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Recent Quaternary fossil mammals of Chrafate and Ez Zarka. The origin of modern fauna in the Northern Rif (NW Morocco, Northern Africa)

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ABSTRACT

The Northern Rif (Northern Morocco, Northwestern Africa) was characterised in the late Pleistocene and the Holocene by mammal assemblages, which included species with different biogeographic origins. Saharian, Saharo-Mediterranean, Sahelian species as well as some forms adapted to the Mediterranean climatic regime have been recorded. The fossil mammal assemblages recovered from two new localities in karstic infills (Chrafate and Ez Zarka) correspond well with this palaeobiogeographic setting and suggest that this region was a crossroad of palaeoartic and palaeotropical species. The variety observed in the fossil mammal assemblages and in the present mammal fauna resulted from a long period of aridity, which coincided with the late Pleistocene post-glacial stage and was followed by a Holocene humid phase. This palaeoclimatic change resulted from the equator ward shift of the high-pressure cell belt, which allowed the southward shift of less arid Mediterranean climatic zones.

KEYWORDS **Mammals. Faunistic types. Late Pleistocene-Holocene. Northern Morocco. Northwestern Africa. Western Mediterranean.**

INTRODUCTION

The Northern Rif is a region located in Northern Morocco. In opposition to other regions in this country (i.e. Southern and Central Morocco, along the Atlantic coast), the Rif had to date a very poorly known fossil mammal record. Only a few localities were known in the vicinity of the cities of Tetuan, Tangier, Chefchauen and Azilah. Other scarce faunal remains had been reported resulting from an archaeological campaign by Tarradel (1955). As a consequence, this zone had been considered as paleontologically barren.

Two new fossiliferous karstic localities in the Northern Rif (Chrafate and Ez Zarka) delivered four Quaternary (late Pleistocene-Holocene) fossil mammal assemblages, a fact that has improved substantially the palaeomastological record in the region. This study deals with the analysis of the distribution of different species of Pleistocene-Holocene micromammal and large mammal assemblages in the Northern Rif. One of the aims of this contribution is to characterise these assemblages taking into account the specific palaeobiogeographic meaning of this region during the late Pleistocene-Holocene time span, when noticeable palaeoclimatic changes took place.

GEOLOGICAL SETTING

The Pleistocene-Holocene mammal assemblages that are the object of this paper were collected from karstic infill deposits (Figs. 1 to 3). The karstic fissures which

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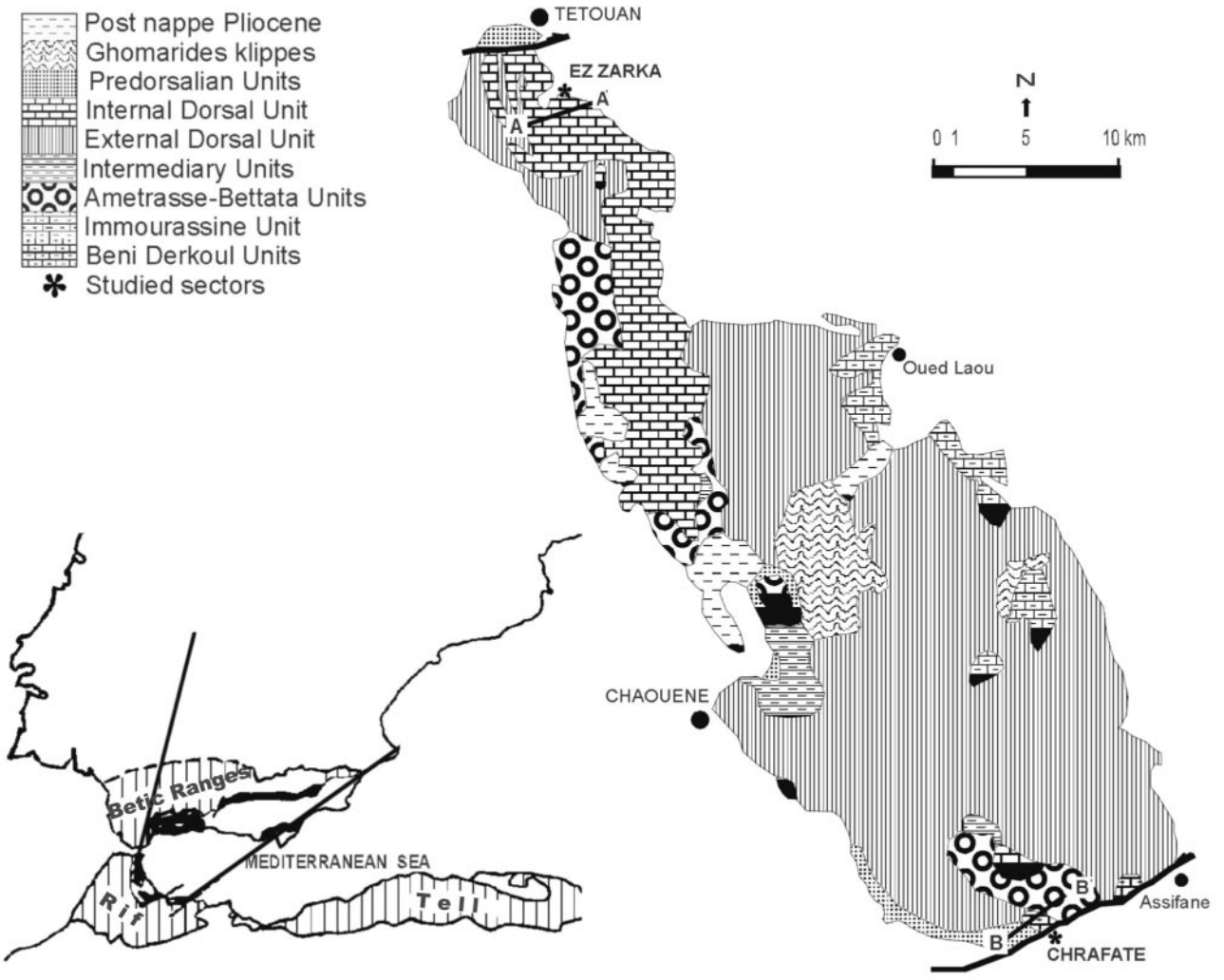


