

# Multiple taxon–multiple locality approach to providing oxygen isotope evidence for warm-blooded theropod dinosaurs

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## ABSTRACT

Oxygen isotope ratios of fossil remains of coexisting taxa from several different localities can be used to help investigate dinosaur thermoregulation. Focusing on the Late Cretaceous, oxygen isotope ratios of crocodile tooth enamel from four separate localities exhibit less of a decrease with latitude than do ratios of tooth enamel from coexisting theropod dinosaurs. A shallower latitudinal gradient for crocodiles is consistent with how oxygen isotope ratios should vary for heterothermic animals having body temperatures coupled with their environments ("cold blooded"), while a steeper gradient for theropods is consistent with how these ratios should vary for homeothermic animals having constant body temperatures independent of their environments ("warm blooded"). This inferred homeothermy in theropods is likely due to higher rates of metabolic heat production relative to crocodiles and is not an artifact of body size.

**Keywords:** thermoregulation, dinosaur, oxygen isotopes, phosphate.

## INTRODUCTION

Despite several decades of study, the paleobiological particulars of dinosaurian thermoregulation have remained enigmatic. Among extant vertebrates, the thermoregulatory strategies of reptiles, on one hand, and birds and mammals, on the other, have long served as a basis for elucidating dinosaurian function. Reptiles are characterized by low rates of metabolic heat production and a reliance on external heat sources to maintain body temperatures (bradythermic ectothermy), and there is typically a daily to seasonal covariance between environmental and body temperatures ("cold-blooded" heterothermy). In contrast, birds and mammals maintain higher rates of metabolic heat production (tachythermic endothermy), and this allows their body temperatures to remain relatively constant ( $\pm 2$  °C) regardless of changes in environmental temperature with season or geographic location ("warm blooded" homeothermy). It is also possible that large dinosaurs had low metabolic rates similar to those of reptiles, but were able to maintain relatively constant body temperatures at any given location as a result of body size (gigantothermy; Paladino et al., 1989; Spotila et al., 1991; O'Connor and Dodson, 1999), or that some dinosaur groups may have had metabolic rates and body temperatures intermediate between those of reptiles and birds and/or mammals (Greenberg, 1980).

## STRATEGY

Conclusive evidence relating to the above hypotheses has been difficult to obtain via traditional analyses of fossil remains. Even cases of exceptionally preserved internal organs (Ruben et al.,

1999; Fisher et al., 2000) have led to differing interpretations of dinosaur physiology, and thus the nature of their thermoregulation remains elusive. A fundamentally different way to address this question is to measure the oxygen isotope ratio ( $\delta^{18}\text{O} = [(^{18}\text{O}/^{16}\text{O})_{\text{sample}} / (^{18}\text{O}/^{16}\text{O})_{\text{standard}}] \times 1000$ ) of phosphate found in vertebrate fossils themselves. Tooth enamel and bone are composed of apatite, and oxygen bound to phosphorus in this mineral is resistant to isotopic exchange during diagenesis (Kolodny et al., 1983). More important is that oxygen isotope ratios can be used to make inferences about the body temperatures at which the phosphate formed. These characteristics were first explored by Barrick and Showers (1994, 1996), who used  $\delta^{18}\text{O}$  values of phosphate in bone apatite to provide evidence for seasonal homeothermy in theropods from a locality in Montana.

Here we report a new, independent way in which oxygen isotope ratios of biogenic phosphate can be used to delineate the thermoregulatory strategies of extinct terrestrial vertebrates. In this case, ratios are measured from phosphate in tooth enamel ( $\delta^{18}\text{O}_{\text{ep}}$ ) rather than bone. However, the most unique aspect of this research is that  $\delta^{18}\text{O}$  values of fossil teeth are compared among a suite of localities to create a broad latitudinal framework of isotopic data. This comparative strategy is advantageous because the way in which  $\delta^{18}\text{O}$  of enamel phosphate varies with latitude is predicted to depend on taxon-specific thermoregulation strategies.

