

First Pleistocene faunas from the Arabian Peninsula: An Nafud desert, Saudi Arabia

Découverte des premières faunes pléistocènes de la péninsule Arabique dans le désert du Nafoud (Arabie Saoudite)

Herbert THOMAS¹, Denis GERAADS², Dominique JANJOU³, Denis VASLET³, Abdallah MEMESH⁴, Daniel BILLIOU⁵, Hervé BOCHERENS⁵, Gauthier DOBIGNY⁶, Véra EISENMANN⁷, Mireille GAYET⁸, France de LAPPARENT DE BROIN⁷, Germaine PETTER⁷ et Mohammed HALAWANI⁴

¹ Collège de France et laboratoire de paléontologie, Ura 12 CNRS, Muséum national d'histoire naturelle, 8, rue Buffon, 75005 Paris, France

² Musée de l'Homme, UMR 152 CNRS, place du Trocadéro, 75116 Paris cedex 05, France

³ BRGM, 3 av. C.-Guillemin, B.P. 6009, 45060 Orléans cedex 2, France

⁴ Ministry of Petroleum and Mineral Resources, Deputy Ministry for Mineral Resources, Jeddab, Kingdom of Saudi Arabia

⁵ Laboratoire de biogéochimie isotopique, UMR 162 CNRS, université Pierre-et-Marie-Curie - Inra, case 120, 4, place Jussieu, 75252 Paris cedex 05, France

⁶ Laboratoire de mammalogie, Muséum national d'histoire naturelle, 55, rue Buffon, 75005 Paris, France

⁷ Laboratoire de paléontologie, Ura 12 CNRS, Muséum national d'histoire naturelle, 8, rue Buffon, 75005 Paris, France

⁸ UMR 5565 CNRS, UFR Sciences de la Terre, Université Claude Bernard - Lyon I, 29, bd du 11-novembre-1918, 69622 Villeurbanne cedex, France

ABSTRACT

Three Pleistocene vertebrate localities in lacustrine deposits which accumulated in interdune depressions were discovered in the south-western part of the An Nafud sand sea (northern Saudi Arabia). Although the fossil vertebrate fauna is restricted in diversity, its composition and stage of evolution suggest an Early Pleistocene age in contrast with the recent Pleistocene or Holocene lake beds occurring in several other interdune depressions in central and southern An Nafud. The Nafud fauna has clear African affinities whereas faunas from the Levant, dating from the Middle Pleistocene onwards, contain typically European elements. © Académie des sciences / Elsevier, Paris.

Keywords: Arabian Peninsula, Saudi Arabia, Pleistocene, Fauna, Vertebrates

RÉSUMÉ

Trois niveaux lacustres pléistocènes à Vertébrés terrestres ont été découverts dans des dépressions interdunaires de l'extrémité sud-ouest du désert du Nafoud (Arabie Saoudite). Bien que très fragmentaires, certains éléments de la faune et leur niveau d'évolution suggèrent un âge Pléistocène inférieur. Cet âge ancien contraste avec l'âge bien plus récent (Pléistocène supérieur à Holocène) d'autres dépôts lacustres affleurant dans la zone centrale et méridionale du Nafoud. Contrairement aux faunes du Levant soumises à de fortes influences paléarctiques à partir du Pléistocène moyen, celles du Nafoud présentent encore un cachet éthiopien très net. © Académie des sciences / Elsevier, Paris.

Mots clés : Péninsule Arabique, Arabie Saoudite, Pléistocène, Faune, Vertébrés

Version abrégée (voir p. 151)

Note présentée par Yves Coppens.

Note remise et acceptée le 17 novembre 1997.

1. Introduction

Until now, between the Holocene and the Late Miocene (6–8 Ma) almost no vertebrate remains were known from the entire Arabian peninsula, with the exception of a single molar of *Hippopotamus* (Holm, 1960) and a few buffalo remains reported from Late Quaternary lake sediments in the south-western part of the now extremely arid Rub' al Khali desert (McClure, 1976, 1978). The lack of fossils documenting the recent faunal history of the Arabian Peninsula is now remedied by the discovery of three fossil vertebrate localities in Pleistocene lacustrine deposits in the interdune depressions of the large, sandy, An Nafud desert in the north-western part of Saudi Arabia. These localities, which occur in the south-western end of the An Nafud and which yielded several hundred specimens, were discovered by two of us (D.J. and D.V.) in 1988 and 1995 during investigations as part of the joint mapping and exploration programs of the Saudi Deputy Ministry for Mineral Resources and the French Bureau de Recherches Géologiques et Minières.

2. Geological context

The An Nafud sand sea occurs in the north-western part of Saudi Arabia. In An Nafud, the present dune system occupies about 95 % of the surface, and is overlain by Late Cenozoic eolian and lacustrine deposits that crop out on its western edge as well as in the interdune depressions. In the south-western part of An Nafud (figure 1), the Late Cenozoic succession is composed of the following succession from base to top: Ajfar Formation (Middle Miocene); Ancient dune system; Lacustrine deposits (vertebrate bearing); Present dune system.

2.1. Ajfar Formation

The Ajfar Formation is best exposed on the south-western edge of An Nafud (figure 1), where it forms white to yellow cuestas, capped either by a ferruginous surface or by lacustrine limestone. It is composed of fluvial, lacustrine and paludal detritic siliciclastic to calcareous deposits. The Ajfar Formation was dated Middle Miocene on the basis of vertebrate remains discovered in the Tayma quadrangle (Vaslet et al., 1994).

