeth of which are unknown. At Ahl al

Oughlam, the upper carnassial is short, and M2 is large compared to M1. This small fox probably deserves a new specific name.

Arambourg [2] reported a medium-sized *Vulpes* from Ain Hanech, but acknowledged that its origin is doubtful. Tighenif has also yielded a fox that is only slightly larger than that of Ahl al Oughlam, and about the same size as *V. rueppelli*; it also shares with both these forms a strong cingulum on the upper molars, completely surrounding the protocone, and can be referred to *Vulpes* cf. *rueppelli*.

All these North African foxes are clearly distinct from the European foxes, which have shorter upper molars compared with the carnassial, but from the early Middle Pleistocene of Thomas Quarry onwards, there is a fox more similar to the living North-African *Vulpes vulpes atlantica*.

The third canid of Ahl al Oughlam is about the same size as *Nyctereutes* but can be readily distinguished from it by the reduced crushing part of its dentition compared to the carnassials and premolars. The M1 is short and broad, without anterior cingulum; on m1 the metaconid and entoconid are small, and the latter cuspid is not connected to the hypoconid by a crest. This feature would exclude it from *Canis* according to Tedford and Qiu [45], but as the crest can be quite faint in this genus, it may be doubted that it can really define it. Alternatively, the material could be referred to *Eucyon*; Tedford and Qiu [45] listed, as the single apomorphic feature of this genus among the Canini, only shared by the "wolf group", the presence of a second posterior accessory cuspid on p4. However, evidence for this purportedly critical feature of the genus in the various species or specimens assigned to it is very slender. The p4 may be unknown (*Eucyon* "monticinensis" from Brisighella [41,43]; *E. cf. odessanus* from Sarikol Tepe [21]), missing or lacking the second cuspid (*E. intrepidus* from Lukeino [27]), said to possess the second cuspid but not illustrated, or lacking it on the figure (*E. zhoui* and *E. davisi* from China [45]; *Eucyon* sp. from Megalo Emvolon [22]), or definitely lacking this second cuspid (*E. adoxus* from Saint-Estève, and at Ahl al Oughlam). This cuspid is definitely present in *E. marinae* [44], but is so small that it is hard to give it much weight. Further revisions may clarify canine systematics, but at present, it looks as if this genus has become a waste basket, and I prefer to leave the Ahl al Oughlam canid as cf. *Canis* sp.

True jackals appear only in the late Middle Pleistocene, e.g., at Sidi Abderrahmane. They cannot be separated from *Canis aureus*.

A few teeth from the early Middle Pleistocene of Tighenif, Grotte des Rhinocéros and Thomas Quarry belong to a *Lycaon* of large size. The talonid of m1 is unicuspid, but on M1 the hypocone is perhaps still more distinct from the trigon than it is in *L. pictus*. The *Lycaon* from the late Middle Pleistocene of Doukkala is more similar to the recent form.

There is no large canid at Ahl al Oughlam but Arambourg [2] described as *Canis cf. atrox* the maxilla of a large canid from Ain Hanech. It was recently referred to *Lycaon* ([25] fig.1H, not 1G as indicated in their caption), but it has a premolar row that is labially concave in occlusal view, a large hypocone on M1, and an M2 that is as large as in *Canis lupus*. I can see no reason for putting it on the *Lycaon* lineage, and it is probably closer to what is called *Canis falconeri* in Europe.

Among the Mustelidae, the otters include only representatives of *Lutra*, as there is no *Aonyx* or *Enhydriodon* in North-western Africa, in contrast to the rest of the continent. At Ahl al Oughlam, the main characters of this *Lutra* are the rather large size, crowded premolars, large canine and small incisors, and talonid of m1 short and flat, narrower than the trigonid. This species is certainly close to the group of otters including *Lutra lutra*, *L. maculicollis*, and *L. simplicidens* from Europe [53], but comparisons are difficult because *Lutra* is very rare in the Pliocene of Europe and Africa; it is certainly distinct from *Torolutra ougandensis* from Uganda and Omo, which has a longer jaw, with less crowded premolars. There is also an otter at Tighenif, probably of the same group, with a large canine, slender premolars and narrow carnassial.

Mellivora, the honey badger, is represented at Ahl al Oughlam by a form of rather small size, but the available material cannot be distinguished from the modern species, which is very variable, especially in the size and proportions of m1. A closely related species is also present in the Middle Pleistocene, at Tighenif and Thomas Quarry, but its skull is perhaps more expanded at mastoid level, as in *Mellivora sivalensis*. The genus is known in North Africa until today, but never reached Europe. The other large European mustelids, *Meles* and *Gulo*, are unknown in North Africa.

Small mustelids are almost exclusively known from Ahl al Oughlam, probably because this is the only site where large amounts of sediment have been screened, as already mentioned.

A few teeth, including three P4 and an m1, have been referred [11] to *Prepoecilogale cf. bolti*. The upper carnassials are broad but much shorter than in *Ictonyx*, but they are otherwise rather similar, with a very strong anterior cingulum, an incipient parastyle, and a long protocone that does not reach much anterior to the main part of the tooth. This species has been reported from South Africa [8] and Laetoli [31], and the genus is unknown outside Africa.

A second species is slightly smaller, the protocone is directed more anteriorly (longer than in *Mustela*), and the parastyle more salient labially; these characters are like those of the living *Poecilictis*, a living genus or subgenus with a circum-Saharan distribution. In true *Ictonyx* the protocone is much thicker and more transverse. All these small mustelids are probably closely related, and are definitely of African type, and quite unlike the European *Mustela* or *Baranogale*. *Mustela* itself is a recent introduction, and has been reported only from the upper Pleistocene [1].