In general,  $\delta^{18}\text{O}$  of precipitation decreases regularly from the equator to the poles due to changes in mean annual temperature (MAT; Dansgaard, 1964). Animals ingest water from surface reservoirs, such as streams, ponds, and plants, that have an ultimate source in local

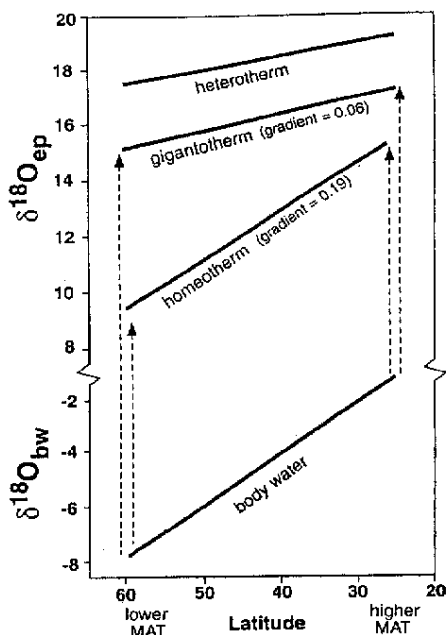
precipitation, with the result that the  $\delta^{18}\text{O}$  of body water for all animals also decreases with increasing latitude (Fig. 1). What is most important to consider, however, is the temperature dependency of oxygen isotope fractionation (Longinelli and Nuti, 1973) that occurs during the subsequent precipitation of enamel phosphate from the body water of an animal. Because of this dependency, the way in which animals regulate their body temperatures relative to the local environment has a strong influence on the way in which  $\delta^{18}\text{O}_{\text{ep}}$  decreases with latitude.

For example, ideal endothermic homeotherms presumably have a constant body temperature regardless of location and/or latitude, and therefore oxygen isotope fractionations will be constant (Fig. 1). If we use a body temperature of 38 °C, the result is a  $\delta^{18}\text{O}_{\text{ep}}$ -latitude relation for the present day with a slope of 0.19‰/lat (Fig. 1), which is consistent with empirical data for mammals and birds (Kohn, 1996). In contrast, body temperatures of ideal ectothermic heterotherms are assumed to mirror those of their environment, and therefore mean annual temperature, at a given latitude. The resulting  $\delta^{18}\text{O}_{\text{ep}}$ -latitude gradient is shallower than the one for endothermic animals, because oxygen isotope fractionation is smaller at higher temperatures relative to cooler temperatures (Fig. 1).

In the case of gigantotherms, it is more difficult to estimate body temperatures and hence predict the nature of the  $\delta^{18}\text{O}_{\text{ep}}$ -latitude relation. Thermoregulatory models suggest that gigantothermy has the potential to produce seasonally constant body temperatures that are greater than ambient conditions at any given location (e.g., Paladino et al., 1989; Spotila et al., 1991; O'Connor and Dodson, 1999). The degree to which gigantothermy can modify body tem-

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Figure 1. Decrease in  $\delta^{18}\text{O}$  of enamel phosphate for animals with different thermoregulatory strategies predicted using present-day mean annual temperature (MAT) and isotopic data. Body water  $\delta^{18}\text{O}$  (lower part of figure,  $\delta^{18}\text{O}_{\text{bw}}$ ) is first determined by combining the observed decrease in  $\delta^{18}\text{O}$  of precipitation over middle latitudes (Dansgaard, 1964) with physiological model that accounts for fluxes and fractionations of oxygen into and out of body of animal (Kohn, 1996). Resulting relations between  $\delta^{18}\text{O}_{\text{bw}}$  and  $\delta^{18}\text{O}$  of precipitation are not one to one (Kohn, 1996), but they are predicted to have similar slopes of  $-0.75$  regardless of type of animal, and here we use relation for mammalian herbivores ( $\delta^{18}\text{O}_{\text{bw}} \sim [0.74] \cdot \delta^{18}\text{O}_{\text{pl}} + 2.47$ ) to represent generalized terrestrial animal (Kohn, 1996). Using these  $\delta^{18}\text{O}$  values of body water, we then calculate  $\delta^{18}\text{O}$  of enamel phosphate ( $\delta^{18}\text{O}_{\text{ep}}$ ) for heterothermic, homeothermic, and gigantothermic animals using body temperatures as described for each in text (upper part of figure). In case of heterotherms, note how isotopic fractionation between phosphate and water (dashed lines) increases as MAT decreases, while for homeotherms isotopic fractionation remains constant regardless of MAT. As result, homeotherms have steeper  $\delta^{18}\text{O}_{\text{ep}}$ -latitude gradient.



