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MAMMALS OF ALGERIA

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1991

3. EVOLUTION OF MAMMAL FAUNA

The following survey includes material concerning the whole of North-West Africa, i.e. the territory of contemporary Morocco, Algeria and Tunisia. Information on evolution of the mammal fauna for the whole Africa has been compiled by MAGLIO and COOKE (1978).

FROM THE PALAEOCENE TO THE MIOCENE

At the beginning of the Tertiary, in the Palaeocene, the continent of Africa was already similar in its basic outline to its present form. Placentals and Marsupials were already developing there, though knowledge of them is very incomplete. The oldest known African fauna of Eutheria is from the southern part of the Quarzatzate Basin in Morocco (CAPETTA et al. 1978). It includes two species of Palaeoryctidae, representatives of Proviverrinae and Miacidae. As the material excavated is composed of isolated teeth, a closer determination of their systematic status has not been possible.

In Eocene layers of Gour Lazib in the Hammada of Dra, Algeria, a fauna of terrestrial mammals has been found (SUDRE 1975, 1979). It includes *Azibius trerki* (Primates), *Megalohyrax gevini, Titanohyrax mongereaui* and *Microhyrax lavocati* (Hyracoidea), together with *Helioseus insolitus*, the last being of uncertain systematic status. The age of the fauna has been determined as the Early or Middle Eocene.

The Early Eocene locality El Kohol near Brezina, Algeria, yielded a mammal fauna including a representative of the marsupial family Peradectinae, *Garatherium mahboubii* (MAHBOUBI et al. 1983, CROCHET 1984), a member of Hyracoidea, *Seggeurius amourensis* (CROCHET 1986), a creodont *Koholia atlasense* (CROCHET 1988) and a primitive species of Proboscidea, *Numidotherium koholense* (MAHBOUBI et al. 1984a, b, 1986). An Early Eocene fauna has also been found at Chambi in Central Tunisia. It included Marsupialia (*Kasserinotherium tunisiense*), Hyracoidea (cf. *Pachyhyrax*, cf. *Sagatherium*), Macroscelidea (*Chambius kasserinensis*), Insectivora, Chiroptera, Rodentia, and probably Primates (HARTENBERGER, MARTINEZ, BEN SAID 1985, HARTENBERGER 1986, CROCHET 1986) (Table I).

Late Eocene age is attributed to the fauna from Bir el Ater on the southern slope of the Nementscha Mts. in eastern Algeria (COIFFAIT et al. 1984). It contained remains of proboscidians (*Moeritherium* sp.), of hyracoids (*Bunohyrax* sp.) and of Anthracotheriidae. *Biretia piveteaui* belonging to catarrhinian primates, is the oldest representative of this family of monkeys so far discovered (BONIS et al. 1988). The site revealed also the oldest specifically determined rodents from the whole of Africa (JAEGER, DENYS, COIFFAIT 1985). Among them were representatives of the family Phiomyidae (*Protophiomys algeriensis*) and Anomaluridae (*Nementschamys lavocati*).

Table I

Fossil Mammals of the Maghreb from Palaeocene to Miocene.
P — Palaeocene, E — Eocene, O — Oligocene, MM — Middle Miocene, LM — Late Miocene

Species	Period				
	P	E	O	MM	LM
Incertae sedis					
Helioseus insolitus SUDRE, 1979	—	●	—	—	—
Marsupialia					
Garatherium mahboubii CROCHET, 1984	—	●	—	—	—
Kasserinotherium tunisiense CROCHET, 1986	—	●	—	—	—
Insectivora					
Protechinus salis LAVOCAT, 1961	—	—	—	●	—
Schizogalerix moedlingensis (RABEDER, 1973)	—	—	—	●	—
Crocidurinae indet.	—	—	—	●	—
Chiroptera					
Megaderma gaillardi (TROUESSART, 1896)	—	—	—	●	—
Megaderma jaegeri SIGÉ, 1976	—	—	—	●	—
Rhinolophus mellali LAVOCAT, 1961	—	—	—	●	—
Hipposideros vetus (LAVOCAT, 1961)	—	—	—	●	—
Tadarida sp.	—	—	—	●	—
Vespertilionidae indet.	—	—	—	●	—
Primates					
Azibius trerki SUDRE, 1975	—	●	—	—	—
Biretia piveteaui BONIS, JAEGER, COIFFET, 1988	—	●	—	—	—
Colobus flandrini (ARAMBOURG, 1959)	—	—	—	—	●
Macaca sp.	—	—	—	—	●
Carnivora					
Agnotherium cf. *antiquum* KAUP, 1833	—	—	—	●	—
Martes khelifensis GINSBURG, 1977	—	—	—	●	—
Mellalictis mellalensis GINSBURG, 1977	—	—	—	●	—
Genetta sp.	—	—	—	●	—
Tungurictis punica KURTÉN, 1978	—	—	—	●	—
Ictitherium cf. *arambourgi* OZANSOY, 1965	—	—	—	●	—
Hyaenictis graeca GAUDRY, 1861	—	—	—	●	—
Capsatherium luciae KURTÉN, 1978	—	—	—	●	●
Allohyaena algeriensis (ARAMBOURG, 1959)	—	—	—	●	—
Lycyaena crusafonti KURTÉN, 1978	—	—	—	—	●
Indarctos aff. *arctoides* (DEPERET, 1895)	—	—	—	●	—
Felis sp.	—	—	—	●	—
Vampyrictis vipera KURTÉN, 1978	—	—	—	●	—
Machairodus robinsoni KURTÉN, 1978	—	—	—	●	—
Messiphoca mauretanica MUIZON, 1981	—	—	—	●	—
Creodonta					
Koholia atlasense CROCHET, 1988	—	●	—	—	—
Palaeoryctidae indet.	●	—	—	—	—
Proviverrinae indet.	●	—	—	—	—
Miacidae indet.	●	—	—	—	—