2.2. Ancient dune system

The ancient eolian deposit is white in color, slightly consolidated, and is exposed below the present dune system in the interdune depressions (figure 2A). It is composed of white, fine- to medium-grained sandstone, that shows giant trough cross stratification. Each set has very regular, tabular, mm-thick and variably consolidated laminations, which give them a leaf-trough aspect. This ancient dune system overlies the Palaeozoic Tayma Group along the south edge of An Nafud, but its geometric relations with the Ajfar Formation are not clear.

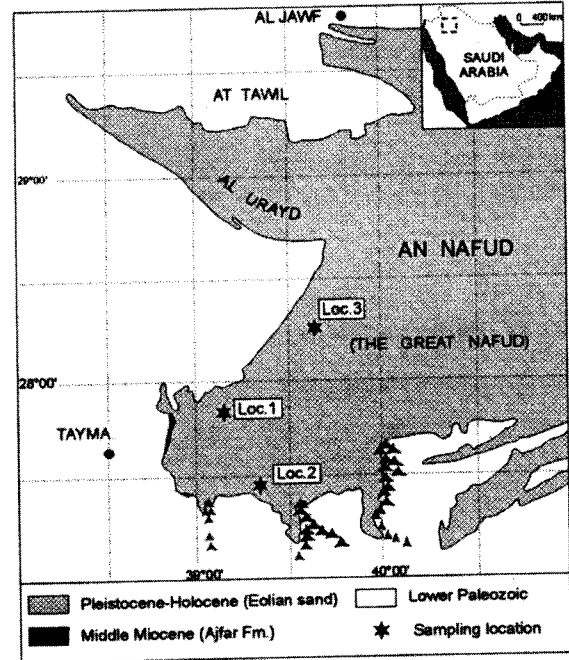


Figure 1. Geologic context and sampling location.

Situation géologique des localités fossilifères.

2.3. Lacustrine deposits (with vertebrate remains)

The lacustrine deposits occur locally within An Nafud in interdune depressions, where they overlie the white sands of the palaeodune system, the Ajfar Formation, and the Palaeozoic rocks, below the present dunes. The lithologic succession varies from outcrop to outcrop.

These lacustrine deposits fill concave depressions on top of the old white eolian sand and are commonly covered laterally by the present dune system (figure 2A); this indicates that they were formed in several isolated lakes which were probably not synchronous.

Three localities have yielded vertebrate remains. Localities 1 and 2, visited in 1995, lie in interdune depressions in the south-western tongue of An Nafud. Locality 3, which was visited in 1988, is situated in the western part of An Nafud.

The bone remains of locality 1 were collected from the surface of the lacustrine deposit and those of locality 2 come from a thin siltstone layer interbedded between the ancient eolian sand and a dm-thick bed of lacustrine carbonate (figure 2B).

The geologic context of locality 3 is similar to that of the preceding one. The host rocks for the vertebrate remains are white coarse-grained sand overlain by white siltstone interbedded with coarse-grained sand. This succession is overlain and laterally covered by the present sand-dunes (figure 2B).

2.4. Present dune systems

The predominant deposits in the south-western An Nafud are represented by large, stabilized, mostly barchan-shaped dunes, many of which are linked to form long

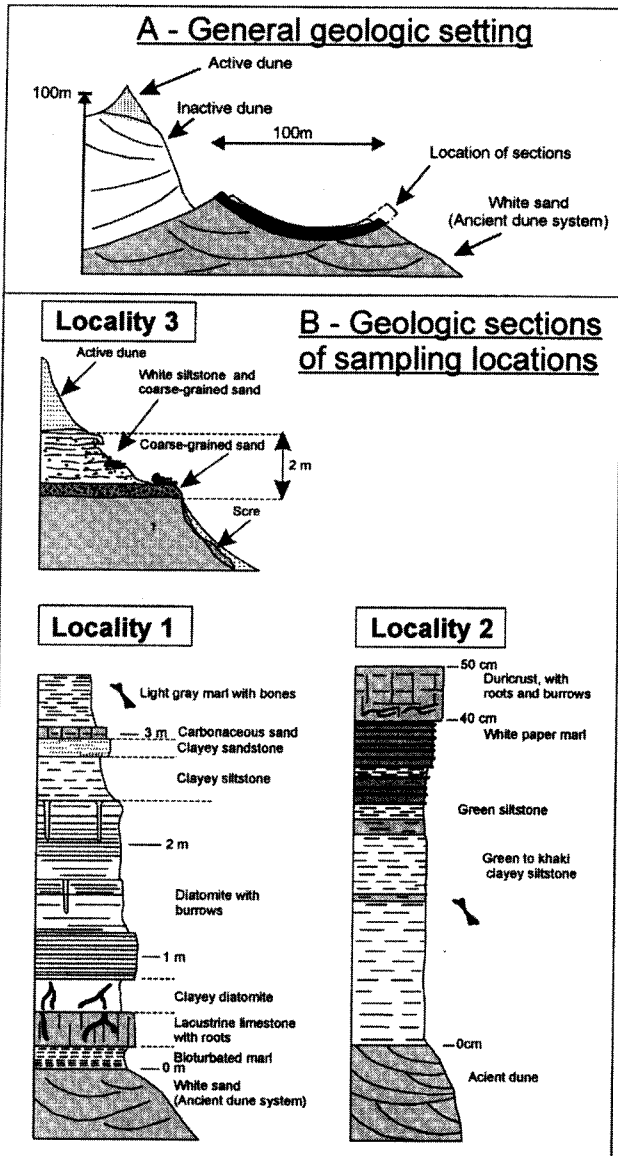


Figure 2. General geologic setting and geologic sections of sampling locations.

