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Palaeogeography, Palaeoclimatology, Palaeoecology 221 (2005) 153–174

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Diets of modern and late Miocene hippopotamids: Evidence from carbon isotope composition and micro-wear of tooth enamel

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Received 17 September 2004; received in revised form 20 January 2005

Abstract

Carbon isotope composition and micro-wear analyses of tooth enamel were used to reconstruct the diet of late Miocene hippopotamids unearthed in the Toros-Ménalla area, Chad, contemporary to the oldest known hominids. A large sample of wild modern *Hippopotamus amphibius* from various locations in Africa was also analysed for comparison. Isotopic analyses showed that the modern hippo, reputedly a strict grazer, has a more varied diet than usually thought, including a significant amount of C_3 plants in closed to moderately open environments. Enamel formed before weaning was on average 3‰ depleted in ^{13}C compared to post-weaning enamel, a pattern that could be partially explained by milk consumption. The observed micro-wear pattern of the modern hippo differs from that of other modern ungulates. We explain the very abundant fine scratches and small pits found on these hippo teeth by the preference for fresh short grasses with low silicon content. The diet of the late Miocene hippopotamid was probably close to that of the modern *Hip. amphibius*, but included a larger amount of C_3 plants. This contradicts previous palaeoecological findings based on relative hypsodonty degree and indicates that the modern feeding behaviour of large hippos was already developed at the end of the Miocene, when C_4 grass exploitation by large ungulates became much more frequent in Africa. Finally, it also indicates that C_4 grasses were a significant component in late Miocene environments of Central Africa.

Keywords: Palaeodiet; Hippopotamidae; Tooth enamel; Carbon stable isotopes; Dental micro-wear; Late Miocene; Chad; Africa

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doi:10.1016/j.palaeo.2005.02.010

1. Introduction

Fossil mammals are a major source of data for reconstructing late Neogene environments of Africa. However, many taxa are not or rarely considered for that purpose, although they may be of great palaeoecological significance. The fossil hippopotamids fall into this scheme. A recent work stresses the potential value of these mammals for palaeoenvironmental studies in Asia (Jablonski, 2003). This should also apply to African hippopotamids, which are among the most common mammals found in the late Neogene deposits of this continent (Coryndon, 1978; Harris et al., 1988; Harris, 1991; Faure, 1994; Harrison, 1997; Brunet and M.P.F.T., 2000; Alemseged, 2003; Weston, 2003). Moreover, the extant common hippo, *Hippopotamus amphibius*, is a keystone species of the lakes, rivers, and their surroundings in Sub-Saharan Africa (Kingdon, 1979; Eltringham, 1999). This semi-aquatic mammal directly and significantly influences different components of aquatic and peri-aquatic ecosystems. The trails of the modern common hippo modify the substrates of these ecosystems at both local and regional levels, inducing localized sedimentological structures (Deocampo, 2002) and shaping the geomorphology of hydrographical networks (McCarthy et al., 1998). Under water, hippos affect trophic inputs (Verheyen, 1954; Kingdon, 1979; Grey and Harper, 2002), water stratification (Wolanski and Gereta, 1999) and nutrient suspension (Verheyen, 1954). Above all, because of their conservative habitat, large size and grazing preferences, the common hippos play a dramatic role in the composition and regeneration of wetland terrestrial vegetation, with great consequences for the other herbivores (Laws, 1968a; Field, 1970; Lock, 1972; Olivier and Laurie, 1974; Kingdon, 1979; Eltringham, 1999).

Despite these promising characteristics, a full integration of fossil hippos in the study of African palaeoenvironments still requires major advances in the knowledge of their ecology and diet. Reconstruction of fossil hippo diets has often been based on superficial observations of the cranio-dental morphology. Grazing or browsing diets have been assessed by using the degree of hypsodonty of the cheek teeth, the morphology of the anterior dentition (Coryndon, 1977; Gèze, 1985), and general morphological comparisons with the modern species (Coryndon, 1967). The resulting assumptions are rather inaccurate. On one hand, the hypsodonty degree is weakly variable in hippos, being quite low even in the extant grazer *Hippopotamus amphibius* (Janis, 1988), and moreover can be misleading for diet recognition (Solounias et al., 1988; MacFadden et al., 1999). On the other hand, the anterior teeth of the Hippopotamidae take an insignificant part in the feeding process. Their morphology is mostly constrained by intraspecific competition, as part of a cranial morphology heavily specialized for biting (Herring, 1975; Kingdon, 1979). Unfortunately, these adaptations are likely to preclude correct identifications of many of the morphological features associated to grazing or browsing that were recognized and used for other ungulates (Solounias and Dawson-Saunders, 1988; Solounias et al., 1988; Janis, 1995). Until now, the most reliable data on fossil hippo diet have been provided by carbon isotope analyses in tooth enamel (Morgan et al., 1994; Bocherens et al., 1996; Kingston, 1999; Zazzo et al., 2000; Franz-Odendaal et al., 2002; Cerling et al., 2003b; Schoeninger et al., 2003). The work of Cerling et al. (2003b) is the most significant, being based on a large sample of late Miocene/basal Pliocene hippopotamids from one locality, Lothagam (Turkana basin, Kenya).

This study is an attempt to characterize the diet of a Miocene hippopotamid from Toros-Ménalla (Central Africa, Chad) combining carbon isotope and dental micro-wear analyses. Results obtained on the fossils were compared with those obtained on a large sample of living *Hippopotamus amphibius*.

2. The Toros-Ménalla fossiliferous area

The Toros-Ménalla (TM) area is located just above 16°N and between 17°E and 18°E, in the Djurab erg, i.e. the most southern extension of the Sahara in Northern Chad. The monotonously flat substrate of TM is composed of aeolian and perilacustrine sandstones, and lacustrine deposits (Vignaud et al., 2002). Those sediments are patchily covered by active aeolian sands and sand dunes that isolate outcrops. Between 1997 and today, the Mission Paléoanthropologique Franco-Tchadienne (MPFT) collected more than 10,000 fossil vertebrates in these outcrops. The hippos studied here were found in association with a