Cetacea					
Physeteridae indet.	—	—	—	●	—
Proboscidea					
Numidotherium koholense JAEGER, 1986	—	●	—	—	—
Moeritherium sp.	—	●	—	—	—
Prodeinotherium hobleyi (ANDREWS, 1911)	—	—	—	●	—
Palaeomastodon serridens ANDREWS and BEDNELL, 1902)	—	—	●	—	—
Gomphotherium angustidens (CUVIER, 1806)	—	—	—	●	●
Gomphotherium pygmaeum (DEPERET, 1897)	—	—	—	—	●
Tetralophodon longirostris KAUP, 1832	—	—	—	—	●
Zygolophodon cf. *turicensis* (GAUDRY, 1862)	—	—	—	—	●
Perissodactyla					
Paradiceros mukirii HOOIJER, 1968	—	—	—	●	—
Dicerorhinus primaevus ARAMBOURG, 1959	—	—	—	●	—
Diceros douariensis GUÈRIN, 1966	—	—	—	—	●
Hipparion africanum ARAMBOURG, 1959	—	—	—	●	—
Hipparion primigenium (VON MEYER, 1825)	—	—	—	●	●
Hyracoidea					
Seggeurius amourensis CROCHET, 1986	—	●	—	—	—
Cf. *Pachyhyrax*	—	●	—	—	—
Cf. *Sagatherium*	—	●	—	—	—
Bunohyrax sp.	—	●	—	—	—
Megalohyrax gevini SUDRE, 1979	—	●	—	—	—
Titanohyrax mongereaui SUDRE, 1979	—	●	—	—	—
Microhyrax lavocati SUDRE, 1979	—	●	—	—	—
Parapliohyrax mirabilis LAVOCAT, 1961	—	—	—	●	—
Tubulidentata					
Orycteropus mauritanicus ARAMBOURG, 1959	—	—	—	●	—
Artiodactyla					
Anthracotheriidae indet.	—	●	—	—	—
Merycopotamus anisae BLACK, 1972	—	—	—	—	●
Nyanzachoerus devauxi (ARAMBOURG, 1968)	—	—	—	●	●
Listriodon juba GINSBURG, 1977	—	—	—	●	—
Hippopotamus sp.	—	—	—	—	●
Palaeotragus lavocati HEINTZ, 1976	—	—	—	●	—
Palaeotragus germaini ARAMBOURG, 1959	—	—	—	●	●
Samotherium africanum CHURCHER, 1970	—	—	—	●	—
Benicerus theobaldi HEINTZ, 1973	—	—	—	●	—
Pachytragus solignaci ROBINSON, 1872	—	—	—	●	—
Damalavus boroccoi ARAMBOURG, 1959	—	—	—	●	—
Gazella praegaudryi ARAMBOURG, 1959	—	—	—	●	—
Rodentia					
Protophiomys algeriensis JAEGER, DENYS, COIFFAIT, 1985	—	●	—	—	—
Paraphiomys occidentalis (LAVOCAT, 1961)	—	—	—	●	—
Megapedetes sp.	—	—	—	●	—
Nementschamys lavocati JAEGER, DENYS, COIFFAIT, 1985	—	●	—	—	—
Metasayimys jebeli (LAVOCAT, 1961)	—	—	—	●	—
Africanomys pulcher (LAVOCAT, 1961)	—	—	—	●	—
Africanomys minor JAEGER, 1977	—	—	—	●	—
Africanomys major JAEGER, 1977	—	—	—	●	—
Africanomys katarati JAEGER, 1977	—	—	—	●	—
Testouromys solignaci ROBINSON and BLACK, 1977	—	—	—	●	—

cont. of Table I

	P	E	O	MM	LM
Irhoudia robinsoni JAEGER, 1977	—	—	—	—	●
Atlantoxerus tadlae (LAVOCAT, 1961)	—	—	—	●	●
Microdyromys ambiguus (LAVOCAT, 1961)	—	—	—	●	—
Microdyromys chaabi JAEGER, 1977	—	—	—	●	—
Eliomys truci MEIN and MICHAUX, 1970	—	—	—	—	●
Protalactaga maghrebiensis JAEGER, 1977	—	—	—	●	—
Mellalomys atlasi (LAVOCAT, 1961)	—	—	—	●	—
Dakkomys zaiani (JAEGER, 1975)	—	—	—	●	—
Myocricetodon parvus (LAVOCAT, 1961)	—	—	—	●	—
Myocricetodon cherifiensis (LAVOCAT, 1961)	—	—	—	●	—
Myocricetodon irhoudi JAEGER, 1977	—	—	—	●	—
Myocricetodon magnus JAEGER, 1977	—	—	—	●	—
Myocricetodon seboui JAEGER, 1977	—	—	—	●	●
Myocricetodon ouedi JAEGER, 1977	—	—	—	●	—
Myocricetodon trerki JAEGER, 1977	—	—	—	●	—
Myocricetodon ouaichi JAEGER, 1977	—	—	—	—	●
Myocricetodon ultimus JAEGER, 1977	—	—	—	—	●
Zramys dubius JAEGER, 1977	—	—	—	●	—
Zramys naichai JAEGER and MICHAUX, 1973	—	—	—	●	—
Zramys semmenensis JAEGER, 1977	—	—	—	●	—
Zramys jaegeri ROBINSON, BLACK, KRISHTALKA, DAWSON, 1982	—	—	—	●	—
Zramys salemi JAEGER, 1977	—	—	—	—	●
Zramys gueltae AMEUR, 1984	—	—	—	●	—
Protatera algeriensis JAEGER, 1977	—	—	—	—	●
Cricetus cf. *barrierei* MEIN and MICHAUX, 1970	—	—	—	—	●
Anthracomys sp.	—	—	—	●	—
Progonomys cathalai SCHAUB, 1938	—	—	—	●	—
Progonomys cf. *woelferi* BACHMAYER and WILSON, 1975	—	—	—	—	●
Paraethomys miocaenicus JAEGER, MICHAUX and THALER, 1966	—	—	—	—	●
Apodemus cf. *jeanteti* MICHAUX, 1966	—	—	—	—	●
Senoussimys hanifiae AMEUR, 1984	—	—	—	●	—
Hystrix sp.	—	—	—	—	●
Lagomorpha					
Kenyalagomys mellalensis JANVIER and MUIZON, 1976	—	—	—	●	—
Prolagus cf. *michauxi* LOPEZ, 1975	—	—	—	—	●
Macroscelidea					
Chambius kasserinensis HARTENBERGER, 1986	—	●	—	—	—

The Oligocene fauna of Africa was still endemic to a large extent. Mammals of this period are virtually unknown from the Maghreb, except for the scant relics of *Palaeomastodon serridens* (Proboscidea) from Tunisia (ARAMBOURG and BUROLLET 1962).

