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20. From the Eggers similarity solution, one can show that the Reynolds number is ≈1. This situation is distinct from other models considered (*1*, *12*).
21. Tjahjadi *et al.* (*6*) observed a different hydrodynamic phenomenon that also had a fractal spatial structure. By allowing a stretched drop to relax, they found a sequence of droplets with sizes that decreased in a geometric progression. Our situation differs from theirs in that the repeated formation of necks is a property of the singularity itself and not the result of multiple breakup events.
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Thermophysiology of *Tyrannosaurus rex*: Evidence from Oxygen Isotopes

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The oxygen isotopic composition of vertebrate bone phosphate (δ_p) is related to ingested water and to the body temperature at which the bone forms. The δ_p is in equilibrium with the individual's body water, which is at a physiological steady state throughout the body. Therefore, intrabone temperature variation and the mean interbone temperature differences of well-preserved fossil vertebrates can be determined from the δ_p variation. Values of δ_p from a well-preserved *Tyrannosaurus rex* suggest that this species maintained homeothermy with less than 4°C of variability in body temperature. Maintenance of homeothermy implies a relatively high metabolic rate that is similar to that of endotherms.

Dinosaurs dominated the terrestrial landscape for 163 million years, from their origin in the mid-Triassic to their extinction at the end of the Cretaceous (*1*). Whether they were warm-blooded (tachymetabolic endotherms), cold-blooded (bradymetabolic ectotherms), or something in between (*2*) has been uncertain. A group as successful and diverse as the Dinosauria may have employed a wide range of thermal physiological strategies, some of which are not represented in extant terrestrial vertebrates.

Endothermy is a pattern of thermoregulation in which body temperature depends on a high and controlled rate of metabolic heat production (*3*). In ectothermy, body temperature is dependent on behaviorally and autonomically regulated uptake of heat from the environment. These patterns of thermoregulation are end members along a continuum of physiological strategies. In homeothermy, cyclic body temperature variation, either nyctohemerally or seasonally, is maintained within ±2°C despite much larger variations in ambient temperature (*3*). Large dinosaurs must have grown quickly to reach sexual maturity within an ecologically feasible length of time. The high metabolic rates of endotherms and the high efficiency of energy production of ectotherms are contrasting physiological strategies for solving this problem (*2*). Arguments for particular strategies of thermoregulation have been based on posture, bone histology, predator-prey relations, feeding mechanics, brain size, postulated behaviors, and paleobiogeography. Though innovative, these lines of evidence have ultimately proven to be inconclusive.

In this study, we used the oxygen isotopic composition of bone phosphate (δ_p) to calculate the body temperature variability of *Tyrannosaurus rex*. The phosphate-water isotopic temperature scale was developed for marine invertebrates (*4*) and later confirmed to be accurate for fish (*5*) and mammals (*6*). Vertebrate δ_p is a function of the body temperature at which bone forms and of the isotopic composition of body water (*7*, *8*). The isotopic composition of body water (δ_{bw}) depends on the $\delta^{18}O$ of water ingested during feeding and drinking as well as on the metabolic rate relative to water turnover rates (*8*, *9*). The body water of air-breathing vertebrates is at a physiological steady state but is not in equilibrium with environmental water. Several studies have demonstrated that δ_p is linearly offset from the $\delta^{18}O$ values of the local meteoric water, from the relative humidity, or from the ambient water (in the case of marine mammals) (*10*). Without knowledge of the $\delta^{18}O$ values (*11*) of body water for each fossil species, it is not possible to calculate actual body temperatures. However, all body water compartments in individual mammals have essentially identical $\delta^{18}O$ values (*12*). The variations in δ_p among skeletal elements in an individual should therefore reflect relative differences in body temperature. Temperature differences between the core body (the trunk) and the extremities can be calculated by use of the bone isotopic differences ($\Delta\delta_p$) and the slope of the phosphate-water paleotemperature equation (*4*, *5*).

An assessment of the isotopic integrity of the fossil bone material being examined is crucial for paleophysiological interpretations. We analyzed a *T. rex* specimen from the Maastrichtian Hell Creek Formation for δ_p and for the isotopic composition of both the structural bone carbonate (δ_c) and the coexisting calcite cements (δ_{cc}) (*13*). This specimen was chosen because of its excellent preservation (*14*). Two lines of evidence demonstrated that the bone phosphate analyzed was likely to reflect the original isotopic signal of growth. One test compared δ_p and the isotopic composition of structural carbonate (δ_c) with the isotopic composition of the diage-

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netic calcite cements (δ_{cc}) (Fig. 1). Covariance was strong between δ_c and δ_{cc} ($r = 0.92$), which indicates that the structural carbonate isotopic composition had been diagenetically altered. Covariance with δ_p was weak ($r = 0.17$), which suggests that δ_p was not in equilibrium with the isotopic composition of the diagenetic carbonate and was therefore isotopically unaltered. In addition, an isotopic comparison can be made between the cancellous bone samples and the compact bone samples. Bone mineral fills 10 to 30% of the total volume of cancellous bone and 95% of the total volume of compact bone (*15*). Thus, cancellous bone is more susceptible to diagenetic alteration because its exposed surface area is greater than that of compact bone. Complete equilibration of the whole bone with the ground water had not occurred, as was demonstrated by the isotopic disequilibrium of the phosphate and diagenetic carbonate phases. Diagenesis partially altering δ_p would result in an isotopic offset between cancellous and compact bone, and this is not evident.

