Proceedings of the 9th Conference of the International Council of Archaeozoology, Durham, August 2002

Series Editors: Umberto Albarella, Keith Dobney and Peter Rowley-Conwy

An offprint from

The Future from the Past

Archaeozoology in wildlife conservation and heritage management

Edited by
Roel C. G. M. Lauwerier and Ina Plug

ISBN 1 84217 115 1

Contents

Zooarchaeology and Wildlife Conservation Issues

Archaeozoology and Heritage Management

9th ICAZ Conference, Durham 2002
The Future from the Past (eds Roel C. G. M. Lauwerier and Ina Plug) pp. 34–50

4. Holocene Faunas of the Eastern Sahara: Zoogeographical and Palaeoecological Aspects

Joris Peters and Nadja Pöllath

Due to the northward shift of the tropical rain belt the Eastern Sahara witnessed an increase in precipitation during the Early and Middle Holocene. This led to the formation of several vast palaeodrainage systems. Faunal and botanical remains collected by geological and archaeological research teams evidence that plants and animals dispersed from the fringes of the Pleistocene hyperarid desert into its centre. In this paper we focus on zoogeographical and palaeoecological aspects of this process. Beyond the contribution to the Holocene development of the Saharan environment, the results of this study can be of relevance for future nature conservation measures in the study area.

Introduction

In the past, the development of deserts, their expansion and contraction, took place largely independent of human activities. An excellent case study of such a cycle is provided by the late Pleistocene and Holocene climatic history of the Eastern Sahara. During the last 12,000 years, the Sahara was exposed to drastic climatic changes, from hyper-arid conditions at the end of the Pleistocene to semi-humid conditions during the first half of the Holocene, and back to hyper-aridity in the course of the last 3,000 years. At the beginning of the 8th millennium calBC, the tilt of the earth's axis was stronger than it is today, and the perihelion was at the end of July (Berger 1978). This led to stronger insolation in the northern Hemisphere in summer and to an increase in the amplitudes of the seasonal cycles. The enhancement of the land-ocean temperature contrast amplified the African and Indian monsoons (*e.g.* Kutzbach and Otto-Bliesner 1982; Kröpelin and Petit-Maire 2000), causing an increased precipitation in the Sahara and resulting in the formation of vast drainage systems with numerous lakes (Pachur 1999; Hoelzmann *et al.* 2001).

The Holocene hydrological conditions favoured the dispersion into the Sahara of species previously restricted to ecozones located south and north of the Late Pleistocene hyperarid desert. Evidence for this can be found in rock art (*e.g.* Lutz & Lutz 1995) as well as in the botanical and faunal samples from archaeological excavations in the Eastern Sahara (*e.g.* Gautier 1982; Gautier and Van Neer 1982; 1989; Peters 1987; Neumann 1989; Van Neer and Uerpmann 1989; Berke 2001; Peters *et al.* 2002).

The vertebrate remains discussed in this contribution have been collected during field work in the frame of three long-term scientific research projects, financed by the German Science Foundation (DFG). The first one, 'Arid Climate, Adaptation and Cultural Innovation in Africa' (University of Cologne, SFB 389), is a multidisciplinary project established in 1995. Scientists from different research disciplines from both the natural (*e.g.* geography, (palaeo)botany, (archaeo)zoology) and social sciences (*e.g.* archaeology, egyptology, social and cultural anthropology, ethnology, linguistics) are involved. Two subprojects deal with the interaction of changing environments and cultural development in the Egyptian and the Sudanese part of the Eastern Sahara during the Holocene climatic optimum. From 1995 onward, numerous sites have been excavated, the animal remains of which being currently under study. A wealth of faunal data has also been collected in the course of an earlier project, 'Besiedlungsgeschichte der Ostsahara' (Settlement history of the Eastern Sahara; University of Cologne, B.O.S.-project), the forerunner of SFB 389. Sampling of faunal remains also took place in the frame of a third project, 'Geo-scientific Research in Arid and Semi-Arid

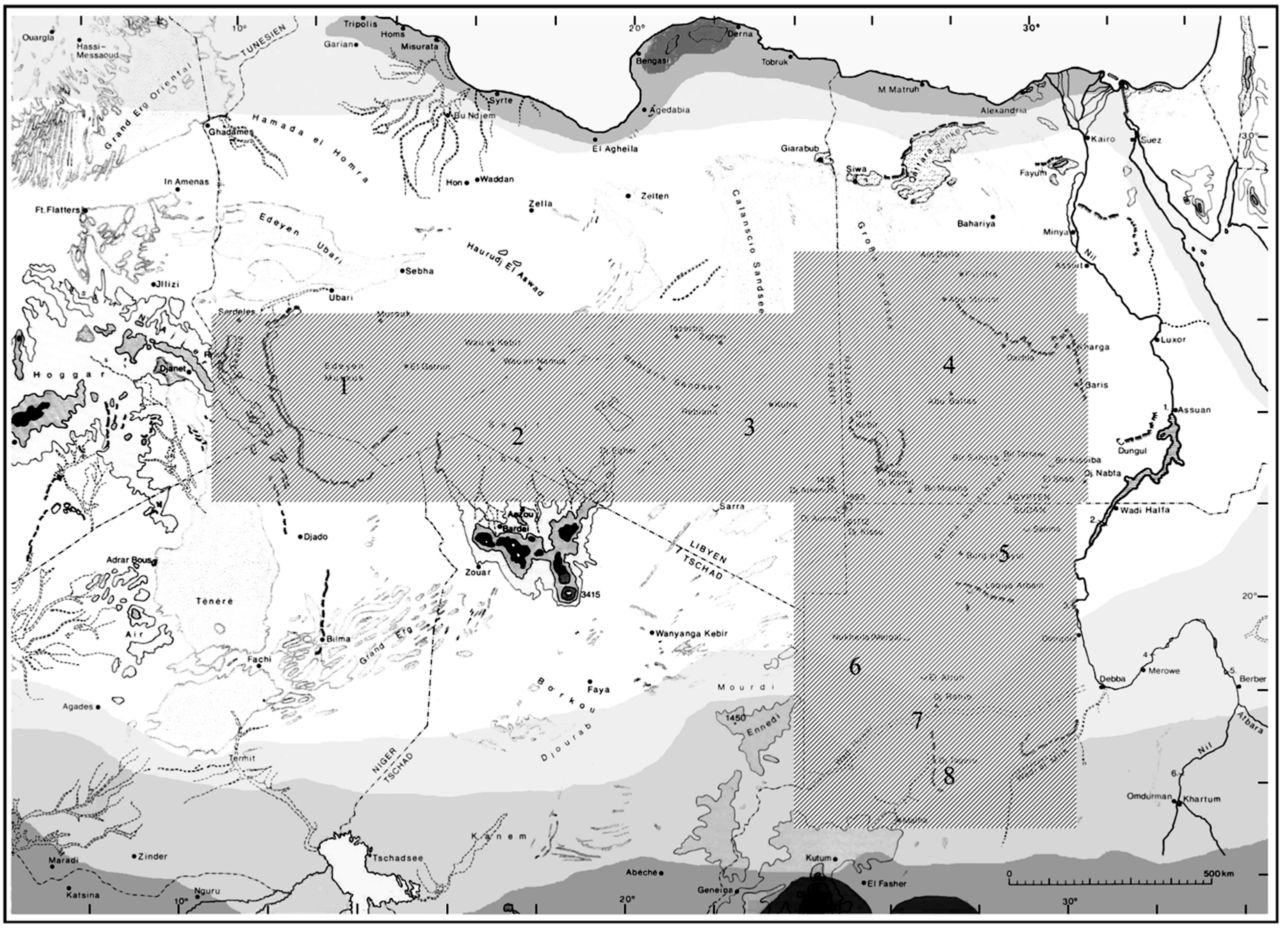

Fig. 1. Map of the Eastern Sahara indicating the present-day vegetationzones, the two transects and the study areas: (1) eastern foreland of the Acacus mountains and the Erg of Murzuq; (2) northern foreland of the Tibesti mountains; (3) Kufra Basin; (4) Western Desert; (5) Laqyia area and Selima Sandsheet; (6) West Nubian Palaeolake area; (7) Wadi Howar; (8) Jebel Tageru area and Meidob Hills.

Areas' (University of Berlin, SFB 69). Though in the latter case research essentially focussed on geological and geographical issues, animal remains were considered of interest because of their significance for the reconstruction of late Quaternary climatic events.

Sampling of faunal remains occurred grosso modo along two transects. The first transect runs about 1,600 km in a West-East direction along the Tropic of Capricorn (Pachur 1999) (Fig. 1). Within this area vertebrate remains were collected in (1) the eastern foreland of the Acacus mountains and the Erg of Murzuq, (2) the northern foreland of the Tibesti mountains, (3) the Kufra Basin and (4) the Egyptian part of the Eastern Sahara (the so-called Western Desert). The North-South transect stretches some 1,200 km along latitude 26°–28°E, *i.e.* from (5) the Laqyia area and Selima Sandsheet in the North to (6) the West-Nubian Palaeolake, (7) the Wadi Howar, and (8) Jebel Tageru area and the Meidob Hills in the South. Today, the North-South transect crosses different ecozones, from the hyperarid desert (< 5 mm precipitation per year) in Egypt and northern Sudan to a zone with contracted desert vegetation in the Middle Wadi Howar region, to a northern Sahel Savanna near the Meidob hills, with an annual precipitation of *c.* 100 mm (Neumann 1989). The West-East transect comes across a single ecozone, the hyper-arid desert.

As said, the faunal remains analysed originated from natural (geological) as well as cultural (archaeological) deposits. Taxonomic composition may therefore differ. The material analysed in the frame of the geo-scientific project comes from fluviatile, limnetic, and semi-lacustrine sediments. The animals encountered in these deposits died naturally, most likely as a result of changes in (micro-)environmental conditions (see below). Given the nature and origin of these deposits, the samples essentially will contain remains from species associated with aquatic and riparian habitats. No doubt, part of the vertebrate remains collected along the seasonal water courses may represent secondary depositions, *e. g.*, animal carcasses and/or bones transported downstream by occasional high floods, but there are also primary contexts, *e.g.* along lake shores, where skeletons of vertebrates still in connection were found. Fossil remains from archaeological contexts have different life and taphonomic histories. They predominantly reflect the palaeodietary habits of the site inhabitants. Thus, whereas geological finds can be considered the outcome of natural phenomena, anthropogenic accumulations mirror a selection, primarily in terms of animal proteins, by communities of hunter-fisher-gatherers or pastoralists. Whichever the origin of the assemblage, only a minor segment of the once existing vertebrate fauna will be present. Besides animal remains, information about late Quaternary environmental conditions and species distribution can also be deduced from rock art, recorded from all major mountain ranges of the study area.

