International Journal of Environmental Sciences & Natural Resources
ISSN: 2572-1119

Juniper Publishers
key to the Researchers

Research Article
Volume 36 Issue 1 - November 2025
DOI: 10.19080/IJESNR.2025.36.556432

Int J Environ Sci Nat Res


# Paleozoology of Sudan: 3. Mammalian fossils

**Muna A Mohmed[1] and Zuheir N Mahmoud[2]***

[1]*Department of Biology, Taibah University, Sudan*

[2]*Department of Zoology, University of Khartoum, Sudan*

**Submission:** November 09, 2025; **Published:** November 24, 2025

***Corresponding author:** Zuheir N Mahmoud, Department of Zoology, Faculty of Science, University of Khartoum, Sudan

**Abstract**

Fossilized mammalian remains recovered from various localities in Sudan have been assigned to 59 distinct taxa. The earliest recorded specimen is a fossil buffalo skull, first documented in 1876. Major fossil-bearing sites across Sudan include Singa–Abu Hugar, Lower Wadi Howar, the Upper Atbara Valley, central and eastern Sudan, Sabaloka, and Al-Khiday. Hominin fossils, comprising cranial and postcranial remains, have been excavated from five principal sites. Among these, the Singa Skull, dated to the Late Pleistocene (~160,000 years before present), represents the earliest known hominin fossil from Sudan. At least 20 carnivoran species have been identified from the fossil assemblages. These include *Hydrictis* indet., *Aonyx* indet., *Genetta* indet., *Caracal* indet., and *Leptailurus* indet. Notably, the golden jackal (*Canis aureus*) is now locally extinct in the region. However, other carnivorans such as *Herpestes sanguineus*, *Mungos mungo*, *Hyaena hyaena*, and *Lycaon pictus* continue to inhabit portions of these areas. Additional carnivores, *Mellivora capensis*, *Viverra civetta*, *Felis silvestris*, *Panthera pardus*, and *Panthera leo*, are extant but occur outside the studied fossil localities. Among herbivorous taxa still present at the fossil sites are *Gerbillus pyramidium*, *Procavia capensis*, *Arvicanthis niloticus*, *Lepus* spp., and *Gazella dorcas*. Other herbivores such as *Phacochoerus aethiopicus*, *Syncerus caffer*, *Sylvicapra grimmia*, *Damaliscus korrigum*, and *Papio cynocephalus* remain extant but are no longer found at the fossil localities. Several herbivorous species identified from the fossil record are now regionally extinct. These include *Elephas* spp. (Asian elephant), *Hippotigris quagga* (zebra), *Diceros bicornis* (black rhinoceros), *Ceratotherium simum* (white rhinoceros), *Giraffa camelopardalis* (giraffe), and *Bubalus bubalis* (water buffalo). Two extinct species, *Homotoceras singae* nov. gen. nov. sp. (a long-horned buffalo) and *Hystrix astasobae* sp. nov., have been described as new to science.

**Keywords:** Sudan; Fossils; Amphibians; Reptiles; Aves

## Introduction

Fossilized plant and animal remain have long served as critical biological proxies for reconstructing past environmental conditions. In the Sahara Desert, the Nile River system is intersected by several paleochannels, remnants of early Holocene fluvial networks, including the now-inactive systems of Wadi Mugaddam, Wadi Al Milk, and Wadi Howar, among others [1]. According to radiocarbon dating conducted by Williams et al. [2], these river systems were active between approximately 9500 and 7500 years before present (BP). However, subsequent geomorphological processes such as erosion, aridification, and shifts in regional precipitation patterns led to their abandonment, redirection, or burial beneath aeolian sands, resulting in the formation of numerous paleochannels. These paleochannels are rich repositories of both paleontological and archaeological material. Notable discoveries have been made in Wadi Howar [3], the Holocene paleochannels of Wadi Farja [4], and the western Dongola Reach [5].