FIGURE 1 **Location of the new Quaternary fossil mammal localities in a geological sketch of the Northern Rif. Note the location of the simplified cross sections in Figs. 2 and 3 (Nold et al., 1981).**

include the Chrafate deposits developed in the unit of Jebel Lakraa Nappe, which is made up of up to 300 m of limestone and dolomite successions (Jbel Lakrra). The karstic infill is situated in the Chrafate region, at the side of the road between Ketama and Chefchauen (X = 527.5; Y = 496.2), in the so-called External Limestone Dorsal (Fig. 2). This locality is an ancient abandoned quarry where two fossiliferous levels (Chrafate 1 -CH1- and Chrafate 2 -CH2-) occur. Chrafate 1 consists of a soft, brown clay layer, which is overlain by partially hardened lighter-coloured clay, which in its turn yielded the Chrafate 2 mammal assemblage.

The Ez Zarka karstic deposits occur in the Hafa-Ferkennix thrust sheet (Fig. 1). This second locality (X = 506.6; Y = 545.5) is localised in the Ez Zarka region, to the south of Tetuan, in the so called Internal Limestone Dorsal (Fig. 3). It is a currently active lime quarry. Two new fossiliferous levels were recognised in this locality (Ez Zarka 1 -ZRK1- and Ez Zarka 2 -ZRK2). The ZRK1 layer is composed of rather dark clay, which is overlain by a dark red mudstone where the ZRK2 mammal assemblage was found.

PALAEOFAUNISTIC ASSEMBLAGES

The fossil mammal collection was carried out by selectively sampling the karstic infillings, taking into account their relative stratigraphic position and major lithological characteristics. The mudstones sampled from the karstic infills were treated according to the cleaning techniques (mudstone washing and seaving) described by Freudenthal et al. (1976) and López-Martínez (1989). The magnetic fraction of the washed and dried material was extracted using an electric magnet. After sorting out the material it appeared that it was composed mainly of isolated teeth and bones.

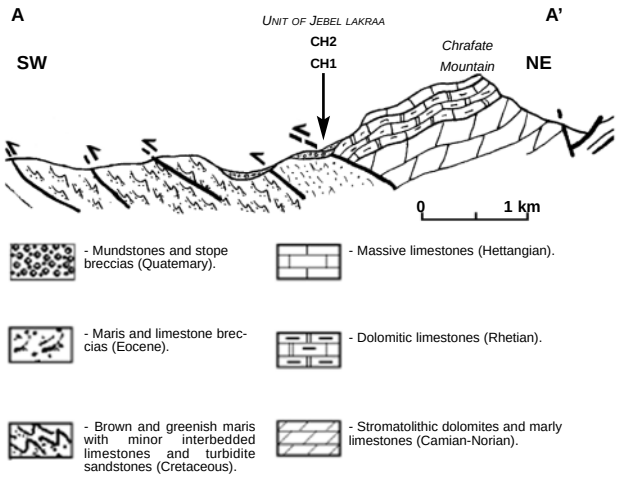


FIGURE 2 | **Geological cross section showing the location of the Chrafate localities. See location in Fig. 1.**

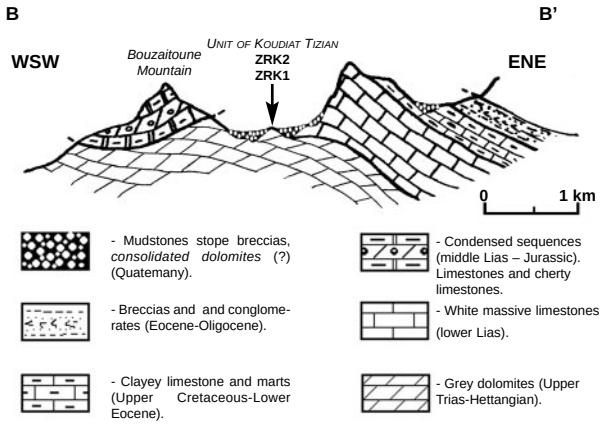


FIGURE 3 | **Geological cross section showing the location of the Ez Arka localities. See location in Fig. 1.**

A variety of rodents, carnivores, lagomorphs, chiropters, artiodactyls, primates, insectivores and macroscelides constitute the four mammal assemblages studied. Their composition is summarised in Table 1 and their age and overall biogeographic affinities are discussed here.

AGE OF THE FOSSIL ASSEMBLAGES

The assessment of the faunal content in the studied sites shows that each fossil assemblage has yielded a more or less diverse faunal association, suggesting that each one corresponds to different ages, which range from the end of the late Pleistocene to the Holocene.

The CH1 faunal assemblage appears to be the oldest, as it can be deduced from the occurrence of *Psammomys obesus*, *Asellia tridens* and the absence of some characteristic forms as *Crocidura russula* (Fig. 4J). As a consequence an early late Pleistocene age is suggested for this association.

The faunal assemblage of the CH2 locality (which overlies CH1) shows close similarity to ZRK1. Nevertheless both localities are distinguished by the appearance of the species *Apodemus sylvaticus* in ZRK1 (Fig. 4F) and its absence in CH2. A latest late Pleistocene (Soltanian) is suggested for CH2 and an early Holocene age (Rharbian) is suggested for the ZRK1 association.

The fossil assemblage ZRK2 was found in a layer that overlies ZRK1 and is clearly younger taking into account the appearance of *Mus musculus* (Fig. 4G). A late Holocene age is suggested for this association.

BIOGEOGRAPHIC AFFINITIES

The four fossil assemblages are varied and display some affinities and differences when compared to the present mammal fauna in Northern Morocco and other neighbouring regions. Nevertheless, the study and zoogeographic analysis of the reported associations show some peculiar trends that enable the assembly of the reported taxa into nine faunistic types. This subdivision was used by Kowalski and Rzebik-Kowalska (1991) and Aulagnier (1992).

1) Saharan type (in strict sense), which includes characteristic taxa of desert zones. These forms are considered to be endemic fauna of the Sahara and include, for instance, *Gazella dorcas*, which shows a present distribution mainly linked to the arid bioclimatic Saharan regions (Sahara of the Arabian Peninsula (?)). Moreover, *Asellia tridens*, a chiropter which occurs in the arid zones of North Africa, Arabia and as far as central Asia, can also be cited.

