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Variable enamel growth rates in hippopotamid canines: Implications for seasonality reconstructions using inverse modeling of intra-tooth isotope data

Antoine Souron[1], Maëlle Couvrat[2], Éric Pubert[1], Frédéric Santos[1], Deming Yang[3], Delphine Frémondeau[4], Clarisse Nékoulnang[5], and Olga Otero[6]

[1]Univ. Bordeaux, CNRS, Ministère de la Culture, PACEA, UMR 5199, F-33600 Pessac, France
[2]Laboratoire Méditerranéen de Préhistoire Europe Afrique (LAMPEA), Aix-en-Provence, France
[3]Division of Anthropology, American Museum of Natural History, New York, NY, United States
[4]Institute of Archaeology, University College London, London, United Kingdom
[5]Centre National de la Recherche et du Développement, Chad
[6]Université de Poitiers, PALEVOPRIM (UMR 7262-CNRS-UP), Poitiers, France

Seasonal variations in climatic variables, and the resulting changes in vegetation, are strong factors governing ecosystem dynamics in modern and ancient times. Stable isotope ratios recorded in tooth enamel document isotopic variations in the environment at the time of enamel formation and thus reveal the intensity and duration of seasonal dietary and climatic variations. However, the long and multi-phased process of enamel mineralization causes a dampening of the original input signal. An inverse model previously developed for ever-growing canines of *Hippopotamus amphibius* proposes to recover the original input signal and assumes constant enamel growth rate, appositional angle, and maturation length. The present study aims to test these assumptions. To do so, we integrated data from histological thin sections, microtomodensitometric analyses, and stable isotope analyses on teeth of extant *H. amphibius* specimens (3 upper canines, 1 lower canine, 1 third molar) to quantify the geometric and temporal patterns of enamel mineralization. To estimate enamel extension rates (EER, in µm/increment), we counted the number of increments representing the position of appositional front for each segment of 5 mm along the enamel-dentine junction in thin sections made along the growth axis of each tooth. We used microtomodensitometry to determine the pattern of enamel maturation using grey values profiles of X-ray radiographies as a proxy for enamel mineralization degree. Serial sampling along one upper canine of an individual from Chad, coming from an environment with one rainy season per year, allowed us to document the intra-tooth $d^{13}C$ and $d^{18}O$ variations over 6 years and thus provided an independent temporal control on histological variations. The histological study showed that the enamel apposition phase is strongly irregular over time within the canines, with no clear temporal trend. EERs vary strongly among teeth and within each tooth (50-200 µm/increment, 100-350 µm/increment, and 80-200 µm/increment for the 3 upper canines; 150-550 µm/increment for the lower canine; 70-130 µm/increment for the third molar). The median EER value from the upper canine of the juvenile individual (ca. 180 µm/increment) is

significantly higher than median EER values from the upper canines of two adult individuals (ca. 110 µm/increment). Similar variations are also observed in apposition angles (3°-8°, 2.5°-4.5°, 3°-7° for the 3 upper canines; 2°-8° for the lower canine; 6°-18° for the third molar). The enamel mineralization parameters vary with age and tooth type (canine vs. molar). Based on strongly correlated seasonal variations in $d^{13}C$ and $d^{18}O$, we also confirm cyclic dietary variations with higher proportions of C_4 plants consumed during the dry seasons. Using the range of enamel mineralization parameters observed within one single hippo canine, we conducted sensitivity tests on the inverse modeling method, producing different modeled input signals that suggest a wider range of uncertainty. In conclusion, the documented intra-canine variability of EER, as well as other histological parameters (apposition angle, maturation length), reveals challenges when applying the current inverse model to wild populations. Future work would benefit from a systematic histological investigation into the sources of variation of enamel growth and mineralization patterns.