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Identifying aquatic habits of herbivorous mammals through stable isotope analysis

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ABSTRACT

Large-bodied, semiaquatic herbivorous mammals have been a recurring component of most continental ecosystems throughout the Cenozoic. Identification of these species in the fossil record has largely been based on the morphological similarities with present-day hippopotamids, leading to the designation of this pairing of body type and ecological niche as the hippo ecomorph. These morphological characters, however, may not always be diagnostic of aquatic habits. Here, enamel $d^{13}C$ and $d^{18}O$ values from living hippopotamuses were examined to define an isotopic signature unique to the hippo ecomorph. Although $d^{13}C$ values do not support unique foraging habits for this ecomorph, living and fossil hippopotamids typically have low mean $d^{18}O$ values relative to associated ungulates that fit a linear regression ($d^{18}O_{hippopotamids} = 0.96 \pm 0.09 * d^{18}O_{fauna} - 1.67 \pm 2.97$; $r^2 = 0.886$, $p < 0.001$). Modeling of oxygen fluxes in large mammals suggests that high water-turnover rates or increased water loss through feces and urine may explain this relationship. This relationship was then used to assess the aquatic adaptation of four purported hippo ecomorphs from the fossil record: *Coryphodon* (early Eocene), *Moeritherium* and *Bothriogenys* (early Oligocene), and *Teleoceras* (middle–late Miocene). Only fossil specimens of *Moeritherium*, *Bothriogenys,* and large species of *Coryphodon* had $d^{18}O$ values expected for hippo ecomorphs; $d^{18}O$ values for *Teleoceras* and a small species of *Coryphodon* were not significantly different from those of the associated fauna. These results show that the mean $d^{18}O$ value of fossil specimens is an effective tool for assessing the aquatic habits of extinct species.