Dinosaur Body Temperatures Determined from Isotopic (^{13}C-^{18}O) Ordering in Fossil Biominerals

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The nature of the physiology and thermal regulation of the nonavian dinosaurs is the subject of debate. Previously, arguments have been made for both endothermic and ectothermic metabolisms on the basis of differing methodologies. We used clumped isotope thermometry to determine body temperatures from the fossilized teeth of large Jurassic sauropods. Our data indicate body temperatures of 36° to 38°C, which are similar to those of most modern mammals. This temperature range is 4° to 7°C lower than predicted by a model that showed scaling of dinosaur body temperature with mass, which could indicate that sauropods had mechanisms to prevent excessively high body temperatures being reached because of their gigantic size.

For the majority of the time since dinosaurs were first named in 1842, it was assumed that their metabolism was similar to ectothermic "cold-blooded" reptiles that derive the heat they need to function from the environment, rather than endothermic "warm-blooded" mammals and birds, which have higher and more stable body temperatures regulated by internal metabolic heat production. However, in the 1960s and 1970s, evidence began emerging that endothermy could be more consistent with observations on the behavior, paleogeographic distribution (for example, polar dinosaurs), and anatomy of nonavian dinosaurs (1–3). The initial case for dinosaur endothermy was largely made on the basis of interpretations of the inferred physical performance and behavior of dinosaurs, such as estimating running speeds from preserved tracks and predator/prey ratios determined by comparing biomass estimates from the fossil record to those ratios in modern ecosystems (3–5). These methods have been extensively debated (5) and have sparked several decades of study on dinosaur thermoregulation by using biophysical and behavioral modeling (6–10), bone histology and growth rate analysis (11), anatomical observations (12), and oxygen isotope paleothermometry (13–15). Despite progress in these methods, a consensus opinion has not been reached (16, 17).

Sauropod dinosaurs are the largest terrestrial animals that have ever lived, and therefore understanding their physiology poses a particular challenge (18). Perhaps the most convincing argument in favor of endothermy in sauropod dinosaurs comes from the analysis of bone histology, which suggests very high growth rates that could not be sustained by a low basal metabolic rate (11, 18–22). Conversely, the case for ectothermy in sauropods has been made by modeling heat exchange by animals with the environment, suggesting that endothermic sauropods would have severe problems with overheating (6, 23–25). Recently, Gillooly et al. presented a biophysical model that is based on allometric scaling laws and dinosaur growth rate analysis, predicting that dinosaur body temperatures would increase as their mass increased, reaching over 40°C for the largest sauropods (9). Such models imply that dinosaurs were ectotherms, but that some dinosaurs would achieve high body temperatures because of their large mass. This phenomenon has been termed "gigantothermy" or "inertial homeothermy" and can be observed in some modern ectotherms, such as leatherback turtles (23, 24, 26). However, this modeling result was not supported by a study on smaller dinosaur taxa that used enamel phosphate oxygen isotope isotopes to reconstruct dinosaur body temperatures of around 33° to 38°C from Cretaceous dinosaurs with body weights spanning the range of 10 to 9000 kg (15).

We applied a different approach to this problem, using clumped isotope thermometry to determine the body temperatures of large Jurassic sauropods by analyzing material from six sites (figs. S1 and S2) (27). This technique is founded on the thermodynamic preference of rare heavy isotopes of carbon (^{13}C) and oxygen (^{18}O) to bond with each other (^{13}C-^{18}O), or "clump," in carbonate-containing minerals (28, 29). Unlike the well-established oxygen isotope thermometer, application of clumped isotope thermometry is not dependent on knowing or assuming the oxygen isotope composition of the water from which a mineral grew (28). The parameter mea-

sured in this approach is the Δ_{47} value [supporting online material (SOM) text] of CO_2 liberated from the carbonate component of tooth bioapatite [generalized as $Ca_5(PO_4, CO_3)_3(OH, CO_3, F, Cl)$] (28). Bioapatite Δ_{47} values follow a temperature dependence indistinguishable from inorganic calcite ($CaCO_3$) over the range of 22° to 37°C, and a theoretical model predicts that this should be the case even over a greater range of temperatures (29). This approach is capable of reconstructing the expected body temperatures of modern and fossil mammals and ectotherms with an accuracy of ~1°C and a precision (1 SE) of 1° to 2°C. Comparison with instrumental measurements of reptile body temperatures indicates that clumped isotope measurements of teeth probably reflect average body temperatures in ectotherms, rather than peak body temperatures (which could be similar to those seen in mammals in some cases) (7, 29, 30).

Fossils of Brachiosaurus brancai [recently assigned to a new genus, Giraffatitan (SOM text)] and a sauropod tentatively identified as being from the subfamily Diplodocinae from the Tendaguru Beds in Tanzania were analyzed, as were fossils of Camarasaurus sp. from five sites in the Morrison Formation (SOM text). A crucial component of our approach was the examination of whether the fossil material preserves primary physiological information or instead reflects isotopic modification during burial alteration. It has been shown that ^{13}C-^{18}O bond ordering can be preserved in the carbonate mineral lattice of calcite much older than Jurassic in age, providing that isotope exchange does not occur with the environment through dissolution/reprecipitation reactions or diffusion (the latter is a factor only at temperatures greater than ~200°C) (31). We focus our interpretations on tooth enamel as the most desirable record of primary growth temperature on the basis of multiple lines of evidence suggesting that the large and closely packed apatite crystals in enamel, as well as its organic-poor nature, can permit the preservation of geochemical signatures even over long time scales (32, 33). We have adopted several approaches to establish the state of preservation of each sample. First, we analyzed dentin from the same teeth, bone, and sparry calcites from each site in order to define diagenetic end-members, with the expectation that well-preserved enamel should yield distinct δ^{13}C and δ^{18}O values when compared with materials that are known to be altered or are secondary precipitates (fig. S3). Because the conditions associated with alteration will likely differ from primary (living body) conditions, the calculated Δ_{47}-based temperatures and water δ^{18}O compositions should also be distinct, barring a fortuitous similarity (fig. S3). Second, we determined phosphate δ^{18}O ($\delta^{18}O_{PO4}$) for each specimen analyzed and compared these values with δ^{18}O values of carbonate in apatite (fig. S4). Because the oxygen isotope composition of phosphate groups is thought to be especially well preserved over geologic time scales, deviations from this offset can be used as

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