

A vacant niche? The curious distributions of African Perissodactyla

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Why are there no perissodactyls in sub-Saharan West Africa? There are no records of hipparions or zebras in that region and records of rhinoceroses are peripheral and sparse. Absence of records is not information of absence. More than a century of palaeontological and archaeozoological research has yielded thousands of skeletal specimens of late Tertiary or Quaternary mammals throughout most of Africa with equid and rhinocerotid specimens well represented from North, East and South Africa, but not saharan, sahelian or soudanian West Africa. This paper explores the evidence of this absence but offers no solution.

Keywords: West Africa, Saharan, sahelian, soudanian, perissodactyls, African distribution, Chalicotheriidae, Rhinocerotidae, Hipparioninae, Equinae, rhinoceroses, hipparions, zebras, asses, Quaternary, Pleistocene, Holocene, palaeontology.

INTRODUCTION

Three main clades of Perissodactyla or odd-toed ungulates are present in the fossil record of Africa. These are the atypical browsing clawed Chalicotheriidae, the massive browsing or grazing and near graviportal Rhinocerotidae and the cursorial mixed grazing Equidae. The latter comprise the tridactylous (three-toed) Hipparionini and the monodactylous (single-toed) Equini.

The extinct chalicotheres (*Butleria* [= *Chalicotherium*], *Chemositia*, & *Ancylotherium*) are present from the Early Miocene to the Early Pleistocene (Butler, 1978; Coombs & Cote, 2010); the rhinoceroses from the Early Miocene (*Aceratherium*, *Brachypotherium* & *Chilotheridium*), Early Miocene (*Dicerorhinus* & *Paradicerus*), and Late Miocene to Recent/Holocene extant grazing (*Ceratotherium*) and browsing (*Diceros*) forms (Geraads, 2010; Hooijer, 1978); and hipparions and zebras (Equidae), with the extinct hipparions (*Hipparion* s.l. spp.) of the Middle Miocene to Middle Pliocene of North and East Africa, and Late Pliocene to Middle Pleistocene of North, East, Central and South Africa, to Middle to early Late Pleistocene of North and East Africa, and extant zebras (*Equus* spp.), possibly from Pliocene to Recent/Holocene of North, Northeast, East, and South Africa, and asses *Equus* (*Asinus*) spp. from Middle Pleistocene (Olduvai Bed II; Churcher, 1982) but mainly Late Pleistocene or Holocene (in archaeological contexts) of North and Northeast Africa (Churcher & Richardson, 1978; Bernor *et al.*, 2010). It is the absence of many of these forms from the fossil record of sub-saharan sahelian and soudanian West Africa (SSS WA) that poses the problem.

PALAEONTOLOGICAL HISTORY

Chalicotheres

African Chalicotheres (Chalicotheriidae) are recorded only from the East and South African Miocene to Pleistocene. They probably entered twice, first from Asia (Chalicotheriinae, 23.5–14.0 My) over the Sinai or by a dry Red Sea corridor and second from Asia or southern Europe (Schizotheriinae, 7.2–1.33 My) over a Sicilian-Tunisian landbridge (Butler, 1978;

Coombs & Cote, 2010). They are sparsely known in the African fossil record which may reflect less utilization of grassland biomes and a greater presence in wooded or forested areas and thus a lessened chance of fossilization (Figure 1). The first African chalicotheres (Chalicotheriinae) are known from the East African Early Miocene (Kenya, 9 or 10 sites; Coombs & Cote, 2010). The second influx (Schizotheriinae) includes *Butleria* (= *Chalicotherium*) *rusingensis* from the Rusinga Early Miocene (Uganda, 1 site), and Latest Miocene to Pliocene (Tanzania, 2 sites) Olduvai Pliocene, Bed I, *Ancylotherium cheboitense* (Guérin & Pickford, 2005); Kenya (Tugen Hills, 3 sites); *Ancylotherium hennigi*, Leakey (1971), from the Laetoli, Tanzania, Pliocene (Dietrich, 1942); Uganda, 1 site (Kaiso); Kenya, 1 site (Baringo); Ethiopia, 2 sites (Omo & Konso); and the South African Early Pleistocene (Makapansgat Limeworks), *Ancylotherium* [= *Metaschizotherium*] *hennigi* (= *transvaalensis*) (George, 1950, Coombs & Cote, 2010).

Chalicotheres are unknown from the rest of Africa, including SSS WA.

Rhinoceroses

Rhinoceroses (Rhinocerotidae) have a long and varied African history from Late Oligocene to Recent with seven genera (Butler, 1978, Hooijer, 1978) or 10 genera (Geraads, 2010). The fossil distribution includes the northern Mediterranean tier of five countries, the East African cluster of six countries with representation near Lake Chad and Congo, and Namibia and South Africa. Geraads (2010) lists six fossil sites in South Africa, all but Langebaanweg have both *C. simum* and *D. bicornis*. Langebaanweg has *Ceratotherium* sp. (= *praecox*) only, dating at 5.5–0.5 My. Namibia has five occurrences dating at 19.5–6.0 My and includes *D. australis*, *Ceratotherium* sp. and Rhinocerotidae indet. The modern distribution is disjunct with two populations – East Africa (from Lake Chad to South Sudan and into Kenya and Tanzania (Tanganyika) and South Africa, from Cape Province, north to southern Angola and east to the Kwa-Zulu lowlands, and north to the Zambesi and into southern Zambia (Rookmaker, 2007: Fig. 2, insets E & F). All modern and fossil