The Miocene saw a great migration of Asiatic mammals into Africa. There is no material from the Sahara belonging to the Miocene. Nevertheless it seems that what is now Sahara already constituted an important barrier for Asiatic migrants; they had to use two independent routes to penetrate into Africa: to the west along its northern coast or to the south along its eastern shores. No direct migration of fauna between

Europe and North Africa during the Miocene until its final stage has been sufficiently demonstrated. The Maghreb of that period contained numerous sea basins cutting into the coastline.

The oldest fauna of mammals of the Miocene is that from Beni Mellal in Central Morocco (LAVOCAT 1961, GINSBURG 1977a, b, c, GUÈRIN 1976, HEINTZ 1973, 1976, JAEGER 1977b, JANVIER, MUIZON 1976, LEGENDRE 1982, REMY 1976, SIGÉ 1976). It includes many endemic African elements, e.g. *Orycteropus mauritanicus* (Tubulidentata), *Parapliohyrax mirabilis* (Hyracoidea), *Prodeinotherium* (Proboscidea), and rodents of the family Thryonomyidae: *Paraphiomys occidentalis* and *Megapedetes* sp. At the same time, however, a significant part of this fauna is made up of elements of Asiatic origin, e.g. *Protechinus salis* and a representative of Crocidurinae (Insectivora), numerous Carnivora and Artiodactyla, and rodents from the families Cricetidae, Gliridae, and Ctenodactylidae. The composition of the fauna suggests a warm but dry climate, with savanna as the dominant vegetation type.

Cricetidae of Beni Mellal are represented by the endemic subfamily Myocricetodontinae. Its further evolution can be observed in the slightly younger fauna of Pataniak 6, found at Jebel Irhoud in southern Morocco (JAEGER 1975c). This fauna is composed almost exclusively of rodents including Sciuridae (the genus *Atlantoxerus*, the only representative of that family in the fauna of the Maghreb) and very diversified Myocricetodontinae. There is also a species of Dipodidae: *Protalactaga maghrebiensis*. The presence of this latter species, similarly to that of Ctenodactylidae, points to the existence of an arid environment of the steppe or savanna type.

A fauna of similar age is known from Testour of the Beja region in Tunisia (ROBINSON, BLACK 1973). It includes *Testouromys solignaci* and *Africanomys* sp. of the family Ctenodactylidae, *Mellalomys atlasi* of Cricetidae, specifically undeterminable Gliridae and Ochotonidae. Large mammals are represented by *Gomphotherium angustidens* (Proboscidea).

The fauna of Bou Hanifia in north-western Algeria was studied mainly by ARAMBOURG (1954, 1959). CHABBAR-AMEUR, JAEGER and MICHAUX (1976) obtained data on its absolute age by use of the $^{40}Ar/^{39}Ar$ method: 12.18 ± 1.03 MY; they also gathered a material of rodents, completed subsequently by AMEUR (1979, 1984). The fauna of large mammals from that locality includes among others *Orycteropus mauritanicus, Allohyaena algeriensis, Dicerorhinus primaevus* (GERAADS 1986), *Hipparion africanum, Palaeotragus germaini, Nyanzachoerus devauxi, Damalavus boroccoi* and *Gazella praegaudryi*. Rodents still include Myocricetodontinae (*Zramys dubius*) but Muridae make their first appearance (*Progonomys cathalai*). The emergence of *Hipparion africanum* (EISENMANN 1980) and *Progonomys cathalai* (JAEGER et al. 1977) points to a new migration of mammals from Asia — the same wave of migration has been recorded from Europe. The climate of the Maghreb seems to have been dry at that time.

Undetermined precisely as to the age, yet probably related to the same period, is the fauna of the Beglia formation, Tunisia, known from several of its layers (BLACK 1972, ROBINSON 1972, ROBINSON, BLACK 1974, KURTÉN 1978, ROBINSON et al. 1982, ROBINSON 1986). They include only large mammals; rodents of the same period are known in Tunisia from Jebel Semmene (JAEGER 1977a).

The Miocene locality Koudiet el Tine, also known as Feid El Atteuch, situated south of Beni Saf in Algeria was discovered by DALLONI in 1915, who recorded the presence of *Hipparion* sp. there. AMEUR (1979) noted *Zramys naichai* and *Myocricetodon ouedi* from the same site.

A rich fauna of rodents has been found at Oued Zra in northern Morocco (JAEGER, MICHAUX, DAVID 1973, JAEGER 1977a). Its absolute date has been established as 9.7—10 ± 0.5 MY. The fauna still contains *Progonomys cathalai*, but Ctenodactylidae, Gliridae, and Myocricetodontidae show significant differences in relation to older representatives of their evolutionary lines.

The Amama 1 locality in the El Eulma basin, eastern Algeria, and the slightly younger one of Sidi Salem situated above layers containing large mammals at Bou Hanifia (western Algeria) provided rodent faunas exhibiting differences from those discussed above (JAEGER 1977b). It suggest their position to be near the borderline between the Vallesian and the Turolian (Table II).