With respect to the absolute age of the animal remains analysed, radiocarbon dates suggest an Early to Middle Holocene age for the bulk of the faunal material obtained from the natural deposits (*e.g.* Kröpelin 1999, Pachur 1999; Pachur and Peters 2001). Because of their less fossilised appearance, however, a number of bone specimens come from later deposits, notably the remains from gazelles, Scimitar oryx, and Addax. It has been noted, moreover, that some of these geological samples yielded material from multiple, subsequent events. Though within individual samples relative chronologies can be established using criteria such as the degree of fossilisation, the major problem will be to correlate findings from different locations, in particular when dating is restricted (at best) to one or few datable specimens. Palaeoecological and -zoogeographical interpretations based exclusively on geological samples will therefore suffer from considerable imponderabilities.

No doubt, well-dated archaeofaunal assemblages could help to compensate for this caveat, but for the moment, the Early to Middle Holocene archaeo(zoo)logical record of the Eastern Sahara still is too poorly known, with the possible exception of the Acacus mountains in south-west Libya (Gautier and Van Neer 1982; Corridi 1998), the Gilf Kebir and Abu Ballas regions in south-west Egypt (Van Neer and Uerpmann 1989; Berke 2001), and the Middle Wadi Howar / Westnubian Palaeolake region in northwest Sudan (Van Neer 1988; 1989a; 1989b; Van Neer and Uerpmann 1989; Berke 2001; Peters *et al.* 2002).

Considering absolute dating in rock art, this issue appears extremely problematic. For the mountain ranges of south-west Libya, for example, a late Pleistocene age has been postulated for the initial stage of rock art (so-called *Bubalus antiquus* phase) (Mori 1965). Since the climate was hyperarid and living conditions even drier than today at that time (Kröpelin 1999), such an early age can be rejected. However, whether the earliest naturalistic depictions of game species were made by Early Holocene hunter-gatherers (*e.g.* Lutz and Lutz 1995), or whether these petroglyphs postdate the 5th millennium calBC arid spell and should therefore be attributed to Middle Holocene hunter-gatherers and/or pastoralists (Muzzolini 1995; Le Quellec 1998, 232 ff.), still is a matter of much debate. Be that as it may, it can be safely assumed that sub-Saharan fauna wildlife depicted in rock art and the animal taxa recognised in Early to Middle Holocene natural or archaeological deposits are broadly contemporaneous.

In the following, zoogeographical aspects, *e.g.* quantitative and qualitative differences, geographic origin of aquatic and herbivorous vertebrate communities inhabiting the Eastern Sahara during the Holocene climatic optimum, as well as palaeoecological issues, in particular habitat diversity in the palaeodrainage systems of West Nubia and in the Erg of Murzuq in south-west Libya, will be addressed.

The Holocene Fauna of the Eastern Sahara: Zoogeographical Aspects

Quantitative and Qualitative Differences along the Two Transects: Some Examples

Fig. 2 gives an overview of the vertebrate spectrum identified on the basis of the bone samples. At least 23 fish, 8 reptile, 17 bird and 49 mammal taxa, as well as four domestic species (cattle, sheep, goat, dog) could be recognised. The majority of the identified taxa today inhabits ecozones located to the south of the Eastern Sahara, with the exception of some species, well-adapted to arid living conditions, *e. g.* dorcas and dama gazelle, addax, scimitar oryx and fennec, and a few taxa of Palaearctic origin, *e.g. Bos*.

A comparison of the Early to Middle Holocene faunas from the sub-regions outlined above reveal interesting differences, not only for the North-South transect, as may be expected because of latitude related changes in precipitation and vegetation cover, but also in a West-East direction along the Tropic of Capricorn, illustrated by the frequency of artiodactyl taxa. Whereas the samples from the Erg of Murzuq yielded evidence for at least 15 taxa, only 7 taxa have been recorded in the samples from south-west Egypt so far (Fig. 2). It should be noted, that this difference is not an artefact of sample size, since the number of bone fragments analysed from the latter region is more than ten times higher (> 100,000).

Along the West-East transect, also qualitative differences between the faunas can be observed, *e.g.* the occurrence in the western half of the Eastern Sahara of species associated with aquatic habitats, such as fishes, bohor reedbuck, hippopotamus, Nile crocodile *etc.* (Fig. 3). Thus, the complete absence of taxa associated with semo-arid environments in the Western Desert on the one hand and their relative abundance in the Erg of Murzuq (n=8) on the other hand – the Kufra Basin occupying an intermediate position (n=4) – is again

Transect	West – East				North – South			
	Erg of Murzuq – Acacus mountains	Tibesti forelnad	Kufra Basin	Western Desert	Selima Oasis – Dry Selima – Laqiya area	West Nubian Palaeolake region	Middle Wadi Howar – Jebel Rahib	Jebel Tageru – Wadi Magrur – Meidob hills
FISH								
Polypterus sp.	–	–	–	–	–	+	+	+
Heterotis, *Heterotis niloticus*	–	–	–	–	–	–	+	–
Mormyridae indet.	–	–	–	–	–	–	+	–
Alestes sp.	–	–	–	–	–	–	+	–
Characidae indet.	–	–	–	–	–	–	+	–
Citharinidae indet.	–	–	–	–	–	–	+	–
Bynni, *Barbus bynni*	–	–	–	–	–	–	+	–
Labeo sp.	–	–	–	–	–	+	+	+
Cyprinidae indet.	–	–	–	–	–	–	+	+
Bagrus sp.	–	–	–	–	–	+	+	+
Chrysichthys sp.	–	–	–	–	–	–	+	–
Auchenoglanis sp.	–	–	–	–	–	–	+	+
Widehead catfish, *Clarotes laticeps*	–	–	–	–	–	–	+	–
Schilbeidae indet.	–	–	–	–	–	–	+	–
Clarias sp.	+	–	+	–	–	+	+	+
Heterobranchus sp.	–	–	–	–	–	+	–	+
Clarias/Heterobranchus	+	–	+	–	–	+	+	+
Wahrindi, *Synodontis schall*	–	–	–	–	–	+	–	–
Synodontis sp.	+	–	+	–	–	+	+	+
Nile perch, *Lates niloticus*	–	–	–	–	–	+	+	+
Banded jewelfish, *Hemichromis fasciatus*	–	–	–	–	–	–	+	–
Tilapiini indet.	+	–	+	–	–	+	+	+
Globefish, *Tetraodon lineatus*	–	–	–	–	–	+	–	+
REPTILES								
African soft–shelled turtle, *Trionyx triunguis*	–	–	–	–	–	+	+	+
Pelusios sp.	–	–	–	–	–	–	+	–
Cyclanorbis sp.	–	–	–	–	–	–	+	–
Testudo/Geochelone	+	–	–	+	+	+	–	+
Nile monitor, *Varanus niloticus*	–	–	–	–	–	–	+	–
Varanus sp.	–	–	–	+	–	–	–	–
Nile crocodile, *Crocodylus niloticus*	+	–	–	–	–	+	+	+
African rock python, *Python sebae*	–	–	–	–	–	+	+	+
BIRDS								
Ostrich, *Struthio camelus*	+	–	–	+	+	–	–	+
Great crested grebe, *Podiceps cristata*	+	–	–	–	–	–	–	–
Little grebe, *Podiceps ruficollis*	+	–	–	–	–	–	–	–
Podiceps sp.	+	–	–	–	–	–	–	–
Common moorhen, *Gallinula chloropus*	+	–	–	–	–	–	–	–
Great egret, *Casmerodius albus*	–	–	–	–	–	–	–	+
Yellow–billed stork, *Mycteria ibis*	+	–	–	–	–	–	–	–
Spur–winged goose, *Plectopterus gambensis*	–	–	–	–	–	–	–	+
Mallard, *Anas platyrhynchos*	+	–	–	–	–	–	–	–

Fig. 2. Subregions of the Eastern Sahara and their early to middle Holocene faunal spectra.