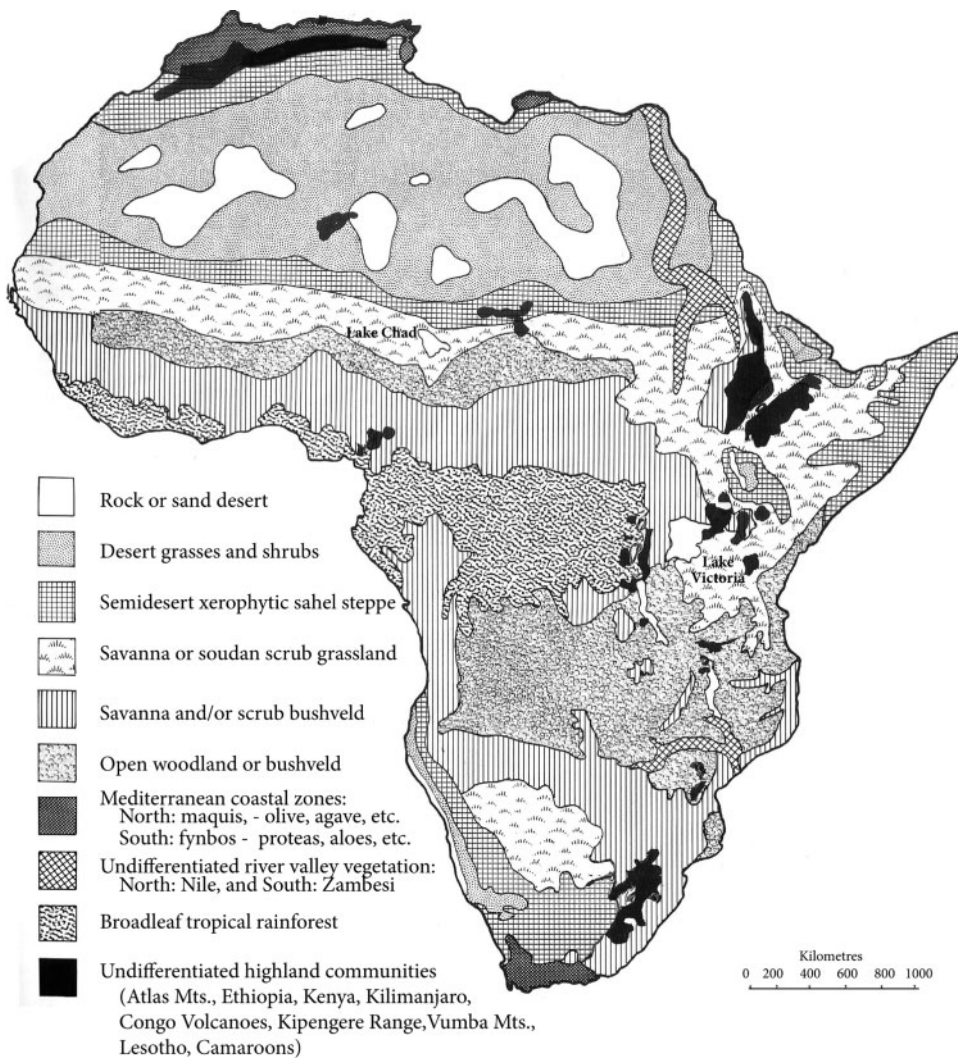


Figure 1. Vegetational zones of Africa. Note the N–S latitudinal banding of zones south of the Sahara Desert and north of the Congo Basin–West African Coastal tropical forests. In southern Africa the banding slopes SW–NE (modified from Cooke, 1978, Fig. 2.2, in Cooke & Maglio, 1978).

records are located in ancient or modern savanna and bushveld zones in Eastern and Southern Africa except those in SSS WA and in well wooded or forested areas. Rookmaker's (2007) records of 18th century hunting kills support the palaeontological distribution in southern Africa.

Square-lipped rhinoceroses (*Ceratotherium simum*) did not range much west beyond Lake Chad (Rosevear, 1953; Ansell, 1971; Geraads, 2010). Black rhinoceroses (*Diceros bicornis*) ranged into northern Cameroon (Flynn *et al.*, 1987) and west of Lake Chad (Rosevear, 1953). Modern records of either species from further west are suspect (Ansell, 1971): some archaeological records of black rhinoceroses (*D. bicornis*) appear solid though intrusive deposition is possible. Both rhinoceroses have their modern Holocene northeastern distributional limits in the Sudans.

Rhinoceroses are the earliest known perissodactyl immigrants into Africa and probably entered during later Oligocene time across the Sinai isthmus (Butler, 1978): there is no evidence to support this. Guérin (1980) surveyed the records of fossil rhinoceroses of Africa, listing 116 sites without noting one in SSS WA. Geraads (2010) lists 106 fossil sites in north, east and south Africa but none in the Saharan or SSS WA areas. A peripheral record of *Ceratotherium simum* from the

Koro Toro Fm., 500 km NE of Lake Chad in Chad (latitude 16° 10' N, longitude 18° 30' E) is dated as Pleistocene (Coppens, 1966). Ansell (1971) considered the northwest limits of the white rhinoceros' recent distribution to be uncertain, but that it may have ranged as far west as Lake Chad (*vide* Schomber, 1966) and may have been restricted to the Ubangi-Uele savanna zone. Hooijer (1978) lists only 21 sites, none of which are from within SSS WA, and omits the Koro Toro record. Guérin and Fauré (1983) report *Diceros bicornis* and cf. *Ceratotherium simum* from the late Quaternary (Neolithic, 7,000 BP) of the Taoudenni Basin in northern Mali between Algeria and Mauretania (*ca* latitude 22° 30' N, longitude 3° 00' W). The cf. *C. simum* metapodial fragment is poorly preserved and hard to identify. However, the Toudenni Basin lies south of the Maghreb (ancient Mauretania) where reliable *Ceratotherium* records are known. A left humeral shaft fragment agrees in size and morphology with modern individuals of *Diceros bicornis* and is a secure identification. It is the most northwesterly record of the black rhinoceros.

Ansell (1971: 3) reviews the distribution of *Diceros* north of the African lakes and presents a confused record but with some certainty that once it existed throughout the South Sudan (Equatoria). "Further west, *Diceros* once ranged

through the central areas of the Central African Republic at about 23° E; southern Chad; northern Cameroun; north-eastern Nigeria; and the vicinity of N'guigmi on the north-western side of Lake Chad, just within the boundary of the present Niger Republic." He concludes by saying that it "may have survived between Lake Chad and the upper Niger (about Niamey and Tillaberi, 13°–14° N, 01°–02° E) until fairly recent times, ... [and] ... no locality west of northeastern Nigeria has ever been confirmed by a collected specimen."

There are therefore no substantiated records of either *Ceratotherium* or *Diceros* within the SSS WA area.

Hipparions

Hipparions, or three-toed horses, are first known in Africa from *Hipparion* cf. *primigenium* in late Middle Miocene (not Middle Miocene; Churcher & Richardson, 1978) deposits of the Magreb (noted by Thomas [1884a, b] and described by Pomel [1897]). Their origin was in North America but immigration was presumably through southern Europe, from Asia through Sinai, or Asia Minor, as the Mediterranean and Red sea basins were partly dry for periods during Middle or Late Miocene times. Hipparions then speciated and spread widely into the Maghreb (*Cremohipparion* [= *H.* *sitifense*] and south to East Africa (*Eurygnathohippus* [= *H.* *turkanense*] and later into South Africa, with further speciation, e.g., Pliocene *Eurygnathohippus* [*H.*] c.f. *baardi*, at Langebaanweg (Hendey, 1984) and early Pleistocene as the widely distributed *Eurognathohippus* (= *Stylohipparion*) *steyleri*, with further speciation.

Bernor *et al.* (2010) revise the Eurasian and African hipparions into early *Hipparion* s.s. (9.5–6.5 My), *Cremohipparion* (9.7–4.0 My), *Cormohipparion* (16.0–10.5 My), *Sivalhippus* s.s. (9.6–6.5 My), *Eurygnathohippus* (6.5–0.5 My). These taxa include North, East and South Africa in their ranges, but not SSS WA.

African hipparions were extinct by the Middle Pleistocene, possibly due to competition from the antelope radiation that took place in the Late Pliocene and Early Pleistocene. Hipparions are known from the North African Magreb (Morocco, Algeria, Tunisia), East Africa (Uganda, Kenya, Ethiopia, Tanganyika [mainland Tanzania]), and from Central (Zambia, Zimbabwe) and South Africa only. There is only one recorded hipparion tooth from northeastern Africa, from Egypt (as *Cormohipparion* [= *H.*] *africanum*, from Wadi el-Natrun, Boné and Singer, 1965), possibly because of the absence of suitable late Tertiary deposits in Egypt, Libya and the Sudans.