Coupes géologiques des localités fossilifères.

transverse dunes oriented along a northwest–southeast trend. A superimposed set of smaller active dunes overlies the large stable dunes. Except in a few locations, this active set of dunes is usually limited in extent to the crest of inactive dunes. The interdune depressions are commonly occupied by ancient eolian and lacustrine deposits as well as rare exposures of Palaeozoic rocks.

3. Palaeontology–Systematics (table 1)

3.1. Pisces

Teleostei, Osteoglossiformes

The only fish fossil (JMI 134) corresponds to the posterior part of a maxilla about 155 mm long. The alveolar series is composed of 12 antero–posteriorly flattened oval alveoli

and two small round alveoli located at the start of the posterior plate. Such a maxilla, which would have been armed with antero–posteriorly compressed teeth in closely spaced rows, occurs in certain osteoglossiform teleosts. In comparison with fossil and living osteoglossiforms, the Nafud fossil is closer to certain marine forms from the beginning of the Tertiary (*Brychaetus* or *Musperia*) or to the extant genus *Arapaima* from South America rather than to the extant African genus *Heterotis*. The Arabian fresh water osteoglossiform was a large specimen, which would originally have been more than a meter long.

3.2. Chelonii

Testudinidae: *Geochelone (Centrochelys) cf. sulcata*

One of the two collected specimens is an anal part of a xiphiplastron. The other (JMI 131) is the medial part of a carapace. It was a large male that had a carapace about 80 cm long and 56 cm wide. The morphological characteristics of the preserved elements (particularly the entoplastron), the reduced thickness of the plates, the decoration, the shape of the sulci on the scutes and their disposition, indicate a tortoise belonging to the same lineage as the extant *Geochelone sulcata*. The elements of the carapace are consistent with the Holocene and extant species, rather than with the Mio–Pliocene species.

The *Geochelone sulcata* lineage is known from the northern part of Africa and from Arabia since the Middle Miocene but it is now restricted to the Sahelian part of Africa (Lapparent de Broin and van Dijk, in press). It is the largest terrestrial tortoise of Africa and the Nafud specimen conforms in size to large extant adult males. Nowadays, *G. sulcata* occurs in dry and warm environments.

3.3. Mammalia

3.3.1. Carnivora

Hyaenidae: *Crocota crocota*

A left mandible (ANA 2) with P_2 – M_1 clearly belongs to *Crocota crocota*. A precise identification at the subspecific level has been attempted using a PCA based on 30 specimens of living spotted hyenas (*C. c. crocota*), and 24 of cave hyenas (*C. c. spelaea*) from Lunel-Viel and Jaurens, and nine variables (length and width of the teeth and length of P_2 – M_1). The graph shows an overlap in the two samples, some specimens of *C. c. crocota* from South Africa plotting among those of *C. c. spelaea* from Lunel-Viel, which themselves appear to be smaller than those from Jaurens, as noted by several authors (e.g. Ballésio, 1979). As to specimen ANA 2, axis 1 which accounts for 70.7 % of the variance, and which is determined by the length of P_2 , P_3 , P_4 , the breadth of P_3 and a little less by the length of M_1 , does not allow its distinction from the cave hyenas. Whatever the case may be, the Saudi *Crocota* cannot be used for estimating the date of the site and its large size may be only related to the environment.

Felidae: *Panthera cf. gombaszoegensis*

A left metacarpal III (JMI 27) of a large felid appears to correspond in size and proportions with the metacarpal IV

from Oubeidiyeh referred to *P. gombaszoegensis* (Ballésio, 1986), a species known in Europe from the Early to Middle Pleistocene.

Canidae: *Vulpes cf. vulpes*

A right metatarsal V (JMI 25) cannot be differentiated from that of a modern *Vulpes vulpes*.

3.3.2. Proboscidea

Elephantidae: gen. et sp. indet. (cf. *Elephas recki*)

An incomplete molar plate JMI 58 was certainly very hypsodont. It bears no median expansion or loop, and certainly does not belong to *Loxodonta*. Among a few carpals and tarsals, the most significant are two semilunars. They differ from those of *Elephas maximus* by their steeply inclined lunar facet and by the relative narrowness of the palmar part of the radial facet. Thus, if all specimens belong to a single species, which is the most likely hypothesis, it is neither of the two living ones. The very large size of some of the bones is reminiscent of the Pleistocene African *Elephas recki*, an identification that we propose very tentatively.

3.3.3. Perissodactyla

Equidae: *Equus sp.*

A fragmentary maxilla with very worn M^1 – M^3 (JMI 57), a third metatarsal (JMI 300), a distal fragment of third metacarpal (JMI 12), a talus (JMI 30), and several other fragmentary limb bones may all belong to a single species of *Equus* which may be stonine or zebra. The talus is bigger than in any modern zebra, including the largest living species, *Equus grevyi*. Several of its dimensions fall outside the range of variation of *Equus mauritanicus* from Tighenif (Algeria). The size and proportions are compatible with those of fossil zebras from Upper Bed II of Olduvai, Tanzania (about 1.4 Ma), and from Garba III, Melka Kunture, Ethiopia. In Europe, the 'young stonines' of Akhal-kalaki, Georgia or Süssenborn, Germany (about 0.6 Ma), are either bigger or more slender. The talus could belong to an *Equus stononis* such as the one from Saint-Vallier (France), but the protocones are too long. In conclusion, the data presently at our disposal support an attribution to a species resembling the *Equus* of Upper Bed II at Olduvai or of the 'Acheulean' of Garba III.