2) Saharan type (in a broader sense), which includes *Psammomys obesus*, a rodent which lives all along the border of the Sahara as well as in the Arabian Peninsula.

3) Saharan and Mediterranean type, with forms which occur in the arid southern zone (semi-desert and steppe) of the Southern Mediterranean areas (i.e. *Gerbillus campestris* and *Meriones shawi*) (Figs. 4D and 4E).

4) Sahelean type, which encompasses forms living in dry savannas and are distributed in the Afro-tropical regions to the south of the Sahara (i.e. *Lemniscomys barbarus* and *Arvicanthis niloticus*) (Figs. 4A and 4B).

5) Tropical-type species, which dwell tropical Africa and Eurasia regions (i.e. *Panthera pardus*) (Fig. 4K).

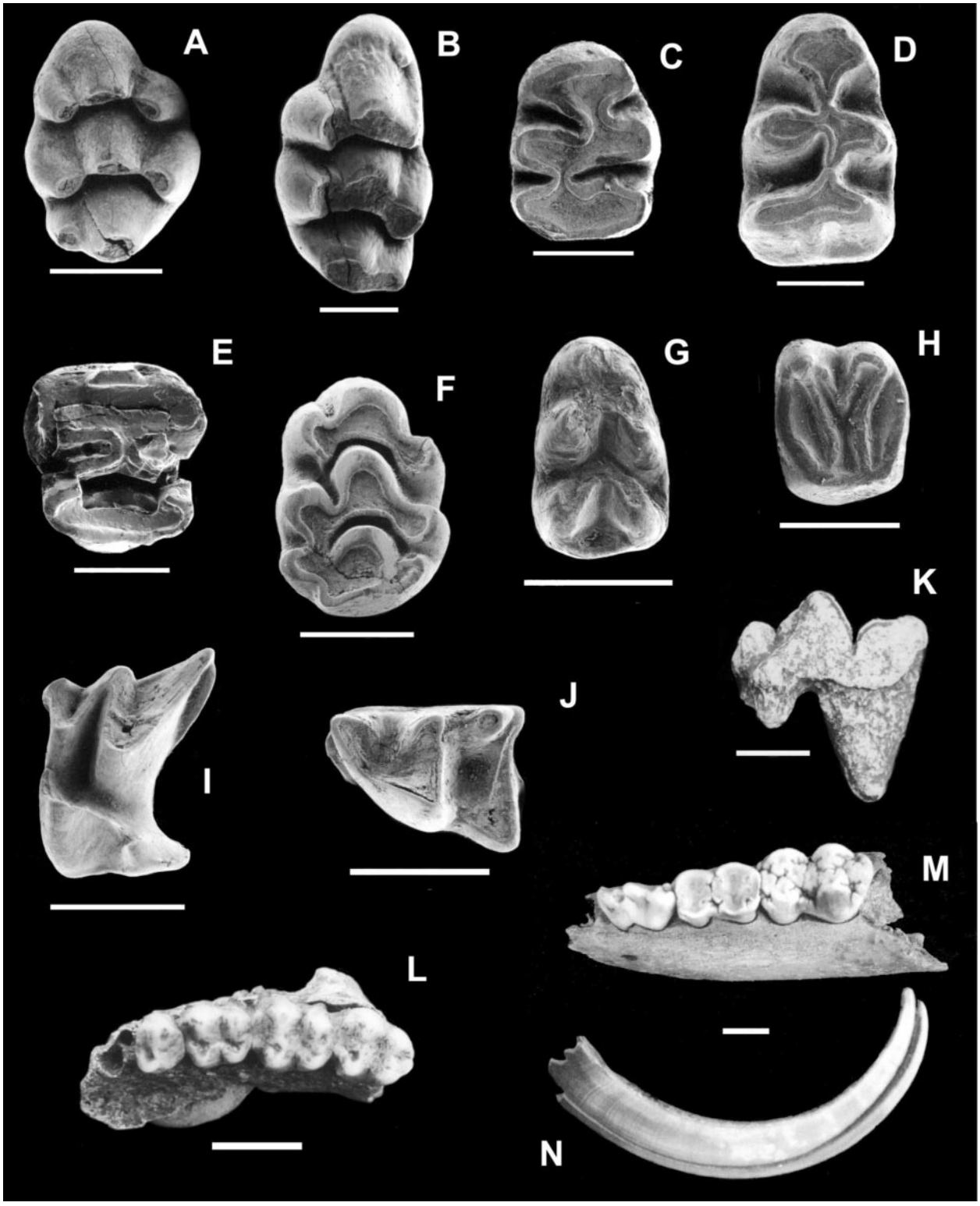


FIGURE 4 **Characteristic taxa recorded in the new Quaternary fossil mammal localities of the Northern Rif. A) M1 upper right, *Lemniscomys barbarus*, Locality: ZRK2-248. B) M1 upper left, *Arvicanthis niloticus*, Locality: ZRK1-1353. C) M1 lower right, *Dipodillus maghrebi*, Locality: CH1-52. D) M1 upper right, *Gerbillus campestris*, Locality: CH1-44. E) M2 upper right, *Meriones shawi*, Locality: CH2-305. F) M1 upper right, *Apodemus sylvaticus*, Locality: ZRK1-408. G) M1 lower right, *Mus musculus*, Locality: ZRK1-192. H) M2 upper right, *Eliomys quercinus*, Locality ZRK1-468. I) M1 upper left, *Crocidura whitakeri*, Locality: ZRK1-1178. J) M1 lower left, *Crocidura russula*, Locality: ZRK1-1238. K) PM upper right, *Panthera pardus*, Locality: ZRK1-1850. L) PM2-M3 lower *Macaca sylvanus*, Locality: CH2-786. M) PM3-M2 lower left, *Sus scrofa*, Locality: CH2-549. N) C lower, *Sus scrofa*, Locality: CH2-551.**

6) Mediterranean-type forms, which are found on the boundary of the Mediterranean basin, Europe, Asia and non-Saharan North Africa (i.e. *Mus spretus* and *Crocidura whitakeri*) (Fig. 4I).