Zebras

Fossil equids were first recognised in South Africa in the 19th century in surficial deposits near Cape Town, but were thought to be remains of Dutch settlers' horses because of the bones' robust size and apparent recent origins. Broom (1909) first identified a fossil equid from Swartklip, Table Bay, as a European horse but later described it as the robust Cape zebra, *Equus capensis*. Remains of this animal were subsequently reported from widespread sites in Southern and Central Africa. Conspecific equid remains were described from Pleistocene and Holocene deposits in East Africa north to southern Ethiopia, but under the name *E. oldowayensis* (Hopwood, 1937; Churcher & Hooijer, 1980) on materials recovered from Laetoli and Olduvai Gorge: this animal is also known from the Lake Turkana and Omo beds and elsewhere (Churcher, 1981, 2007). The living Grevy zebra, *E. grevyi*, is considered the surviving relict of this East African population

and is probably conspecific with the ancestral *E. capensis*/*E. oldowayensis* population. Bernor *et al.* (2010: 705) review the large zebras *E. (Dolochohippus) koobiforensis* and *E. (D.) oldowayensis*, and consider *E. (D.) oldowayensis* to be "the most widespread and abundant horse in the Plio-Pleistocene deposits of Ethiopia, Kenya, and Tanzania (from 2,33 My at Shungura Member G to 1.0 My at Ologesailie)."

Fragmentary equid remains are reported from Late Palaeolithic sites in the Plain of Kom Ombo by Gaillard (1934) and Churcher (1972). Gaillard assigned all of the isolated equid teeth except three to *E. asinus*; the exceptions are an M³, a ?LP₄ and a RP₂ assigned to *E. caballus*. Churcher (1972) assigned only a fragment of a right lower molar to *E. caballus*. Both Gaillard's and Churcher's lower molar specimens, assigned to *E. caballus*, have rounded metaconids and metastylids and could well represent *E. capensis*.

Remains of a similarly robust zebra have also been recovered from early Middle Pleistocene and Holocene levels in Dakhleh Oasis, Egypt (Churcher, 1986, 2007). These specimens are considered to represent a population of a robust zebra species that for much of the Quaternary ranged from the Cape to Cairo: the name *Equus capensis* is used for this fossil form (although *E. oldowayensis* has continued in use for the East African fossil population). Grevy's zebra (*E. grevyi*, Figure 2, inset B; Sidney, 1965, Map 2) is the name for the threatened extant Kenyan, Ethiopian and Somali population that is morphologically identical to the Cape zebra and whose scientific name has priority. However, it is convenient to have names to use for the southern and eastern African extinct populations. This animal is a species of the subgenus *Equus*.

A large zebra, probably *E. capensis*, was reported by Bate (1951) from Nilotic deposits in the central Sudan as *E. numidicus*. Bernor *et al.* (2010) and Eisenmann (1980) also record this species from Ain Boucherit, Algeria (ca 2.4–2.0 My).

The situation in western North Africa (the Maghreb) is less clear. The presence of a larger equid identified as *E. numidicus* in Tunisia and Libya (Petrocchi, 1940; Churcher, 1972) may represent *E. capensis* and may have been part of the *E. capensis* population recognised from Dakhleh Oasis (Churcher, 1986). A smaller equid described as *E. mauretanicus* by Thomas (1884a, b) and Pomel (1897) has been shown by Boule (1899 [1900], 1900) to closely resemble the zebra *E. burchelli* (= *E. quagga*). *E. tabeti* from Algeria (Arambourg, 1970) is also dentally similar to *E. burchelli* and is too large to be a form of *Asinus*. Arambourg remarked that fossil 'asses' from the Maghreb, generally assigned to *E. mauretanicus*, are probably *E. burchelli* or *E. quagga*. Eisenmann (1992) considers *E. mauretanicus* possibly to be conspecific with *E. burchelli*, in fact a small zebra. Thus there was a population in the Maghreb of equids larger than the wild asses and probably representing an equid of similar size and morphology to, if not conspecific with, *E. burchelli*. Four upper cheekteeth, identified only to *Equus*, are reported from the Taoudenni Basin in Mali (Guérin & Fauré, 1983); one is dated at between 4,100 and 3,400 BP, i.e. Late Holocene or ca 1750 BC, and may well be Pharaonic.

E. capensis occurs together with fossils of a more gracile zebra, *E. quagga*, throughout its distribution (Figure 2, inset D), within a plains or tree savanna, and accompanied by a typical African plains fauna. A zebra, tentatively assigned to *E. quagga* s.l., is also present with *E. capensis* in the Early Middle Pleistocene Iron Balls Fauna of Dakhleh Oasis, Egypt (Churcher & Kleindienst, 2006), but has not been found in