Table II

Miocene Fossil Mammal Localities in North-West Africa

MY	Continental chronology	Morocco	Algeria	Tunisia
6 7 8 9	Turolian	Aïn Guettara Khendek el Ouaich (7.4 MY)	Marceau (?) Raz el Aïn Amama 2 Sidi Salem Amama 1	Douaria (?)
10 11 12	Vallesian	Oued Zra (9.7 MY)	Koudiet el Tine Bou Hanifia (12.2 MY)	Jebel Semene Beglia (?)
13 14 15	Mellalian	Pataniak 6 Beni Mellal		Testour

(?) — stratigraphic position uncertain

Amama 2 yielded the oldest representative of Gerbillinae in the whole of the Maghreb, *Protatera algeriensis*. According to JAEGER (1977b), Gerbillinae might have originated from Myocricetodontinae in Maghreb. The entire Amama 2 fauna suggests an increasing aridity of the climate.

The Khendek El Ouaich in eastern Morocco could be dated to 7.4 ± 1.2 MY thanks to the presence of volcanic activity at that time. Remains of *Hipparion primigenium* and a rich fauna of rodents have been recorded there. It is dominated by Myocricetodontidae, but *Paraethomys miocaenicus* is also present (JAEGER, MICHAUX, THALER 1975).

The findings of large Miocene mammals from Algeria cannot be dated precisely. It is certain, however, that they must be classified as belonging to the Late Miocene. ? *Macaca* sp., ? *Colobus flandrini, Allohyaena algeriensis, Indarctos* aff. *arctoides, Hipparion primigenium* and *Palaeotragus germaini* are known from Menacer (French Marceau) (DELSON 1974, THOMAS, PETTER 1986). The rhinoceros *Diceros douariensis*, mastodonts and giraffes have been found at Douaria (GUERIN 1986, 1988). Remains of the genus *Hipparion* and of several mastodon species, impossible to date precisely, have also been found in Miocene sediments in many other localities of the Maghreb.

The final period of the Miocene is represented by the fauna from Ain Guettara, north-eastern Morocco (BRANDY, JAEGER 1980). It includes *Apodemus* aff. *jeanteti, Paraethomys miocaenicus, Cricetus* cf. *barrierei, Eliomys truci,* and *Prolagus* aff. *michauxi*. It is identical with the mammal fauna of Spain from the same period, suggesting a temporary junction between Europe and Africa in the Gibraltar region, probably during the Messinian episode.

It may be mentioned that remains of Miocene sea mammals, Physeteridae and *Messiphoca mauretanica*, are known from Raz El Ain near Oran, Algeria (MUIZON 1981).

It seems that because of the aridity of the Saharan climate, which was already of desert type in the Miocene, North Africa was to a large extent isolated from the rest of the African continent at that time. Some endemic elements of the old African fauna still survived, but their number was decreasing with time. Later migrations from the south seem to be of minor importance.

It is Asia that was the main source of the North African Miocene mammal fauna, as its composition in the Mellalian suggests. Many groups consequently underwent evolution and differentiation (it is particularly true of rodents, the best-studied group). A number of taxa in other orders became extinct at the end of the Miocene (Anthracotheriidae, Palaeotragini, Agrotheriidae).

The next wave of Asiatic migrants in the beginning of the Vallesian included the genus *Hipparion* and the earliest Muridae. Their simultaneous appearance in Europe is a result of parallel migration along both coasts of the Mediterranean rather than that of a direct exchange of fauna.

Throughout the whole of the Miocene, the climate of the Maghreb was rather dry and savanna-type vegetation dominated. However, variations in humidity did occur. The final part of the Miocene (the Messinian) was particularly dry.

During the Messinian, the land junction between the Baetic Cordillera and the Rif took place. On the other hand, this region was largely isolated from both the rest of Africa and Europe by sea channels. Its fauna was uniform and included at that time a mixture of African and European elements in what now belongs to Africa (THOMAS, BERNOR, JAEGER 1982) as well as in regions situated in present-day Europe (JAEGER, MICHAUX, THALER 1975, JAEGER et al. 1977). The fauna exchange in more distant areas of the two continents is little marked.

THE PLIOCENE AND THE QUATERNARY

After the short period of direct contact with Europe during the Messinian, which did not leave many lasting traces in the fauna of the Maghreb, the animal world of the region developed in relative isolation. The Sahara has had its present-day desert vegetation since the beginning of the Pliocene and had already become a successful barrier against animal migrations. Periods of increased humidity permitted the penetration of some species of large mammals originating from savannas south of the Sahara, which survived for various periods of time in the north. The desert barrier was more difficult to negotiate for smaller mammals, yet even some of them managed to penetrate into the Maghreb (e.g. the genus *Arvicanthis*). Migrations from Europe are more difficult to demonstrate, for the same species might have travelled from West Asia along the northern coast of Africa.

The period of the Pliocene is usually difficult to distinguish from the oldest Pleistocene and has been jointly termed Villafranchian, with the analogy to the stage of mammal fauna development in Europe (ARAMBOURG 1979). The Late Villafranchian of Europe (from 1.8 MY BP) is presently recognized as a part of the Pleistocene.

Older Pliocene localities of the Maghreb still contain the mastodon, *Anancus osiris*, and among the carnivores the genus *Machairodus*; while pigs are represented by *Nyanzachoerus jaegeri*, rhinoceroses by *Dicerorhinus africanus*, and equids by *Hipparion primigenium*. Among the rodents murids of the genus *Paraethomys* are still present, yet Myocricetodontinae are already absent. The beginning of the Pliocene is marked by the appearance of elephants (*Mammuthus africanavus*). Close ties with West Asia are exemplified by the composition of the fauna of small mammals from Oued Athmenia (COIFFAIT, COIFFAIT 1981), very similar to that of the Maritsa fauna from Rhodes (Table III).

