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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), paleontological 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 $\text{Ca}_5(\text{PO}_4, \text{CO}_3)_3(\text{OH}, \text{CO}_3, \text{F}, \text{Cl})$] (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 $\sim 1^\circ\text{C}$ 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/precipitation reactions or diffusion (the latter is a factor only at temperatures greater than $\sim 200^\circ\text{C}$) (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 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ 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 $\delta^{18}\text{O}$ compositions should also be distinct, barring a fortuitous similarity (fig. S3). Second, we determined phosphate $\delta^{18}\text{O}$ ($\delta^{18}\text{O}_{\text{PO}_4}$) for each specimen analyzed and compared these values with $\delta^{18}\text{O}$ 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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Table 1. Δ_{47} derived body temperature determinations on well-preserved dinosaur tooth enamel. Number of analyses represent the total number of Δ_{47} measurements made on distinct extractions of CO_2 gas from tooth enamel material from each locality. Values for individual measurements and averages for

Species	Site	Number of analyses*	Δ_{47} [per mil (‰)]	Δ_{47} temperature (°C)
<i>Brachiosaurus brancai</i> , acquisitions from 3 teeth	Tendaguru, Tanzania	5	0.591 ± 0.004	38.2 ± 1.0
Diplodocinae, acquisitions from 2 teeth	Tendaguru, Tanzania	3	0.609 ± 0.017	33.6 ± 4.0
<i>Camarasaurus</i> sp., acquisitions from 3 teeth*	Oklahoma	7	0.596 ± 0.004	36.9 ± 1.0
<i>Camarasaurus</i> sp., acquisitions from 1 tooth†	Howe Quarry, Wyoming	3	0.614 ± 0.010	32.4 ± 2.4
<i>Camarasaurus</i> sp., average acquisitions from 4 teeth‡	Wyoming and Oklahoma	10	0.601 ± 0.005	35.7 ± 1.3

*One of the four specimens from Oklahoma was suspected of alteration and so was excluded from the final body temperature determinations presented here and in Fig. 1. †One of the two tooth specimens from Howe Quarry was suspected of alteration and so was excluded from the final body temperature determinations presented here and in Fig. 1. ‡All of the specimens from the Utah Quarries and Como Bluffs, Wyoming, were suspected of alteration and so were excluded from the final body temperature determinations presented here and in Fig. 1.

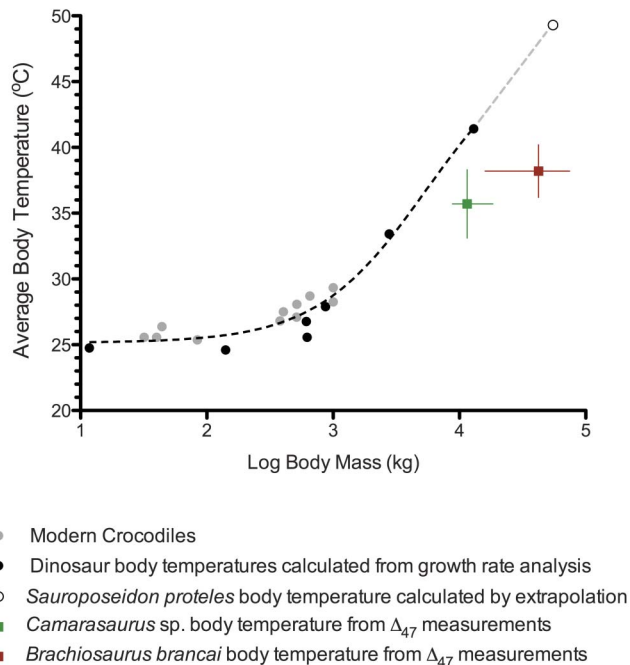
an indicator of alteration of the carbonate component because of reactions with diagenetic fluids (fig. S4). Thin sections of representative tooth samples were also examined petrographically (fig. S5 and SOM text).

On the basis of these parameters, we were able to identify samples that were clearly altered and some samples that appear to be well preserved (table S1 and SOM text). From apparently well-preserved tooth enamel material from the Tendaguru Beds, we measured average body temperatures of $38.2 \pm 1.0^\circ\text{C}$ (1 SE) from three *Brachiosaurus* teeth and $33.6 \pm 4.0^\circ\text{C}$ from two sauropod teeth of a Diplodocinae (Table 1). Three of four *Camarasaurus* teeth analyzed from the Morrison Formation in Cimarron County Oklahoma appeared to be well preserved and yielded an average temperature of $36.9 \pm 1.0^\circ\text{C}$ —a value that decreases slightly to $35.7 \pm 1.3^\circ\text{C}$ when a well-preserved *Camarasaurus* tooth from the Howe Ranch Quarry in Wyoming is included (Table 1). All material from the Utah Quarries and Nail Quarry, Wyoming, appeared to be altered (SOM text). Because their precise taxonomic identification was uncertain and temperature determinations were also relatively uncertain owing to the few measurements that were possible (Table 1), we did not consider data from Diplodocinae in the physiological interpretations of our data (Fig. 1) and instead focused on the more precisely constrained data from *Brachiosaurus brancai* and *Camarasaurus* sp.