peratures, however, depends in part on the radiative input of heat via solar insolation, and both solar insolation and MAT decrease with latitude. Therefore latitudinal changes in the body temperatures of gigantothermic animals should remain coupled to changes in MAT, even if the two temperatures are not identical (O'Connor and Dodson, 1999). Body temperatures of gigantotherms are thus assumed to be 10 °C higher than MAT at each latitude. The resulting  $\delta^{18}\text{O}_{\text{ep}}$ -latitude relation has a slope that is the same as that for ectotherms, but with lower  $\delta^{18}\text{O}_{\text{ep}}$  values because of the higher body temperatures and/or smaller isotopic fractionation (Fig. 1).

It is important to note that these different  $\delta^{18}\text{O}_{\text{ep}}$ -latitude relations depend primarily on differences in thermoregulation. As a result, they should remain detectable even if latitudinal gradients in MAT and  $\delta^{18}\text{O}$  of precipitation change over time.

#### SAMPLES

In this study we characterize the thermoregulatory strategies of extinct taxa by comparing isotopic data obtained from fossil samples with the preceding predictions. Teeth of theropod dinosaurs and coexisting crocodiles from six different formations in North America, Madagascar, and India are used to construct latitudinal gradients in  $\delta^{18}\text{O}_{\text{ep}}$ . The North American localities (Judith River Formation, Montana; Aguja Formation, Texas; Dinosaur Park Formation, Alberta; Prince Creek Formation, Alaska) can all be placed in the late Campanian to early Maastrichtian (Conrad et al., 1990; Rowe et al., 1992; Eberth and

Hamblin, 1993; Rogers et al., 1993). Until recently, the Maevarano Formation of Madagascar was also considered to be Campanian, but new stratigraphic data indicate that upper reaches of the unit are most likely Maastrichtian (Rogers et al., 2000). The Lameta Formation of India is also Maastrichtian in age (Khajuria et al., 1994).

The teeth used in this analysis were collected as isolated specimens from localities spanning narrow stratigraphic intervals within each formation. The paleoenvironments of the sampled localities are broadly similar, representing fluvial and floodplain settings likely characterized by seasonal fluctuations in precipitation. Sedimentological data suggest that the Maevarano Formation may have been deposited under somewhat more arid conditions than the other units (Rogers et al., 2000). The theropods analyzed range from the small to intermediate body sizes of *Spotilia* et al. (1991). There is no indication that any of the crocodilians used in this study ventured from the terrestrial settings where their fossils were recovered.

Because of the small size of the teeth, isotopic measurements were made by removing all of the enamel on a tooth and analyzing it using a method of graphite reduction (O'Neil et al., 1994). Not all theropod teeth from Texas were large enough to analyze in this manner, and an ultraviolet laser-based microanalytical technique was used in two cases (Jones et al., 1999; Table 1 here).

#### DIAGENESIS AND LATITUDINAL GRADIENTS

Isotopic exchange and secondary precipitation of apatite during diagenesis are important

