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A Biophysical Analysis of Possible Thermoregulatory Adaptations in Sailed Pelycosaurs

In: *The Ecology and Biology of Mammal-like Reptiles*. Nicholas Hotton III, Paul D. MacLean, Jan J. Roth and E. Carol Roth (eds.). Smithsonian Institution Press, Washington, D.C. 1986. pp. 195-206.

Introduction

The spectacular dorsal sails of some members of the synapsid order Pelycosauria have placed these animals among the most easily recognized of fossil tetrapods. Not surprisingly, these structures have generated much conjecture regarding their function. The large surface area of the sail is suspected to have been useful in temperature regulation—specifically in increasing rates of heat gain and loss (Romer, 1948), 1966; Bramwell and Fellgett, 1973; Spotila, 1980). However, it has also been suggested that the sail could have been used in intraspecific displays (Bakker, 1971).

Although a direct resolution of the function of a sail is impossible, we can apply biophysical models of heat transfer to analyze the conditions under which a sail might have functioned in thermoregulation. With the advanced sphenacodont pelycosaur *Dimetrodon* as an example, specific questions to be entertained are: Does the sail play a role in promoting homeothermy? How do body size, body form, and sail size interact to determine the body temperature at which *Dimetrodon* habitually may have regulated? What bearing does thermoregulation in *Dimetrodon* have on the ultimate attainment of endothermic homeothermy by early mammals?

Regulation of Heat Exchange in Reptiles

Modern reptiles are known for their ability to control heat exchange with the environment,

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and hence body temperature, by behavioral mechanisms such as regulating time of activity, microhabitat selection, basking, and postural orientation with respect to the sun or wind (Cowles and Bogert, 1944); Bogert, 1949; Brattstrom, 1965; Health, 1965; Huey and Pianka, 1977; Muth, 1977; James and Porter, 1979; Huey, 1982). Reptiles also supplement behavioral adjustments with sophisticated physiological adjustments that influence rates of heat exchange by altering distributions of blood flow within the body, evaporative heat loss through panting, and control of body color (Cowles, 1958; Bartholomew and Lasiewski, 1963; Bartholomew and Tucker, 1963; Norris, 1967; Baker and White, 1970; Weathers, 1970, 1971; Weathers and White, 1971; Smith, 1979; White, 1976; Voight and Johnson, 1977; Grigg, Drane, and Courtice, 1979). Indeed, except for a few very small species, reptiles use this physiological control so that the rates at which they cool are almost always lower than the rates at which they warm (Fig. 1; Table 1).

Difference in rates of warming and cooling have been explained as resulting from control of blood flow between the core and skin of the torso of an animal (Cowles, 1958). Subsequently, it has been argued on theoretical grounds that blood flow to the appendages is probably more important in controlling heat exchange than is blood flow between the core and skin of the torso (Turner, in press). Empirical evidence from *Alligator*, and from two genera of lizards, support this hypothesis (Turner, Hamond, and Tracy, 1980; Turner and Tracy, 1983; Turner, unpublished data). These recent findings, combined with morphological evidence that the sails of pelycosaurs were well supplied with blood (Romer and Price, 1940), feed the suspicion that pelycosaur sails—in essence, accessory heat exchangers—had an important role in thermoregulation.

The size of a reptile influences its heat exchange with the environment. For example, very large reptiles have capacities for storage of thermal energy, and, consequently, fluctuations in their body temperatures are invariably smaller than fluctuations in the thermal environment; this has been called "inertial homeothermy" (McNab, 1978; Spotila, 1980). Additionally, large reptiles can control thermal exchange with the environment by shunting heat around their bodies by varying the distribution of blood flow (Turner and Tracy, this volume). In contrast, very small reptiles have small capacities for storage of thermal energy and, therefore, a limited