7) Palaeoarctic species, which split into two groups: (a) Some taxa which come from West Europe (remote Western Palaeoarctic) and the Maghreb (i.e. *Crocidura russula*); (b) Other taxa which are distributed in Northern Africa, Europe and Asia in colder and temperate climatic regions of the Mediterranean (i.e. *Myotis blythi*, *Apodemus sylvaticus* and *Eliomys quercinus*) (Fig. 4H).

8) Endemic types, including very localised species (i.e. *Dipodillus maghrebi* and other endemic types of Northern Africa: *Elephantulus rozeti* and *Macaca sylvanus*) (Figs. 4C and 4L).

9) Cosmopolitan forms, whose distribution covers at least three continents (Africa, Europe and Asia) regardless of their geographical origin and being able to inhabit regions with very varied climates (i.e. *Mus musculus*).

COMPARISON OF THE LATE PLEISTOCENE-HOLOCENE AND PRESENT MAMMAL ASSEMBLAGES

The comparison between the fossil mammal assemblages and the recent mammal fauna in the Rif and other Northern Africa regions reveals a large variety and some differences. The analysis of the diverse major taxonomic groups confirms this fact.

Rodentia

For the Rodents, it appears that the variation is clear-cut while analysing families (Table 2). Thus, Gerbilidae is well represented by four species in most of the studied deposits. Apart from the endemic species *Dipodillus maghrebi*, the other Gerbilidae recorded in the late Pleistocene-Holocene assemblages are widespread in Northern Africa. Some of them even extend their distribution area to the Arabian Peninsula and the Middle East, where they seek affinities or even origin from central Asia. All these rodents migrated through Saharan paths. Therefore, we can distinguish two faunal types according to their distribution: 1) North African *Gerbillus* and *Meriones* species, which are characteristic of arid environments and currently display adaptive capacities to less desertic biotopes and also to increasing anthropisation of the environment; 2) Saharan species in broader sense of the term, of desert origin, with a distribution over the North African edges of the great desert (*Psammomys obesus*).

The family Muridae presents a very varied current distribution, which for anthropophile forms is independent from the bioclimatic variables. However, it remains rather varied in North Africa by comparison to the countries situated to the south of the Sahara desert (18 species in Senegal, Aulagnier, 1992). The two main migration paths that opened up for all species during some period of the middle and late Pleistocene were the Northeast Libyco-Egyptian path and the subtropical and Southwestern paths of the Western Saharan way (Petter, 1974; Kowalski and Rzebik-Kowalska, 1991). These migration ways gave rise to the settlement of *Mus* and *Lemniscomys barbarus* at the beginning of middle Pleistocene and *Arvicanthis niloticus* at the end of middle Pleistocene on the Atlantic front of the Sahara desert (Simpson, 1969; Jaeger, 1975a, b); It is during this period that the subsaharian tropical influence is the most remarkable. *Apodemus sylvaticus* appears on the Mediterranean coast in the late Pleistocene (Jaeger, 1975a, b). At present, seven species occur in this region. One of them is *Rattus norvegicus*, which has recently entered and spread to all cities situated to the west of the Atlas Mountains. In 1910, it was only known in port cities of the Tangiers Peninsula. Ten years later, it inhabited all cities of the Rif Mountains (Cabrera, 1932). *Rattus rattus* was also involuntarily introduced by man and became cosmopolitan

The family Hystricidae has not been recorded in the studied fossil assemblages. It currently occurs in the same northern region and is represented by the species *Hystrix cristata*, which belongs to the palaeotropical faunal type. This species extends up to the Saharan edges.

The Gliridae contribute to this diversity only by a single taxon, *Eliomys quercinus*, which has been reported in all the fossil assemblages and is also present in the recent mammal association. Gliridae is a rather conservative family and its occurrence in the Maghreb has been shown to be ancient (Jaeger, 1975a). Neverless its present-day genus did not appeared in Morocco until the Pliocene or even Pleistocene (Cabrera, 1932). Then it differentiated there or migrated from neighbouring regions to Europe and in particular to the Near East because of climatic fluctuations, to which this family is particularly sensitive. Probably the Sahara desert often acted as a barrier for it.