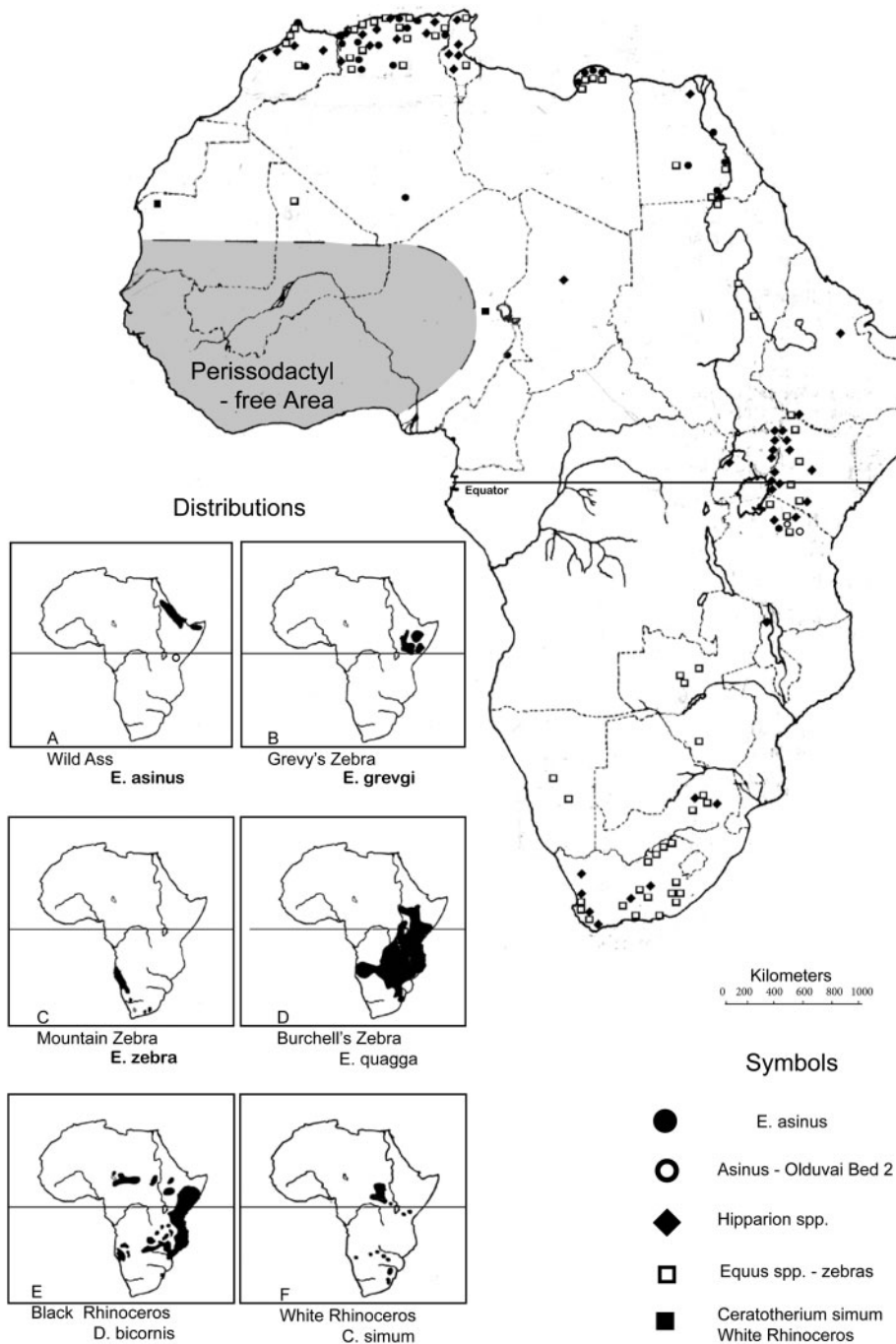


Figure 2. Distribution of limital recovery sites for the Rhinocerotids *Diceros* and *Ceratotherium* and the Equids *Hipparion* and *Equus* in Africa. Based on and adapted from Churcher & Richardson (1978), with additional data from Ansell (1971), Butler (1978), Flynn *et al.* (1987), Jousse (2006), Jousse & Chenal-Velarde (2001–2002), Jousse *et al.* (2003), Kaber & Raimbault (1997) and Rosevear (1953). The main figure plots the main occurrences of hipparions, asses and zebras, and white and black rhinoceroses, to demonstrate the absence of Perissodactyla in Sub-Sub-Saharan West Africa. Some isolated equid records in the Sahara or near Lake Chad are considered unreliable to species. The inset sketch-maps are adapted from Haltenorth & Diller (1980) and Dorst & Dandelot (1970). Black areas indicate where the named taxon is considered to have occurred recently, based on 19th and 20th century records. Many of these are no longer current, e.g. Grevy's zebra (inset B) has recently been much restricted outside Kenya due to drought, land settlement and hunting, and the common zebra or quagga (inset D) now exists in scattered populations, mainly in game reserves, with its former extended plains range fragmented and much reduced by farming and ranching.

Holocene contexts. A small equid, identified to *E. quagga s.l.* or *E. burchelli* is commonly found associated with *E. capensis* in South and East African sites and is often identified on isolated teeth or fragmentary skeletal elements. It is probable that *E. capensis* formed mixed herds with the smaller quagga-like zebras throughout its range as does the modern *E. grevyi* (Churcher, 1993).

There are no prehistoric records of a large *Equus* from the SSS WA. Bernor *et al.* (2010: Fig. 35.20) show no equids present in the central Sahara or coastal West Africa.

Asses and donkeys

Palaeontological records of asses are scant. A right metapodial III, similar to that of the modern ass or donkey, was

recovered *in situ* from Bed II in Olduvai Gorge, (1.5–1.7 My BP; Churcher, 1982: Fig. 2) and indicates that a wild ass was present in East Africa in Middle Pleistocene time. Eisenmann (1992: 165) stated that “asinine (*A.?*) metacarpals are found in member G 5 of the Shungura formation (Ethiopia)”, below the KF and Chari tuffs in East Turkana (Kenya), and in Olduvai Bed I (Site FLK N1; Tanzania), but gave no details. The occurrence below the Chari tuff dates at >1.4 Ma and the Shungura G occurrence at between 2.33 and 1.9 My (Brown *et al.*, 1985). Eisenmann suggests that the African ass may have evolved in the Maghreb region from *E. tabeti* through *E. melkensis* at ca 1.4 My.

Otherwise palaeontological or archaeozoological evidence of the wild ass is present only in Latest Pleistocene or Holocene sites. It is perhaps confused with remains of the domestic donkey from the earliest mid-Holocene deposits (5,000 BC), but mainly from Pre-Dynastic or Old Kingdom Pharaonic (ca 2500 BC) times in Egypt (Churcher & Kleindienst, 2006). Remains of *Equus asinus* are reported from sites in northeastern Africa: Kom Ombo, Egypt, by Gaillard (1934), Reed (1965), Reed & Turnbull (1969), Churcher (1972) and Wadi Halfa, by Gautier (1968); Hagfet et Tera Cave, Libya (Cyrenaica), by Blanc (1956) and Hagfet ed-Dabba Cave (Bate, 1955); and in the Nile Valley, Sudan, at Singa and Abu Hugar, by Bate (1951), but these may all be domesticates.

Sparse remains of caravan donkeys appear as trade increased between the north-eastern Nile Valley and southern SSS zones (Jousse & Escarguel, 2006), and spread from northeast to southwest during Predynastic and Old Kingdom times (4000–2000 BC). Jousse (2006) reported Mid-Holocene fossil asses from Amekni in the Hoggar Massif at 8670 ± 150 BP (ca 6670 BC) and Zmeilet el-Barka in the southern margin of the Atlas Mountains at 7700 ± 180 BP (ca 5700 BC). Recent wild asses were alleged to exist in the Western Sahara ca 1900 AD, but is unconfirmed.

MODERN DISTRIBUTIONS OF EXTANT PERISSODACTYLA IN AFRICA

Rhinoceroses are widely known. The black rhinoceros (*Diceros bicornis*) today has a disjunct distribution in an arc around the Congo Basin from Lake Chad to the Angolan coast and on Africa’s east coast from central Somalia to Beira in Mozambique, with a Zululand outpost (Figure 2, inset D). In the past, its range was from the Cape of Good Hope to the Sudans and Lake Chad, excluding the Congo Basin. Rosevear (1953, 120 & Map 208) notes *Diceros* as “very rare and local” and in “mostly Sudan savannah” in northeast Nigeria. He plots three localities (Map 208) centred on Biu, ca 360 km southwest of Lake Chad. The White rhinoceros (*Ceratotherium simum*) also has two disjunct populations: in Kenya and the eastern South Sudan, and in Kwa-Zulu-Natal, Lesotho and extreme southern Mozambique. During the Pleistocene and Quaternary, its range was probably much as for the black rhinoceros except that it ranged further west than Lake Chad to the Atlantic coast near Cape Verde (Baie du Levrier), Mauretania, on the northwest limit of the SSS zone (Jousse, Kaber & Raimbault, 2003: Fig. 3–2). It is recorded from the Langebaanweg Pliocene, near Cape Town (Hendey, 1976) and Swartklip (Klein, 1986).