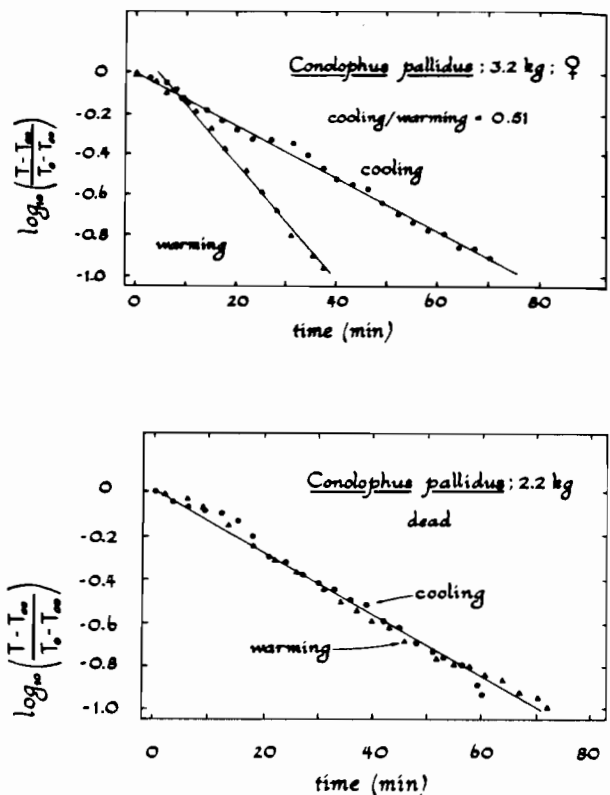


Figure 1. The body temperatures of Galapagos land iguanas (*Conolophus pallidus*) while cooling and warming in a water bath. Top: cooling and warming curves for a 3.2 kg female; bottom: cooling and warming curves for a 2.2 kg dead lizard. (Tracy and Christian, unpublished data.)

Key: T = cloacal temperature, T_0 = body temperature at the beginning of the temperature transient, T_{∞} = equilibrium body temperature at any time during the transient.

ability to regulate heat exchange within the body; they must rely primarily upon behavioral adjustments to restrict fluctuations in body temperature. Between extremes of size, reptiles can effectively use both behavioral and physiological mechanisms to regulate body temperature.

Homeothermy

Recent studies (Christian, Tracy, and Porter, 1983) have suggested that homeothermy, per se, plays an important role in the animal's life history. Indeed, actual body temperature may be less important than the ability to maintain a given body temperature for a long period of time (Christian, Tracy, and Porter, 1983). This suggests that selection favors homeothermy. While hypotheses have been advanced to explain the advantage of homeothermy (Alexandrov, 1967; Prosser, 1973; Hochachka and Somero, 1973; Heinrich, 1977; Else and Hulbert, 1981), the

Table 1.—Ratios of cooling to warming in some lizards

<i>Species</i>	<i>Mass(kg)</i>	<i>Cooling/warming</i>	<i>Source</i>
Varanidae			
<i>Varanus acanthurus</i>	0.016	1.13	(a)
<i>Varanus gouldii</i>	0.094	0.94	(a)
<i>Varanus gouldii</i>	0.144	0.83	(a)
<i>Varanus punctatus</i>	0.186	0.94	(a)
<i>Varanus varius</i>	0.735	0.74	(a)
<i>Varanus gouldii</i>	0.736	0.85	(a)
<i>Varanus varius</i>	0.774	0.85	(a)
<i>Varanus gouldii</i>	1.060	0.72	(a)
<i>Varanus varius</i>	4.008	0.89	(a)
Agamidae			
<i>Amphibolurus barbatus</i>	0.294	0.74	(b)
<i>Amphibolurus barbatus</i>	0.520	0.76	(b)
Teiidae			
<i>Cnemidophorus sexlineatus</i>	0.005	0.80–1.01	(c)
Iguanidae			
<i>Sceloporus undulatus</i>	0.010	0.73–0.80	(c)
<i>Dipsosaurus dorsalis</i>	0.050	0.75	(d)
<i>Amblyrhynchus cristatus</i>	0.652	0.50	(e)
<i>Amblyrhynchus cristatus</i>	1.360	0.55	(e)
<i>Conolophus pallidus</i>	3.200	0.51	(f)
<i>Conolophus pallidus</i>	2.900	0.53	(f)

(a) Bartholomew and Tucker, 1964; (b) Bartholomew and Tucker, 1963; (c) McKenna and Packard, 1975; (d) Turner *et al.*, unpublished; (e) Bartholomew and Lasiewski, 1965; (f) Tracy and Christian, unpublished data.