The mammalian fossil record of Sudan plays a significant role in understanding both the region's prehistoric biodiversity and its zoogeographic context. Bate [6] first described a new species of African fossil long-horned buffalo, and subsequently [7] provided a broader overview of Sudanese fossil mammals. Vacek [8] reported a fossil buffalo skull with horn morphology markedly different from that of *Syncerus caffer*, associated with large *Hippopotamus* remains in fluviatile deposits near Khartoum. Lydekker [9] described a molar belonging to a Pliocene *Equus* species from Nubia, and Andrews [10] examined an elephant molar recovered from Nile alluvium near Khartoum.

Bate [7] also conducted a detailed study of mammalian fossils from Singa and Abu Hugar, located on the western bank of the Blue Nile, identifying 11 species, including three extinct taxa. Among these was the holotype of the long-horned buffalo *Homotoceras singae* nov. gen. nov. sp. Subsequent contributions to the Sudanese mammalian fossil record have been made by multiple researchers [11-21].

## Methods

The information presented herein is derived from literature-based research. The following acronyms and abbreviations are used throughout the text:

Ex = Extinct, L. Ex = Locally extinct (extinct at the study site but extant elsewhere in Sudan) and √ = Extant (present at the study site and elsewhere in Sudan).

nov. gen. = *novum genus* (new genus), nov. sp. = *nova species* (new species), indet. = Indeterminate (taxonomic identification not possible beyond a certain level) and cf. = *confer* (to be compared with).

IUCN Red List category included: LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered and CR = Critically Endangered.

BP = Before Present (calibrated radiocarbon years) and YA = Years Ago.

## Findings and Discussion

### Important mammalian fossil sites in Sudan

**a) Singa-Abu Hugar site**: Located in the western bank of the Blue Nie and is stretching 340-360km south of Khartoum. Both sites yielded fossils from various prehistoric mammals, including extinct elephants, rhinos, and other mega fauna. Excavations were by [7].

**b) Lower Wadi Howar site**: Lower Wadi Howar between Gebel Rahib and Nile River, Northern Sudan. Pachur & Kropelin [2] reported found from this site mammalian fossil remains belonging to 14 species.

**c) The Upper Atbara Valley site**: Marks et al. [11] findings from this valley produced early mammalian fossils, contributing significant visions into Sudan's ancient fauna.

**d) Central and Eastern Sudan site**: Peters [12] studied the Central Nile valley, Central Nile Hinterland, Nile-Atbara junction and upper Atbara Valley and produced evidence of early mammalian fossils, offering insight into the fauna of prehistoric Sudan. His compilation covered the period between 9,000 to 3,500BP.

**e) Sabaloka site:** Sukova et al. [22] excavated the Sphinx (SBK.W-60) 3.5km north west of the Sabaloka cataract (the 6$^{th}$ cataract) about 80km from Khartoum.

**f) Al-Khiday site:** Dunne et al. [23] stated that Al-Khiday site is located 25km south of the city of Omdurman and 3 km west of the White Nile. Al- The site is situated on a sandy ridge rising around 4m above the surrounding plain [24].

### Hominid fossils

Hominin fossil discoveries in Sudan are relatively rare. One of the most notable finds is the so-called "Singa Skull," first described by Woodward [25] as belonging to an ancestral "Bushman" and subsequently deposited in the Natural History Museum, London. Wells [26] provided a more detailed anatomical description, while Stringer [27] later re-examined the specimen and concluded that it represents *Homo sapiens*, rejecting Woodward's earlier classification that placed it at the upper morphological range of the "Bushman" type.

The Singa Skull has been dated to the Late Pleistocene, approximately 160,000 years ago [28]. McDermott et al. [29] applied uranium-thorium and electron spin resonance (ESR) dating techniques, yielding an estimated age of 133,000 ± 2,000 years. They suggested that the specimen may represent a rare member of an early African population potentially ancestral to all modern *Homo sapiens*.

Additional hominin remains have been reported from sites along the Nile, particularly near Wadi Halfa. These include a *Homo sapiens* mandible found in association with Upper Palaeolithic lithic tools [12,13]. Shiner [15] recovered two cranial fragments among the skeletal remains of 38 individuals, dated to approximately 8,000 years ago. Anderson [14] described 68 Late Palaeolithic individuals, dated between 14,000 and 11,600 years ago. Furthermore, Sausse [30] examined human skeletal remains recovered from the archaeological site of Soleb.