Transect	**West – East**				**North – South**			
	Erg of Murzuq – Acacus mountains	**Tibesti forelnad**	**Kufra Basin**	**Western Desert**	**Selima Oasis – Dry Selima – Laqiya area**	**West Nubian Palaeolake region**	**Middle Wadi Howar – Jebel Rahib**	**Jebel Tageru – Wadi Magrur – Meidob hills**
Anas sp.	+	–	–	–	–	+	–	–
Ferruginous duck, *Aythya nyroca*	+	–	–	–	–	–	–	–
Vanellus sp.	–	–	–	–	–	–	–	+
African fish eagle, *Haliaeetus vocifer*	+	–	–	–	–	–	–	–
Falconiformis indet.	+	–	–	–	–	–	–	–
White stork, *Ciconia ciconia*	+	–	–	–	–	–	–	–
Helmeted guinea fowl, *Numida meleagris*	–	–	–	–	–	–	–	+
Common quail, *Coturnix coturnix*	–	–	+	–	–	–	–	–
WILD MAMMALS								
Brown hare, *Lepus capensis*	+	–	–	+	–	–	–	–
Lepus sp.	–	–	+	+	–	+	+	+
North African crested porcupine, *Hystrix cristata*	–	–	–	–	–	–	–	+
Greater cane rat, *Thryonomys swinderianus*	–	–	–	–	–	+	+	+
Golden jackal, *Canis aureus*	+	–	–	+	–	–	–	+
Rueppell's fox, *Vulpes rüppelli*	–	–	–	+	–	–	–	–
White–tailed mongoose, *Ichneumia albicauda*	—	–	–	–	–	–	+	+
Striped hyena, *Hyaena hyaena*	–	–	–	+	–	–	–	+
Spotted hyena, *Crocuta crocuta*	–	–	–	–	–	–	–	+
Wild cat, *Felis silvestris*	–	–	–	+?	+	–	–	+
Serval, *Leptailurus serval*	+	–	–	–	–	–	–	–
Caracal, *Felis caracal*	–	–	–	+	–	–	–	–
Leopard, *Panthera pardus*	+	–	–	–	–	–	–	–
Aardvark, *Orycteropus afer*	–	–	–	–	–	+	–	+
African Elephant, *Loxodonta africana*	+	–	–	+	–	+	+	+
Cape hyrax, *Procavia capensis*	–	–	–	+	–	–	–	–
African wild ass, *Equus africanus*	+	–	–	–	+	–	–	–
Burchell's zebra, *Equus burchellii*	–	–	–	–	–	–	–	+
Equidae indet.	–	–	–	–	–	+	–	+
White rhinoceros, *Ceratotherium simum*	–	–	–	–	–	–	–	+
Black rhinoceros, *Diceros bicornis*	–	–	–	–	–	–	–	+
Ceratotherium/Diceros	+	–	–	–	+	–	–	+
Warthog, *Phacochoerus aethiopicus*	+	–	–	–	–	+	+	+
Hippopotamus, *Hippopotamus amphibius*	+	–	–	–	–	+	+	+
Giraffe, *Giraffa camelopardalis*	–	–	–	+	+	+	+	+
Small bovids:								
Sylvicapra/Ourebia	+	–	–	–	–	–	–	–
Dorcas gazelle, *Gazella dorcas*	+	+	+	+	+	+	–	–
Unidentified *Small Bovids*	+	+	+	+	+	+	+	+
Medium bovids:								
Bohor reedbuck, *Redunca redunca*	+	–	+	–	–	+	–	+
Kob, *Kobus kob*	–	–	–	–	–	–	–	+
Kobus sp.	–	–	–	–	–	+	–	+

Fig. 2. continued.

Transect	West – East				North – South			
	Erg of Murzuq – Acacus mountains	Tibesti forelnad	Kufra Basin	Western Desert	Selima Oasis – Dry Selima – Laqiya area	West Nubian Palaeolake region	Middle Wadi Howar – Jebel Rahib	Jebel Tageru – Wadi Magrur – Meidob hills
Slender–horned gazelle, *Gazella leptoceros*	–	–	–	+	–	–	–	–
Red–fronted gazelle, *Gazella rufifrons*	+	–	–	–	–	–	+	+
Barbary sheep, *Ammotragus lervia*	+	–	–	+	+	+	–	–
Unidentified *Medium Bovids*	+	–	+	+	+	+	–	+
Large Bovids:								
Addax, *Addax nasomaculatus*	+	–	+	+	+	–	–	–
Scimitar–horned oryx, *Oryx dammah*	+	–	–	+	+	+	–	+
Hartebeest*, Alcelaphus buselaphus*	+	–	–	+	–	–	+	+
Alcelaphus/Damaliscus	+	–	–	–	–	+	–	–
Waterbuck, *Kobus ellipsiprymnus*	+	–	–	–	–	–	–	+
Roan antilope, *Hippotragus equinus*	+	–	–	–	–	–	–	+
Dama gazelle, *Gazella dama*	–	–	+	+	+	–	–	–
Unidentified *Large Bovids*	+	–	+	+	+	+	+	+
Very large Bovids :								
Giant eland, *Taurotragus derbianus*	–	–	–	–	–	+	–	+
African buffalo, *Syncerus caffer*	+	–	–	–	–	+	+	+
Giant buffalo, *Syncerus (caffer) antiquus*	+	–	–	–	–	+	+	+
Syncerus sp.	–	–	–	–	+	–	–	+
Unidentified *Very large Bovids*	+	–	+	–	–	+	–	+
DOMESTIC MAMMALS								
Dog	–	–	–	–	+	–	+	–
Cattle	+	–	+	+	+	+	+	+
Sheep	+	–	–	+	+	–	+	–
Sheep/Goat	+	–	–	+	+	+	+	–
Goat	–	–	+	+	+	+	–	–

Fig. 2. continued.

indicative of a West-East gradient in humidity along the Tropic of Capricorn. The presence of vast mesic habitats in south-west Libya during the climatic optimum is also illustrated by rock engravings of species associated with aquatic habitats such as Nile crocodile (Fig. 4) and Hippopotamus (Fig. 5).

As said, a North-South gradient in terms of precipitation and vegetation cover can be postulated. One illustration of this can be found looking at the ungulate taxonomic composition and diversity in the different faunal assemblages (Fig. 6).

Geographic Origin of Holocene Fish Populations in the Eastern Sahara

Relic populations of Nilo-Sudanic fish still occur in the present-day Sahara, but taxonomic diversity is very low (Van Neer 1989b). Species present are characterised by low ecological demands and particular physiological adaptations (see below).

In view of the actual distribution patterns of Nilo-Sudanic fish taxa, it can be assumed that their Early to Middle Holocene presence in the western half of the Eastern Sahara (Erg of Murzuq, Acacus mountains, Kufra Basin) reflects a northern extension of a large hydrological basin, presently located to the south. Conceivably

Taxon	**Erg of Murzuq**	**Kufra Basin**
Clariid, *Clarias/Heterobranchus* sp(p).	+	+
Mochokid, *(Brachy)synodontis* sp(p).	+	+
Cichlid, *Tilapia/Sarotherodon* sp(p).	+	+
Nile crocodile, *Crocodylus niloticus*	+	–
African River Eagle, *Haliaeetus vocifer*	+	–
Hippopotamus, *Hippopotamus amphibius*	+	–
Bohor Reedbuck, *Redunca redunca*	+	+
Waterbuck, *Kobus ellipsiprymnus*	+	–

Fig. 3. Taxa associated with Holocene aquatic habitats along the West-East Transect.

Fig. 4. Crocodile, Wadi Imrawen. (Lutz and Lutz 1995, Fig. 119).

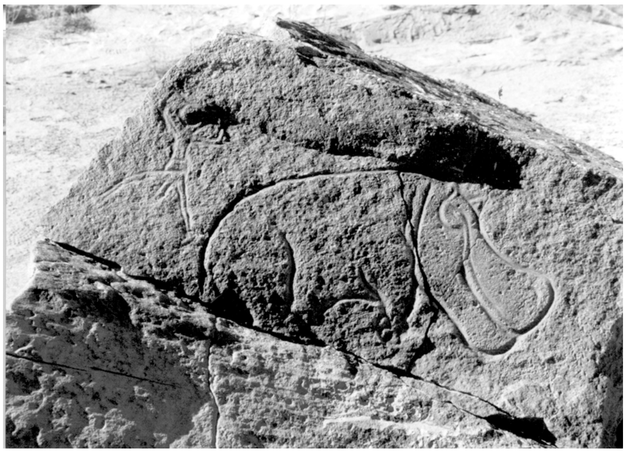

Fig. 5. Hippopotamus, Upper Wadi Aramas. (Lutz and Lutz 1995, Fig. 118).

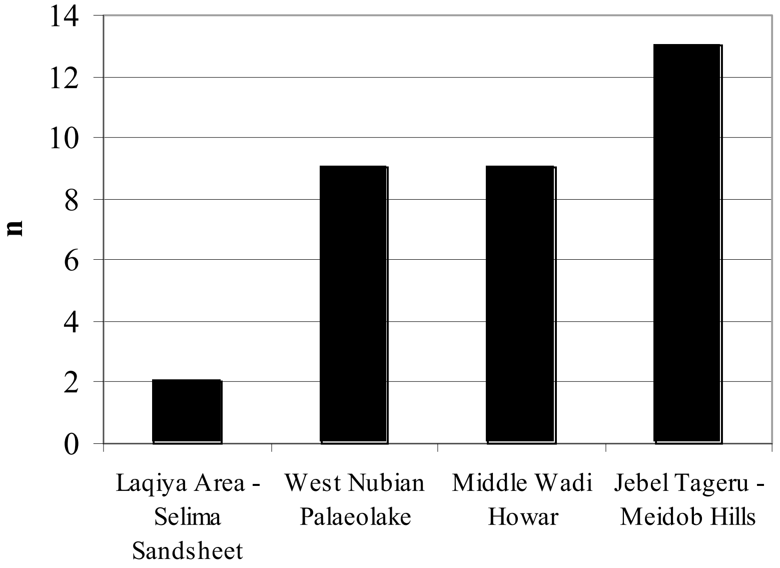

Fig. 6. Early to middle Holocene Ungulate taxonomic composition in the Eastern Sahara in a North-South direction along 26°–28°E.