We analyzed 54 samples from 12 bones of the Montana *T. rex* for δ_p (Fig. 2). Samples were taken sequentially from the outer dense bone to the inner cancellous bone. The range of δ_p within each skeletal element varied between 0.4 and 0.9 per mil. If this variability were solely a result of fluctuations in body temperature, it would correspond to a range of 1.7° to 3.8°C. Thus, the bone in each skeletal element appears to have been deposited under homeothermic conditions, with the most variability in the legs and dorsal vertebrae and the least variability in the ribs and caudal vertebrae. Intrabone isotopic heterogeneity is also affected by bone resorbtion and redeposition (*16, 17*). In human adults, mean annual remodeling rates can vary between 1 and 10%, depending on bone type and skeletal element (*17, 18*). At these rates, bones are completely replaced in 10 to 100 years. Seasonal effects on δ_p produced by changes in thermoregulation or in body water isotopic composition would be recorded by intrabone heterogeneity.

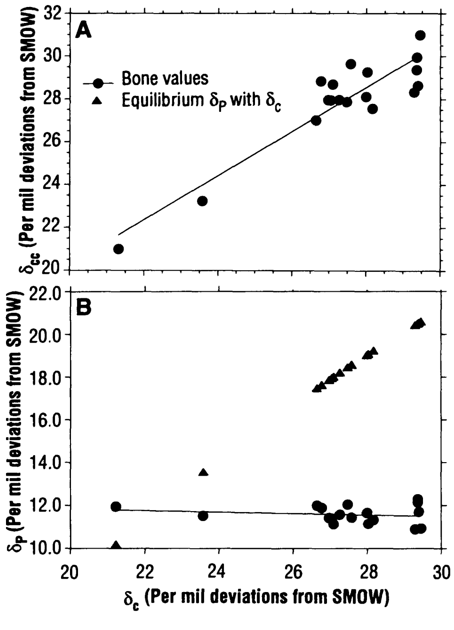

Fig. 1. (**A**) Comparison of the oxygen isotopic composition of the coexisting calcite cements (δ_{cc}) to the oxygen isotopic composition of the structural carbonate (δ_c). (**B**) Comparison of the oxygen isotopic composition of bone phosphate (δ_p) to that of the structural carbonate (δ_c). Triangles represent phosphate isotopic values expected for diagenetically altered bone phosphate in equilibrium with the diagenetic carbonate.

Samples taken across a bone record physiological conditions over time. Homeotherms should have little δ_p variation. Heterotherms should have large δ_p variation, which should not be consistent within different body regions. The largest intrabone δ_p variation in heterotherms should be in the extremities, which lose heat more rapidly than does the core body. Migratory animals should have similar δ_p variability in all bones. Because the intrabone isotopic variation of this *T. rex* specimen is not the same for each skeletal element, it is likely that changes in δ_{bw} were not the only cause of variability. If changes in body temperature had been the sole cause of the intrabone variability, core body temperatures could have fluctuated no more than 3.0°C, whereas temperatures in the extremities could have fluctuated by 3.8°C. Such variability in body temperatures is well within the limits defining homeothermy (*3*). Any part of the intrabone variability that was caused by changes in δ_{bw} would further reduce the possible temperature variation.

Differences in interbone δ_p values can be used to estimate average temperature differences between skeletal elements. To account for the effects of remodeling, we averaged the replicate data for each skeletal element. The overall body temperature variation between skeletal elements for this *T. rex* was 4.2°C, which is within ±0.1°C of the variation specified in the definition of homeothermy (Fig. 3). The warmest bones (those most isotopically negative) were from the core body (ribs and dorsal vertebrae), whereas the coldest bones were from the extremities (leg and foot bones and distal caudal vertebrae) and from one of the gastralia (stomach ribs). The proximal caudal vertebra yielded temperatures as warm as those for the core body, whereas the more distal bones yielded progressively cooler temperatures. The temperature difference between the core body and the legs was the same as that between the core body and the tail.

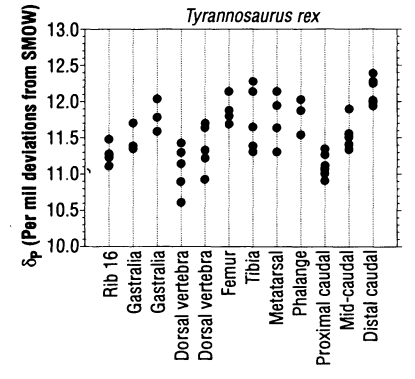

Fig. 2. The δ_p values for each skeletal element that was analyzed, plotted from anterior to posterior.