Table III

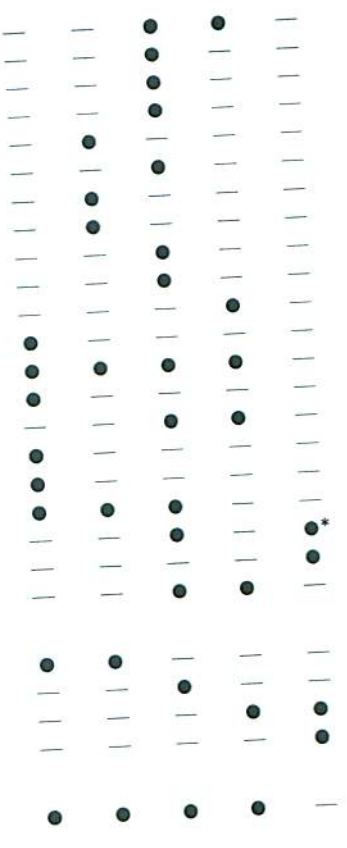
Fossil Mammals of the Maghreb from Pliocene to Holocene. P — Pliocene, EPl — Early Pleistocene, MPl — Middle Pleistocene, LPl — Late Pleistocene, H — Holocene (only species recorded as fossils)

Species	Period				
	P	EPl	MPl	LPl	H
Insectivora					
Erinaceus algirus LEREBOULLET, 1842	—	—	—	●	●
Episoriculus maghrebiensis RZEBIK-KOWALSKA, 1988	—	●	—	—	—
Crocidura jaegeri RZEBIK-KOWALSKA, 1988	—	●	—	—	—
Crocidura marocana RZEBIK-KOWALSKA, 1988	—	—	●	—	—
Crocidura whitakeri DE WINTON, 1897	—	—	●	—	—
Crocidura cf. *viaria* GEOFFROY SAINT-HILAIRE, 1834	—	—	●	—	—
Crocidura russula (HERMANN, 1780)	—	—	●	●	—
Chiroptera					
Rhinolophus cf. *ferrumequinum* (SCHREBER, 1774)	—	—	●	—	—
Miniopterus cf. *schreibersi* (KUHL, 1819)	—	—	●	—	—
Myotis sp.	—	—	●	●	—

Primates					
Macaca sylvanus (LINNAEUS, 1758)	●	●	●	●	●
Theropithecus atlanticus (THOMAS, 1884)	—	—	●	—	—
Carnivora					
Canis cf. *atrox* BROOM, 1948	—	—	●	—	—
Canis aureus LINNAEUS, 1758	—	—	●	●	●
Lycaon sp.	—	—	●	●	●
Vulpes vulpes (LINNAEUS, 1758)	—	—	—	●	●
Ursus arctos LINNAEUS, 1758	—	—	●	●	●
Mustela nivalis LINNAEUS, 1766	—	—	—	●	—
Mellivora capensis (SCHREBER, 1776)	—	—	●	—	—
Genetta genetta (LINNAEUS, 1758)	—	—	—	●	●
Herpestes ichneumon (LINNAEUS, 1758)	—	—	—	●	●
Percrocuta sp.	●	—	—	—	—
Crocuta crocuta (ERXLEBEN, 1777)	●	—	●	●	●
Hyaena hyaena (LINNAEUS, 1758)	●	—	●	●	●
Felis silvestris SCHREBER, 1777	—	—	—	●	●
Felis serval SCHREBER, 1776	—	—	—	—	●
Lynx caracal (SCHREBER, 1776)	—	—	—	●	●
Lynx thomasi GERAADS, 1980	—	—	●	—	—
Panthera leo (LINNAEUS, 1758)	—	—	●	●	●
Panthera pardus (LINNAEUS, 1758)	—	—	●	●	●
Homotherium latidens (OWEN, 1845)	●	—	●	—	—
Proboscidea					
Anancus osiris ARAMBOURG, 1945	●	—	—	—	—
Loxodonta atlantica (POMEL, 1879)	—	—	●	—	—
Loxodonta africana (BLUMENBACH, 1797)	—	—	—	—	●
Mammuthus africanavus (ARAMBOURG, 1952)	●	—	—	—	—
Mammuthus meridionalis (NESTI, 1825)	—	●	●	—	—
Elephas iolensis POMEL, 1895	—	—	●	●	—
Elephas recki DIETRICH, 1916	—	—	—	●*	—
Perissodactyla					
Dicerorhinus africanus ARAMBOURG, 1945	●	●	—	—	—
Dicerorhinus hemitoechus (FALCONER, 1858)	—	—	●	●	—
Ceratotherium simum (BURCHELL, 1817)	●	●	●	●	●
Hipparion primigenium (VON MEYER, 1829)	●	—	—	—	—
Hipparion sitifense POMEL, 1897	●	●	—	—	—
Hipparion libycum POMEL, 1897	●	●	●	—	—
Equus numidicus POMEL, 1897	—	●	●	—	—
Equus burchelli (GRAY, 1824)	—	●	●	●	●
Equus algericus BAGTACHE, HADJOUIS, EISENMANN, 1984	—	—	—	●	—
Equus melkiensis BAGTACHE, HADJOUIS, EISENMANN, 1984	—	—	—	●	—
Equus africanus (FITZINGER, 1866)	—	—	—	—	●*
Hyracoidea					
Procavia capensis (PALLAS, 1766)	—	—	—	—	●*
Tubulidentata					
Orycteropus afer (PALLAS, 1766)	—	—	—	—	●*
Artiodactyla					
Nyanzachoerus jaegeri COPPENS, 1971	●	—	—	—	—
Colpochoerus phacochoeroides THOMAS, 1884	—	—	●	—	—
Phacochoerus aethiopicus (PALLAS, 1767)	—	—	●	●	●
Sus scrofa LINNAEUS, 1758	—	—	●	●	●