Roman historical records of wild asses in Africa are restricted to the northern Atlas Mountains and coasts from Atlantic Morocco to Libya and Egypt’s Western Desert, at least during Dynastic times (Osborn with Osbornova, 1998), and south through the Red Sea Hills and coast to Eritrea, Djibuti

and Somaliland. Specimens exist for asses ranging through the Western Desert of Egypt, south into western Sudan (Dharrfur), and possibly southwest as far as Lake Chad, but probably represent Dynastic pack animals. The wild asses of Africa constitute the only species within its subgenus as *Equus (Asinus) asinus* (Dorst & Dandelot, 1970) or *E. (Asinus) africanus* (Haltendorff & Diller, 1980). Both authorities divide the species into two subspecies, respectively, *E. (A.) asinus africanus* or *atlanticus* of the Maghreb, and Libya to Egypt, and *E. (A.) a. somaliensis* or *somalicus* of Sudan, Eritrea and Ethiopia. The former was still extant until about 300 AD and was found in the Atlas Mountains and along the Mediterranean coast to Cyrenaica. The latter was found along the coasts of Egypt and the Red Sea hills, Sudan, Eritrea and Lake Chad. Wild asses are included in the extant fauna of Egypt as *E. asinus taeniopus* by Hoogstraal (1964) who cites them as “fairly common north of the Q’ena-Q’eseir road” (observed by Barron & Hume [1902] and Gee [1964]), who quotes Talbot (1960), and disputes whether wild asses occurred in the coastal Red Sea mountains (?Gebel Elba) or the coastal plain. Whether these animals are wild, feral, or just unattended, is disputed by scientists though the local *badawin* claim to own them! Setzer (1957) does not consider an ass as part of the modern fauna of Libya. The domestic donkey probably originated from tamed *E. a. atlanticus* (Churcher & Kleindienst, 2006).

No reported evidence of either zebra exists from sites in SSS WA (from Nigeria to Senegal: Rosevear [1953] pointedly omits any equid from the Nigerian mammal faunal list) and no equid from the Quaternary of the Maghreb (Tunisia, Algeria, Morocco) has been confirmed as conspecific with the Cape zebra. *E. mauritanicus* (= *E. quagga*) was described from Algeria by Pomel (1870). It is reported from the Maghreb by Eisenmann (1992) and as *E. cf. mauritanicus* from Mauretania by Jousse *et al.* (2003; Tab. 2, Berouâga [Kaber & Raimbault, 1997], Chomi [Petit-Maire, 1979], Dhar Tichitt [Amblard-Pison, 1999]) and Khatt Lemaiteg [Bathily *et al.*, 1998]). It is also reported from near the village of Rayo, north of Garoua, northern Cameroon, in Pleistocene sediments, as *Equus cf. mauritanicus* (Flynn *et al.*, 1987). Three of five interred specimens of horses from northern Cameroon are radiocarbon dated to 660–780, 1020–1160 & 1280–1390 AD (1310 ± 60, 950 ± 50 & 680 ± 50 BP, respectively; MacEachern *et al.*, 2001) and represent domestic animals (personal communication December 2012).

The natural absence of fossil or recent equids in SSS WA is enhanced by the absence of black rhinoceroses (*Diceros*) and sparse and peripheral records of Pleistocene/Holocene white rhinoceroses (*Ceratotherium*), the other widespread African perissodactyls in Holocene and modern faunas, and by the absence of hipparions in that region in the Pliocene and Early and Middle Pleistocene beds, although these three-toed equids were present over similar North and East African areas during Miocene and Pliocene times. The absence of hipparions in the SSS WA region in the Pliocene and Early and Middle Pleistocene, although present over assumed ecologically similar North and East African areas during Miocene and Pliocene times, supports the validity of the inquiry!

DISCUSSION AND CONCLUSIONS

The Cenozoic distribution of the African Perissodactyla involves the Maghreb (Roman Mauretania or modern Morocco, Algeria and Tunisia), East and South Africa, and northeast Africa because of the Sinai landbridge as a route for

immigrants. All African Perissodactyla, with the probable exception of chalicotheres, are recovered from savanna or bushveld biomes, frequently in caves in North and South Africa, and in sedimentary deposits within the Great Rift Valley in East Africa. Preservation of fossils in heavily forested areas such as the Congo Basin or East African highlands is problematical because of humic acid solution of the skeleton, and thus chalicotheres and forest hipparions would have had small chance of skeletal preservation.

Recovered fossil evidence of hipparions and zebras is distributed within the grassy savanna, treeveld or broken rocky country and avoids the forested Congo Basin, the Mau and Kinankop rift mountains or volcanoes in Kenya, and the Ethiopian highlands. However, evidence is plentiful from caves along the Mediterranean coast and in Southern Africa, at least during the wetter periods before the final Saharan drying of the latest Pleistocene and Holocene and in fluvial, pan and cave deposits in Eastern and Southern Africa. The question arises “Why are there no evidences of these equids in the saharan, sahelian and soudanian zones of West Africa during the wetter periods before the final Saharan drying of the latest Pleistocene and Holocene?” Evidence for rhinoceroses is almost as scant, with a few records of white rhino from west of Lake Chad and coastal Mali (Jousse, Kaber & Raimbault, 2003: Tab. 2; Berouâga [Kaber & Raimbault, 1997], Chomi [Petit-Maire, 1979] & Dhar Tichitt [Amblard-Pison, 1999]; Rosevear, 1953: 120, Map 207). Saharan Middle Stone Age and Neolithic petroglyphs and rock drawings include few depictions of asses (as opposed to donkeys with packs or riders), and few striped equids that could be zebras, and almost no rhinoceroses.

But this question begs a deeper question “Why does this gap in the distribution of the eminently successful zebras and rhinoceroses also apply to the known distribution of the extinct Miocene to Pleistocene hipparions?” or “What is it about West Africa that is inhospitable to perissodactyls when artiodactyls flourish there?”

Is there room in the West African faunas for the typical African perissodactyla? Rosevear (1953) surveyed the mammals of Nigeria and recorded 239 species. If species of Insectivora (15), Chiroptera (61), Lagomorpha (3) and Rodentia (66) are deducted, 94 larger mammal species remain, of which 31 are Artiodactyla and only 1 Perissodactyla (*Diceros* [black rhinoceros]). The East African equivalent latitudinal ecological zones contain 135 mammal species (based on surveys of major game parks which, if trimmed as for the Nigerian mammal count – Insectivora (6), Chiroptera (19), Lagomorpha (2) and Rodentia (13) – leaves 95 larger mammal species, of which 44 are Artiodactyla and 4 are Perissodactyla (Williams & Arlott, 1967). The endemic faunas of larger mammals in the two equatorial regions are equally varied when taphonomic tastes are allowed for, and smaller taxa discounted. Thus, apparently the West African ungulate fauna could accommodate some perissodactyl taxa.

