Fossil evidence for perennial lake conditions during the Holocene at Etosha Pan, Namibia

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E TOSHA PAN, A LARGE (4760 km²), ENDORHEIC depression situated in north-central Namibia, has been claimed to be essentially a wind-deflated landform. The pan was assumed by some researchers to have developed under persistent semi-arid conditions, which were alleged to have prevailed in the region for at least the last 140 000 years. Recent field evidence points to the contrary. This evidence includes a significant number of fossils belonging to, amongst others, semi-aquatic antelopes such as sitatunga, which are diagnostically indicative of perennial lake conditions in the area. These species have previously never been reported from Etosha National Park, either as fossils or extant. Here we indicate the significance of these findings and their implications for the palaeo-environment of the Etosha region.

Unlike the rest of the Mega-Kalahari, the climatic conditions at and around Etosha in north-central Namibia (Fig. 1) were considered by some researchers to have been as semi-arid as today for the last 1.8 million years (Myr). Field evidence supporting that premise was primarily based on the presence of the so-called lunette dunes situated in the western and northwestern margins of the Etosha Pan. Sediments at depth of this landform were dated to at least 140 kyr ago and their sedimentation record since then was deemed to reflect continuous accumulation of surface deposits. Such a conclusion firmly attributed the development of Etosha Pan to aeolian action, supplemented only occasionally by seasonal water erosion.

An earlier postulate was that this endorheic depression arose from a desiccated palaeolake. Advocates of this hypothesis assumed that the Kunene, one of the great rivers of the subcontinent, was an endorheic system like the neighbouring Okavango River today. Thus, like the modern-day Okavango Delta of Botswana, a large lake existed over the Pliocene and Early Pleistocene. Since then, the progressive drying-out at Etosha translated into the desiccation of the lake, leaving behind successive shorelines in its western and northwestern margins as the water level receded. These shorelines are the same landforms interpreted as lunette dunes by proponents of an aeolian origin for Etosha Pan.

These two contrasting hypotheses, one perceiving Etosha Pan as a deflation hollow and the other as a dried-up lake, have sparked a debate as to how this feature formed and under what climatic regime. Such a debate is not just an academic exercise. The Etosha Pan, regarded by Giess in his classification of the major vegetation zones of the territory as a ‘saline desert with dwarf shrub savanna fringe’, is an integral part of a unique life-support system under such climatic conditions. The pan is a magnet for a high density of animals (more than 70 animals per 10 square kilometres), a diverse population of wildlife (114 mammal and 340 bird species) and the accompanying tourism industry that it supports under the flagship of the Etosha National Park. Understanding the mechanics that controlled its development is thus germane to the prudent management of the ecosystem. A host of fossil sites was recently discovered at Etosha Pan that has a bearing on its origin and development. This article contextualizes the significance of the fossil remains and their implications for the palaeo-environment of the Etosha region.

The new fossils

The reconstruction of the Mega-Kalahari, the largest continuous sand body on earth, has been hindered by a lack of fossils and natural exposures. Such was also true for the Etosha region. In the past, the only notable fossils found at Etosha were pieces of struthious eggshell and stromatolites. The stromatolites proved to be difficult to interpret owing to the various ages that different authors assigned to them. Those ages ranged between the Pliocene and Late Pleistocene. Nor was agreement reached about the environment in which these stromatolites lived. Other significant fossils found in the area are molluscs. Like the stromatolites, the molluscs were considered to be either freshwater or marine. The most common species found at Etosha was identified as Xerocrastus burchelli, which thrive under a wide range of ecological conditions, including a seasonally wet terrestrial environment.
More recently, Hipondoka\(^2^3\) reported at least 10 different fossil types from Etosha Pan and its immediate surroundings (Figs 2, 3). They include pieces belonging to fish, birds, and antelopes. The fish fossils belong to a \textit{Clarias} species, with some specimens comparable to a modern individual measuring some 90 cm. These fossil fragments were found in cemented, lower and middle river terraces of the Ekuma River and the Oshigambo Peninsula. Others were found in the loose sediments of the Ekuma Delta and in the middle of the pan at a depth ranging between 70 and 190 cm. As far as can be ascertained, these fish species are by far the largest individuals known from mainland Namibia, save for its perennial border rivers (the Kunene, Okavango and Orange).

Among the \textbf{Clariidae}, six species of the genus \textit{Clarias}, and one each of \textit{Clariellates} and \textit{Heterobranchus} are known to exist in southern Africa today. However, only the genus \textit{Clarias} occurs in the Cuvelai system,\(^2^5\) which is a maze of shallow watercourses with perennial tributaries found in the upper catchment in Angola,\(^2^6\) courses with perennial tributaries found near Kunene and Okavango rivers.\(^2^7\) \textit{Clarias} is the only genus that lives in southern Africa today. However, only the genus \textit{Clarias} occurs in the Cuvelai system,\(^2^5\) which is a maze of shallow watercourses with perennial tributaries found in the upper catchment in Angola,\(^2^6\) courses with perennial tributaries found near Kunene and Okavango rivers.\(^2^7\) \textit{Clarias} is the only genus that lives in southern Africa today. However, only the genus \textit{Clarias} occurs in the Cuvelai system,\(^2^5\) which is a maze of shallow watercourses with perennial tributaries found in the upper catchment in Angola,\(^2^6\) courses with perennial tributaries found near Kunene and Okavango rivers.\(^2^7\)

Fig. 2. Fossil fragments of \textit{Clariidae} fish. Key: Etosha 215: pectoral spine (1), dentale (2), skull fragments (3), supraoccipital (4), Etosha 215 Delta: supraoccipital (5), Etosha 228: supraoccipital (6).