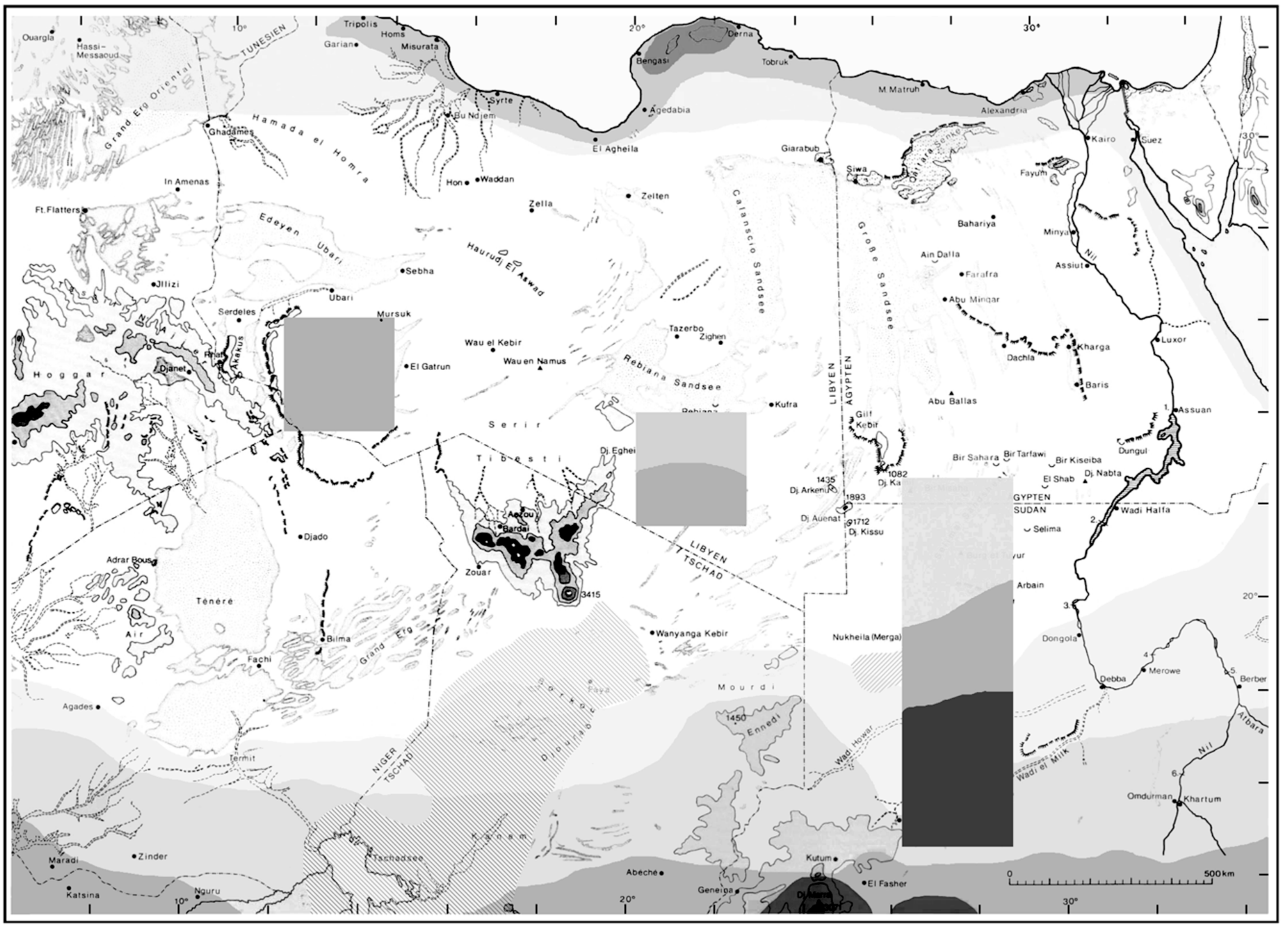

Fig. 7. Estimated position of the biomes during the Holocene climatic optimum on the basis of faunal remains from natural depostits and archaeological sites in the Eastern Sahara.

the palaeodrainage system of the Erg of Murzuq was interconnected with the Chad Basin, which extended much further north during the Holocene optimum. Thus, the Nilo-Sudanic fish taxa present in the Erg of Murzuq most likely originated from the Mega-Chad palaeodrainage system (Fig. 7).

As said, the Holocene climatic optimum witnessed the development of vast palaeodrainage systems, with numerous lakes, ponds and river-like wadis. The most important of these water courses is Wadi Howar in the eastern half of the Eastern Sahara, the largest Saharan tributary of the Nile. Originating in an almost unexplored area in the Ennedi region, Wadi Howar runs 1,100 km in a northeasterly direction to reach the Nile just north of Ed Debba (Pachur and Kröpelin 1987). During much of the Early and Middle Holocene, Wadi Howar may have been a perennial river, but due to aridification in the course of the Holocene, the water level dropped leading to a string of isolated water bodies, *e.g.* pools, swamps, and smaller lakes, interconnected only seasonally (Kröpelin 1993; 1999). Some 150 km north of the middle section of Wadi Howar, the Holocene optimum also witnessed the formation of a chain of palaeolakes. The largest of these is the so-called West Nubian Palaeolake. It had a maximum depth of 15 m and a maximum extent of some 5330 km^2 (Hoelzmann *et al.* 2001). Whilst these palaeodrainage systems already existed at the very beginning of the Holocene optimum (Kröpelin 1993; Pachur 1999), human presence along the Middle Wadi Howar and in the West Nubia Palaeolake region can only be attested from the 5th millennium calBC onward (Keding 1997a; 1997b; 1998; Jesse 1998; Hoelzmann *et al.* 2001). With increasing aridity during the 4th and 3rd millennium calBC, year round human habitation in this region became restricted to ecologically favourable settings with permanent water. From the 2nd millennium calBC onward, man's presence in this area becomes increasingly ephemeral.

Contrary to the Erg of Murzuq, the presence of Nilo-Sudanic fish in Holocene West Nubia (Fig. 1) cannot be explained by a northward dispersion from of a hydrological basin located to the south, but on present evidence solely by a south-westerly migration of aquatic organisms along the Wadi Howar (Van Neer 1989a; 1989b; Peters *et al.* 2002). This Nile tributary served as a migration

Species	**Desert <100 mm**	**N–Sahel 100–250 mm**	**S–Sahel 250–500 mm**	**Sudan Savanna 500–1000 mm**	**Guinea Savanna 1000–1500 mm**
Addax, *Addax nasomaculatus*	+	+	+	–	–
Dorcas gazelle, *Gazella dorcas*	+	+	+	–	–
Dama gazelle, *Gazella dama*	+	+	+	–	–
Scimitar oryx, *Oryx dammah*	–	+	+	–	–
African wild ass, *Equus africanus*	–	+	+	–	–
Red–fronted gazelle, *Gazella rufifrons*	–	–	+	+	–
Aardvark, *Orycteropus afer*	–	–	+	+	+
Warthog, *Phacochoerus africanus*	–	–	+	+	+
Hippopotamus, *Hippopotamus amphibius*	–	–	+	+	+
Giraffe, *Giraffa camelopardalis*	–	–	+	+	+
Bohor reedbuck, *Redunca redunca*	–	–	+	+	+
Waterbuck, *Kobus ellipsiprymnus*	–	–	+	+	+
Korrigum, *Damaliscus lunatus*	–	–	+	+	+
Hartebeest, *Alcelaphus buselaphus*	–	–	+	+	+
Giant eland, *Taurotragus derbianus*	–	–	+	+	+
African buffalo, *Syncerus caffer*	–	–	+	+	+
Greater cane–rat, *Thryonomys swinderianus*	–	–	–	+	+
Kob, *Kobus kob*	–	–	–	+	+
Black rhinoceros, *Diceros bicornis*	–	–	–	+	+

Fig. 8. Herbivore species and their preferred biomes.

path during the Holocene climatic optimum when the two water courses were still interconnected. Though fish populations were separated after the connection with the Nile was interrupted, a diverse ichthyofauna continued to survive in aquatic habitats of the wadi. As to the West Nubian Palaeolake region, it is for the moment impossible to say how the fish migrated into this palaeodrainage system. A connection with the Middle Wadi Howar seems unlikely because of an important topographical barrier, a massive sandstone ridge (Hoelzmann *et al.* 2001). An Upper Wadi Howar origin of the ichthyofauna has been suggested by Peters *et al.* (2002), but need to be verified by future field work.

Palaeozoogeography of Herbivore Communities

Strictly herbivorous species are particularly suitable for zoogeographical studies. They depend on the availability of characteristic food plants and will therefore be encountered in specific biomes. Fig. 8 gives an overview of the different herbivore taxa recognised in the Early to Middle Holocene assemblages of the Eastern Sahara and a rough appreciation of the vegetation zones frequented by these taxa today. If for each sub-region the taxa with the highest ecological demands in terms of plant cover and precipitation are considered representative for the local vegetation during the Holocene climatic optimum, the herbivore record of the Erg of Murzuq, for example, indicate environmental conditions comparable to those prevailing actually in the southern Sahel Savanna (250–500 mm precipitation/year) and/or in the northern Sudan Savanna (500–600 mm precipitation/year). At present, a mammalian fauna similar to the one described from the Erg of Murzuq is recorded from north-east Nigeria (11–12°N; 12–15°E; Happold 1987, 355 ff), *i. e.* some 12–13° further south! Faunal composition in deposits north-east of the Tibesti suggests that the vegetation resembled a mixture of a northern (100–250 mm precipitation/year) and a southern Sahel Savanna, whilst the contemporaneous fauna from the Western Desert (south-west Egypt) is indicative of a northern Sahel Savanna. The West Nubian Palaeolake and the Middle Wadi Howar region witnessed a southern Sahel Savanna and perhaps even a (northern) Sudan Savanna in ecological more favourable settings, whereas the southernmost part of the study area (Wadi Magrur, Jebel Tageru, Meidob Hills) was probably located in a Sudan Savanna.

Based on the actual position of the vegetation belts, the Holocene faunas can be used to estimate how far these would need to shift northward to explain the presence of the taxa encountered. Provided that in the past vegetation zones ran almost parallel to their actual positions, the following assumptions can be made: A southern Sahel/northern Sudan Savanna in the Erg of Murzuq would correspond to a northward shift of the present-day sub-Saharan biomes of some 900 to 1200 km. No doubt, the formation of Lake Mega Chad, which, at its maximum, had a surface somewhat similar to the present-day Caspian Sea (Pachur 1999), favoured the dispersal of sub-Saharan plant and animal communities in this part of the Eastern Sahara. To maintain a northern /southern Sahel Savanna to the north-east of the Tibesti mountains and a northern Sahel Savanna in the Western Desert, a northward shift of 600 to 800 km of the present-day biomes has to be invoked (Kröpelin 1989; 1999; Neumann 1989). To explain the herbivore communities recorded near the West Nubian Palaeolake and in the Middle Wadi Howar region, a northward shift of the present-day biomes of some 400–550 km must be postulated. Finally, taxonomic composition in the assemblages from Jebel Tageru and Meidob Hills indicate that vegetation belts were located some 300 to 400 km further north during the Holocene optimum. All in all, these estimates fit the results obtained by (palaeo)botanists and geoscientists working in the Eastern Sahara (*e.g.* Wickens 1982; Neumann 1989; Kröpelin 1989, 1999; Pachur 1999) and compare well with the palaeoclimatic reconstructions based on faunal remains from Holocene archaeological sites along and to the east of the Nile (*e.g.* Gautier 1983; Peters 1989).