The Ursidae were quite uncommon before the Late Pleistocene. Besides an *Agriotherium* from the Late Miocene of Menacer [35], the earliest bear from northwest Africa is the one from Ahl al Oughlam, which is represented by a few isolated teeth. It is a small primitive form close to *Ursus etruscus* or *Ursus minimus*, with an extremely small protocone on P4, but there is already some elongation of the talon of M2.

No bear is known during the lower Pleistocene, but this is not surprising, as they are quite rare both at Ahl al Oughlam and Tighenif, where a few remains document a form the size of *U. deningeri*.

Later in the Middle Pleistocene, bears become more common. In Thomas and Oulad Hamida Quarries, and at the Grotte des Ours of Sidi Abderrahmane, there is a large form with elongated last molars, but with narrow teeth (especially the lower ones); it also differs from the *deningeri-speleaeus* lineage in the lack of extra tubercles on p4 and m1. Thus, we are probably dealing with an endemic North African branch, the valid name of which is *Ursus bibersoni* [9], perhaps directly descended from the Ahl al Oughlam species. If, as seems likely, there were true *U. arctos* after that, a second migration from the North must have occurred, replacing this endemic *U. bibersoni* lineage. Bears went extinct in the Maghreb in historical times [16].

An unexpected discovery at Ahl al Oughlam was that of a member of the Odobenidae, a group which was previously unknown in the Eastern Atlantic south of Belgium. There are some differences from the modern *Odobenus*, such as the larger condylar foramen, the position of the last teeth below the root of the zygomatic, the thin mandibular corpus, which is thickened in the modern form, and there are also some differences in the post cranial bones. Called *Alachtherium africanum* [11], this walrus has recently been referred to the widespread Atlantic species *Ontocetus emmonsii* [20].

3. Conclusion

Ahl al Oughlam shows that, under favourable taphonomic conditions, at least 20 carnivore taxa can be associated ([13], fig. 2); much less diverse assemblages found in other sites in North Africa (and elsewhere) are therefore so impoverished by taphonomic or collecting bias that attempting to recognize turnover patterns would be futile. The only site with a reasonable carnivore collection is Tighenif, although it lacks small species. Table 1 compares the number of cranial and dental specimens of large and medium-sized carnivores at these two sites. It shows that the proportions of the various groups do not change much between the Late Pliocene and the earliest Middle Pleistocene, given that Ahl al Oughlam is a cave site more likely to shelter hyaenids.

| | Hyaenidae | Felidae | Canidae | large Mustelidae | Ursidae |
|----------|-----------|---------|---------|---------------------|---------|
| AaO | 145 | 69 | 102 | 8 | 7 |
| Tighenif | 39 | 35 | 60 | 9 | 6 |

The main events between these two sites are the replacement of a diverse hyaenid assemblage by the modern tandem, of a true *Nyctereutes* by some related form, and the arrival of a (or more probably, several) large canid(s).

More positive conclusions can be drawn from biogeography. Although carnivores often have wide geographic ranges, the Ahl al Oughlam carnivore fauna shares with East and South Africa a number of taxa which are unknown in Eurasia at that time: *Herpestes*, *Ichneumia*, *Viverra leakeyi*, *Genetta*, *Crocuta*, *Chasmaporthetes nitidula*, *Panthera*, presumably omnivorous *Vulpes*, *Prepoecilogale*, and *Ictonyx* s. l., whereas it lacks many Eurasian taxa (*Viverra*, *Megaviverra*, *Puma*, *Cuon*, *Vulpes* with long carnassials, *Baranogale*, *Martes*, *Mustela*). The most definite immigrations from the North are *Lutra* and *Ursus* (and *Ontocetus* !); it must be noted that all are good swimmers. *Pliocrocuta perrieri* could be descended from the Aïn Brimba hyaenid; *Nyctereutes* could be an immigrant from Spain, but African forms need revision.

In the early Middle Pleistocene, *Lynx thomasi* is certainly an immigrant from the North, perhaps together with the strange *Nyctereutes*, but other carnivores could well be of African origin.

A bivariate diagram of factors 1-2 of a factor analysis on some carnivore faunas is shown in Figure 3. The results should be viewed with caution because the two axes explain less than 30% of the variance, but the distinction between African (to the right) and Eurasian sites (to the left) is very clear; Ahl al Oughlam definitely plots among the former, but Tighenif and Late Pleistocene Moroccan sites become less distant from European ones.

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Captions to figures

Fig. 1 : Plot of P3 length vs. P4 length in some *Homotherium*-like forms.

Fig. 1 : Graphique longueur de P3 x longueur de P4 chez quelques formes du groupe de *Homotherium*.

Fig. 2 : cf. *Homotherium* sp., Ahl al Oughlam. Fragment of muzzle with incisors, canine, P3 and incomplete P4. Scale = 50 mm.

Fig. 2 : cf. *Homotherium* sp., Ahl al Oughlam. Fragment de museau avec la canine, P3 et la P4 incomplète. Echelle = 50 mm.

Fig. 3 : Factor analysis of carnivore faunas of some Late Pliocene to Late Pleistocene African, European and Western Asiatic sites. Sites in roman, taxa in italics, North-western African sites in bold.

Fig. 3 : Analyse factorielle des faunes de carnivores de quelques sites du Pliocène supérieur au Pleistocène supérieur d'Afrique, d'Europe et d'Asie Occidentale. Sites en romain, taxons en italiques, sites du Maghreb en gras.