Fig. 3. Fossil fragments of selected mammals. Key: Etosha 231: \textit{Kobus} sp., horn core (1); Etosha 233: \textit{Equus quagga}, pelvis bone (2); \textit{Dama}, metacarpal (3 and 4); \textit{Taurotragus} (sittinga), metatarsal (5) and metatarsal (6).

The most provocative evidence for swampy conditions at Etosha is the presence of sittatunga, the most aquatic of the antelopes.\(^2^9^–^3^1\) The habitat of the sittatunga is so specialized that it spends the greater part of its life in swampy areas characterized by dense papyrus, \textit{Cyperus papyrus}, and reed beds, \textit{Phragmites mauritianus}. At night, they may emerge from swamps and venture into adjacent woodland. The nearest place to Etosha Pan where they occur today is the Okavango Delta and along the Chobe River, some 600 km away.\(^2^9\) The tribe Reduncini, to which \textit{Taurotragus} belongs, is surpassed by no other antelope for its dependence on water, with the exception of the sittatunga.\(^3^0\) All three possible species to which a horn core belongs, is surpassed by no other antelope for its dependence on water, with the exception of the sittatunga.\(^3^0\) All three possible species to which a horn core belongs, is surpassed by no other antelope for its dependence on water, with the exception of the sittatunga.\(^3^0\) All three possible species to which a horn core belongs, is surpassed by no other antelope for its dependence on water, with the exception of the sittatunga.\(^3^0\) All three possible species to which a horn core belongs, is surpassed by no other antelope for its dependence on water, with the exception of the sittatunga.\(^3^0\) All three possible species to which a horn core belongs, is surpassed by no other antelope for its dependence on water, with the exception of the sittatunga.\(^3^0\) All three possible species to which a horn core belongs, is surpassed by no other antelope for its dependence on water, with the exception of the sittatunga.\(^3^0\)}
Tsessebe also have a distinct habitat requirement that is not met in the present-day Etosha National Park. Like the sitatunga and Reduncini tribe, tsessebe thrive in areas with permanent water. They favour floodplains, where they spend most of the time during the dry season. Penetrating into adjacent woody vegetation is attempted only when water is available. Again, the Okavango Delta is the nearest place to Etosha where they occur today. Except for the horn core, all other fossils were found in the eroded northern shoreline of the Etosha Pan. The horn core was found on the surface of the Ekuma Delta, but we believe that it was eroded from a nearby terrace, capped with calcrite blocks. The age of the horn could not be determined because of its lack of collagen.

A pelvis of the now extinct quagga was successfully subjected to carbon dating, using accelerator mass spectrometry (AMS). The dated sample was obtained from the site where all other antelope fossils, except the horn core fragment, were found. It yielded an age of 4275 ± 80 years 14C BP (lab. ref. no. LuS0116–Eto 233). Applying the shcal02.12c calibration curve in conjunction with McCormac et al., 32 to derive the calendar years, that age was adjusted to 5.0–4.5 cal kyr BP. This date overlaps a thermoluminescent date of 5.6 ± 2.2 kyr BP, assigned to the sediments taken from the so-called inner-lunette dunes situated in the western margin of the Etosha Pan. 43 The dated sediments were taken from a depth of 120 cm. These authors interpreted sediments of these ridges as being wind-excavated from the surface of the Etoha Pan in the course of the development of the pan, and subsequently deposited on the leeward side to form what they called lunette dunes.

Buch and Zöller, Buch et al. 2 and Buch, amongst others, have emphatically ruled out even a single phase of humid or perennial lake conditions at Etoha, particularly over the last 140 kyr. This is clearly in direct conflict with the fossil evidence presented above, which unambiguously points to perennial lake conditions at Etoha Pan within this time frame. Inevitably, a premium is attached here to field evidence, and the sand ridges situated in the western margin of the pan are now re-interpreted as shorelines, and not lunette dunes as previously postulated. If this is so, then the Etoha Pan does not owe its development to aeolian processes. As Hipondoka 23 noted, the explanation of how the pan developed still needs refining, but it excludes aeolian action as the primary agent of formation.

The significance of the fossils from

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10. Wellington J.H. (1938). Fatlings, in particular, unequivocally point to the existence of perennial lake conditions at Etoha. Moreover, the absolute age obtained from a representative sample, which was taken from the site where most fossil fragments of semi-aquatic antelopes were discovered, placed that glimpse of lacustrine environment at Etoha in the Holocene. This date singularly dispels the earlier assertion that the climate at Etoha was as dry as today for the last 1.8 Myr and that not even a single episode of a wet phase occurred at the pan since the Pleistocene. Second, apart from the semi-aquatic fauna that are now locally extinct, the presence of extant antelopes in the fossil record of Etoha, as presented above, indicates their pre-existence in the area and that of a diverse fauna, with varying ecological requirements. The present, extraordinarily high diversity and large number of mammals, for the climate of present-day Etoha, that concentrate in the fringes of the pan is therefore most likely a remnant of a faunal population that gravitated around a once swampy environment, which was surrounded by a heterogeneous habitat.

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