cont. of Table III

	P	EPl	MPl	LPl	H
Hippopotamus amphibius LINNAEUS, 1758	●	●	●	●	—
Camelus thomasi POMEL, 1893	●	—	●	●	●
Giraffa camelopardalis LINNAEUS, 1758	—	●	●	—	—
Sivatherium maurusium POMEL, 1892	●	●	●	—	—
Cervus elaphus LINNAEUS, 1758	—	—	—	●	●
Megaloceros algericus (LYDEKKER, 1890)	—	—	—	●	—
Tragelaphus gaudryi (THOMAS, 1889)	●	—	—	—	—
Tragelaphus maroccanus ARAMBOURG, 1938	—	—	—	●	—
Tragelaphus algericus GERAADS, 1981	—	—	●	—	—
Tragelaphus oryx (PALLAS, 1766)	—	—	●	●	●
Oryx cf. *dammah* (CRETZSCHMAR, 1826)	●	●	●	●	—
Leptobos sp.	●	—	—	—	—
Bos bubaloides ARAMBOURG, 1979	—	—	●	—	—
Bos primigenius BOJANUS, 1827	—	—	●	●	●
Hippotragus sp.	—	—	●	●	—
Permularis ambiguus (POMEL, 1894)	—	—	●	—	—
Kobus sp.	—	—	—	●	—
Connochaetes taurinus (BURCHELL, 1823)	—	—	●	●	●
Redunca redunca (PALLAS, 1767)	●	●	●	●	●
Rabaticeros arambourgi ENNOUCHI, 1953	—	—	●	●	●
Oreanagor tournoveri THOMAS, 1884	●	—	—	—	—
Antidorcas sp.	●	—	—	—	—
Alcelaphus buselaphus (PALLAS, 1766)	—	—	●	●	●
Gazella atlantica BOURGIGNAT, 1870	—	—	●	●	—
Gazella tingitana ARAMBOURG, 1957	—	—	—	●	—
Gazella thomasi POMEL, 1895	—	—	●	—	—
Gazella setifensis POMEL, 1895	—	—	●	—	—
Gazella dracula GERAADS, 1891	—	—	●	—	—
Gazella cuvieri (OGILBY, 1841)	—	—	—	—	●
Gazella dorcas (LINNAEUS, 1758)	—	—	●	●	●
Antilocapra crassicornis ARAMBOURG, 1949	●	—	●	—	—
Ammotragus lervia (PALLAS, 1777)	—	—	—	●	●
Rodentia					
Thryonomys swinderianus (TEMMINCK, 1827)	—	—	—	—	●*
Irhoudia bohlini JAEGER, 1971	●	●	●	—	—
Ctenodactylus gundi (ROTHMANN, 1776)	—	—	—	●	—
Hystrix cristata LINNAEUS, 1758	—	●	●	●	●
Atlantoxerus huvelini JAEGER, 1975	—	●	—	—	—
Atlantoxerus cf. *rhodius* DE BRUIJN, DAWSON, MEIN, 1970	●	—	—	—	—
Eliomys truci MEIN and MICHAUX, 1970	●	—	—	—	—
Eliomys quercinus (LINNAEUS, 1766)	—	—	●	●	—
Jaculus sp.	—	—	●	●	●
Ellobius barbarus (POMEL, 1892)	—	—	●	—	—
Ellobius zimae JAEGER, 1988	—	—	●	—	—
Ellobius africanus JAEGER, 1988	—	—	●	—	—
Ellobius atlanticus JAEGER, 1988	—	—	●	—	—
Mascaramys brimbensis TONG, 1989	●	—	—	—	—
Mascaramys medius TONG, 1986	—	—	●	—	—
Gerbillus abdallahi TONG, 1989	—	●	●	—	—



Gerbillus campestris LOCHE, 1867
Gerbillus cingulatus TONG, 1986
Gerbillus grandis TONG, 1989
Gerbillus jebileti TONG, 1989
Gerbillus minutus TONG, 1989
Gerbillus major TONG, 1986
Gerbillus ochrae TONG, 1989
Gerbillus robustus TONG, 1989
Meriones maghrebianus TONG, 1989
Meriones maximus TONG, 1986
Meriones shawi (DUVERNOY, 1862)
Ruscinomys sp.
Mus sp.
Paraethomys anomalus DE BRUIJN, DAWSON, MEIN, 1970
Paraethomys filfilae PETTER, 1968
Paraethomys athmeniae COIFFAIT and COIFFAIT, 1980
Pelomys europaeus DE BRUIJN, DAWSON, MEIN, 1970
Praomys sp.
Arvicanthis niloticus (DESMAREST, 1822)
Apodemus sylvaticus (LINNAEUS, 1758)
Lemniscomys barbarus (LINNAEUS, 1758)

Lagomorpha
Prolagus sp.
Lepus sp.
Lepus cf. *capensis* LINNAEUS, 1758
Oryctolagus cuniculus (LINNAEUS, 1758)

Macroscelidea
Elephantulus cf. *rozeti* (DUVERNOY, 1833)

* — known from Sahara only
(New scientific names used only in unpublished theses are not listed)

Large Pliocene and earliest Pleistocene mammals are known from Tunisia, especially from the localities of Hammada Damous (Base), Garaet Ichkeul, and Djebel Mellah (ARAMBOURG, 1970, COPPENS 1971a, b, 1974), and also from Algerian localities (ARAMBOURG 1949a, b, 1952, 1957a, b, 1962, EISENMANN 1980). A more complete image of the rodent fauna of that period has emerged lately as a result of research on its localities in Tunisia: Garaet Ichkeul, Djebel Mellah, Ain Brimba (JAEGER 1971a, 1975a, c), in Algeria: Djebel Orousse, Bel Hacel, Oued Athmenia, Amama 3 (AMEUR 1977a, 1979, AMEUR-CHABBAR et al. 1975), and in Morocco: Sais (JAEGER 1975c) (Table IV).

The Pliocene fauna suggests a climate initially quite dry and a vegetation of the savanna type. The cooling of the Mediterranean at the beginning of the Pleistocene must have influenced the climate in North Africa.

The knowledge of fauna of large mammals from the Pliocene-Pleistocene transition is based, to a large extent, on findings which cannot be accurately dated. According to COPPENS (1971b), *Mammuthus africanavus* was no longer present in Tunisia at that time; on the other hand, *Equus burchelli* appears for the first time. Small mammals from the Pliocene-Pleistocene transition are best known from Irhoud Ocre, Morocco (JAEGER 1971b, 1975c, RZEBIK-KOWALSKA 1988, TONG 1989). This locality

contains *Irhoudia bohlini* of the family Ctenodactylidae, murids of the genera *Praomys*, *Paraethomys*, and *Mus*, two species of *Atlantoxerus*, the genera *Jaculus* and *Gerbillus* and lagomorphs of the genus *Prolagus*. The presence of the genus *Episoriculus* (Insectivora) points to a migration from Asia or Europe.