Insectivora

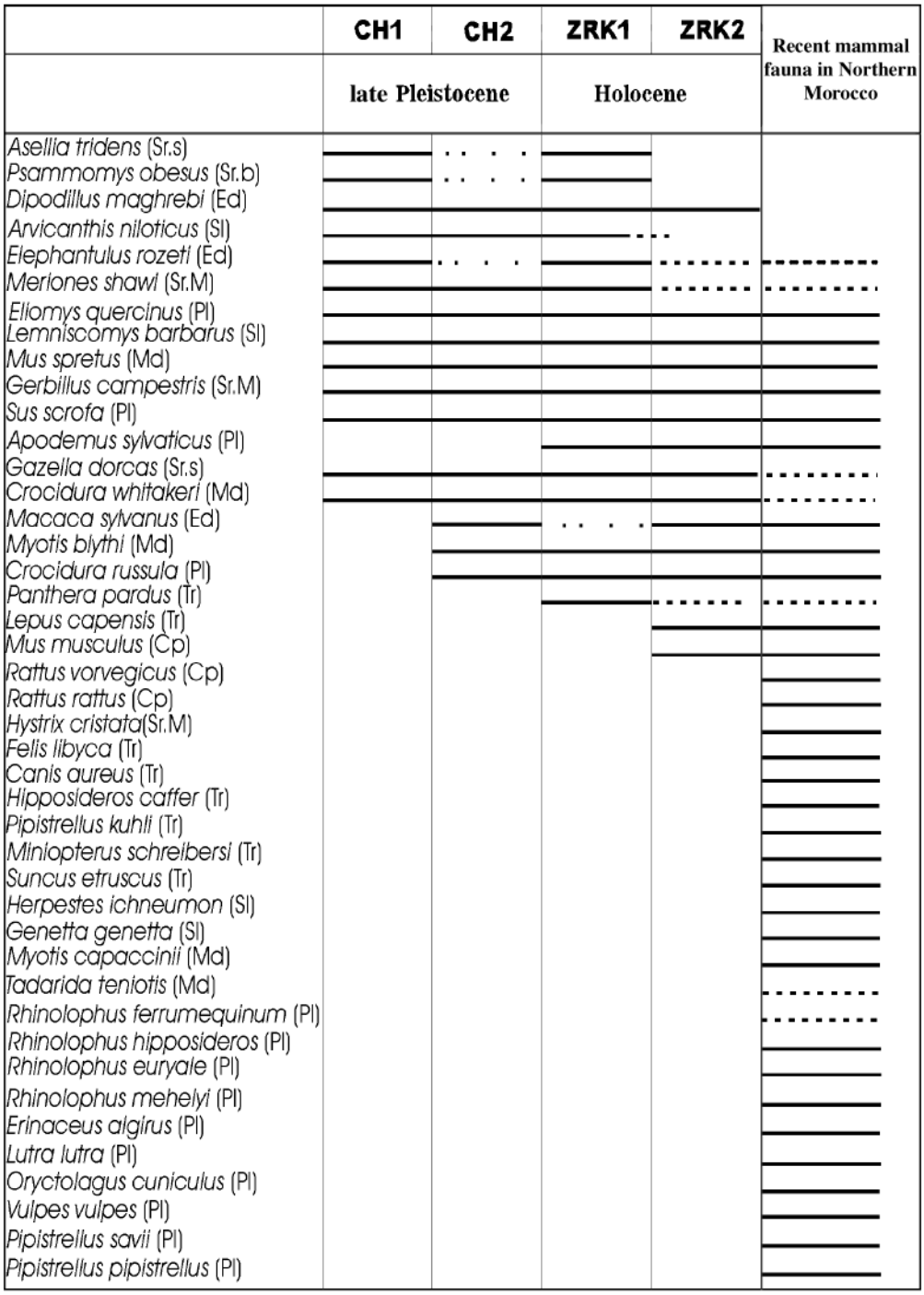
The Insectivora species occurring in the Quaternary localities include some palaeoarctic forms, mainly the Mediterranean ones. They are characterised by a very slight penetration into the desert edge zones. However, the Sahara constituted an efficient gateway to the immigration of palaeotropical species, which are relatively not very numerous in Western Africa. Nine species occur in Senegal, eleven in Mali, and twelve in Burkina Faso (Nicol and Rathburn, 1990). The two species of *Crocidura* found in the deposits of Ez Zarka and Chrafate are extensively

TABLE 1 **Fauna list of mammals of Chrafate and Ez Zarka deposits (*) and fauna list of the present mammals of the North of Morocco (**). Data obtained from the guiding map of protected areas 1996 and the catalogue of the wild mammals of Morocco (Aulagnier and Thevenot, 1986).**

ORDERS *Species*	**CH1***	**CH2***	**ZRK1***	**ZRK2***	**Recent mammal fauna in Northern Morocco****
RODENTIA					
Eliomys quercinus (Pl)	+	+	+	+	+
Apodemus sylvaticus (Pl)	-	-	+	+	+
Lemniscomys barbarus (Sl)	+	+	+	+	+
Mus musculus (Cp)	-	-	-	+	+
M. spretus (Md)	+	+	+	+	+
Arvicanthis niloticus (Sl)	+	+	+	-	-
Rattus rattus (Cp)	-	-	-	-	+
R. norvegicus (Cp)	-	-	-	-	+
Hystrix cristata (Sr.M)	-	-	-	-	+
Gerbillus campestris (Sr.M)	+	+	+	+	+
Dipodillus maghrebi (Ed)	+	+	+	+	-
Meriones shawi (Sr.M)	+	+	+	-	~
Psammomys obesus (Sr.b)	+	-	+	-	-
CARNIVORA					
Panthera pardus (Tr)	-	-	+	-	~
Canis aureus (Tr)	-	-	-	-	+
Vulpes vulpes (Pl)	-	-	-	-	+
Lutra lutra (Pl)	-	-	-	-	+
Genetta genetta (Sl)	-	-	-	-	+
Herpestes ichneumon (Sl)	-	-	-	-	+
Mustela nivalis (Pl)	-	-	-	-	+
Felis libyca (Tr)	-	-	-	-	+
LAGOMORPHA					
Lepus capensis (Tr)	-	-	-	+	+
Oryctolagus cuniculus (Pl)	-	-	-	-	+
CHIROPTERA					
Myotis blythi (Pl)	-	+	+	+	+
M. capaccinii (Md)	-	-	-	-	+
Asellia tridens (Sr.s)	+	-	+	-	-
Rhinolophus ferrumequinum (Pl)	-	-	-	-	~
R. hipposideros (Pl)	-	-	-	-	+
R. euryale (Pl)	-	-	-	-	+
R. mehelyi (Pl)	-	-	-	-	+
Hipposideros caffer (Tr)	-	-	-	-	+
Pipistrellus pipistrellus (Pl)	-	-	-	-	+
P. kuhli (Tr)	-	-	-	-	+
P. savii (Pl)	-	-	-	-	+
Miniopterus schreibersi (Tr)	-	-	-	-	+
Tadarida teniotis (Md)	-	-	-	-	~
ARTIODACTYLA					
Gazella dorcas (Sr.s)	+	+	+	+	~
Sus scrofa (Pl)	+	+	+	+	+
PRIMATES					
Macaca sylvanus (Ed)	-	+	-	+	+
INSECTIVORA					
Crocidura russula (Pl)	-	+	+	+	+
C. whitakeri (Md)	+	+	+	+	~
Erinaceus algirus (Pl)	-	-	-	-	+
Suncus etruscus (Tr)	-	-	-	-	+
MACROSCELIDEA					
Elephantulus rozeti (Ed)	+	-	+	-	~

~ : rare species and/or not very much localised; (Pl): palaeoarctic type; (Sl): Sahelean type; (Cp): cosmopolitan type; (Md): Mediterranean type; (Sr.M): Saharan and Mediterranean type; (Ed): endemic type; (Sr.b): Saharan type in a broader sense; (Sr.s): Saharan type in strict sense; (Tr): tropical type.