TABLE 1. OXYGEN ISOTOPE RATIOS OF TOOTH ENAMEL FOR CROCODILES AND THEROPOD DINOSAURS

Sample	$\delta^{18}\text{O}_{\text{ep}}$	Avg. $\delta^{18}\text{O}_{\text{ep}}$
Madagascar (~30°S)		
Crocodile -1	20.2	20.9 ± 0.5
Crocodile -2	21.2	
Crocodile -3	21.1	
Theropod -1	21.6	21.5 ± 1.6
Theropod -2	23.2	
Theropod -3	23.2	
Theropod -4	20.2	
Theropod -5	19.6	
Texas (~40°N)		
Crocodile -1	16.8	16.8 ± 0.2
Crocodile -2	17.1	
Crocodile -3	16.7	
Crocodile -4	16.7	
Theropod -1*	17.0	17.6 ± 0.7
Theropod -2*	18.3	
Theropod -4	17.5	
Montana (~55°N)		
Crocodile -1	14.7	14.7 ± 0.8
Crocodile -2	16.2	
Crocodile -3	15.4	
Crocodile -4	14.1	
Crocodile -5	14.7	
Crocodile -6	15.0	
Crocodile -7	14.9	
Crocodile -8	13.4	
Crocodile -9	14.1	
Theropod -1	12.9	13.5 ± 1.2
Theropod -2	12.5	
Theropod -3	13.5	
Theropod -4	13.1	
Theropod -5	14.8	
Theropod -6	11.8	
Theropod -7	15.4	
Theropod -8	14.1	
Alberta (~60°N)		
Crocodile -1	13.9	14.2 ± 0.6
Crocodile -2	13.6	
Crocodile -3	14.6	
Crocodile -4	14.7	
Crocodile -5	11.6	
Theropod -1	11.6	12.8 ± 0.7
Theropod -2	13.2	
Theropod -3	12.6	
Theropod -4	13.0	
Theropod -5	13.4	
Alaska (~75°N)		
Theropod -1	10.2	10.2 ± 0.7
Theropod -2	9.8	
Theropod -3	10.4	
Theropod -4	10.2	
India (~30°S)		
Crocodile -1	17.2	16.9 ± 0.2
Crocodile -2	17.0	
Crocodile -3	16.6	

Note: All samples were analyzed using the method of O'Neil et al. (1994) except where noted by an asterisk. Montana, Alberta, and Alaska theropods are classified as *Albertasaurus*, Madagascar theropods as *Majungatholus*, and Texas theropods as the smaller taxon *Saurornitholestes*. Crocodilian taxa are not resolved to lower taxonomic levels. Approximate paleolatitudes are from Scotese (1999) and are shown in parentheses.

concerns when analyzing fossil samples from the Late Cretaceous. Unfortunately, there are no methods of demonstrating conclusively whether these processes have affected  $\delta^{18}\text{O}_{\text{ep}}$  values. In general, oxygen in phosphate should not undergo isotopic exchange as a result of inorganic processes (Kolodny et al., 1983), and the crystals of apatite that make up tooth enamel are large and densely packed. This arrangement greatly reduces the surface area available for interaction with diagenetic fluids and for the secondary pre-

precipitation of apatite. More specifically, the data from each locality indicate that primary oxygen isotope ratios are preserved by enamel phosphate. In each case there is a measurable difference in average  $\delta^{18}\text{O}_{\text{ep}}$  between theropod and crocodile teeth (Fig. 2). These isotopic offsets between taxa would not occur if isotopic alteration was extensive, because isotopic exchange with groundwaters or secondary precipitation of apatite during diagenesis would result in uniform  $\delta^{18}\text{O}$  values of phosphate. Thus, the existence of these offsets provides the most concrete evidence for preservation of primary isotopic information in these late Mesozoic enamel samples. Similar offsets have also been observed for early Cenozoic samples (Fricke et al., 1998).

Considering the data from a more global standpoint, the  $\delta^{18}\text{O}$  of enamel phosphate for both dinosaurs and crocodiles decreases from lower to higher paleolatitudes (Fig. 2), as observed in the teeth of modern animals (Kohn, 1996). These data provide evidence that both  $\delta^{18}\text{O}$  of precipitation and temperature decreased with latitude during the Late Cretaceous. Of particular note, however, is the shallower gradient in  $\delta^{18}\text{O}_{\text{ep}}$  for crocodiles relative to theropod dinosaurs (Fig. 2). Closer to the equator, crocodiles have lower  $\delta^{18}\text{O}_{\text{ep}}$  values than theropods regardless of taxon, hemisphere, or inferred environmental setting, while at higher latitudes  $\delta^{18}\text{O}_{\text{ep}}$  of crocodiles is higher than that of theropods at two different North American localities. Regression lines for the theropod and crocodile data and confidence intervals for the slopes (Fig. 3) indicate that the taxa define two statistically different  $\delta^{18}\text{O}_{\text{ep}}$ -latitude relations.