The beginning of the Middle Pleistocene coincides with the first glaciations in Europe; climatic changes, however, seem to have been milder in the Maghreb. Nevertheless, the composition of the fauna suggests a certain cooling. The first human remains found here date back to that period; they represent *Homo erectus* and came from Ternifine (Tighennif) in Algeria (ARAMBOURG, HOFSTETTER 1955).

Table IV

Principal Pliocene and Pleistocene Fossil Mammal Localities in North-West Africa

MY	Stratigraphical units	Morocco	Algeria	Tunisia
0.1	Upper Pleistocene	Irhoud Neanderthal	Jebel Filfila	
0.7	Middle Pleistocene	Sidi Abderrahman Irhoud Lanz Salé Irhoud Derbala V. Thomas 1 Aïn Hanech Sidi Abdallah	Tadjera Aïn Mefta Aïn Rouina Ternifine (Tighennif)	
1.8	Lower Pleistocene	Irhoud Ocre	Oued Kremia	Sidi Bou Kouffa Hammada Damous (top)
	Pliocene	Saïs	Djebel Orousse Bel Hacel Amama 3 Oued Athmenia	Bulla Regia 1 Aïn Brimba Jebel Melah Ichkeul Hammada Damous (base)

The same locality (GERAADS 1981, GERAADS et al. 1986) together with Ain Hanech (ARAMBOURG 1970) and quarries from Casablanca region (BIBERSON 1961, GERAADS 1980a, b, GERAADS, BERIRO, ROCHE 1980) are the main sites for the fauna of large mammals of the Middle Pleistocene. Small mammals, mostly rodents, are known from Moroccan localities: Sidi Abdallah, Thomas-1, Irhoud-Derbala Virage, Irhoud-Lanz-3, and Sidi Abderrahmane (JAEGER 1975a, b, c, 1988) and from Algeria: Ain Mefta (AMEUR 1977b, RZEBIK-KOWALSKA 1988a), Ain Rouina (AMEUR 1979) and Ternifine (Tighennif) (JAEGER 1969, TONG 1986).

A review of Middle Pleistocene fauna of mammals in the Maghreb is given by JAEGER (1975 a, b). According to him, three stages in the development of fauna can be

distinguished in this period. The earliest one is represented by Ain Hanech (large mammals) and Sidi Abdallah (rodents). Some archaic elements known from earlier periods were found there, e.g. *Irhoudia bohlini*. *Canis* cf. *atrox* is known from this period only.

The second stage is represented by the fauna of Ternifine (Tighennif) (DENYS, PATOU, DJEMMALI 1984). It witnesses the first appearance in Maghreb of *Loxodonta atlantica, Ursus arctos, Connochaetes taurinus,* and, in only slightly later faunas from Casablanca, *Bos primigenius*. Rodents include the genera *Ellobius, Meriones,* and *Arvicanthis*.

The latest phase of the Middle Pleistocene is represented by the faunas of the Atlantic coast, associated with the periods of the Tensiftian and the Praesoltanian, which immediately precede the Late Pleistocene. Those faunas include *Phacochoerus aethiopicus* and *Sus scrofa*. Still present is the genus *Ellobius*, the only representative of Arvicolidae in the North-West African faunas (JAEGER 1988). Extant species of Gerbillinae were already present then: *Meriones shawi* and *Gerbillus campestris*.

The dominant vegetation of the Middle Pleistocene was probably of savanna type. Ecological differences in fauna composition can be seen on the coast, where *Elephas iolensis* was present while the rodent *Arvicanthis* was absent, as compared to the hinterland, where *Loxodonta atlantica* and *Arvicanthis* were found. Generally, the fauna of large mammals was clearly African in its character with numerous antelopes of genera present then, and to a considerable extent even now, in sub-Saharan Africa. The climate must have been humid enough to permit migration of animals through the Sahara, possibly along the Atlantic coast. This migration included only occasional small mammals (*Arvicanthis*). At the same time, the fauna is being gradually enriched with Palaearctic elements. Their most probable migration route was the one from Asia. Their successive appearance demonstrates that this route acted as a kind of a filter: it is not an emergence of a new fauna but rather an accidental migration of particular species.

The period of the Late Pleistocene is known from very numerous localities in river, limnic, and cave sediments (ARAMBOURG 1929, 1932/1933, ROMER 1938, GINSBURG, HILLY, TAQUET 1968, PETTER 1968, HADJOUIS 1985, 1986). Unfortunately it is mainly represented in older excavations, and most of them are devoid of detailed stratigraphical data which would permit a study of changes in the animal world and in climate. A catalogue of species known from this period has been compiled by ROMER (1928). Many elements of Afrotropical fauna disappeared and species of deer emerged for the first time (*Megaloceros algericus* and *Cervus elaphus*).

The end of the Pleistocene brought about a further reduction of the older fauna of African origin (e.g. *Elephas iolensis*), yet also of some Palaearctic elements (e.g. *Megaloceros algericus*). Instead, *Loxodonta africana* appeared and donkeys replaced zebras, the latter present up to then. Of the rodents, *Apodemus sylvaticus* made its appearance. Numerous sub-Saharan species survived in the Holocene well into the Neolithic age but gradually became extinct, some of them clearly under human influence. Few as yet precisely dated localities (e.g. in the Tebessa region of Algeria: LUBELL et al. 1985) permit study of the fauna of this period.

THE SAHARA

The western Sahara is almost devoid of fossil localities with mammal faunas, and those that are known date back to more humid periods and usually contain savanna species, presently absent from this region.