TABLE 2 | **Progressive appearance and extinction of northern Morocco mammals from late Pleistocene to present.**



Types: see legend in Table 1

sympatric and have a large current distribution. However, *Crocidura whitakeri* is currently absent from the Tangiers Peninsula and rare in other localities (regions of Al Hoceima and Nador). On the contrary, *Crocidura russula* is present in the whole north of the country.

Two additional species of Insectivora occur currently in the region, associated with the previous ones. The possibility of their introduction by man and their mode of recent settlement remain open. This is the case of *Suncus etruscus*, a Mediterranean and Turkistanian insectivor,

whose distribution is limited to the most northern part of the country and spreads along the Mediterranean basin to Asia and to some subsaharan countries (Corbet, 1978). The other species, *Erinaceus algirus*, belongs to the Family Erinaceidae and is widely spread throughout the north and reaches both pre-Saharan and Saharan regions and even the Mediterranean coast. It is considered an endemic species of the Maghreb with palaeoarctic affinity (Kowalski and Rzebik-Kowalska, 1991; Aulagnier, 1992).

Chiroptera

The Chiroptera recognised in the deposits of Ez Zarka and Chrafate (Table 1) are represented only by two species showing an interesting contrast: while *Asellia tridens* is a strictly Saharan species, and therefore does not occur today in Northern Morocco, *Myotis blythi* is purely palaeoartic.

Yet, several other species of Chiroptera live now in the same region, making it among the richest zones with 12 species of varied faunal types (Table 1):

- Palaeoarctic species, with a distribution limited to the most northern part of the country*: Pipistrellus pipistrellus, P. savii, Rhinolophus hipposideros, R. euryale, R. mehelyi, Myotis blythi* and *Rhinolophus ferrumequinum* (absent from the Tangiers Peninsula because of the competition with the important colonies of *Rhinolophus mehelyi* and *Myotis blythi*).

- Mediterranean species, *Myotis capaccinii, Tadarida teniotis;* as to *Pipistrellus kuhli* and *Miniopterus schreibersi,* they have an extensive distribution in Africa and Eurasia.

- Palaeotropical species, *Hipposideros caffer*, which occurs mainly in the Southern Sahara, but has been spotted in Tangier (Cabrera, 1932).

From this distribution we conclude that most of the species which currently represent this order in the study zone are Mediterranean or palaeoartic forms (Kowalski and Rzebik-Kowalska, 1991), with a wide distribution in Europe and Asia. These are species that colonised the Maghreb recently due to their great capacity of dispersion, by crossing the Strait of Gibraltar or by using the Siculo-Tunisian path. It can be emphasised that Northern Morocco is closer to Iberia and Italy than to Egypt, which apparently has no palaeoartic chiropteran species.

Macroscelida

Macroscelidae is represented by *Elephantulus rozeti*. This is an endemic species of North Africa which has been recorded in CH1 and ZRK1 (Table 1). The distribution of this species covers mainly arid bioclimatic biotopes and spreads to the south of the Saharan floor, although without penetrating into the heart of the Sahara. It also extends to the north in the semi-arid environments (Seguignes, 1983), in spite of the predominant craggy landscape. Likewise, it spreads from the west of Morocco up to the west of Libya, whereas its affinities are definitely palaeotropical. It occurs also on the slope of the Atlas Mountains, while in the Rif Mountains is currently localised in the eastern zone of Al Hoceima and in the region of Melilla. It is completely absent from the Tangiers Peninsula.

Lagomorpha

A species of Lagomorpha (*Lepu*s cf. *capensis*?) has been recorded in the Ez Zarka 2 locality, although it has not been identified with certainty. On the other hand, the present mammal association in Northern Morocco includes two species, *Lepus capensis* and *Oryctolagus cuniculus*. *L. capensis* is a cosmopolitan species which lives in Africa and Eurasia, including the tropical and subtropical zone that spreads along Morocco from the Tangiers Peninsula up to the Sahara regions. On the other hand, *O. cuniculus* spreads over a more restricted area limited to some parts of North African and Western Europe. It was probably introduced by man from Europe heading for Africa or vice-versa. In Morocco this species occupies the northern part of the country.

Artiodactyla

The record of Artiodactyla in the studied fossil assemblages is widespread although is reduced to the two species *Gazella dorcas* and *Sus scrofa* (Figs. 4M and 4N). *G. dorcas* is a typical Saharan form well adapted to arid environments. It has been recorded in the four localities and is absent or nearly absent in the present mammal assemblage in Northern Morocco. *S. scrofa* is also common in the studied fossil assemblages. It is a typical Mediterranean-European form, also currently present in Northern Mo-rocco.

Primates

The species *Macaca sylvanus* has been recorded in two localities (Table 1) and is endemic of North Africa. Thus, it is classified among the Mediterranean Palaeoarctic fauna. We can also find it on the other maritime edge of the rock of Gibraltar, whose colonies have been periodically renewed with captured specimens from Morocco (Aulagnier, 1992).

Carnivora

The record of Carnivora in the studied fossil assemblages is very scarce and to date is reduced to the species

Panthera pardus. The extinction of *P. pardus* from Northern Morocco hardly affected the important distribution of other tropical Carnivores in the same region, whose settlement dates back to a recent past. We note the presence of *Canis aureus* and *Felis libyca*, which show a large distribution throughout the country. They show an uncommon ecological ability that enables them to live in very varied environments.

Other species (*Vulpes vulpes*, *Mustela nivalis* and *Lutra lutra)* of faunal Palaeoarctic type are distributed from the Tangiers Peninsula up to the Sahara. Finally some Palaeotropical forms (*Genetta genetta* and *Herpestes ichneumon)* can even reach the Saharan areas through the colonization of suitable environments related to sufficient water resources.