3.3.4. Artiodactyla

Hippopotamidae: *Hexaprotodon sp. ?*

Several tarsal and carpal bones of a hippopotamid have been recovered from locality 1. Among them, a complete metacarpal V (JM 301) although morphologically similar to that of *Hippopotamus*, is much more slender, a characteristic of *Hexaprotodon* according to Harrison (1997). Therefore we refer it tentatively to the latter genus rather than to the former, known in the Middle East until the Holocene.

Camelidae: gen. et sp. Indet.

JMI 50 is a camelid maxilla with a poorly preserved M^1 and the roots of P^3 and P^4 . It differs from *Camelus dromedarius* and from a complete, unpublished, skull of *Camelus thomasi* from the Lower/Middle Pleistocene of Tighenif, Algeria, by its palatine foramen which is both larger and more posteriorly situated (at the level of M^1), while it is small and more anteriorly positioned in the living domestic camel. This makes the Nafud camelid more like the Bactrian camel, although the difference is not clear-cut. Other fossil camels have been described from a number of Late Cenozoic sites throughout the Old World, but almost always from very incomplete material, making comparisons difficult.

Bovidae

Bovini: *Pelorovis cf. oldowayensis*

Two horn-core fragments (JMI 322 and 324), a maxilla fragment with M^2 – M^3 (JMI 325), a left mandible (ANA 1), an astragalus (ANA 16), and phalanges I, II and III (ANA 48, 21, 22) attest to the presence of a giant buffalo. The derived structure of the P_4 , which is extremely molarized, suggests that the Nafud buffalo does not belong to the Asiatic genus *Bubalus*. The mandible differs from those of aurochs by the moderate height of the horizontal ramus and the morphology of the interalveolar portion. By its dimensions (length of M_1 – M_3 : ca 100 mm), the Nafud bovine is comparable to the large fossil buffalos of Africa, *Pelorovis*. The same applies to the proportions of the astragalus, which resemble those of the ancient buffalo of Djelfa (Algeria), *P. antiquus*, even though it is larger. In contrast, the ungual phalanx (ANA 22) of which the internal border of the plantar surface is curved—which distinguishes it from the genus *Bos*—is astonishingly well-developed antero-posteriorly and is larger than its counterpart in the Djelfa specimen. The length of the plantar surface is about 103 mm. The Nafud *Pelorovis*, which was undoubtedly a thickset form, was adapted for moving on a soft substrate judging from the exaggerated development of the hooves.

The genus *Pelorovis* comprises four species, of which three are mainly known from East Africa: *P. kaisensis* from the Plio-Pleistocene beds of Kaiso in Uganda; *P. oldowayensis* known above all from Olduvai where it survives up to, but probably beyond, Bed III, but also from Kanjera and from Melka Kunture and in the Shungura Formation in the Omo; and finally *P. turkanensis* from East Turkana and other localities, contemporary with the Olduvai form.

The ancient buffalo, *P. antiquus* which probably descended from *P. oldowayensis*, is widely represented in the whole African continent, where it persisted until the onset of the Late Pleistocene, perhaps even to the Holocene.

Outside Africa, *P. oldowayensis* has been reported from the Lower Pleistocene of the Levant at Oubeidiyeh. Finally, several rare bones and teeth indicate the existence of a large buffalo in the southern part of the Arabian Penin-

sula, in the south-west of the Rub' al Khali desert and in the Tihama on the west coast of Yemen (Garcia et al., 1991).

The two horn-cores, even though broken, suggest that the Nafud buffalo is close to *P. oldowayensis*. Their oval cross-section, only slightly compressed dorso-ventrally, is closer to that of *P. oldowayensis* than to that of *P. antiquus* where it is strongly compressed and dorsally flattened.

Alcelaphini indet.

Only a few isolated lower and upper molars from localities 1 and 2 belong to an alcelaphine.

Hippotragini: *Oryx* sp.

Most of the cranial, dental and skeletal remains from locality 2 belong to an oryx. This is shown by features such as: horn-cores rather far from orbit, strongly inclined backwards, with an almost circular cross-section, slightly compressed antero-posteriorly; extensive frontal sinuses; short muzzle with a short pre-dental part of the maxilla; very posterior infra-orbital foramen; humerus with a distal trochlea which is cylindrical rather than conical and with a slightly inclined postero-lateral border; tibia with an anterior fibular facet medially positioned.

Today, this genus includes four groups in widely separated areas. The larger species (*O. gazella*), south of the Sahara, has almost straight horn-core, but they can be sometimes divergent, while the smaller species of the Saharo-Arabian belt (*O. dammah* and *O. leucoryx*) may have more curved but parallel horns. These desert-dwelling forms also differ from *O. gazella* by their teeth, which have a simpler occlusal pattern with a weak entostyle, if any, and less bowed pillars on the upper molars. The Nafud oryx resembles them by its tooth characteristics and curved horn-core, but differs from all four living species by clear horn-core divergence (about 35°), and therefore appears to be distinct from them.