Jousse, Kaber & Raimbault (2003) recognise 21 species of artiodactyls and Jousse and Escarguel (2006) 24 species from Holocene faunal archaeological sites in SSS WA. Walker (1985) lists 34 species of artiodactyl in East Africa, of which 19 are congeneric or conspecific with one of the SSS WA taxa, and which inhabit the same ranges within zones in East Africa as the two species of zebra and two species of rhinoceros. The Plio-Pleistocene Olduvai Beds 1 and II faunas include 16 genera of bovids (Leakey, 1971) of which 9 are present in SSS WA archaeofaunal deposits. These Oldowan beds

yield both Eurognathohippus (= *Stylohipparion*) and *Equus* cf. *oldowayensis* (= *capensis*) (Leakey, 1971) and a small equid, *E. cf. quagga*, none of which are recorded from SSS WA.

Thus the general savanna biodiversity in East Africa resembles that in SSS WA in all ways except for the presence of zebras and rhinoceroses. The ecological zones that are available range from tropical forest near the coast, through intensely treed or scattered bushveld with low growing shrubs and seasonal grasses, to isolated trees or woody xerophytes and to generally bare mineral surfaces to vegetationless desert (Figure 1). These are the saharan, sahelian, soudanian (SSS) and forest zones that run east to west in latitudinal bands in sequence from north to south across North Equatorial Africa. Similar zones exist in southern Africa parallel to the Indian Ocean coast but disturbed by the coastal ranges, Lesotho and Swazi highlands and, in East Africa, by the Rift Valley marginal mountains, the three major rift volcanoes and the Ethiopian highland massif. The seasonally dry grass savannas, tree savannas and broken montane environments throughout these zones but east of Lake Chad are or were inhabited by hipparions and zebras. Trees, woody bushes, forbs and grasses in these zones are often congeneric or conspecific or clinally related from south to north and west, and even north to the Mediterranean coast. Thus there is no apparent biological or ecological reason why equids, and possibly rhinocerotids, should be naturally absent from SSS WA.

The history and distribution of the African asses complicates these questions. Until an ass was recovered *in situ* from Bed II in the Olduvai Gorge sequence, their African history appeared simple: immigration through the Sinai sometime during the early Late Pleistocene and subsequent gradual colonization of Africa's Mediterranean and Red Sea-Gulf of Aden coasts, with expansion into the interiors of Libya, the Maghreb, the Atlas Mountains and Sudan. The many published records of subfossil asses in the Maghreb probably mostly represent a smaller zebra attributable to *E. quagga s.l.*, although Eisenmann (1992) suggests that *E. tabeti* and *E. melkensis* may be early ancestral asses. Tamed asses or donkeys then become a small but constant element in Late Neolithic and Pre-Dynastic sites (Churcher & Kleindienst, 2006). The presence of a certified African ass in the Olduvai Middle Pleistocene (Bed II) deposits implies an earlier immigration, and one that would allow time for dispersal some 5000 km to south of the Equator by that date, or a rapid speciation event to select a wild ass. This suggests at least an Early Pleistocene date for the first immigration. It also implies that asses were equally unsuccessful in colonizing the Sahara and West Africa and suffered a severe reduction in range during the later Pleistocene, after initially extending to central Tanzania (Tanganyika).

What could be a reason for the absence of equids and the paucity of rhinocerotids in the West African savannas? Could it be that there is an unknown local pathogen that targets equids? That seems unlikely as introduced horses and asses apparently thrive if properly cared for. Could it be that some plant occurs that causes infertility and thus prevents the build-up of a resident population? Again, that is disproved by the present domestic breeding of horses and donkeys in the region. What could prevent the colonization of West Africa by both black and white rhinoceroses? Could it be that there is something in or absent from the minerals of the region that has a dietary effect on wild equids or rhinocerotids and makes them liable to lessened ecological fitness? This also

seems unlikely for equids as domestic equids kept by the local peoples today are seldom fed nutritional supplements that might overcome dietary deficiencies, but still thrive. And even if a possible factor along these lines were to be identified, there is still the mystery of the absence of Pliocene hipparions from the region and the scarcity or possible absence of the rhinoceroses.

The search for a possible causative factor to explain the strange absence of Perissodactyla in West Africa from the Miocene to the Holocene remains a curious matter for future research.