The δ_p data suggest that the Montana *T. rex* was definitely a homeotherm, but was this a result of endothermy or of mass homeothermy? Large ectotherms such as leatherback turtles are capable of maintaining core body temperatures above the ambient temperature in cold environments by countercurrent heat exchange mechanisms (*19*). The thermal differences between the core body and the extremities of the *T. rex* suggest that it also may have used heat exchange. However, if *T. rex* were a mass homeotherm in a seasonally cold environment, countercurrent heat exchange would have been expected to produce a more pronounced difference in temperature between the extremities and the core body as well as greater temperature variations in the extremities than were measured. In environments where there is little seasonal temperature variation, large ectotherms should be able to maintain homeothermy with this mechanism. In especially warm climates, heat dumping would be a greater problem than heat retention (*20*). The climate was warmer in the Cretaceous than it is at present because of larger amounts of atmospheric CO_2 (*21*). However, global climate model calculations also suggest that mid-continent seasonality was high during the Cretaceous (*22*). Leaves from the lower Hell Creek Formation (which was at ~53°N latitude) suggest mean annual tem-

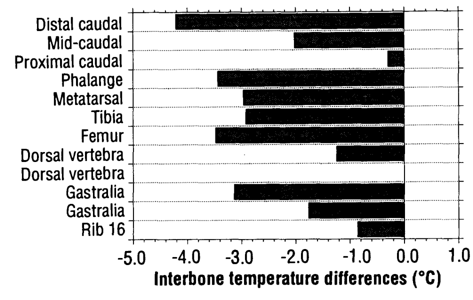

Fig. 3. Body temperature differences between each skeletal element and the warmest bone in the body core. Replicate analyses were averaged and the temperature differences were calculated from mean values.

peratures of ~11° to 13°C, though seasonal temperature variability is unclear (*14, 23*). Physiological models for a 5000-kg bradymetabolic hadrosaur predict that annual core body temperature variation would be large (~20°C, which is equivalent to a 4.5 per mil δ_p variation) in a simulated Cretaceous environment, though monthly temperature variability would be small (1° to 3°C) (*24*). A minimum isotopic variability of 3.5 per mil (15°C) is suggested even if individuals were capable of always maintaining body temperatures above 20°C, the minimum temperature at which most extant ectotherms can digest food. Because of its similar size (~6000 kg) (*14*), temperature variability should be similar in a bradymetabolic *Tyrannosaurus*. The small intrabone δ_p variation indicates that this *T. rex* was not an ectotherm. The lack of increased intrabone variation in the limbs and tail and the small interbone variation suggest that this *T. rex* was also not a mass homeotherm using heat exchange mechanisms to dump heat through the extremities during warm periods and retain core body heat during colder periods. However, if it can be shown that there was little seasonal temperature variability (that is, less than 8° to 10°C) during early Hell Creek time, then mass homeothermy remains a valid interpretation of the data.

Because this *T. rex* does not have either large intrabone or interbone δ_p variability, we conclude that it was a nonmigratory endotherm. The metabolism of *T. rex* may or may not have been as high as that of modern endotherms, but it was high enough that body temperatures were largely maintained by a controlled metabolic rate, unlike the metabolism of modern ectotherms. The difference in metabolic rates for ectotherms and endotherms narrows at larger sizes (*25*), but the difference is still important when extrapolated to weights of 6 or 7 tons. It is therefore likely that *Tyrannosaurus* metabolic rates were closer to those of a modern 6-ton endotherm (such as a bull African elephant) than to those of a postulated 6-ton ectotherm. Metabolic rates may, however, have undergone seasonal shifts (*2*) in order to maintain homeothermy. Endothermy would have allowed tyrannosaurs the aerobic stamina (*26*) to be active predators or scavengers (or both) that were independent of ambient temperature fluctuations.

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The Role of the Tropical Super Greenhouse Effect in Heating the Ocean Surface

Dan Lubin

Measurements made by a Fourier transform infrared (FTIR) spectroradiometer operating in the middle infrared (5 to 20 micrometers, with a spectral resolution of one inverse centimeter) imply that there is an anomalously large greenhouse effect over equatorial oceans that is caused by water vapor. As sea-surface temperature increased from 297 to 303 degrees kelvin, the net infrared cooling at the surface decreased by 30 to 50 watts per square meter. Thus, according to the FTIR data, the super greenhouse effect that had been inferred from satellite measurements contributes directly to radiative heating of the sea surface. The data demonstrate that most of this heating occurs in the middle infrared by means of the continuum emission window of water vapor and that tropical deep convection contributes substantially to this super greenhouse effect.

The western tropical Pacific Ocean has the hottest sea-surface temperatures and the largest burden of tropospheric water vapor in the world. Thus, greenhouse forcing by water vapor might be expected to be greatest there. Two major international experiments were conducted from late 1992 to early 1993 (*1*), whose object was to evaluate the climate feedbacks in the region.

In the western tropical Pacific, sea-surface temperature rarely exceeds 303 K (*2*). This upper limit is most apparent in regions of extensive convection (*3*). Ramanthan and

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