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Was the Early Eocene proboscidean *Numidotherium koholense* semi-aquatic or terrestrial? Evidence from stable isotopes and bone histology

Numidotherium koholense, *un proboscidien primitif de l'Eocène inférieur, était-il terrestre ou semi-aquatique ? Contribution de l'analyse des isotopes stables et de l'histologie osseuse*

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A B S T R A C T

The Early Eocene deposits of El Kohol, Algeria, have yielded numerous remains of *Numidotherium koholense*, one of the most primitive and oldest known proboscideans in Africa. The Upper Eocene proboscideans of the Fayum locality (Egypt), *Barytherium* sp. and *Moeritherium* sp., were recently interpreted as aquatic or semi-aquatic, according to the stable isotopic compositions ($\delta^{13}C$ and $\delta^{18}O$) of their tooth enamel. These data led us to reinvestigate the adaptations of *N. koholense*. Stable isotopic analysis and observations of histological sections of its long bones reveal that it was essentially terrestrial. According to its position within the phylogenetic tree of Eocene proboscideans, the adaptation to semi-aquatic life appears to have evolved independently in different lineages of Middle and Upper Eocene proboscideans during their adaptive radiation in Africa. Moreover, these new results reopen the debate about the hypothesis that Eocene to Recent proboscideans are derived from semi-aquatic ancestors.

Mots clés :
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R É S U M É

Le gisement de l'Eocène inférieur d'El Kohol (Algérie) a livré de nombreux restes de *Numidotherium koholense*, l'un des proboscidiens les plus primitifs et les plus anciens de la radiation de cet ordre en Afrique. Les proboscidiens de l'Eocène supérieur du Fayum en Égypte, comme *Barytherium* sp. et *Moeritherium* sp. étaient semi-aquatiques d'après des données des isotopes stables ($\delta^{13}C$ et $\delta^{18}O$) de leur émail dentaire. Ces données nous ont conduits à réexaminer le mode de vie de *N. koholense*. Les analyses des isotopes stables et l'examen des coupes histologiques des os longs révèlent qu'il était plutôt terrestre. Compte-tenu de la position qu'il occupe dans l'arbre phylogénétique des proboscidiens

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éocènes, l'adaptation à la vie semi-aquatique serait donc développée indépendamment dans différentes lignées de proboscidiens primitifs au cours de leur radiation adaptative éocène. Par ailleurs, ces résultats rouvrent le débat concernant l'hypothèse de l'adaptation semi-aquatique de l'ancêtre des proboscidiens primitifs.

1. Introduction

The evolutionary history of proboscideans is documented over 60 million years (Gheerbrant, 2009). The first radiation is that of the Eocene lophodont taxa (Gheerbrant and Tassy, 2009), whose phylogenetic relationships were established by Delmer (2009) (Fig. 1). His phylogeny supports the hypothesis of an ancestral morphotype with lophodont molars that gave rise to semi-aquatic forms such as *Moeritherium* that displayed bunolophodont molars, and later to bunodont forms, including the elephantiforms (Gheerbrant et al., 1998, 2005). Previous stable isotopic work showed that *Moeritherium* and *Barytherium*, proboscideans from the Upper Eocene of Fayum, were semi-aquatic mammals (Liu et al., 2008). *Numidotherium koholense*, one of the oldest and basalmost proboscideans, comes from the Early Eocene of El Kohol (Algeria). It was described on the basis of rich and well-preserved material that documents almost its entire skeleton (Mahboubi et al., 1986). An Ypresian age, between 52 Ma and 51 Ma, was recently estimated for this deposit, based on a magnetostratigraphic study (Coster et al., 2012).

According to the detailed description of Court (1994a), the postcranial morphology of *N. koholense* differs significantly from that of the later elephantiform proboscideans. The fusion of the distal radius and ulna in a semi-supinated position, a character also observed in aquatic mammals such as Pinnipedia and Sirenia, could indicate an aquatic mode of life (Court, 1994a; Savage, 1957). However, Court (1994a) concluded that there is “little else in the limb skeleton of *N. koholense* to suggest an aquatic mode of life”. Furthermore, the abducted members and ambulatory gait of this animal reflect a compromise between aquatic and terrestrial lifestyles (Court, 1994a).