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REFERENCES

- AMBLARD-PISON, S. 1999. Communautés villageoises néolithiques des Dhars Tichitt et Oualeta (Mauretanie). Université Paris I, Thèse de doctorat d'état, 1–850.
- ANSELL, W.F.H. 1971. Part 14, Order Perissodactyla, 1–14. In Meester, J. A.J. & Setzer, H.W. (Eds), *The Mammals of Africa: An identification manual*. Washington, DC, Smithsonian Institution Press.
- ARAMBOURG, C. 1970. Les vertébrés du Pléistocène de l'Afrique du nord. *Archives de la Museum National d'Histoire Naturelle, Paris* **10**: 1–126.
- BARRON, T. & HUME, W.F. 1902. Topology and geology of the Eastern Desert of Egypt (Central Portion). Survey Department, Cairo, 105–108.
- BATE, D.M.A. 1951. The mammals from Singa and Abu Hugar. In *The Pleistocene Fauna of Two Blue Nile Sites*. Fossil Mammals of Africa, no. 2, 1–28.
- BATE, D.M.A. 1955. Vertebrate faunas of Quaternary deposits in Cyrenaica, app. A. In McBurney, C.B.M. & Hey, R.W. (Eds), *Prehistory and Pleistocene Geology in Cyrenaican Libya*. Cambridge, Cambridge University Press, pp. 274–291.
- BATHILY, M.S., OULD-KHATTAR, M., VERNET, R., CHUZEL, C. & OTT, J.M. 1998. *Les sites néolithiques de Khatt Lemaiteg (Amatlich) en Mauretanie occidentale*. Meudon, CMA, 1–233.
- BERNOR, R.L., ARMOUR-CHELU, M.J., GILBERT, H., KAISER, T.M. & SCHULZE, E. 2010. 35. Equidae. In Werdelin, L. & Saunders, W.J. (Eds), *Cenozoic Mammals of Africa*. Berkeley, CA, University of California Press, pp. 685–721.
- BLANC, G.A. 1956. Sulla esistenza di *Equus (Asinus) hydruntinus* Regalia nel Pleistocene del Nord Africa. *Bollitino della Societa Geologica del Italia* **75**: 176–187.
- BONÉ, E.L. & SINGER, R. 1965. *Hipparion* from Langebaanweg, Cape Province, and a revision of the genus in Africa. *Annals of the South African Museum* **48**: 273–397.
- BOULE, M. 1899 [1900]. Observations sur quelques équidés fossiles. *Bulletin del la Société Géologique de France* **27**: 531–542.
- BOULE, M. 1900. Étude paléontologique et archéologique sur la station paléolithique du Lac Karâr (Algérie). *Anthropologie* **11**: 1–21.
- BROOM, R. 1909. On the evidence of a large horse recently extinct in South Africa. *Annals of the South African Museum* **7**: 281–282.
- BROWN, F.H., MCDUGALL, I., DAVIES, T. & MAIER, R. 1985. An integrated Plio-Pleistocene chronology for the Turkana Basin. In Delson, E. (Ed.), *Ancestors: The hard evidence*. New York, Liss, pp. 82–90.
- BUTLER, P.M. 1978. 18 Chalicotheriidae. In Maglio, V.J. & Cooke, H.B.S. (Eds), *The Evolution of African Mammals*. Cambridge, MA, Harvard University Press, pp. 368–370.
- CHURCHER, C.S. 1972. Late Pleistocene vertebrates from archaeological sites in the Plain of Kom Ombo, Upper Egypt. *Life Sciences Contribution, Royal Ontario Museum*, no. **82**: 1–172.
- CHURCHER, C.S. 1981. Zebras (Genus *Equus*) from nine Quaternary sites in Kenya, East Africa. *Canadian Journal of Earth Sciences* **18**: 330–341. doi:10.1139/e81-025
- CHURCHER, C.S. 1982. Oldest ass recovered from Olduvai Gorge, Tanzania, and the origin of asses. *Journal of Paleontology* **56**: 1124–1132.
- CHURCHER, C.S. 1986. Equid remains from Neolithic horizons at Dakhleh Oasis, Western Desert of Egypt. In Meadow, R.H. & Uerpmann, H.-P. (Eds), *Equids in the Ancient World*. Wiesbaden, Dr. Ludwig Reichert Verlag, pp. 413–421.
- CHURCHER, C.S. 1993. *Equus grevyi*. *Mammalian Species* no. **453**, 1–9. doi:10.2307/3504222
- CHURCHER, C.S. 2007. Distribution and history of the Cape Zebra (*Equus capensis*) in the Quaternary of Africa. *Transactions of the Royal Society of South Africa*, **61**: 89–95. doi:10.1080/00359190609519957
- CHURCHER, C.S. & HOOIJER, D.A. 1980. The Olduvai zebra (*Equus oldowayensis*) from the later Omo Beds, Ethiopia. *Zoologische Mededelingen* **55**: 265–280.
- CHURCHER, C.S. & KLEINDIENST, M.R. 2006. A Pre-Dynastic ass (*Equus asinus*) from the Sheikh Muftah cultural horizon of the Dakhleh Oasis, Western Desert, Egypt. In Kroeper, K. & Kobusiewicz, M. (Eds), *Archaeology of Early Northeastern Africa*; Poznan Archaeology Museum, Studies in African Archaeology vol. **9**, pp. 425–435.
- CHURCHER, C.S. & RICHARDSON, M.L. 1978. 20 Equidae. In Maglio, V.J. & Cooke, H.B.S. (Eds), *The Evolution of African Mammals*, Cambridge, MA, Harvard University Press, pp. 379–422.
- COOKE, H.B.S. 1978. Africa: The physical setting. In Maglio, V.J. & Cooke, H.B.S. (Eds), *The Evolution of African Mammals*, Cambridge, MA, pp. 17–45.
- COOMBS, M.C. & COTE, S.M. 2010. 33. Chalicotheriidae. In Werdelin, J. & Saunders, W.J. (Eds), *Cenozoic Mammals of Africa*. Berkeley, CA, University of California Press, pp. 659–667.
- COPPENS, Y. 1966. Essai de biostratigraphie du Quaternaire de la région de Koro-Toro (Nord-Tchad). *Colloque internationaux du CNRS*, no. **163**, pp. 589–595.
- DIETRICH, W.O. 1942. Altestquartäre Säugetiere aus der südlichen Serengeti, Deutsch-Ostafrika. *Paläontographica* **94A**: 44–130.
- DORST, J. & DANDELOT, P. 1970. Order Perissodactyla. A Field Guide to the Larger Mammals of Africa. London, Collins, pp. 159–170.
- EISENMANN, V. 1980. Les chevaux (*Equus sensu lato*) fossiles et actuels: cranes et dents jugales supérieur. *Cahiers de Paléontologie*. Paris, CNRS, 186 pp.
- EISENMANN, V. 1992. Origins, dispersals, and migrations of Equus (Mammalia, Perissodactyla). *Courier Forschungsinstitut Senkenberg* **153**: 161–170.
- FLYNN, L.J., BRILLANCEAU, A., BRUNET, M., COPPENS, Y., DEJAX, J., DUPERON-LAUDOUEINIX, M., EKODECK, G., FLANAGAN, K.M., HEINTZ, E., HELL, J., JACOBS, L.L., PILBEAM, D.R., SEN, S. & DJALLO, S. 1987. Vertebrate fossils from Cameroon, West Africa. *Journal of Vertebrate Paleontology* **7**: 469–471. doi:10.1080/02724634.1988.10011676