Bovidae: gen. et sp. indet. 1

JMI 38 is the rear part of a skull, including the occipital, the cranial base and the auditory region. Only a small fragment of the cranial vault remains, but enough to show that the parieto-occipital angle was rather open (between 130° and 140°). The occipital is wide over the supra-mastoid crest, but rapidly narrows upwards; it bears a well-marked crest in the sagittal plane, with two small depressions on either side of its upper end. The mastoid exposures are mainly directed backwards. On the basi-occipital, the posterior tuberosities are strong and widely separated by a deep groove. The anterior tuberosities are long and prominent but much narrower than the posterior ones.

This occipital does not match any living species. It is certainly not of *Oryx*. It is unlike alcelaphines in that the anterior tuberosities are narrow and at the same level as the *foramen ovale*. The latter feature is sometimes found in tragelaphines, but in this case it is due to lengthening of the basi-occipital, which in this species is rather short. Whatever the case, this extinct form confers an archaic aspect to the Nafud fauna.

Bovidae: gen. et sp. indet. 2

The base of a left spiralled horn-core (ANA 49) has a basal index of 28.4×19.7 (ratio 0.69). The lateral side is slightly flatter than the medial one; there is no anterior keel but a well marked postero-lateral one. The horn-core is curved backwards in side view and has a clear clockwise torsion. There is a well-marked post-cornual fossa. It cannot be referred either to a tragelaphine or to a caprine. No species of the latter group has spiralled horns, except some domestic forms and a few Asiatic ones such as *Capra falconeri* and *Pseudois*, but the horn-cores of the latter two taxa are much flatter internally than externally, in sharp contrast to the Nafud one. The basal cross-section of tragelaphine horn-cores is usually more or less triangular, or even sub-circular (e.g. *T. imberbis*). Furthermore, tragelaphines have only a poorly indicated post-cornual fossa, if any. It is clear, therefore, that this horn-core does not fit with any living species. However, a few horn-cores of doubtful affinities from the Plio-Pleistocene of Africa share some similarities with the Nafud one. This is true, in particular, of a horn-core from the Upper Ndolanya beds at Laetoli (Antilopini sp. 1) which, according to Gentry (1987), is almost identical with some from Olduvai Middle and Upper Bed II and the surface of Bed I (Gentry and Gentry, 1978). According to Gentry (pers. comm.), the local conformation at the posterolateral base of the Nafud horn-core is quite similar to *Antilope* from the Shungura Formation at Omo (Member C) although it is uncompressed and has a slight posterolateral keel. As none of these horn-cores can be definitely identified with the Nafud one, the nature of which remains problematical, it might belong to a new species, or even to a new genus.

Table 1 Fossil vertebrates from the Pleistocene of An Nafud desert

	loc. 1	loc. 2	loc. 3
Pisces Osteoglossiformes		+	
Reptilia, Chelonii:			
<i>Geochelone (Centrochelys) cf. sulcata</i>		+	
Mammalia			
Carnivora			
Hyaenidae: <i>Crocuta crocuta</i>			+
Felidae: <i>Panthera cf. gombaszoegensis</i>		+	
Canidae: <i>Vulpes cf. vulpes</i>		+	
Proboscidea:			
gen. et sp. indet. (cf. <i>Elephas recki</i>)			+
Perissodactyla: <i>Equus</i> sp.	+	+	
Artiodactyla			
Hippopotamidae: <i>Hexaprotodon</i> sp.?	+		
Camelidae: gen. et sp. indet.		+	
Bovidae			
Bovini: <i>Pelorovis cf. oldowayensis</i>	+		+
Hippotragini: <i>Oryx</i> sp.		+	
Alcelaphini: gen. et sp. indet.	+	+	
gen. et sp. indet. 1			+
gen. et sp. indet. 2			+

4. Palaeoecological implications of carbon isotope abundances

A recently developed approach for palaeoenvironmental reconstruction is the use of carbon (^{13}C) isotopic signatures in mammal enamel. During the life of the individual, this mineralized tissue records the carbon isotopic signature of the diet, which depends mainly on the photosynthetic pathway of the plants consumed by herbivores (Lee-Thorp and van der Merwe, 1987). They are thus indirectly linked to environmental parameters, since in tropical environments grasses are C4-plants whereas trees are C3-plants, with different carbon isotopic signatures. Thus, a closed plant cover will be recorded in herbivore enamel by lower levels of ^{13}C (more C3 plants, such as trees) whereas an open environment will correspond to higher levels of ^{13}C (more C4 plants, such as grasses). Numerous studies strongly suggest that these isotopic signatures are preserved in fossil enamel, even millions of years old (e.g. Lee-Thorp and van der Merwe, 1987; Bocherens et al., 1996).

Small enamel fragments have been sampled from herbivore teeth and treated according to the protocol described in Bocherens et al. (1996) for fossil samples. Isotopic compositions of carbon are measured with a VG Sira 9 isotopic ratio mass spectrometer after reaction with anhydrous orthophosphoric acid at 50 °C, and they are expressed as $\delta^{13}\text{C} = [(^{13}\text{C}/^{12}\text{C} \text{ sample} / ^{13}\text{C}/^{12}\text{C} \text{ standard}) - 1] \times 1\,000$ (‰), where the standard is the carbonate PDB (table II).

Table II. $\delta^{13}\text{C}$ values in enamel fragments from some herbivore teeth.

Valeurs $\delta^{13}\text{C}$ mesurées dans des fragments d'émail de dents d'herbivores.