Here, we reconstruct the ecology of *N. koholense*, through stable isotope analyses of tooth enamel. Using carbon isotopes, we assessed feeding preference. Then, we used oxygen isotopes of tooth enamel to know its lifestyle, as well as histological studies of its long bones. Our study aims to complete and re-evaluate the interpretations of mode of life proposed by Court (1994a). In addition, to obtain more relevant data, we also analyzed the tooth enamel of several proboscideans from Dur At Talah (Central Libya, late Middle Eocene) such as *Arcanotherium savagei*, *Moeritherium* sp., and *Barytherium grave* (Jaeger et al., 2010).

1.1. *Stable isotopes of carbon and diet*

Stable carbon isotope analysis of tooth enamel offers a good proxy for reconstructing terrestrial paleoenvironments, including climate and vegetation, notably providing valuable information regarding the proportions of C_3 and C_4 vegetation in the diet of the herbivores and thus indirectly in their habitat. Although one of the earliest record of C_4 plants is dated around 14 Ma–12.5 Ma (Cerling et al., 1997a; Nambudiri et al., 1978; Tidwell and Nambudiri, 1989), these plants do not constitute a significant part of ecosystem ground before 8 Ma–7 Ma, and became common worldwide only from 6 Ma–5 Ma, (Cerling et al., 1997b).

The $\delta^{13}C$ values for C_3 plants range between −38‰ and −22‰, with an average of −27‰ (Cerling and Harris, 1999; Farquhar et al., 1989; Tieszen, 1991). The $\delta^{13}C$ values of C_4 plants range between −17‰ and −9‰, with an average of −13‰ (Smith and Epstein, 1971). In general, aquatic plants have lower concentrations of $\delta^{13}C$, and some algae and other aquatic plants can have values of $\delta^{13}C$ in the range of C_4 plants (Cerling et al., 1997b).

Herbivorous mammals usually exhibit a +14‰ enrichment for the $\delta^{13}C$ values of carbonate in bioapatite in bones and enamel relative to the type of plant consumed (Cerling and Harris, 1999; Cerling et al., 1997b; Lee-Thorp and Van der Merwe, 1989; Passey et al., 2005). This enrichment for tooth enamel in large mammals compared to their diet is greater than observed in laboratory experiments on very small mammals (Cerling et al., 1997b; DeNiro and Epstein, 1978). In carnivores, the enrichment is +9‰ for bones and enamel apatite (Bocherens and Drucker, 2013; Cerling et al., 1997b; Koch, 1998; Kohn and Cerling, 2002; Lee-Thorp and Van der Merwe, 1989). We take into consideration this enrichment for the interpretation of our results.

1.2. *Oxygen isotopes environment/habitat use*

Two isotopic approaches have been proposed to distinguish terrestrial mammals from aquatic or semi-aquatic ones. First, the hippopotamids of Plio-Pleistocene age in eastern Africa show lower $\delta^{18}O$ values than other associated terrestrial herbivores, which have been related to their semi-aquatic lifestyle (Bocherens et al., 1996). Another approach, proposed by Clementz and Koch (2001) and by Clementz et al. (2008), showed that $\delta^{18}O$ values within a same population of terrestrial animals display considerable variation, significantly higher than in semi-aquatic mammals. The standard deviation of $\delta^{18}O$ measured on a minimum of five specimens of a terrestrial population is higher than 1‰. Aquatic mammals living in isotopically homogeneous water show a much lower variation in their $\delta^{18}O$ values, their standard deviation of $\delta^{18}O$ being generally less than 0.5‰ (Clementz and Koch, 2001; Yoshida and Miyazaki, 1991). It shows that $\delta^{18}O$ of tooth enamel reflects water values during the mineralization of teeth (Andersen and Nielsen, 1983; Hui, 1981). This model was previously applied to distinguish terrestrial and semi-aquatic fossil mammals. According to the results obtained on *Moeritherium* sp. and *Barytherium* sp. from Upper Eocene