### Carnivora fossils

Peter (1991) reported fossil remains representing 15 species of the order Carnivora from central and eastern Sudan. Among these, *Canis aureus* (golden jackal) has since become locally extinct (L. Ex.). Several taxa were identified only to the genus level due to fragmentary remains and were thus classified as indeterminate (*indet.*). These include *Hydrictis* sp. (spotted-necked otter) and/or *Aonyx* sp. (clawless otter), *Genetta* sp. (genet), and either *Caracal* sp. (caracal) or *Leptailurus* sp. (serval).

The remaining taxa were identified to the species level, and their current conservation status—following IUCN categories—is as follows:

Least Concern (LC) are: *Felis silvestris* (wildcat), *Herpestes sanguineus* (slender mongoose), *Herpestes ichneumon* (Egyptian mongoose), *Mungos mungo* (banded mongoose), *Mellivora capensis* (honey badger), *Viverra civetta* (African civet). Near Threatened (NT) is *Hyaena hyaena* (striped hyena). Vulnerable (VU) species are *Panthera pardus* (leopard) and *Panthera leo* (lion). Endangered (EN) included *Lycaon pictus* (African wild dog).

In addition to these findings, *Carnivora* indet. specimens were reported by Suková et al. [22] from sites northwest of the Sabaloka Mountains and by Dunne et al. [23] from the Al-Khiday archaeological site.

### Herbivores fossils

The fossils other than hominoid and carnivora were given in Table 1 with the Red List conservation status of the extant ones.


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The taxonomy arrangement, nomenclature and English names are based on the list of mammals of Sudan existing in Wikipedia (accessed on 15 April 2025).

**Table 1:** Fossils of Herbivores wild mammals.1= Bate [7]; 2=Marks et al. [11]; 3= Pachur & Kropelin [3]; 4= Peter 191; 5= Sukova et al. [22]; 6= Dunne et al. [23].

| Taxon | 1 | 2 | 3 | 4 | 5 | 6 | Red List |
|---|---|---|---|---|---|---|---|
| **Order: Tubulidentata** | | | | | | | |
| *Orycteropus afer* (Aardvark) | | | | L. Ex | L. Ex | | LC |
| **Order: Hyracoidea** | | | | | | | |
| *Procavia capensis* (Rock hyrax) | | | | | √ | | LC |
| **Order: Proboscidea** | | | | | | | |
| *Loxodonta* sp. (Elephant) | | L Ex. | Indet | | | | |
| *Elephas* sp. (Asian elephant) | | Ex. | | | | | |
| *Loxodonta africana* (African elephant) | | | | L Ex. | | L Ex. | |
| **Order: Primates** | | | | | | | |
| *Papio cynocephalus* (Baboon) | | | | Ex. | | Ex. | |
| *Cercopithecus* sp. (Red-tailed monkey) | | | | Ex. | | | |
| **Order: Rodentia** | | | | | | | |
| *Hystrix astasobae* sp. nov. | Ex. | | | | | | |
| *Hystrix cristata* (porcupine) | | | | √ | | | LC |
| *Euxerus erythropus* (Striped ground squirrel) | | | | √ | | | LC |
| Muridae | | | | | Indet | Indet | |
| Gerbilinae | | | | | Indet | | |
| *Gerbillus pyramidium* (Gerbil) | | | | L. Ex | L. Ex | | LC |
| *Tatera* sp. (Tatera gerbil) | | | | Indet | | | LC |
| *Arvicanthis niloticus* (grass rat) | | | √ | √ | | √ | LC |
| *Thryonomys swinderianus* (Cane rat) | | | | L Ex. | | | |
| *Praomys* sp (Multimammate rat) | | | | L Ex. | | | |
| **Order: Lagomorpha** | | | | | | | |
| *Lepus* sp. (Hare) | | | | √ | √ | √ | LC |
| **Order: Chiroptera** | | | | | | | |
| Chiroptera | | | | | Indet | | |
| **Order: Perissodactyla** | | | | | | | |
| *Equus* sp | Indet | | | Indet | | | |
| *Equus afriacus* (wild ass) | | L Ex. | L Ex. | | | | |
| *Hippotigris* sp. | | L Ex. | | | | | |
| *Hippotigris quagga* (zebra) | | | Ex. | | | | |
| *Hipparion* sp. | | Ex. | | | | | |
| *Rhinoceros* sp. | Indet | Ex. | | | Indet | | |
| *Diceros bicornis* (black rhinoceros) | | | Ex. | Ex. | | Ex. | |
| *Ceratotherium simium* (White rhinoceros) | | | | Ex. | | Ex. | |
| **Order: Artiodactyla** | | | | | | | |
| Suidae | cf. | Ex. | | | Indet | | |
| *Phacochoerus aethiopicus* (Warthog) | | | √ | √ | | | LC |
| *Potamochoerus porcus* (Bush pig) | | | | √ | | | LC |
| *Phacochoerus* sp. (Warthog) | | | | | | L Ex. | |
| *Hippopotamus* sp. | | L Ex. | | | | | |



