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Multiple taxon–multiple locality approach to providing oxygen isotope evidence for warm-blooded theropod dinosaurs: Comment and Reply

COMMENT

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Fricke and Rogers (2000) applied a unique approach to the question of theropod metabolism. Their premise was that latitudinal effects on the oxygen isotope composition of meteoric water should be reflected more directly in endothermic homeotherms, because they maintain constant body temperature, than in ectothermic heterotherms, because they will be colder at higher latitudes. The isotope slope of theropods appears steeper than that of crocodiles, and it is possible and perhaps probable that the interpretation of theropod endothermy is correct. However, we believe the authors were premature in dismissing environmental factors and sample bias as explanations for their data. We outline several of these factors to show how they may explain the data, but also to illustrate how Fricke and Rogers' study has further research implications.

Thermoregulation. Fricke and Rogers assume that crocodile body temperatures vary seasonally and latitudinally. However, all extant members of *Crocodylia* use several different strategies to maintain high body temperatures (25–35 °C), despite variations in ambient temperature. More critically, crocodiles only grow at body temperatures above a thermal minimum of ~25 °C (Coulson and Coulson, 1986) and will grow faster at warmer temperatures up to a thermal maximum of ~36 °C. Thus even if high-latitude crocodiles had mean annual body temperatures that were much cooler than equatorial crocodiles, their teeth probably grew at similar temperatures. We believe the theropod-crocodile isotope differences may reflect some factor(s) other than thermoregulation.

Humidity. Fricke and Rogers also assume that the body-water composition of crocodiles and theropods was the same at any given latitude or had the same slope across latitudes. This is not necessarily valid, because of behavior and the "humidity effect": $\delta^{18}O$ in terrestrial animals increases as humidity decreases (e.g., Luz et al., 1990). For example, suppose low-latitude crocodiles were aquatic during the day (low-humidity) and terrestrial during the night (high-humidity), similar to modern saltwater crocodiles, but higher latitude crocodiles were terrestrial during the day and aquatic at night, as are modern alligators. If so, then humidity effects will shallow the crocodile isotope slope relative to terrestrial theropods, even if body temperatures were always identical. This effect would magnify if the crocodile diet differed taxonomically, so that low-latitude crocodiles ate only aquatic animals and high-latitude crocodiles also ate terrestrial vertebrates. Alternatively, suppose all crocodiles were fully aquatic with no humidity effects. The Scotese paleogeographic map for the Late Cretaceous shows that low-latitude sites were drier than high-latitude sites. If so, low-latitude theropods had an extra-high $\delta^{18}O$ compared to their high-latitude cousins, steepening the theropod slope for reasons unrelated to thermoregulation.

Seasonality. Isotope compositions vary seasonally and are recorded in isotope zoning in tooth enamel (Fricke and O'Neil, 1996). In principle, isotope zoning studies on several teeth from a site can resolve the seasonal range of isotope compositions. However, in our experience, abundant fossil teeth of one species at a site often reflect one well-preserved specimen, not a random sample. Because the lifetime of a tooth is typically a few months to a year in crocodiles and in small dinosaurs (Erickson, 1996a, 1996b), the different teeth from each site may in fact represent only a single portion of the year. Homogenization of each tooth for analysis also must have blurred seasonality, which is a special problem for most sites with only 3–4 teeth. We believe that the mean tooth compositions may be biased toward one season, and insofar as seasons can vary by many per mil, that the crocodile-theropod isotope differences at most sites are not yet meaningful.

Tooth growth. Low-latitude tropical crocodiles may replace teeth all year, but high-latitude crocodiles probably will not if their body temperatures drop below the critical minimum. This will skew the isotopic data to higher values for the high-latitude crocodiles, whose teeth represent seasonal tooth deposition, further shallowing the crocodile isotope slope. In contrast, if theropods at high latitudes replaced their teeth all year, teeth representing the low $\delta^{18}O$ winter-spring water will decrease the mean isotopic value relative to crocodiles. It would also create a greater standard deviation in the theropod data at higher latitudes, because some teeth would reflect winter deposition while none of the crocodile teeth would. For the Montana site, the isotope variability for theropods is much higher than for crocodiles. If isotope variability is a principal measure of metabolic physiology rather than behavior, then the Montana tooth data support the authors' original conclusion that theropods maintain a higher metabolic rate than crocodilians.

Implications for paleoclimate analysis. The results also have important implications for the study of paleoclimates, because gradients in meteoric water $\delta^{18}O$ values reflect latitudinal heat distribution. For example, the data show a shallower $\delta^{18}O$ slope (~0.2‰/°lat) at implications of our stable isotope research (e.g., Fricke and Rogers, 1998; Fricke et al., 1998). However, it was clear to us that in order to estimate $\delta^{18}O$ of Cretaceous precipitation, it was first necessary to resolve the nature of theropod thermoregulation. We feel that the data now available do provide reasonable evidence for theropod homeothermy, and we are in the process of preparing a more detailed report of how stable isotope data from theropods and other taxa can provide exciting new insights into Cretaceous climate.

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