DISCUSSION

The palaeoclimatic factor

Although many evidences related to the present Sahara desert show its great influence on the evolution of the mammal population in Northwestern Africa, it must not be forgotten that an early desert belt already existed in the Miocene (Jaeger, 1975a, b; Thomas, 1979). Asiatic mammals migrated in great number to Africa in the Miocene. It appears that the present-day Sahara prevented Asiatic species from migrating, forcing them to take two different ways to embark on Africa: one along the northern coast, the other in the south along the eastern shores. The then Maghreb abounded with sea basins that edged with coastline. The oldest population of mammals is that encountered in Beni Mellal, Central Morocco (Lavocat, 1961; Ginsburg, 1977a, b, c; Guèrin, 1976; Heintz, 1973, 1976; Jaeger, 1977; Janvier and Muizon, 1976; Legendre, 1982; Remy, 1976; Sigé, 1976; Tong, 1986; Kowalski and Rzebik-Kowalska, 1991). Rodentia, Insectivora, Macroscelida, among others, formed the ancient mammal population of that time and stayed in the region because they encountered the appropriate conditions for dispersion and/or speciation of some taxa.

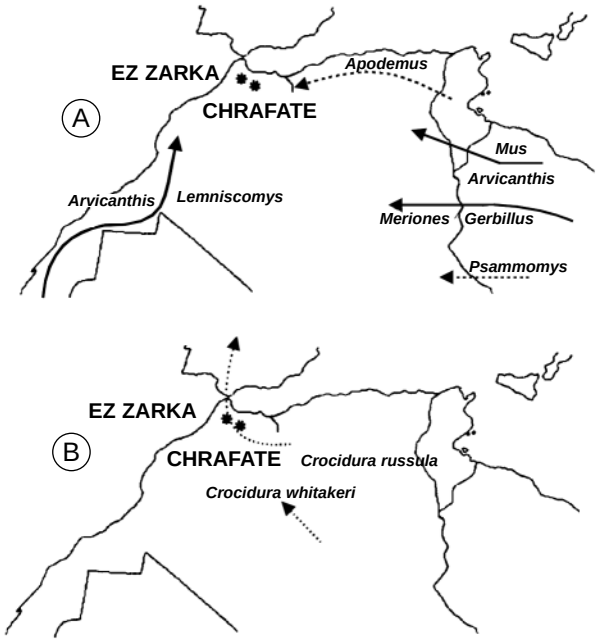


FIGURE 5 **Palaeobiogeographic scenario showing the main faunal changes in Northern Africa from the Pleistocene to Holocene. A) Pliocene-early Pleistocene (full arrows), late Pleistocene (discontinuous arrows). B) Holocene. The evolutionary stage (A) was characterised by arid-humid conditions, (B) by humid conditions (Jaeger, 1975a, b; Tong, 1986; Aulangnier, 1992).**

The climate in the Maghreb during the whole period of the Miocene was quite dry and characterised by a vegetation of savannah type. There were variations in humidity, but the end of the Miocene (the Messinian) was very dry (Kowalski and Rzebik-Kowalska, 1991) while the Betic Cordillera and the Rif were joined. Sea channels caused this Betic-Rifean region to be isolated from Europe and the other parts of Africa. The fauna was uniform and there was a blend of African and European species of the present-day Africa (Thomas et al., 1982).

Starting in the Pliocene, the Sahara had acted as a barrier for migrant rodents and was covered with present-day vegetation (Figs. 5A and 5B). Predominantly humid climatic regimes were favourable for some species of large mammals that came from Southern Saharan savannas; they managed to persist in the north for rather long periods. But smaller mammals found it even more difficult to overcome the desert barrier, although some of them found their way into the Maghreb (Kowalski and Rzebik-Kowalska, 1991).

Most families of smaller mammals were formerly introduced in the Maghreb, but present-day genera had not appeared in Morocco until the Pliocene or even Pleistocene. The Saharan influence is particularly perceptible on the population; the Sahara plays the role of barrier or way of migration according to the species.

As a result of research carried out in a few regions of Tunisia (Jaeger, 1971, 1975a, b), in Algeria (Ameur, 1977a, 1979; Ameur-Chabbar et al., 1975) and in Morocco (Jaeger, 1975b), our knowledge of rodent populations living in that period has recently been completed.

From the fauna encountered at the outset of the Pliocene, we can infer that climate was rather dry and the predominant vegetation was of savannah type. Thus, the

climate of North Africa was greatly influenced by the effect of cooling of the Mediterranean at the beginning of the Pleistocene (Kowalski and Rzebik-Kowalska, 1991).

During the early Pleistocene, the climate was characterised by long, arid seasons that alternated with relatively wet ones. This climatic regime became very arid in the middle Pleistocene and gave rise to a widespread desertification (Ameur-Chehbeur, 1988). Palaeolimnological studies carried out in the Maghreb, which focused on variations concerning the lacustrine water level and salinity of ancient lakes and their dating by isotopic methods, have enabled to reconstitute their history with certainty since 20000 years B.P. (Petit-Maire, 1984). These studies revealed the development of a late Pleistocene, (18000 to 12000 B.P.) major period of aridity, which coincided with a post-glacial period during which the Northern Morocco was considered as a Sub-Mediterranean zone. This period of aridity should be significant in terms of influencing the distribution and extent of the ancient desert zones.

The distribution of the desert belt, with all its associated consequences, gradually changed at the end of the late Pleistocene and during the Holocene (Soltanian-Rharbian) as a consequence of increasing rainfall**.** The larger input of fresh water through a significant change of the regional atmospheric circulation over the continent could be related to increasing rainfall coming from equatorial zones (thus linked to the northward shift of the intertropical front) or from the Mediterranean regions (in connection with the penetration of the rainfalls related to the Polar front). The increasing humidity enabled the fauna of the African savannas to reach Northern Africa and to come into contact with the fauna of the palaeoartic steppes.

The biogeographic and climatic regions that we distinguish currently were remarkably shifted during the last Quaternary pluvial period, dating back to about 10000 years B.P. This fact resulted in the increase of rainfall in areas that today are desert regions (Petter, 1974). The major wet phases ended in around 4000 years B.P.

Biogeographic significance of the Rif region

Although it is situated in Northwestern Morocco (the northwestern corner of Africa) the Rif was a biogeographic crossroad zone, where significant immigration, exchange and speciation processes took place during the late Pleistocene-Holocene time span. The presence of some Saharan and Sahelian elements in the Quaternary and recent fauna of the Rif rules out the idea that the mammal association of Northern Morocco is typically Mediterranean in origin, as previously proposed by Smith (1983).