It should be stressed, however, that such estimates are only rough approximations. One major problem is the fact that due to the lack of precise dates, faunal data cannot be used, for example, to trace small-scale oscillations in climate and precipitation. In absence of consistent absolute chronologies – dating being limited to a few taxa of a limited number of assemblages –, only site stratigraphy (archaeological materials) and degree of fossilisation (geological samples) can be used to group 'contemporaneous' taxa. Interestingly, in much of the study area herbivores adapted to drier environments co-existed with taxa preferring wetter living conditions. This suggests that during the Holocene wet phase, moist and semi-arid vegetation types may have co-existed, *e.g.* Sudan Savanna and southern Sahel Savanna or southern Sahel/ northern Sahel Savanna *etc*. If the taxa in these Holocene faunal communities indeed were contemporaneous, it is likely that herbivores with higher ecological demands were mainly confined to well-watered areas with associated vegetation (gallery forest, reeds, grasses), whereas species less dependant on water intake populated the hinterlands. Given such a vertebrate distribution pattern, the estimates concerning the maximum northerly positions of the sub-Saharan biomes may be somewhat overoptimistic. Conversely, if 'wetter' and 'drier' faunal elements did not occur together but replaced each other at consecutive occasions, the osteological findings must be interpreted as evidence for short term climatic oscillations with alternating wet and dry phases. Correspondingly, taxonomic composition of floral and faunal communities may have varied, as well as the geographic position of the sub-Saharan vegetation belts.

In sum, the late Quaternary faunal record of the Eastern Sahara provides evidence for important environmental changes during the Early and Middle Holocene, which enabled the dispersal into the region of taxa, to date associated with the Sahel and Sudan Savanna biomes. Based on habitat preferences of the ecologically most demanding species, the extent of the northward shift of the vegetation belts has been estimated roughly, but the mixed nature of the samples as well as the lack of means to date individual specimens prevent a more detailed evaluation. But some trends are visible (see above), including the observation that during the Early Holocene wet phase, hyper-arid species, such as dorcas gazelle, dama gazelle, and addax largely disappeared from the (moister) western part of the Eastern Sahara, but did survive in the drier eastern part, where annual precipitation may not have exceeded 100–200 mm even during the Holocene optimum (*e.g.* Peters 1987; Kröpelin 1989; Neumann 1989; Van Neer and Uerpmann 1989).

The Holocene Palaeoenvironment: Two Case Studies

Based on the econiches of the taxa identified, it is possible to describe in more detail some of the landscapes that once characterised the Eastern Sahara. An in-depth evaluation of all faunal data lies beyond the scope of this paper. In the following we will focus upon the Middle Holocene aquatic ecosystem of the Wadi Howar region and the Early Holocene vertebrate community of the Erg of Murzuq.

Palaeoecology of the Mid-Holocene Ichthyofauna from Wadi Howar

The list of the fish taxa identified in the fossil assemblages of the Wadi Howar region is given in Fig. 9. Apart from the samples analysed by the authors the list includes additional data from the Wadi Howar (Van Neer 1988; 1989a; 1989b) and from the Central Nile Valley (Peters 1995; Gautier *et al.* 2002). A comparison of the ichthyofaunas reveals that the assemblages from the Central Nile Valley are richer in taxa than the samples of the Wadi Howar region, except for site Djabarona 84/13 (Van Neer 1988). However, faunal diversity not only depends on the number of taxa present but on their relative frequencies in the samples as well. Using the Shannon-Wiener function (Reitz and Wing 1999, 105–6), it can be illustrated that the ichthyofaunas from the Wadi Howar region indeed have significantly lower diversity indices

	Wadi Howar Region				**Central Nile Valley**			
	Palaeolake S 98/20 & 21	**Jebel Rahib 80/87**	**Middle Wadi Howar 84/13–9**	**Middle Wadi Howar S 96/5–1**	**Abu Darbein**	**El Damer**	**Aneibis**	**Jebel Umm Marrahi**
Date	c. 6000–5300 BP	c. 6000 BP	c. 4500–4000 BP	c. 3300 BP	c. 9000–7000 BP			
Protopterus aethiopicus					4	46	50	1
Polypterus sp.	4		40		12	53	53	216
Heterotis niloticus			23				1	158
Hyperopisus bebe						5	2	
Mormyrops anguilloides					1		4	
Mormyridae indet.			14		41	140	38	14
Gymnarchus niloticus						37	6	8
Hydrocynus sp.					1	3		
Alestes sp.			8		3	54		
Characidae indet.			3			13		
Distichodus sp.					3	58	3	
Citharinus sp.						6		
Citharinidae indet.			2			5	4	
Barbus bynni			8					
Barbus sp.						20	6	
Labeo sp.			4			27	2	
Cyprinidae indet.			39		34	333	24	55
Bagrus bajad					4	2	1	
Bagrus docmak					2	2	1	
Bagrus sp.			10		50	247	48	36
Chrysichthys sp.			2	1				
Auchenoglanis sp.			18	1	1	1		6
Clarotes laticeps			1			4	1	
Schilbeidae indet.			4					
Clariidae indet.	5	385	1189	33	74	926	261	
Clarias sp.		41		2	11	71	9	540
Heterobranchus sp.						1		
Synodontis serratus							2	
Synodontis sorex					1	2		
Synodontis batensoda					1			
Synodontis membranaceus					3			
Synodontis schall					5	6	13	
Synodontis sp.	1	6	172		301	261	455	66
Malapterus electricus						1	1	
Lates niloticus	22	5	45	2	32	217	176	239
Tilapiini indet.	15	109	1896	58	3	42	22	89
Hemichromis fasciatus			13					
Parachanna								2
Tetraodon fahaka		8			1	1	3	1
Total	48	554	3491	97	588	2584	1186	1431

Fig. 9. Species spectrum of fish bone samples from the Wadi Howar region and the Central Nile Valley (NISP).

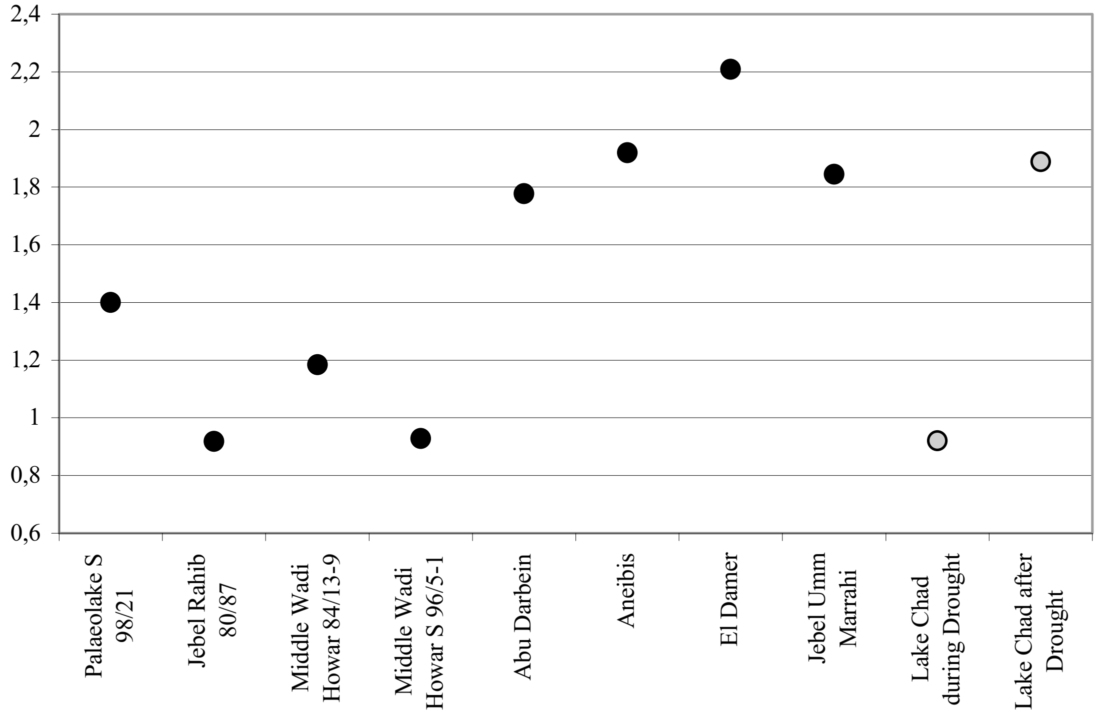

Fig. 10. The diversity (H′) of fish bone samples from sites in the Wadi Howar region, the Central Nile Valley and modern Lake Chad.

(H′) than the values calculated for the fish bone samples from the Central Nile Valley (Fig. 10). To understand these differences, a closer look at the habitat requirements of the species present is needed.

In arid ecosystems water bodies are characterised by daily and seasonal fluctuations in water temperature, high evaporation rates, turbidity and other natural phenomena, all of which affect water chemistry. Studies on Afrotropical fishes demonstrate that some species possess adaptations for coping with extreme changes in water chemistry. For freshwater fishes water temperature is an important factor which influences, *e.g.* spawning behaviour, egg maturation and individual growth. A few species can tolerate extreme temperatures above 35° and/ or a wide temperature range. Tilapiines like *Oreochromis niloticus* and *Tilapia zillii* tolerate even temperature changes from 8°C to 40°C (Lévêque 1997). The importance of water temperature for the reproduction of freshwater fishes shows the example of two closely related Nilo-Sudanic clariid catfishes. Whereas in *Heterobranchus longifillis* spawning will only take place between 25°C and 29°C, the eurytherm *Clarias gariepinus* can reproduce within a much wider temperature range of 19°C to 31°C (Lévêque 1997).

Temperature affects fishes not only directly, but also by its influence on water chemistry, in particular concentration of dissolved oxygen and salinity. Species with high oxygen demands are, for example, *Lates niloticus*, bagrid catfishes and mormyrids (Fish 1956), and will therefore be absent if oxygen becomes reduced. To cope with low oxygen concentrations, some freshwater fishes developed additional organs for aerial breathing, like the clariid catfishes and the African lungfish *Protopterus aethiopicus* (Lévêque 1997). Hence, adult *Clarias gariepinus* can obtain up to 50% of their total oxygen requirements from the air. Other strategies can be found in *(Brachy)Synodontis*, which are able to enhance their haemoglobin production in order to ensure sufficient oxygen supply (Green 1977), whereas the haemoglobin of tilapiines show significantly higher oxygen affinity compared to other species (Fish 1956). Apart from low oxygen contents, shallow water bodies in arid regions are also characterized by high evaporation rates, in particular if rainfall is insufficient reducing the supply of freshwater, which will cause an increase in salinity. Species able to survive high salinity levels are *Clarias gariepinus*, *(Brachy)Synodontis* and tilapias (Lévêque 1997), whereas other taxa, *e.g.* mormyrids, do not tolerate even the slightest increase in salinity (Bénech *et al.* 1983).