There are several ecological, environmental, and sampling biases that could cause isotopic offsets between theropods and crocodiles at any given locality, but none are likely to explain different latitudinal gradients in  $\delta^{18}\text{O}_{\text{ep}}$  for each animal. For example, different habitats or different mechanisms of heat loss and efficiency of water use may have resulted in an offset in average  $\delta^{18}\text{O}_{\text{ep}}$  between theropods and crocodiles at any given locality, but these offsets should be systematic. Therefore, they cannot account for crocodiles having higher  $\delta^{18}\text{O}$  values than theropods in some cases but not in others. Finally, local differences in environmental conditions might impact  $\delta^{18}\text{O}_{\text{ep}}$  values across taxonomic lines, but they cannot account for different isotopic offsets between theropods and crocodiles at different localities. Support for this idea comes from the higher  $\delta^{18}\text{O}_{\text{ep}}$  values of Madagascar theropods and crocodiles relative to those from Texas, which probably reflects higher  $\delta^{18}\text{O}$  values of surface waters associated with more arid conditions (Dansgaard, 1964). Because  $\delta^{18}\text{O}_{\text{ep}}$  of both theropods and crocodiles are affected by aridity, this type of environmental factor cannot account for crocodiles having higher  $\delta^{18}\text{O}$  values than theropods in some cases but not in others. Finally, the  $\delta^{18}\text{O}$  of enamel

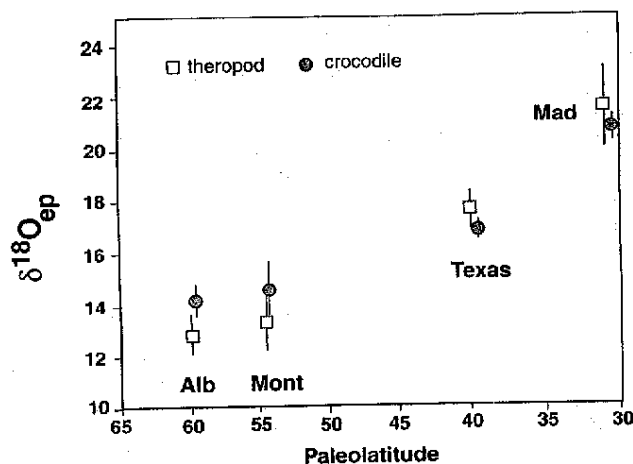
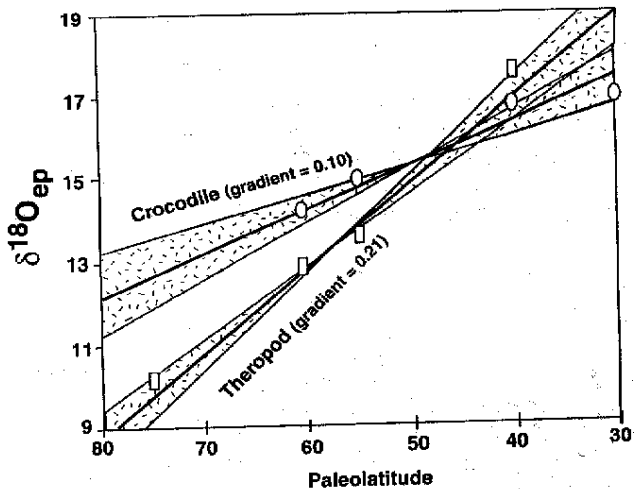


Figure 2. Average  $\delta^{18}\text{O}$  of enamel phosphate ( $\delta^{18}\text{O}_{\text{ep}}$ )  $\pm 1\sigma$  for crocodile and theropod teeth versus absolute paleolatitude for localities where both taxa are present. Alb—Alberta, Mont—Montana, Mad—Madagascar.

Figure 3. Regression lines for  $\delta^{18}\text{O}$  of enamel phosphate ( $\delta^{18}\text{O}_{\text{ep}}$ ) of theropods and crocodiles (excluding arid Madagascar locality) along with 95% confidence intervals for slopes and average  $\delta^{18}\text{O}_{\text{ep}}$  values from Table 1. Gradient for theropod dinosaurs, significantly steeper than that for coeval crocodiles, is similar to that of modeled homeotherms. Even if only North American localities are considered, the two lines are still significantly different (85% confidence). Latitudinal gradient in  $\delta^{18}\text{O}_{\text{ep}}$  for Cretaceous crocodiles is slightly steeper than predicted for



present-day ectotherms or gigantotherms (Fig. 1) because the decrease in MAT with latitude was less during Cretaceous time than it is now (Wolfe and Upchurch, 1987). As a result, isotopic fractionation between crocodile body water and tooth enamel at higher latitudes would have been smaller during Cretaceous time. Theropod  $\delta^{18}\text{O}_{\text{ep}}$  values are higher than predicted for present-day homeotherms (Fig. 1) because  $\delta^{18}\text{O}$  of precipitation was likely different at those times from that of present. In addition, exact body temperatures maintained by theropod dinosaurs may have been lower than body temperatures of mammals and birds. Lower theropod body temperatures would result in greater isotopic fractionation between their body water and tooth enamel (Longinelli and Nuti, 1973).