The Rodentia assemblages appear as the most varied and they were characterised by the early predominance of the Gerbilidae (i.e. Saharan forms), which were later largely substituted by Muridae (i.e. Mediterranean forms), which became dominant. Gerbillidae benefited from steppe strips, or even larger desert zones, which developed and/or spread during dry periods. The very arid climatic regime, which developed in the middle Pleistocene, contributed to the diversification of Gerbillinae. Such diversification accords well with desertification (Ameur-Chehbeur, 1988), the gradual extinction of former archaic mammal lineages and the settlement of *Arvicanthis*.

Muridae, on the contrary, reached this region during relatively more humid climatic episodes. They differentiated locally because of the climatic oscillation suitability and treated tactfully inshore fringe zones characterised by Mediterranean vegetation. Thus, the last Quaternary pluvial period, dating back to about 10000 years, which resulted in the increase of rainfall in areas that today are desertic regions (Petter, 1974), allowed the arrival of *Apodemus sylvaticus* and *Mus musculus*. For these forms the Mediterranean line of Northern Africa constituted a more or less wide path of migration depending on climatic fluctuations.

Compared to Rodentia, Insectivora were characterised by a much slighter penetration into desert areas. In addition, after their settlement by the Libyco-Berber path, the Mediterranean Maghreb became a speciation home and a dispersion centre for most of species of the genus *Crocidura*.

Chiroptera present the same components as other orders of mammals, although their proportions are clearly different. Most of their species are palaeoarctic, but an important proportion is Mediterranean. This composition would have resulted from a recent settlement in the Maghreb coming from Southwestern Europe, because of their great dispersal ability. Chiroptera settled in areas with moderate climatic vagaries of the Mediterranean basin, whereas the cold climatic regime of central Europe and the drought of the Sahara limited their spread. The present-day disruptions of natural ecosystems, such as monoculture and pollution due to the use of pesticides (Qumsiyeh, 1985), are also factors that rapidly modify their area of distribution.

Macroscelidea were isolated from an original population and became an endemic order in North Africa. The migration of the latter probably used large path, either while following some Saharan rivers at the time of periods of very humid climate, or while crossing the more humid Atlantic coast.

Most of the Carnivora recorded in the fossil record and in the recent mammal fauna are tropical (i.e. *Panthera pardus*, *Felis libyca*, *Canis aureus*) palaeotropical (*Geneta*

genetta, *Herpestes ichneumon*) and even palaeoartic (*Vulpes vulpes*, *Mustela nivales*, *Lutra lutra*) in origin. Nevertheless, none of them can be considered typically Mediterranean. This fact can be explained by the recent development of the Mediterranean biome, in comparison to the low speed of the speciation of large-sized animals. This statement can be specially proposed for carnivores that**,** on one hand, have a low capacity to adapt to the environmental constraints because of their size and, on the other hand, as a consequence of their status as predators that exploit easily varied food resources. The carnivore fauna in the Maghreb diverged then with the immigration of some species (*G. genetta, H. ichneumon*) whereas others such as the panther disappear progressively in Europe to the benefit of northern species (Savage and Russell, 1983; Aulagnier, 1992).

According to Le Houerou (1990), other groups of macromammals, such as ungulates, are mainly tropical. They record a flourishing past already attested by the fossil forms, now extinct due to the effect of both climate (desertification) and anthropic action. From the Pan-African forms that invaded the whole Morocco, only few species remains in the Rif. This extinction was neither compensated by the speciation of gazelles (*Gazella dorcas*) during the desertification episodes, nor by the migration of rare Mediterranean and European forms such as *Sus scrofa*. The progressive regression of the ungulates is significant since it resulted from the low adaptive capacity of these herbivores with respect to the ongoing climatic constraints. This situation was opposite to that which affected the micromammal faunas, which were modified by limited palaeoartic and Saharan immigrants or enhanced by the immigration from the Saharan-Arabian belt. They turned out to be more adapted on a large scale to the current environment and reacted to the climatic variations of the Quaternary while adapting to the extreme environments by their evolutionary dynamism. Moreover, since ungulates are generally associated with the presence of a continuous and dense vegetation cover, the Maghreb became an inaccessible, isolated region for these animals as a consequence of being surrounded by the sea and desert (Darlington, 1957).

CONCLUDING REMARKS

The Northern Rif (Northern Morocco, Northwestern Africa) was characterised in the late Pleistocene and the Holocene by mammal assemblages, which included species with different biogeographic origins. The presence of some Saharan and Sahelian elements in the Quaternary fauna of the Rif region rules out the idea that the mammal fauna of Northern Morocco is typically or exclusively Mediterranean in origin. The palaeontological data suggest that this region was in fact a crossroad of palaeoartic and palaeotropical species and a centre of differentiation and exchange of species.

The variety observed in the upper Pleistocene-Holocene fossil mammal assemblages and in the present mammal assemblages resulted in part from the alternative arid and humid periods, which affected this region. The climate was characterised by arid-wet seasons during the early Pleistocene and became very arid in the middle Pleistocene. This fact contributed to the diversification of Gerbillinae and might be related to the settlement of *Arvicanthis* and the gradual extinction of archaic mammal lineages.

The distribution of the desert belt changed at the end of the late Pleistocene and during the Holocene (Soltanian-Rharbian) as a consequence of increasing rainfall. The increasing humidity enabled the mammal immigration from the African savannas into Northern Africa**.**

During the last Quaternary pluvial period (i.e.10000 years B.P.) the increase of rainfall on former desert regions allowed the arrival of Muridae (*Apodemus sylvaticus* and *Mus musculus*), which used the Mediterranean line of North Africa as a way of immigration.

The major wet phases ended in around 4000 years B.P. and this fact led the Northwestern Morocco to become a Mediterranean zone. Despite of this, some tropical forms (i.e. *Lemniscomys barbarus*) have survived until now. Other species with Saharian affinity have declined or migrated from this area (*Psammomys obesus*, *Asellia tridens*). Some Sahelian forms became extinct or disappeared (*Arvicanthis niloticus*). Finally some forms differentiated from others: (i.e. *Crocidura whitakeri* and *C. russula*).

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