Specimen	Taxa	$\delta^{13}\text{C}$ (PDB)
ANA7 (loc. 3)	<i>Pelorovis</i> cf. <i>oldowayensis</i>	2.1
JM166-73 (loc. 2)	(cf. <i>Elephas recki</i>)	0.8
JM1100 (loc. 2)	Alcelaphini indet.	0.1
JM1328 (loc. 1)	<i>Pelorovis</i> cf. <i>oldowayensis</i>	1.4

The measured $\delta^{13}\text{C}$ values range from 0.1 to 2.1 ‰. Such values clearly indicate a C4-plant diet for all analysed samples, by comparison with values measured on modern African faunas (Lee-Thorp and van der Merwe, 1987). These results imply an open savanna at the time the animals lived in Saudi Arabia, as already suggested by some of the species indicative of open arid grassland and/or scrub (alcelaphines, *Oryx*, *Geochelone* cf. *sulcata*) that comprise the bulk of the total sample collected from locality 2. No clear woodland or forest edge species have been recorded from An Nafud but large standing bodies of water were present as suggested by the osteoglossiform fish, the hippopotamid and perhaps by the giant buffalo.

5. Conclusions: biochronology and biogeography

The vertebrate fossil localities from An Nafud in the Arabian peninsula are situated about 420 km east of the southern margin of the Levantine Rift Valley. With the exception of possible passages across the Red Sea during periods of low sea stand, the Levantine Rift Valley, by way of the northern Sinai strait has always been considered as a major crossroad between Africa and Eurasia for faunal and hominid dispersals from Late Pliocene times onwards. The Nafud fauna is therefore of particular significance.

Although the fossil vertebrate fauna from An Nafud is poorly known, its composition and stage of evolution, even though imprecise for biochronology, are nevertheless more indicative of an Early Pleistocene age than of a recent Pleistocene or Holocene one.

With the exception of the fox and the tortoise, there is no element in the fauna that corresponds to a living or Late Pleistocene subfossil form. The Nafud fauna does not have the typical European aspect which characterizes that of the Middle East from the Middle Pleistocene onwards. The elements with African affinities, in particular the artiodactyls, are predominant. It is worth noting the scarcity of North African elements—if any—despite its location at the same latitude. The Ethiopian aspect of the fauna is even more marked if we note the absence of cervids. It is true that the absence of this important group, which emigrated from Eurasia, is probably related to the semi-arid climate indicated by the fauna. Several species may suggest an Early Pleistocene age (*Hexaprotodon* sp.?, *Equus* sp., cf. *Elephas recki*, *Pelorovis* cf. *oldowayensis*). The ancient aspect of the fauna also emerges from the presence of an enigmatic bovid recovered from locality 2. While the three localities may not correspond to a single lacustrine episode, their ages are nevertheless later than the arrival of Ethiopian forms in the Levant, when Palaeartic influences were still minor and when the routes from East Africa into the North across the Saharan–Arabian belt were not completely closed.

According to Schulz and Whitney (1986), various lake beds which occur in diverse interdune depressions in central and southern An Nafud as well as in its southwestern part (diatomite of Bi'r Hayzan) correspond to two major lake periods: the older of Late Pleistocene age dated by radiocarbon between 34 000 and 24 000 BP and the younger of Middle Holocene age. Near Jubba in south-central An Nafud, a section measured in a well proves the existence of an important humid phase which is older, but undated (Garrard and Harvey, 1981). Sanlaville (1992) considered that the Arabian Peninsula experienced at least four humid phases since the last interglacial, but the prior climatic history is almost completely unknown. For Hötzl and Zötl (1978) however, a long intense humid period occurred during the Late Pliocene/Early Pleistocene between 1.2 and 3.5 Ma. This long humid period would have been followed by a semi-arid climate until the end of the Holocene, interrupted by several relatively short humid periods. The Nafud fauna may correspond to the beginning of this period.

VERSION ABRÉGÉE

Introduction

Jusqu'à présent, à de très rares exceptions près (Holm, 1960 ; McClure, 1976, 1978), aucun Vertébré fossile n'était connu, de toute la péninsule Arabique, entre le Miocène supérieur (6 à 8 Ma) et l'Holocène. Cette lacune est aujourd'hui en partie comblée par trois gisements pléistocènes dans des dépôts lacustres situés dans des dépressions interdunaires du désert du Nafoud, dans la partie nord-ouest de l'Arabie Saoudite. Ces sites ont été découverts par deux d'entre nous (D.J. et D.V.) au cours de missions conjointes menées par le Saudi Deputy Ministry for Mineral Resources et le BRGM.

Contexte géologique

Dans le Nafoud, le système dunaire actuel, qui occupe 95 % de la surface, recouvre des sédiments éoliens et lacustres de la fin du Cénozoïque qui comprennent (de la base au sommet) :

- la formation d'Ajfar, formée de dépôts fluviaux, lacustres et palustres, datée du Miocène moyen grâce aux Vertébrés (Vaslet et al., 1994) ; elle affleure au sud et à l'ouest (figure 1) ;
- un système dunaire ancien, de sables clairs faiblement consolidés, à stratifications entrecroisées d'échelle décimétrique ; il recouvre le Paléozoïque, mais ses rapports avec la formation d'Ajfar sont incertains ;
- des dépôts lacustres à Vertébrés, qui recouvrent toujours les formations précédentes, et en particulier le système dunaire ancien, mais sont recouverts latéralement par les dunes récentes (figure 2A) ; ils proviennent donc de lacs isolés, non nécessairement synchrones ; les successions lithologiques observées dans les trois localités fossilifères sont indiquées sur les figures 2B et 2C ;
- le système dunaire actuel, stabilisé à 95 %, recouvre les formations précédentes.