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| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Hippopotamus amphibius* | | | L. Ex | | L. Ex | L. Ex | VU |
| Sivatherine (Short-legged graphoid) allied to Sivatherium. | | | | | | | VU |
| *Giraffa camelopardalis* (Giraffe) | | | Ex | Ex | Ex | Ex | |
| Bovidae | | | | | Indet | Indet | |
| *Alelaphus buselaphus* (hartebeest) | | | √ | | | L. Ex | LC |
| *Damaliscus korrigum* (tiang)? | | | | | | L. Ex | |
| *Damaliscus/Alcelaphus* (Topi and/or Hartebeest) | | | | Indet | | | |
| Antilopine | L Ex. | | | | Indet | Indet | |
| Hippotragine | Indet | | | | | | |
| *Gazella* sp. (about the size of Dorcas gazelle). | √ | | | | | | |
| Antilopine (about size of Grant's gazelle) | Indet | | | | | | |
| *Gazella dorcas* (Dorcas gazelle) | | | √ | | | | VU |
| *Gazella soemmerringi* (Soemmerring's gazelle) | | | | | | | VU |
| *Ourebia ourebi* (Oribi ) | | | | L. Ex | L. Ex | L. Ex | |
| *Homotoceras singae* nov. gen. nov. sp. (Long-horned buffalo) | Ex. | | | | | | |
| *Bubalus bubalis* (Water buffalo) | | | Ex. | | | | |
| *Syncerus caffer* (African buffalo) | | | | L. Ex | | L. Ex | |
| *Hippotragus equinus* (roan antelope) | | | √ | √ | | | |
| *Tragelaphus scriptus* (Bush buck) | | | | √ | | L. Ex | |
| *Tragelaphus strepsiceros* (Greater kudu) | | | | √ | | | |
| *Tragelaphus spekei* (Sitatunga) | | | | √ | | L. Ex | |
| *Slyvicapara grimmia* (Common Bush duiker) | | | | L. Ex | | L. Ex | |
| *Redunca redunca* (Bohor reedbuck) | | | | L. Ex | | L. Ex | |
| *Kobus ellipsiprymnus* (Waterbuck) | | | | √ | | | |
| *Kobus kob* (Kobus) | | | | L. Ex | | L. Ex | |
| Oryx sp. | √ | | | | | | |
| *Addax nasomaculatus* (addax) | | | √ | √ | | | CR |

## General Remarks

The faunal assemblage from Sudanese fossil sites is predominantly composed of extinct species, with extant taxa exhibiting distribution ranges that differ markedly from those observed at the excavation sites. Notable exceptions, species still found at or near the fossil localities, include the rock hyrax (*Procavia capensis*), the striped ground squirrel (*Euxerus erythropus*), the grass rat (*Arvicanthis niloticus*), the gerbil (*Gerbillus pyramidium*), the hare (*Lepus* sp.), and the dorcas gazelle (*Gazella dorcas*).

According to Bate [7], several specimens from the Singa and Abu Hugar sites were too fragmentary for definitive identification but may represent extinct taxa, including a Sivatherine (extinct giraffid) and a probable antilopine. Bate [31] also described the holotype of an extinct nov. sp., reed rat, *Thryonomys arkelli* nov. sp., while Robinson [32] reported a fossil specimen attributed to the murine rodent *Nesokia indica*.