These and other abiotic factors influence species-specific characteristics like feeding and reproduction strategies. Reproductive cycles, for example, are linked to the seasons and to the existence of favourable conditions for the survival of eggs and larvae. In African freshwater ecosystems, therefore, species can be separated according to their spawning strategies. During the rainy season the floodplains yield abundant food and cover for the fry. Many taxa will therefore migrate into these

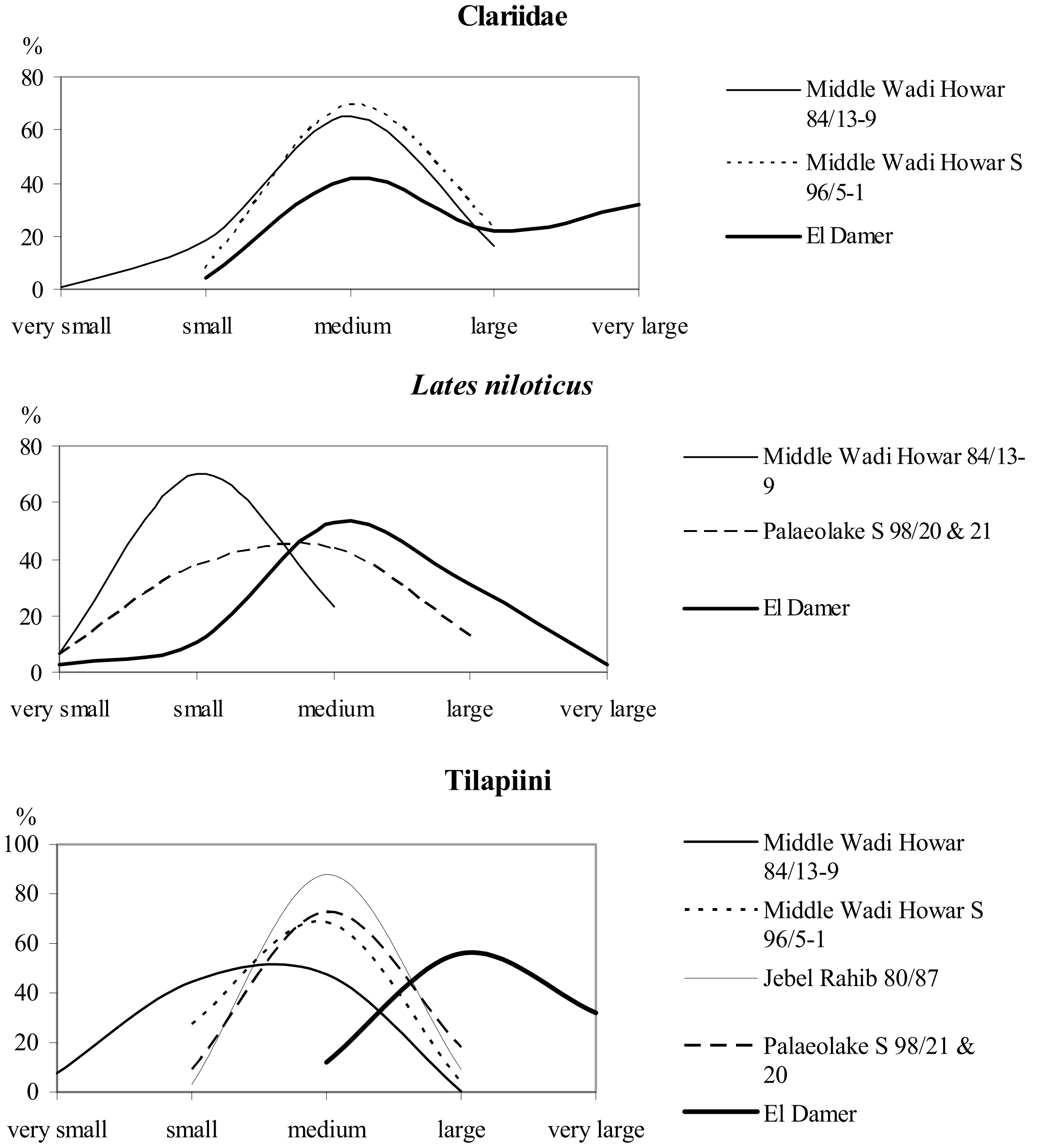

Fig. 11. Size distribution of Clariidae, Lates niloticus*, and Tilapiini from selected sites.*

inundated areas, except for the Nile perch, *Lates niloticus*, which will leave the main river later and only for a very short period, because it cannot withstand the rapidly deteriorating conditions of floodplains for a long time. On the contrary, other taxa, like clariids, tilapiines, *Polypterus*, *Protopterus*, *etc*., will frequent the inundated plains until the waters start to recede, even at the risk of being cut off from the main water body. According to their feeding and/or spawning behaviour, Nilo-Sudanic fish taxa can therefore be roughly classified into two categories, „floodplain dwellers‘, *e.g. Clarias* and tilapiini, and „open water forms‘, *e.g. Lates*, *Synodontis* and bagrids (Van Neer 1989b).

From Fig. 9 it can be seen that remains from Clariids and tilapias form the bulk of the fish bone samples collected in sites of the Wadi Howar region. This suggests that the ecological requirements of the two taxa were largely met within the respective site catchments. To a certain extent, the abundance of these taxa mirrors some constraints imposed by the Holocene environment, *i.e.* low oxygen contents, high temperature, and considerable salinity levels. Isolated bones of *Lates niloticus*, as seen a species with particular ecological demands, were also identified in each assemblage. Consequently more favourable living conditions must have existed, at least in certain parts of the Wadi Howar ecosystem. Considering the relative abundance of the taxa identified and their ecological requirements, it can be assumed that the mid-Holocene Middle Wadi Howar palaeodrainage system primarily consisted of shallow, mostly temporary water bodies. Though, there is also evidence for the presence of some deeper, larger and better oxygenated freshwater habitats in the wadi catchment. Given the low frequencies of fishes associated with these environments, these water bodies may not have been located necessarily in the neighbourhood of the sites excavated until now. During the rainy season, fish presumably migrated from a larger water body upstream (Upper Wadi Howar?) to the inundated areas downstream.

On the basis of taxonomic composition and relative frequencies (Peters *et al.* 2002), much more stable hydrologic conditions can be postulated for the West Nubian Palaeolake compared to the Middle Wadi Howar drainage system. That living conditions in the West Nubian Palaeodrainage system may have been not optimal compared with the Nile, is suggested by the size distribution of the taxa (Fig. 11). Indeed, *Clarias*, *Lates* and tilapias from the Wadi Howar region are, on average, smaller than their relatives caught in the Central Nile. Comparably poor living conditions in the Wadi Howar drainage system could have been the cause, since growth rates correlate with environmental factors (Lévêque 1997), but these seem to have differed between species. Whereas *Clarias* from sites in the study area reached almost the same size as their relatives inhabiting the Nile, the tilapias and the Nile perch remained significantly smaller, suggesting that the habitat was not optimal. With respect to *Lates*, the largest individuals are recorded from sites along the main Nile, whereas the smallest individuals come from the Middle Wadi Howar sites, with *Lates* from the West Nubian Palaeolake region occupying an intermediate position. Conceivably, this large freshwater biotope presented a much more stable aquatic environment compared to the Middle Wadi Howar, but again, did not offer optimal living conditions for species with high ecological demands, hence limiting the species' size. Growth ring studies are necessary to test this assumption. An example of the extent to which climatic changes can affect fish species diversity in inland waters of tropical Africa comes from Lake Chad. In Fig. 10 we added two diversity values obtained from modern Lake Chad (Bénech *et al.* 1983), the first being calculated on the basis of experimental catches at the end of the drought period in 1975, the second at the onset of a new equilibrium since 1977. Of interest is the fact that the first value corresponds well to those obtained for the Wadi Howar sites, while the second fits better the values calculated for the Central Nile Valley sites. From a methodological point of view, a comparison of archaeological samples with modern zoological data is problematic because of fundamental differences between fossil and modern samples as well as sampling methods. For instance, while ichthyologists can sample active present-day freshwater ecosystems, archaeozoologists can only analyse the leftovers of prehistoric human groups. Moreover, fossil fish bone assemblages have been modified by pre- and postdepositional processes that cause differential preservation, *e.g.* a bias in favour of osseous remains of species with a more robust skeleton, such as *Lates niloticus*. Nevertheless, the phenomena observed in the Lake Chad ecosystem provide an interesting model for interpreting the Holocene ichthyofaunal record in the Middle Wadi Howar region. Looking at the taxonomic composition of the fish fauna from Lake Chad at the end of the long drought period (Bénech *et al.* 1983), it may be possible that the habitat features of the mid-Holocene water bodies in the Middle Wadi Howar region may not have been too different.

Ecology of the Early Holocene Vertebrate Fauna from the Erg of Murzuq

Fish, reptiles, birds, and mammals are the vertebrate groups recognised in Early Holocene deposits from the Erg of Murzuq. A comparison of the Wadi Howar ichthyofaunal spectrum with the one from the Murzuq area reveals the taxonomic paucity of the latter (Fig. 1). Until now, the taxa *Clarias*, *(Brachy)Synodontis* and tilapiini could be evidenced. As said, dispersal likely took place via a network of water courses, linking the Erg of Murzuq with the (Mega) Chad Basin, but ecological bottlenecks reduced taxonomic diversity considerably. Based on the observations made above, we can assume that the small mean size of these individuals is indicative of unstable aquatic conditions. Though a good tolerance of hypoxic conditions and salinity has been noted in *(Brachy)-Synodontis,* members of this taxon are less well-adapted to cope with high salinity levels compared to *Clarias* and tilapiini (Lévêque 1997). Interestingly, all *(Brachy)-Synodontis* remains collected so far in the Erg of Murzuq come from sediments of the somewhat larger, more permanent palaeolakes that stretched over 3 km and had estimated maximum depths of *c.* 10 m, whereas remains of the ecologically more tolerant catfish and tilapias have also been found on ancient shores of much smaller water bodies.