Paléontologie – Systématique (tableau I)

• Pisces

- **Teleostei, Osteoglossiformes** : un fragment de maxillaire évoque davantage certaines formes marines du début du Tertiaire que le genre actuel africain *Heterotis*, dulçaquicole comme les autres genres actuels.

• Chelonii

- **Geochelone (Centrochelys) cf. sulcata** : deux fragments de plastron et de carapace appartiennent à une tortue de la lignée de l'actuelle *G. sulcata*, qui remonte au Miocène moyen du Djebel Zelten.

• Mammalia

- Carnivora,

Hyaenidae, Crocuta crocuta : une mandibule d'hyène pourrait être rapportée, soit à l'hyène des cavernes du Pléistocène supérieur d'Europe dont la taille est variable, soit à la sous-espèce actuelle africaine, ou encore à la sous-espèce du Würmien de Palestine, *C. crocuta dorothae*. Une ACP sur les mesures des dents inférieures, qui sépare assez bien les deux premières sous-espèces, ne

permet cependant pas de préciser les affinités de la forme d'Arabie, qui n'apporte donc pas d'indication chronologique.

Felidae, Panthera cf. gombaszoegensis : un métacarpien pourrait appartenir à cette espèce, connue à Oubeydiyeh (Ballésio, 1986).

Canidae, Vulpes cf. vulpes : un métatarsien est très semblable à celui du renard commun.

- **Proboscidea, cf. Elephas recki** : une lame dentaire, très hypsodonte et complètement dépourvue de sinus médian, ne peut appartenir à *Loxodonta*, tandis que quelques carpiens se distinguent de ceux de *E. maximus*, suggérant que l'éléphant du Nafoud n'est pas une espèce actuelle, mais pourrait être *E. recki*.

- Perissodactyla,

Equidae, Equus sp. : quelques éléments de grande taille semblent se distinguer du cheval, mais aussi de la plupart des formes pléistocènes européennes, et se rapprocheraient plus de celles du Pléistocène inférieur et moyen d'Afrique orientale.

- Artiodactyla,

Hippopotamidae, Hexaprotodon sp. ? : parmi quelques carpiens et tarsiens de la localité 1, un métacarpien V ne saurait appartenir à l'espèce actuelle *H. amphibius*, qui vivait encore à l'Holocène au Proche-Orient, car sa forte gracilité évoque plutôt les formes du genre *Hexaprotodon* (Harrison, 1997), auquel nous le rattachons sous toutes réserves.

Camelidae, gen. et sp. indet. : un maxillaire se distingue de celui du dromadaire par la taille et la position du foramen palatin, mais ne peut être identifié avec précision.

Bovidae,

▲ **Bovini, Pelorovis cf. oldowayensis** : quelques éléments, dont des fragments de cornes et une mandibule, se distinguent tant de *Bubalus* que de *Bos*, mais rappellent en revanche le genre *Pelorovis*, représenté par quatre espèces en Afrique et au Proche-Orient. La courbure et la forme de la section des cornes évoquent plutôt *P. oldowayensis*, du Pléistocène inférieur d'Afrique orientale et d'Israël. Un buffle avait déjà été cité, sur la base de matériels fragmentaires, dans le Sud de la péninsule Arabique (Garcia et al., 1991).

▲ **Hippotragini, Oryx sp.** : la plupart des fossiles de la localité 2 se rapportent à ce genre arabo-africain, mais si les dentitions sont semblables à celles des formes désertiques actuelles, les cornes à la fois courbées et divergentes semblent se distinguer de celles de toutes les espèces vivantes.

▲ **Alcelaphini indet.** : quelques dents isolées attestent la présence de cette tribu.

▲ **Bovidae, gen et sp. indet. 1** : un fragment d'arrière-crâne d'assez grande taille, élargi à la hauteur des mastoïdes, mais étroit vers le sommet, est bien différent, non seulement des crânes d'*Oryx*, mais aussi de tous les Bovidés actuels par son basioccipital court et étroit au niveau des tubérosités antérieures.

res, qui sont situées au même niveau que le trou ovale. Cette forme énigmatique confère un caractère archaïque à la faune du Nafoud.

- ▲ **Bovidae, gen et sp. indet. 2** : un fragment de corne spiralée présente une section aplatie latéralement et une carène postéro-externe. Par sa conformation, cette cheville n'évoque ni les Caprini, ni les Tragelaphini ; des similitudes existent en revanche avec quelques spécimens mal connus et d'attribution incertaine, provenant du Plio-Pléistocène est-africain, de Laetoli (Gentry, 1987) ou d'Olduvai (Gentry et Gentry, 1978). Il se peut qu'il s'agisse d'une espèce nouvelle, voire d'un nouveau genre.

Implications paléocéologiques des abondances du ^{13}C

L'abondance relative en ^{13}C dans l'émail dentaire des Mammifères herbivores dépend de la chaîne photosynthétique suivie par les végétaux qu'ils consomment. Si leur alimentation est à base d'herbes tropicales, plantes en C4, le ^{13}C est plus abondant dans l'émail dentaire que s'ils se nourrissent d'autres plantes (Lee-Thorp et van der Merwe, 1987 ; Bocherens et al., 1996). Les valeurs de ^{13}C relevées ici montrent clairement que les herbivores du Nafoud se nourrissaient surtout d'herbes,

Acknowledgements: This study was carried out within the framework of an agreement between the Saudi Arabian Deputy Ministry for Mineral Resources and the French Bureau de Recherches Géologiques et Minières. Publication of these results was made possible thanks to the support and authorization of Dr M.A. Tawfiq (Assistant Deputy Minister for Survey and Exploration, Deputy Ministry for Mineral Resources), to whom the authors express their grateful thanks.