In general, body temperatures of vertebrates reflect the combined influences of metabolism, size, environmental temperature, and in some cases, specialized physiological strategies for heat regulation. Therefore, our data taken in isolation are not unambiguous indicators of endothermy versus ectothermy. However, they do place quantitative constraints on sauropod physiology, limiting the range of possible thermoregulatory strategies.

Clumped isotope body temperature determinations from *Brachiosaurus brancai* and *Camarasaurus* sp. are 5° to 12°C higher than those previously measured from modern and fossil crocodiles and alligators, are within error to those measured from modern and fossil mammals (7, 29, 30), but are lower than most modern birds, which often have body temperatures in

Fig. 1. Comparison of measured dinosaur body temperatures to a previously published model calling for scaling of body temperatures with body mass (9). Crocodile data was derived from modern species. Dinosaur body temperature determination from modeling were for the following taxa (in descending mass in this plot); *Sauroposeidon proteles*, *Apatosaurus excelsus*, *Tyrannosaurus rex*, *Daspletosaurus torosus*, *Gorgosaurus libratus*, *Albertosaurus sarcophagus*, *Massospondylus carinatus*, and *Psittacosaurus mongoliensis*. *S. proteles* body temperature was calculated by Gillooly *et al.* from extrapolation of their model rather than directly from growth rates (9). *Camarasaurus* sp. and *Brachiosaurus brancai* (green square and red square, respectively) body temperature determinations from this study are also presented. We have plotted the average of body mass estimates from the literature versus clumped isotope-derived body temperatures for each sauropod. Body mass estimates are taken from the compilation of Sander *et al.* (18). Error bars in the horizontal axis represent the range of estimates of body mass reported in the literature. Vertical error bars represent 2 SE of the clumped isotope temperature determinations.



excess of 40°C (34). This observation should not be taken as a simple indication that sauropods were endothermic, however; our measured temperatures for both *Camarasaurus* sp. and *Brachiosaurus brancai* are lower than those predicted according to the model of Gillooly *et al.*, even when lower estimates of body mass from the literature and the 2 SE range in the clumped isotope measurement are used (Fig. 1) (9). This result cannot easily be explained as an artifact of burial alteration because diagenetically altered enamel material examined in this study consistently records hotter temperatures than that of material that is inferred to be well preserved (fig. S4 and SOM text). Our data probably reflect temperatures of tooth formation. Further work with models and observations will be required to determine whether large thermal gradients could have existed across the large-bodied sauropods, although

this is not observed in our clumped isotope data from modern taxa, in which isotopically determined body temperatures from teeth were in good agreement with expected body temperatures (29). If our temperature determinations are accurate, then in order for sauropod body core temperatures to be similar to those predicted by the model of Gillooly *et al.* there would have to be a 4° to 7°C temperature gradient between the site of tooth formation and the body.

Therefore, the largest sauropods had body temperatures cooler than the Gillooly model suggests. One possible explanation of this result is that adult sauropods had mechanisms to prevent excessively high body temperatures being reached and so could regulate their body temperatures to some extent. For example, they may have had a tracheal surface and air sac system that served as an internal cooling system (35, 36), and their

long necks and tails could have facilitated heat dissipation by increasing their surface area (37). Overall, our data are most consistent with the hypothesis that sauropods sustained high metabolic rates during ontogeny to reach their gigantic size so rapidly, but that in maturity a combination of physiological and behavioral adaptations and/or a slowing of metabolic rate prevented problems with overheating and avoided excessively high body temperatures (18, 36). An unresolved question is whether such adaptations could have compensated for the high internal heat production associated with endothermy, or whether large adult sauropods must have had both heat-dissipating adaptations and a low basal metabolism to maintain body temperatures in the 36° to 38°C range that we have measured.

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Supporting Online Material

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A Common Scaling Rule for Abundance, Energetics, and Production of Parasitic and Free-Living Species

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The metabolic theory of ecology uses the scaling of metabolism with body size and temperature to explain the causes and consequences of species abundance. However, the theory and its empirical tests have never simultaneously examined parasites alongside free-living species. This is unfortunate because parasites represent at least half of species diversity. We show that metabolic scaling theory could not account for the abundance of parasitic or free-living species in three estuarine food webs until accounting for trophic dynamics. Analyses then revealed that the abundance of all species uniformly scaled with body mass to the $-3/4$ power. This result indicates "production equivalence," where biomass production within trophic levels is invariant of body size across all species and functional groups: invertebrate or vertebrate, ectothermic or endothermic, and free-living or parasitic.

General ecological theory should apply to all species, and thus should include the parasites that represent at least half of species diversity (1–3). A goal of the metabolic theory of ecology is to broadly explain and pre-

dict local species abundance by considering how metabolic rate scales with body size and temperature (4, 5). Although studies have documented the scaling of parasite abundance with body size within individual hosts (6, 7), none have examined

the scaling of parasites alongside co-occurring free-living species. This omission is potentially critical because, in addition to their great diversity, there are other factors indicating that the inclusion of parasites can test and refine general rules for abundance and body-size scaling.

Parasites differ from free-living consumers in ways that can violate assumptions made by current models of abundance and diversity. For instance, because parasites are smaller than their hosts, they invert consumer-resource body-size ratios, which are often assumed to be constant and larger than 1 (4, 8–10). Further, parasites might be rarer than other small consumers, as they tend to occupy higher trophic levels to which the flow of resources is constrained by trophic

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