This part of the Sahara has always had a continental climate, since the Cretaceous transgression. It is only in the north that the sea occupied a large area (present-day Tunisia and East Algeria as far south as Hassi Messaud) until the Eocene. The climate, relatively humid in the Palaeogene, became arid in the Neogene.

The Sahara must have had a desert character since the Miocene, which may be demonstrated, for example, by its having been an effective barrier, isolating the fauna of North Africa and ensuring its independent development. The vegetation of xerophytes, similar to the present one, has settled there since the Pliocene.

Data concerning the climate of the Sahara in the Early and the Middle Pleistocene are very scarce, becoming more complete only for the period of the last European glaciation and for the Holocene (e.g. BAKKER 1979). This last glaciation brought about — just as the earlier ones probably did — a considerate fall in temperature in the coastal region of North Africa. At the same time palaeobotanical data suggest this coast to have been woodless; thus the climate was arid.

Between 40—20,000 Y BP, a period of a relatively mesic climate occurred permitting the development of Palaeolithic cultures in the Sahara. The last maximum of the European glaciation in the Sahara was connected with an increased aridity of the climate. The desert extended about 450 km farther south than it does now, as can be gathered from fossil dunes. It is as late as about 12,000 Y BP that a certain increase in humidity of the climate can be observed. Around 6,000 Y BP, another humid phase brought about a new wave of human culture in the Sahara. This phase was followed by a dry one between 4,700—3,700 Y BP. The climate of the Sahara has since been undergoing some fluctuations in humidity, nevertheless without ceasing to be of desert type.

The climate of the mountains of Central Sahara (among them the Hoggar Mts. in Algeria) was quite mesic at the end of the Pliocene — an influence of nearby great lakes. Forest developed in higher locations. Periglacial phenomena are known from the Pleistocene, suggesting the cold in higher altitudes. The climate became arid during the last European glaciation, the drought being most marked between 20—18,000 Y BP, the influence of monsoon rains became more important.

A locality of Acheulean culture has been found in the Erg Tihodaine on the edge of the Tassili n'Ajjers (ARAMBOURG, BALOUT 1955, DEVILLERS 1948, H. THOMAS 1977). It contained a fauna with *Canis* aff. *aureus, Elephas recki, Ceratotherium simum, Equus* (*Asinus*) sp., two species of zebras, *Hippopotamus amphibius,* cf. *Mesochoerus* sp., *Tragelaphus* cf. *oryx*, *Oryx* aff. *dammah, Alcelaphus buselaphus, Connochaetes* sp., *Rabaticeros arambourgi, Gazella dorcas* and *Bos primigenius.* It was thus a typical fauna of African savanna, with the exception of *Bos primigenius,* a species of Palaearctic origin.

The fauna of the mesic Holocene is known, e.g. from Amekni in the Hoggar region. It includes *Genetta genetta, Herpestes ichneumon, Phacochoerus aethiopicus, Ammotragus lervia, Gazella* sp., *Redunca* aff. *redunca, Alcelaphus buselaphus, Procavia capensis*, and the rodents *Arvicanthis niloticus, Hystrix cristata* and *Thryonomys swinderianus* (BOUCHUD 1969, MONOD 1970). This last species is also known from the region of Tamanrasset, where it has been found together with *Orycteropus afer, Equus africanus, Bos* sp. and *Gazella* sp. (ROMER, NESBITT 1930). These faunas illustrate a shift to the north of the borderline of African savanna during the humid period of the Holocene, probably in the 7th millennium BP (BALOUT, ROUBET 1980).

Rich material relating to the history of the mammal fauna of the Sahara is provided by cave paintings and rock drawings known from the Saharan Atlas, the edges of great wadis (e.g. Saoura) (ALIMEN 1954) as well as from the mountains of Central Sahara. Their precise dating is difficult — the oldest might be determined as originating from a phase of mesic climate in the Neolithic. They show African savanna mammals — elephants, giraffes, rhinoceroses, lions, panthers; also, in the Tassili n'Ajjers, warthog, hippopotamus, and aardvark (MAUNY 1957, LHOTE 1963, 1970, 1976).

FOSSIL RECORD OF MAMMAL SPECIES OF ALGERIA

Insectivora. Erinaceidae came to Africa in the Miocene, probably from Asia. Species known from the Miocene (e.g. *Protechinus salis* from Beni Mellal) do not seem to be ancestors of extant ones. It was a later migration from the north-east, that brought species belonging to the genus *Erinaceus. E. algirus* is not known as fossil until the Late Pleistocene, older remains of hedgehogs being only generically determined.

Soricidae arrived to Africa probably from Asia, and have been known there since the Miocene. „*Sorex dehmi africanus* LAVOCAT, 1961" was described from Beni Mellal but it is a representative of the subfamily Crocidurinae and its systematic position needs further study. The genus *Crocidura*, represented by *C. jaegeri*, is already known from the Pliocene/Pleistocene boundary in Morocco (Irhoud Ocre). Remains of the extant *C. whitakeri* have been recorded from the Middle Pleistocene of Algeria (Ain Mefta). *C. russula* has also been known from Morocco and Algeria since the Middle Pleistocene (RZEBIK-KOWALSKA 1988 a).

Chiroptera. Remains of bats are very scanty in North-West Africa. The genera *Tadarida* and *Rhinolophus* are known since the Early Miocene (Beni Mellal), and *Myotis* sp., *Rhinolophus* cf. *ferrumequinum*, and *Miniopterus* cf. *schreibersi* are known from the Middle Pleistocene of Sidi Abdellah.

Primates. The oldest fossil remains of the genus *Macaca* are known from the Late Miocene of Menacer, Algeria, where they have been found among relics of other monkeys. They are almost identical with specimens ascribed to the genus *Parapapio* JONES, 1937, known from East and South Africa from the same period. It may be assumed that the two genera, *Macaca* and *Parapapio*, originated from a common African ancestor. Remains from the Pliocene of North-West Africa (Ain Brimba, Ichkeul) are identified with the extant species *Macaca sylvanus*, also known from this