- GAILLARD, C. 1934. Contributions à l'étude de la faune préhistorique de l'Égypte. *Archives du Museum d'Histoire Naturelle de Lyons* **14**, Mémoire 3: 1–12.
- GAUTIER, A. 1968. Mammalian remains of the northern Sudan and southern Egypt. In Wendorf, F. (Ed.), *The Prehistory of Nubia*. Vol. 1, Fort Burgwin Research Center, Publication no. 5 and Southern Methodist University Contributions in Anthropology no. 2, Taos, New Mexico. Fort Burgwin Research Center and Southern Methodist University Press, pp. 80–99.
- GEE, E.P. 1964 (1963). The Indian wild ass: a survey. *Journal of the Bombay Natural History Society* **60**: 516–529.
- GEORGE, M. 1950. A chalicothere from the Limeworks Quarry of the Makapansgat Valley, Potgietersrust District. *South African Journal of Science* **46**: 241–242.
- GERAADS, D. 2010. 34. Rhinocerotidae. In Werdelin, J. & Saunders, W.J. (Eds), *Cenozoic Mammals of Africa*. Berkeley, CA, University of California Press, pp. 669–683.
- GUÉRIN, C. 1980. À propos des rhinocéros (Mammalia, Perissodactyla) néogènes et quaternaires d'Afrique: essai de synthèse sur les espèces et sur les gisements. In Leakey, R.E. & Ogot, B.A. (Eds), *Proceedings of the 8th Panafrican Congress of Prehistory and Quaternary Studies*, Nairobi, 5–10 September, 1977. Nairobi, The International Louis Leakey Memorial Institute for African Prehistory, pp. 58–63.
- GUÉRIN, C. & FAURÉ, M. 1983. Mammifères, Ch. 8. In Petit-Maire, N. & Riser, J. (Eds), *Sahara ou Sahel? Quaternaire récent du Bassin de Taoudenni (Mali)*. Editions CNRS, Laboratoire de Géologie du Quaternaire, Paris, pp. 239–272.
- GUÉRIN, C. & PICKFORD, M. 2005. *Ancylotherium cheboitense* nov. sp., nouveau Charicotheriidae (Mammalia, Perissodactyla) du Miocene supérieur des Tugen Hills (Kénya). *Comptes Rendus Palevol* **4**: 225–234. doi:10.1016/j.crpv.2004.10.005
- HALTENORTH, T. & DILLER, H. 1980. Odd-toed Ungulates, Perissodactyla. In *A Field Guide to the Mammals of Africa including Madagascar*. London, Collins, pp. 109–119.
- HENDEY, Q.B. 1976. The Pliocene fossil occurrences in 'E' Quarry, Langebaanweg, South Africa. *Annals of the South African Museum* **69**: 215–247.
- HENDEY, Q.B. 1984. South African Late Tertiary vertebrates. In Klein, R. G. (Ed.), *Southern African Prehistory and Palaeoenvironments*. Rotterdam, AA, Balkema, pp. 81–106 & 361–395.
- HOOGSTRAAL, H. 1964. A brief review of the land mammals of Egypt (including Sinai). 3, Carnivora, Hyaracoidea, Perissodactyla and Artiodactyla. *Journal of the Egyptian Public Health Association* **39**: 205–239.
- HOOIJER, D.A. 1978. Rhinocerotidae, Ch. 19. In Maglio, V.J. & Cooke, H. B.S. (Eds), *The Evolution of African Mammals*. Cambridge, MA, Harvard University Press, pp. 371–378.
- HOPWOOD, A.T. 1937. Die fossilen pferde von Oldoway. *Wissenschaftliche Ergebnisse der Oldoway-Expedition 1913*. Neue Folge **4**: 112–136.
- JOUSSE, H. ET AL. 2003. Aperçu archéozoologique d'un site de chasseurs au Néolithique ancien à Berouâga (Mauritanie nord-occidentale). *Sahara* **14**: 81–88.
- JOUSSE, H. 2006. What is the impact of Holocene climatic changes on human societies? Analysis of West African Neolithic populations dietary customs. *Quaternary International* **151**: 63–73. doi:10.1016/j.quaint.2006.01.015
- JOUSSE, H. & CHENAL-VELARDE, I. 2001–2002. Nouvelles données sur la faune mammalienne de Kobadi (Mali) au Néolithique: implications paléoeconomiques et paléoenvironnementales. *Préhistoire Anthropologie Méditerranéenne* **10.11**: 145–158.
- JOUSSE, H. & ESCARGUEL, G. 2006. The use of Holocene bovid fossils to infer palaeoenvironment in Africa. *Quaternary Science Reviews* **25**: 763–783. doi:10.1016/j.quascirev.2005.06.002
- JOUSSE, H., KABER, N.O.M. & RAIMBAULT, M. 2003. Aperçu archéologique d'un site de chasseurs au Néolithique ancien à Berouâga (Mauritanie nord-occidentale). *Sahara* **14**: 81–88.
- KABER, N.O.M. & RAIMBAULT, M. 1997. Les sites néolithiques de Berouâga en Mauretanie nord-occidentale. *Préhistoire Anthropologie méditerranéennes (Aix en Provence)* **6**: 141–153.
- KLEIN, R.G. 1986. Carnivore size and Quaternary climatic change in Southern Africa. *Quaternary Research (NY)* **26**: 153–170.
- LEAKEY, M. 1971. Appendix B. Olduvai Beds I & II. In Leakey, M.D. (Ed.), *Olduvai Gorge, Vol. 3: Excavations in Beds I & II; 1960–1963*. Cambridge, Cambridge University Press, 290–294.
- MACEACHERN, S., BOURGES, C. & REEVES, M. 2001. Early horse remains from northern Cameroon. *Antiquity* **75**: 62–67.
- MEESTER J.A.J. & SETZER, H.W. (Eds). 1971. *The Mammals of Africa: An Identification Manual*. Washington, DC, Smithsonian Institution Press.
- OSBORN, D.J., with OSBORNOVA, J. 1998. The mammals of Ancient Egypt. In *The Natural History of Egypt*, vol. 4. Warminster, Aris & Phillips, 1–213.
- PETIT-MAIRE, N. 1979. Le Sahara Atlantique à Holocène. Peuplement et écologie. *Memoires du CRAPE* **28**: 1–340.
- PETROCCHI, G. 1940. Ricerche preistoriche in Cyrenaica. *Africa Italiano* **7**, no. 1–2: 1–34.
- POMEL, N.A. 1897. Les équidés. *Carte Géologique de l'Algérie, Paléontologique Monographie*, **12**: 1–44.
- REED, C.A. 1965. A human frontal bone from the Late Pleistocene of the Kom Ombo Plain, Upper Egypt. *Man* **65**: 101–104. doi:10.2307/2797442
- REED, C.A. & TURNBULL, P.F. 1969. Late Pleistocene mammals from Nubia. In van Zinderen Bakker, E.M. (Ed.), *Palaeoecology of Africa and of the surrounding islands and Antarctica*. Vol. IV, covering the years 1966–1968. Cape Town, A.A. Balkema, 55–56.
- ROOKMAKER, L.C. 2007. A chronological survey of bibliographical and iconographical sources on rhinoceroses in southern Africa from 1795–1875: reconstructing views on classification and changes in distribution. *Transactions of the Royal Society of South Africa* **62**: 55–198. doi:10.1080/00359190709519203
- ROSEVEAR, D.R. 1953. *Checklist and Atlas of Nigerian Mammals*. The Nigerian Government, The Government Printer, Lagos, 131, 239 faunal distribution maps & 2 coloured vegetational maps.
- SCHOMBER, H.W. 1966. Die Verbreitung und der Bestand des zentral-afrikanischen Breitmaulnashorns, *Ceratherium simum cottoni* (Lydekker, 1908). *Säugetiere Mitteilungen* **14**: 214–227.
- SETZER, H.W. 1957. A review of Libyan mammals. *Journal of the Egyptian Public Health Association* **32**: 41–82.
- SIDNEY, J. 1965. The past and present distribution of some African ungulates (13–17). *Transactions of the Zoological Society of London* **30**: 1–395.
- TALBOT, L.M. 1960. A look at threatened species. 99. Fauna Preservation Society, London, for *International Union for the Conservation of Nature* (unseen, cited by Gee, 1964, above).
- THOMAS, P. 1884a. Recherches stratigraphiques et paléontologiques sur quelques formations d'eau douce de l'Algérie. *Mémoire de la Société Géologique de France* **3**: 1–51.
- THOMAS, P. 1884b. Sur quelques formations d'eau douce tertiaires d'Algérie. *Comptes Rendus hebdomadaires de l'Académie de Science* **1884**: 311–314 & 381–383.
- WALKER, R. 1985. *A guide to post-cranial bones of East African animals*. Norwich, Hylochoeris Press.
- WILLIAMS J.G. & ARLOTT, N. 1967. *A Field-Guide to the National Parks of East Africa* (edit. 1981). London, Collins.