phosphate reflects only the  $\delta^{18}\text{O}$  of local precipitation during the time period over which the enamel was forming. This period may be as short as several months (Erickson, 1997), and the  $\delta^{18}\text{O}$  of precipitation can vary seasonally (Dansgaard, 1964); thus, it is possible that some of the observed isotopic offsets are due to a biased sampling of teeth formed during different parts of the year. What makes this possibility unlikely is the random selection of specimens for this study that represent teeth formed and replaced throughout the lifetime of the animals.

#### WARM-BLOODED THEROPODS

Given what is currently known or inferred about the taxa in question, the best explanation for different latitudinal gradients in  $\delta^{18}\text{O}_{\text{ep}}$  is that crocodiles and theropod dinosaurs relied on dif-

ferent thermoregulatory strategies. Extant crocodiles are ectothermic and/or gigantothermic reptiles that are unable to maintain a uniform body temperature at different latitudes. As expected from Figure 1, this taxon has a shallower  $\delta^{18}\text{O}_{\text{ep}}$ -latitude gradient, which is consistent with such heterothermy. In contrast to that for crocodiles, the slope of the  $\delta^{18}\text{O}_{\text{ep}}$ -latitude relation for theropod dinosaurs is steeper, and is almost identical to that modeled for present-day homeotherms such as mammals and birds (Fig. 3). This steeper slope indicates that theropods were not heterothermic reptiles or gigantotherms, but were instead true homeotherms able to maintain a constant body temperature regardless of latitude. This result is consistent with previous oxygen isotope studies of theropod dinosaur bone (Barrick and Showers, 1994, 1996).

If the theropods studied here were able to maintain relatively constant body temperatures at any given latitude, then it follows that they had higher rates of metabolic heat production than coeval crocodiles. As in the case of mammals or birds, these higher metabolic rates would be necessary in order to decouple theropod body temperatures from those of the ambient environment at different latitudes, especially for those taxa of small to intermediate body sizes. Therefore it seems most appropriate to consider theropod dinosaurs endothermic animals having metabolic rates distinctly higher than those found in ectothermic reptiles. Because tooth enamel growth appears to occur over regular daily intervals (Erickson, 1997), this inferred endothermy probably represents resting, or routine, metabolic conditions.

Our isotopic evidence for endothermic homeothermy is at odds with recent studies that argue for more reptile-like rates of metabolism in some theropod dinosaurs. An endothermic theropod with high metabolic heat production would require a greater physiological intake of oxygen and water, and recent studies of well-preserved fossils indicate that theropod lung and nasal structures may have been less efficient than those in birds and mammals (Ruben et al., 1996, 1999). As a result, it has been suggested that theropod dinosaurs most likely maintained routine metabolic rates that were similar to ectotherms except for brief periods of much higher metabolic activity (Ruben et al., 1999). This physiological evidence, however, does not definitively exclude the possibility of theropods having higher routine metabolic rates than ectothermic reptiles (Ruben et al., 1996). Therefore, one way in which the isotopic and physiological data can be reconciled is if theropod dinosaurs had routine metabolic rates higher than those of ectothermic reptiles, but lower than those of extant endotherms such as mammals and birds of comparable size. More data are needed to test this hypothesis.

## CONCLUSIONS

A comparison of oxygen isotope data from different taxa and different latitudes indicates that theropod dinosaurs from the Late Cretaceous regulated their body temperatures differently from coeval crocodiles, and that theropods were endothermic to at least a certain degree. More generally, these results demonstrate the tremendous potential of this isotopic method of studying thermoregulation. A wide array of dinosaur taxa, including early birds, and other extinct groups such as therapsida, can be studied using these methods, and the same techniques can be applied to other intervals of the Mesozoic. Comparative studies of oxygen isotope data thus offer a unique way of investigating the evolution of vertebrate thermal physiology.

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