Arkell [33] excavated an early occupation Mesolithic site Khartoum Hospital and Esh Shabeinab and revealed a large collection of animal remains. Peters [19] revised fossils remain from Khartoum hospital and Esh Shaheinab (50km North of Om Durman). From both sites fragments of Gerbillidae indet., *V. civetta*, and *H. amphibius*, were identified. From Khartoum hospital *H. cristata*, *T. swinderianus*, *M. mungo*, *Felis caracal* and/or *F. silvestris*, *P. leo*, *P. aethiopicus*, *G. camelopardalis*, *O. ourebi*, *Sylvicapra gnmmia* ?, *T. scriptus*, *T. spekei*, *R. redunca*, *K. kob*, *Damaliscus lunatus* and/or *Alcelaphus buselaphus*, *H. equinus*, *K. ellipsiprymnus* and *S. caffer*. From Esh Shaheinab, he identified fossil remains of *Lepus* sp., *E. erythropus*, *Canis* sp. Indet, *F. sylvestris*, *L. africana*, *D. bicornis* and/or *Ceratotherium simium*, *Gazella rufifrons*, *Gazella* sp. and *T. strepsiceros*.

Fossils of large, now-extinct herbivores such as elephants (Asian and African), rhinoceroses, hippopotamuses, and buffaloes provide important paleoenvironmental insights, especially regarding the vegetation and habitats once prevalent in the region. According to Chaix et al. [21], these megafaunas are indicative of grassy or wooded savanna ecosystems. Further evidence of habitat diversity comes from the recovery of a *Colobus polykomos abyssinicus* skull from presumed Pleistocene alluvium near Wad Medani in central Sudan [13]. This monkey, now locally extinct, inhabits closed-canopy forests, suggesting that forested environments once extended into this region.


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Marks et al. [11] reported *Papio cynocephalus* (baboon) and three unidentified small cercopithecids (*Cercopithecidae* indet.) from Late Pleistocene to Early Holocene occupations in the Upper Atbara River Valley. Similarly, Dunne et al. [23] described remains of *P. cynocephalus* from Early Holocene layers at the Al-Khiday site, south of Omdurman. Marks et al. [34] and [18] also identified *Cercopithecus* sp. from the Shaqadud site. These primates are currently considered locally extinct in Sudan.

Additional fossil records include a bovid indet. from Pleistocene deposits at Abu Hugar, reported by Wells [10], and remains of giraffe, black rhinoceros, and hippopotamus identified by Chaix et al. [21] at the Kerma site. Tahir [4] recovered radius bones of *Hippopotamus amphibius* along with additional fragments from Wadi Farja. The wild taxa recovered from both Kerma and Wadi Farja are also considered locally extinct.

## Conclusion

a) Mammalian fossils assemblages from Sudan provide valuable insights into species' the ecological adaptability of various species to climatic shifts during the Pleistocene and Holocene epochs.

b) The geographic distribution of both extinct and extant species, inferred from fossil records, helps reconstruct past faunal biogeography and patterns of survival or extinction.

c) The faunal assemblages suggest that the region once supported shallow aquatic environments and extensive grassland vegetation, indicating significant environmental change over time.

d) These findings contribute to a broader understanding of paleoecological dynamics and climate-driven habitat transformation in northeastern Africa.

e) Expanded paleontological research in Sudan has the potential to further elucidate the region's natural history and biodiversity evolution.

f) Several promising but unexcavated sites, including Wadi Al Mugaddam, Wadi Abu Dom, Wadi Abo Suba'a, Wadi Kabna, and the Khor Abu Habil alluvial fan, represent important opportunities for future exploration.

## Ethical Consideration

Ethics approval, consent to participate and publish, human and animal rights, availability of data and materials: Not applicable.

Conflict of interest: The authors declare no conflict of interest, financial or otherwise.

Funding: This research did not receive any hind of fund.

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How to cite this article: Muna A M, Zuheir N M. Paleozoology of Sudan: 3. Mammalian fossils. Int J Environ Sci Nat Res. 2025; 36(1): 556432.
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DOI: 10.19080/IJESNR.2025.35.556432




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