Palaeoenvironmental information also comes from the other vertebrate groups (Fig. 2). The crocodile remains found, for example, are mostly of individuals with lengths below 2.5 m. Smaller crocodiles mainly take up residence in swamps and backwaters, feeding essentially on (cat)fish (Branch 1988). Following the ecological requirements of the different bird taxa, larger (African fish eagle, great crested grebe) as well as smaller (moorhen, pintail) aquatic habitats were present, mainly with shallow, slow-moving (yellow-billed stork, ferruginous duck), fresh to brackish waters (ferruginous duck, pintail), bordered by trees (African fish eagle), reeds and other aquatic vegetation (great crested grebe, pintail, ferruginous duck, moorhen), and surrounded by grasslands and marshes (white stork, yellow-billed stork, moorhen, quail). Most birds present are known to rely on a broad spectrum of plants and/or animals (molluscs, amphibians *etc.*), with the possible exception of the African fish eagle, which

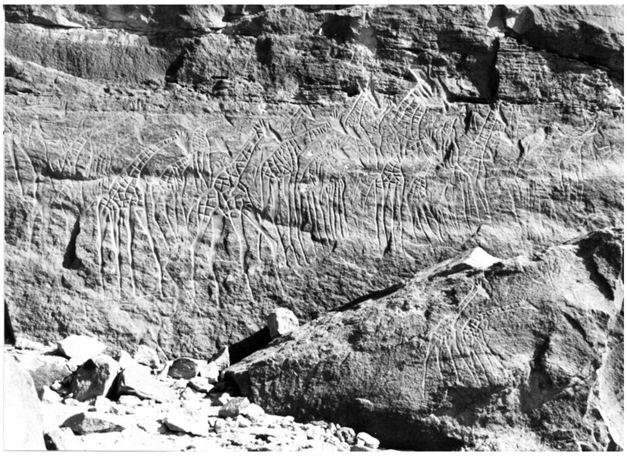

Fig. 12. Giraffe herd, Wadi Aramas. (Lutz and Lutz 1995, Fig. 107).

Fig. 13. African buffaloes, Wadi Alamasse. (Lutz and Lutz 1995, Fig. 108).

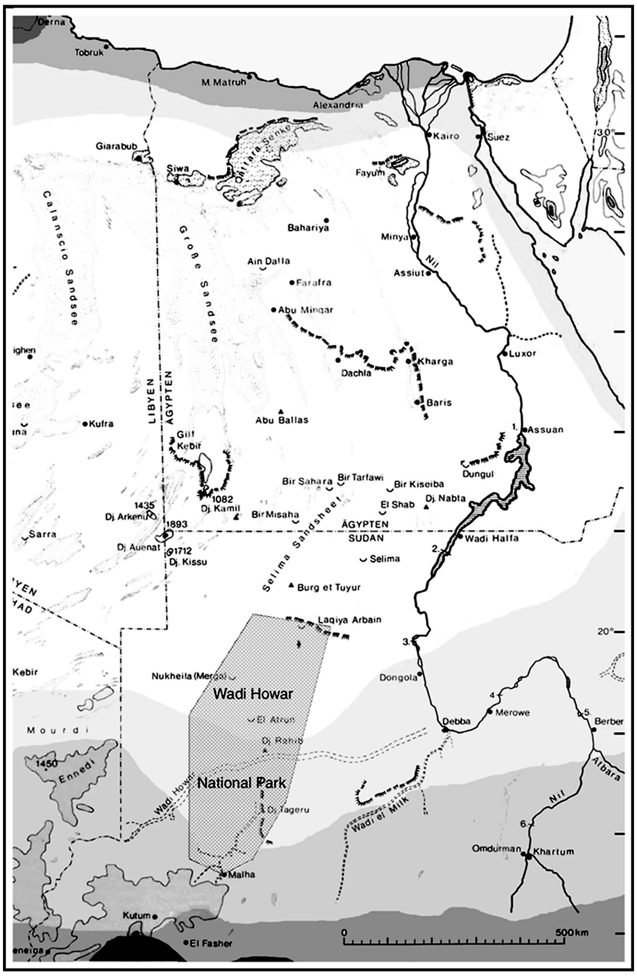

Fig. 14: Location of the Wadi Howar National Park. (Kröpelin 1999, Fig. 11.24).

normally prefers surface-feeding fish up to 1 kg, like catfish, tilapias or lungfish (Brown *et al.* 1982, 313).

As to the terrestrial mammals, their habitat requirements indicate that the dominant vegetation type in the Erg of Murzuq were grasslands and sparse, open woodlands with an abundance of shrubs and some stands of smaller trees (hare, serval, warthog, hartebeest, roan antelope, korrigum, oribi, crowned duiker, red-fronted gazelle), whereas near permanent water bodies large trees and shrubs were found, forming quite dense shady habitats (leopard, buffalo, waterbuck). The vegetation associated with the lakes, marshes and swamps consisted of moist grasslands (hippopotamus, buffalo, waterbuck, korrigum), water plants, tall grasses and reeds (bohor reedbuck, hippopotamus). Animals depicted in rock art (*e. g.* Frobenius 1937; Lutz and Lutz 1995; Muzzolini 1995; Le Quellec 1998) complete the faunal spectrum: African elephant, white rhinoceros, African wild ass, hippopotamus (Fig. 5), giraffe (Fig. 12), giant and African buffalo (Fig. 13), hartebeest, barbary sheep, leopard, and Nile crocodile (Fig. 4).

Based on the foregoing, it can be concluded that the palaeodrainage system and the vegetated dunes of the Erg of Murzuq, as well as the surrounding mountainous areas and wadis, formed a complex, heterogeneous ecosystem with a multitude of habitats and niches.

Concluding Remark

Interdisciplinary long-term geo-scientific and archaeological research programmes provided the faunal materials dealt with in this study. Since the Eastern Sahara represents an area of immense natural and cultural heritage (*e.g.* Kuper 1981; Kröpelin 1999; Hoelzmann *et al.* 2001), efforts have been intensified to prevent at least part of this heritage from being destructed by economic development programmes and tourism (vgl. Kröpelin 2002). It is within this context that 2001 the Wadi Howar National Park was established (Fig. 14; Kröpelin 1999). Future measures might include the re-introduction of sub-Saharan vertebrate species, for which the archaeozoological results presented here may be of relevancy.

Acknowledgements

We are indebted to the members of the research projects mentioned above for the constructive collaboration. The financial support of the Deutsche Forschungsgemeinschaft for these projects is gratefully acknowledged. W. Van Neer kindly provided unpublished data on fish remains from the B. O. S. project. I. Plug and W. Van Neer commented an earlier draft of this paper. This report combines two papers of the authors given at the Durham conference.

References

Bénech, V., Durand, J.-R. and Quensière, J. 1983. Fish communities of Lake Chad and associated rivers and floodplains, pp. 293–356 in Carmouze, J.-P., Durand, J.-R. and Lévêque, C. (eds), *Lake Chad. Ecology and productivity of a shallow tropical ecosystem. Monographiae biologicae* **53**. The Hague, Boston, Lancaster: Junk Publishers.

Berger, A. 1978. Long-term variation of caloric insolation resulting from earth's orbital elements. *Quaternary Research* **9**, 136–67.

Berke, H. 2001. Gunsträume und Grenzbereiche. Archäozoologische Beobachtungen in der Libyschen Wüste, Sudan und Ägypten, pp. 237–56 in Gehlen, B., Heinen, M. and Tillmann, A. (Hrsg.), *Zeit-Räume. Gedenkschrift für Wolfgang Taute. Archäologische Berichte* **14**. Bonn: Selbstverlag der Deutschen Gesellschaft für Ur- und Frühgeschichte e.V. / Dr. R. Habelt.

Branch, B. 1988. *Bill Branch's Field Guide to the Snakes and other Reptiles of Southern Africa.* Cape Town: Struik Publishers.

Brown, L. H., Urban, E. K. and Newman, K. 1982. *The Birds of Africa* **1**. London: Academic Press.

Corridi, C. 1998. Some new archaeozoological data from the Tadrart Acacus, Libya (9th to 5th millennium B.P.), pp. 41–7 in Gautier, A. (ed.), *Animals and people in the Holocene of North Africa. ArchaeoZoologia* **9**. Grenoble: La Pensée Sauvage.

Fish, G. R. 1956. Some aspects of the respiration of six species of fish from Uganda. *Journal of Experimental Biology* **33**, 186–95.

Frobenius, L. 1937. *Ekade Ektab, die Felsbilder Fezzans*. Leipzig, Harrassowitz.

Gabriel, B., Kröpelin, S., Richter, J. and Cziesla, E. 1985. Parabeldünen am Wadi Howar. *Geowissenschaften in unserer Zeit* **3**, 105–22.

Gautier, A. 1982. Neolithic faunal remains in the Gilf Kebir and the Abu Hussein Dunefield, Western Desert, Egypt, pp. 335–9 in El-Baz, F. and Maxwell ,T. A. (eds), *Desert landforms of southwest Egypt. a basis for comparison with Mars*. Washington: NASA Scientific and Technical Information Branch.

Gautier, A., Linseele, V. and Van Neer, W. 2002. The fauna of the early Khartoum occupation on Jebel Umm Marrahi (Khartoum Province, Sudan, pp. 337–44 in Jennerstraße 8 (Hrsg.), *Tides of the Desert. Contributions to the Archaeology and Environmental History of Africa in Honour of Rudolph Kuper.* Africa Praehistorica **14**. Köln: Heinrich-Bart-Institut.

Gautier, A. and Van Neer, W. 1982. Prehistoric fauna from Ti-n-Torha (Tadrart Acacus, Libya). *Origini* **12**, 87–127.