REFERENCES

- Ballésio R. 1986. Les carnivores du gisement pléistocène d'Oubeldiyeh (Israël), in: Tchernov E. (Ed.), *The Lower Pleistocene mammals of Ubeidiya (Jordan Valley)*, Mémoires et travaux du Centre de recherche français de Jérusalem, Assoc. Paléorient, 5, 63-91
- Bocherens H., Koch P.L., Mariotti A., Geraads D. and Jaeger J.J. 1996. Isotopic biogeochemistry (^{13}C , ^{18}O) of mammal enamel from African Pleistocene hominid sites: implications for the preservation of palaeoclimatic isotopic signals, *Palaios*, 11, 306-318
- Garcia M.A., Rachad M., Hadjouis D., Inizan M.-L. and Fontugne M. 1991. Découvertes préhistoriques au Yémen. Le contexte archéologique de l'art rupestre de la région de Saada, *C.R. Acad. Sci. Paris*, 313, série Ila, 1201-1206
- Garrard A.N. and Harvey C.P.D. 1981. Environment and Settlement during the Upper Pleistocene and Holocene at Jubba in the Great Nefud, Northern Arabia, *ATLAL*, 5 (Part IIIb), 137-148
- Gentry A.W. 1978. Pliocene Bovidae from Laetoli, in: Leakey M.D., Harris J.M. (Eds.), *Laetoli, a Pliocene Site in northern Tanzania*, Oxford, Clarendon Press, 378-408
- Gentry A.W. and Gentry A. 1978. Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania. Part I and II, *Bull. Br. Mus. nat. Hist. (Geol.)*, 29 (4), 289-446 and 30 (1), 1-83
- Harrison T. 1997. The anatomy, palaeobiology and phylogenetic relationships of the Hippopotamidae (Mammalia, Artiodactyla) from the Manonga Valley, Tanzania, in: Harrison T. (Ed.), *Neogene Palaeontology of the Manonga Valley, Tanzania, Topics in Geobiology*, 14, 137-190
- Holm D.A. 1960. Desert Geomorphology in the Arabian Peninsula, *Science*, 132 (3437), 1369-1379
- Hötl H. and Zötl J.G. 1978. Climatic Changes During the Quaternary Period, in: Al-Sayari S.S., Zötl J.G. (Eds.), *Quaternary Period in Saudi Arabia*, Springer-Verlag, Wien, New York, 301-311
- Lapparent de Broin F. de and van Dijk P.P. Chelonia from the Baynunah Formation, Late Miocene, Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates: palaeogeographical implications, in: Whybrow P.J. and Hill A. (Eds.), *Fossil Vertebrates of Arabia*, ch. 13, Yale University Press (in press)
- Lee-Thorp J.A. and van der Merwe N.J. 1987. Carbon isotope analysis of fossil bone apatite, *South African J. Sci.*, 83, 712-715
- McClure H.A. 1976. Radiocarbon chronology of Late Quaternary lakes in the Arabian Desert, *Nature*, 263 (5580), 755-756
- McClure H.A. and Ar Rub' Al Khali 1978. in: Al-Sayari S.S. and Zötl J.G. (Eds.), *Quaternary Period in Saudi Arabia*, Springer-Verlag, Wien, New York, 252-263
- Sanlaville P. 1992. Changements climatiques dans la péninsule arabique durant le Pléistocène supérieur et l'Holocène, *Paléorient*, 18 (1), 5-26
- Schulz E. and Whitney J.W. 1986. Upper Pleistocene and Holocene lakes in the An Nafud, Saudi Arabia, *Hydrobiologia*, 143, 175-190
- Vaslet D., Janjou D., Robelin C., Al Muallem M.S., Halawani M.A., Brosse J.M., Breton J.P., Courbouleix S., Roobol M.J. and Dagain J. 1994. *Geologic map of the Tayma quadrangle (Sheet 27C)*, Kingdom of Saudi Arabia: Saudi Arabian Deputy Ministry for Mineral Resources, Geologic Map GM-134, with text, 51 p.

suggérant un milieu de savane ouverte, mais la présence d'animaux aquatiques implique évidemment la présence d'étendues ou de cours d'eau.

Conclusions : biogéographie et biochronologie

La faune du Nafoud tire toute son importance de sa situation géographique, au carrefour des voies de passage entre Afrique et Eurasie, et sa datation est évidemment capitale. Bien qu'elle soit encore très incomplètement connue, il nous semble qu'elle correspond mieux au Pléistocène inférieur qu'à une période plus récente, car plusieurs espèces évoquent des formes anciennes ; en effet, à l'exception de la tortue et du renard, aucun taxon ne s'accorde avec une espèce actuelle. Elle est, de plus, dépourvue des éléments européens, en particulier les Cervidés, qui caractérisent le Moyen-Orient dès la fin du Pléistocène inférieur.

Cette faune pose le problème de l'âge de certains des sédiments lacustres du Nafoud, jusque-là tous datés de l'Holocène ou de la fin du Pléistocène supérieur (Schulz et Whitney, 1986 ; Sanlaville, 1992). Des phases humides sont pourtant attestées au cours des périodes antérieures, encore très mal connues (Hötl et Zötl, 1978 ; Garrard et Harvey, 1981), et la faune du Nafoud pourrait illustrer l'une d'entre elles.