Gautier, A. and Van Neer, W. 1989. Animal Remains from the Late Paleolithic Sequence at Wadi Kubbaniya, pp. 119–61 in Wendorf, F., Schild, R. (assembl.) and Close, A. E. (ed.), *The prehistory of Wadi Kubbaniya 2. Stratigraphy, paleoeconomy, and environment*. Dallas: Southern Methodist University Press.

Green, J. 1977. Haematology and habitats in catfish of the genus *Synodontis. Journal of Zoology* **182**, 39–50.

Happold, D. C. D. 1987. *The Mammals of Nigeria*. Oxford: Clarendon Press.

Hoelzmann, P., Keding, B., Berke, H., Kröpelin, S. and Kruse, H.-J. 2001. Environmental change and archaeology. Lake evolution and human occupation in the eastern Sahara during the Holocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* **169**, 193–217.

Jesse, F. 1998. *Zur Wavy Line-Keramik in Nordafrika unter besonderer Berücksichtigung des Wadi Howar (Sudan) und dort des Fundplatzes Rahib 80/87*. Diss. phil.: Universität zu Köln.

Keding, B. 1997a. *Djabarona 84/13. Untersuchungen zur Besiedlungsgeschichte des Wadi Howar anhand der Keramik des 3. und 2. Jahrtausends v.Chr.* Africa Praehistorica **9**. Köln: Heinrich-Barth-Institut.

Keding, B. 1997b. Prehistoric investigations in the Wadi Howar region. a preliminary report on the 1995–1996 season. *Kush* **1997**, 33–46.

Keding, B. 1998. The Yellow Nile. New Data on Settlement and the Environment in the Sudanese Eastern Sahara. *Sudan and Nubia* **2**, 2–12.

Kröpelin, S. 1989. Untersuchungen zum Sedimentationsmilieu von Playas im Gilf Kebir (Südwest-Ägypten), pp. 183–305 in Kuper, R. (Hrsg.), *Forschungen zur Umweltgeschichte der Ostsahara.* Africa Praehistorica **2**. Köln: Heinrich-Barth-Institut.

Kröpelin, S. 1993. *Zur Rekonstruktion der spätquartären Umwelt am Unteren Wadi Howar (Südöstliche Sahara/NW Sudan).* Berliner Geographische Abhandlungen **54**. Berlin: Geomorphologisches Laboratorium der Freien Universität.

Kröpelin, S. 1996. Suggesting natural heritage sites in remote desert areas, pp. 35–41 in Ayyad, M. A., Kassas, M. and Ghabbour, S. I. (eds), *Conservation and management of natural heritage in Arab countries*. Cairo: UNESCO-MAB.

Kröpelin, S. 1999. Terrestrische Paläoklimatologie heute arider Gebiete. Resultate aus dem Unteren Wadi Howar (Südöstliche Sahara/Nordwest-Sudan), pp. 446–506 in Klitzsch, E. and Thorweihe, U. (Hrsg.), *Nordost-Afrika. Strukturen und Ressourcen. Ergebnisse aus dem Sonderforschungsbereich 'Geowissenschaftliche Probleme in ariden und semiariden Gebieten'*, 446–506. Weinheim: Wiley-VCH.

Kröpelin, S. and Petit-Maire, N. 2000. Paleomonsoon variations and environmental change during the late Quaternary. *Global Planetary Change* 26, vii-viii.

Kröpelin, S. 2002. Damage to natural and cultural heritage by petroleum explotarion and desert tourism in the Messak Settafet (Central Sahara, Southwest Libya), pp. 405–23 in Jennerstraße 8 (Hrsg.), *Tides of the Desert. Contributions to the Archaeology and Environmental History of Africa in Honour of Rudolph Kuper.* Africa Praehistorica **14**. Köln: Heinrich-Barth-Institut.

Kuper, R. 1981. Untersuchungen zur Besiedlungsgeschichte der östlichen Sahara. Vorbericht über die Expedition 1980. *Beiträge zur Allgemeinen und Vergleichenden Archäologie* **3**, 215–75.

Kutzbach, J. E. and Otto-Bliesner, B. L. 1982. The sensitivity of the African-Asian monsoonal climate to orbital parameter changes for 9000 years BP in a low resolution General Circulation Model. *Journal of Atmosphere Science* **39**, 1177–88.

Lévêque, C. 1990. Relict tropical fish fauna in Central Sahara. *Ichthyological Exploration of Freshwaters* **1**, 39–48.

Lévêque, C. 1997. *Biodiversity dynamics and conservation. The freshwater fish of tropical Africa.* Cambridge: Cambridge University Press.

Le Quellec, J.-L. 1998. *Art rupestre et préhistoire du Sahara. Le Messak libyen.* Paris: Payot.

Lutz, R. and Lutz, G. 1995. *Das Geheimnis der Wüste. Die Felskunst des Messak Sattafet und Messak Mellet – Libyen.* Innsbruck: Golf Verlag.

Mori, F. 1965. *Tadrart Acacus, Arte rupestre e culture del Sahara preistorico.* Turin: Einaudi.

Muzzolini, A. 1995. *Les images rupestres du Sahara.* Toulouse: printed by the author.

Neumann, K. 1989. Vegetationsgeschichte der Ostsahara im Holozän. Holzkohlen aus prähistorischen Fundstellen, pp. 13–181 in Kuper, R. (Hrsg.), *Forschungen zur Umweltgeschichte der Ostsahara.* Africa Praehistorica **2**. Köln: Heinrich-Barth-Institut.

Pachur, H.-J. 1999. Paläo-Environment und Drainagesysteme der Ostsahara im Spätpleistozän und Holozän, pp. 366–445 in Klitzsch E. and Thorweihe U. (Hrsg.), *Nordost-Afrika. Strukturen und Ressourcen. Ergebnisse aus dem Sonderforschungsbereich 'Geowissenschaftliche Probleme in ariden und semiariden Gebieten'*. Weinheim: Wiley-VCH.

Pachur, H.-J. and Hoelzmann, P. 2000. Late Quaternary palaeoecology and palaeoclimates of the Eastern Sahara. *Journal of African Earth Sciences* **30**, 929–39.

Pachur, H.-J. and Kröpelin, S. 1987. Wadi Howar. Paleoclimatic evidence from an extinct river system in the southeastern Sahara. *Science* **237**, 298–300.

Pachur, H.-J., Kröpelin, S., Hoelzmann, P., Goschin, M. and Altmann, N. 1990. Late Quaternary fluvio-lacustrine environments of Western Nubia. *Berliner Geowissenschaftliche Abhandlungen (A)* **120.1**, 203–60.

Pachur, H.-J. and Peters, J. 2001. The position of the Murzuq Sand Sea in the palaeodrainage system of the Eastern Sahara. *Palaeoecology of Africa and the Surrounding Islands* **27**, 259–90.

Pachur, H.-J. and Wünnemann, B. 1996. Reconstruction of the Palaeoclimate along 30°E in the Eastern Sahara during the Pleistocene/Holocene transition. *Palaeoecology of Africa and the surrounding Islands* **24**, 1–32.

Peters, J. 1987. The Faunal Remains collected by the Bagnold-Mond Expedition in the Gilf Kebir and Jebel Uweinat in 1938. *Archéologie du Nil Moyen* **2**, 251–64.

Peters, J. 1989. Faunal Remains and Environmental Change in Central and Eastern Sudan from Terminal Pleistocene to Middle Holocene Times. *Academiae Analecta, Mededelingen van de Koninklijke Academie voor Wetenschappen, Letteren en Schone Kunsten van België, Klasse der Wetenschappen* **51**(4), 121–48.

Peters, J. 1995. Mesolithic subsistence between the 5th and the 6th Nile Cataract. The archaeofaunas from Abu Darbein, El Damer and Aneibis (Sudan), pp. 178–244 in Haaland, R. and Magid, A.A. (eds), *Aqualithic sites along the rivers Nile and Atbara, Sudan*. Bergen: Alma Mater.

Peters, J., Pöllath, N. and Driesch, A. von den 2002. Ichthyological Diversity in the Holocene Palaeodrainage Systems of Western Nubia, pp. 325–35 in Jennerstraße 8 (Hrsg.), *Tides of the Desert. Contributions to the Archaeology and Environmental History of Africa in Honour of Rudolph Kuper*. Africa Praehistorica **14**. Köln: Heinrich-Barth-Institut.

Reitz, E. J. and Wing, E. S. 1999. *Zooarchaeology.* Cambridge Manuals in Archaeology. Cambridge: Cambridge University Press.

Van Neer, W. 1988. Fish remains from a holocene site (84/13–9) in Wadi Howar, Sudan. *Archaeozoologia* **2**(1–2), 339–48.

Van Neer, W. 1989a. Holocene fish remains from the Sahara. *Sahara* **2**, 61–8.

Van Neer, W. 1989b. Recent and fossil fish from the Sahara and their palaeohydrological meaning. *Palaeoecology of Africa and the Surrounding Islands* **20**, 1–18.

Van Neer, W. and Uerpmann, H.-P. 1989. Palaeoecological significance of the Holocene faunal remains of the B.O.S.-missions, pp. 309–41 in Kuper R. (ed.), *Forschungen zur Umweltgeschichte der Ostsahara.* Africa Praehistorica **2**, 309–41. Köln: Heinrich-Barth-Institut.

Wickens, G. E. 1982. Palaeobotanical Speculations and Quaternary Environments in the Sudan, pp. 23–50 in Williamson, M. A. J. and Adamson, D. A. (eds), *A Land between Two Nile.* Rotterdam: Balkema.

Joris Peters
State Collection for Anthropology
and Palaeoanatomy in Munich,
Karolinenplatz 2a,
D-80333 Munich, FRG.
and
Institute for Palaeoanatomy and
History of Veterinary Medicine
Kaulbachstr. 37
D-80539 München, FRG.
E-mail: joris.peters@palaeo.vetmed.uni-muenchen.de

Nadja Pöllath,
Sonderforschungsbereich 389
'Arid Climate, Adaptation and Cultural Innovation
in Africa',
Jennerstraße 8,
D-50823 Köln, FRG.
and
State Collection for Anthropology
and Palaeoanatomy in Munich,
Karolinenplatz 2a,
D-80333 Munich, FRG.
E-mail: nadja.poellath@palaeo.vetmed.uni-muenchen.de