principal advantage is probably biochemical conservatism. In the animal that maintains body temperature within narrow limits, biochemical function can specialize for greater efficiency within those limits than at other temperatures. Such an animal has an advantage, at its preferred temperature, over another with a more elaborate biochemical makeup, which, though effective over a broad spectrum of temperatures, may be especially efficient at none. Specialization for high efficiency in a narrow range of temperatures presumably requires but a single set of isozymes, and avoids the genetic and developmental expense of producing multiple sets to accommodate a broad range of body temperatures. In any case, constancy of body temperature is such a common pattern in nature that it would be difficult to dispute that it has adaptive value (Cowles and Bogert, 1944; Bartholomew and Tucker, 1963; MacKay, 1964; Hutchinson, Downing, and Vinegar, 1966; DeWitt, 1967; Fry, 1967; Heath, 1968; Templeton, 1970; Edney, 1971; Bartholomew, 1972; Nagy, Odell, and Seymour, 1972; Whittow, 1970, 1973; Heinrich, 1974; Crompton, Taylor, and Jagger, 1978). Since homeothermy at some stage in life history is almost ubiquitous among extant mammals, but is not restricted to higher vertebrates, it is instructive

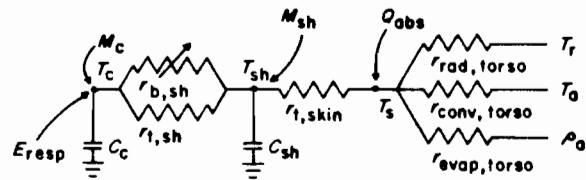
to seek evidence for this characteristic among the reptilian progenitors of mammals.

Biophysical Models

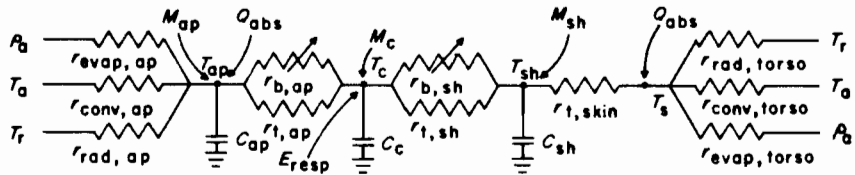
Most biophysical models of energy exchange deal with animals in which rates of influx and efflux of energy are equivalent, and body temperature is constant with respect to time; these are "steady-state" or equilibrium models. More complex biophysical models (Spotila *et al.*, 1973; Porter *et al.*, 1973) deal with animals in which rates of influx and efflux are not equal, and body temperature changes with time (Fig. 2a). Such "transient-state" models are especially important for analyses of large animals, such as pelycosaurs, because large animals are often out of equilibrium with their environment due to their large thermal inertia. Control of blood flow to facilitate heat exchange is probably a crucial adaptation for the regulation of body temperature in large animals; and thus models of energy exchange in pelycosaurs must be transient-state models that include control of blood flow.

We base our analyses for pelycosaurs on a "three-lumped" model (Fig. 2b; Tracy *et al.*, 1980), which tracks the temperatures of three regions (lumps) of the body (torso, shell or skin of

A) 2-LAYER MODEL



B) 3-LAYER MODEL



C) 4-LAYER MODEL

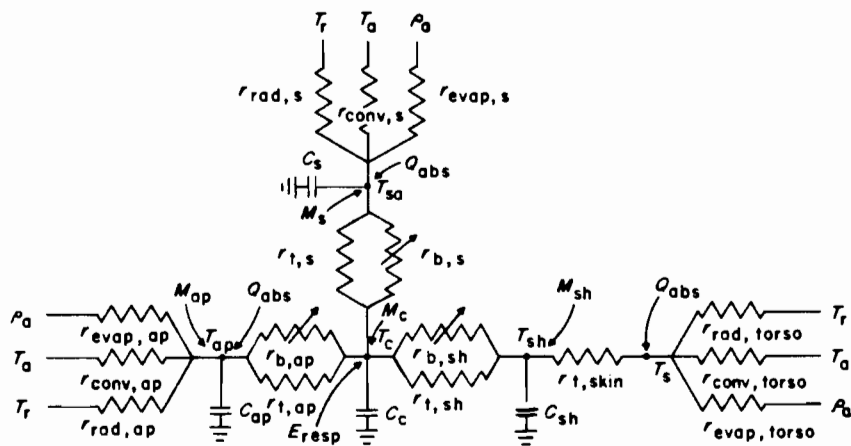


Figure 2. Three transient state energy balance models illustrated like "thermal circuits" (i.e., diagrammed like an electrical circuit, but energy rather than electricity is the current transferred; see Campbell, 1977, for discussion of thermal circuit).

A. A two-layer model, described in Beckman, Mitchell, and Porter (1973), that has been used for describing small lizards as essentially consisting of a core (center of torso) with a temperature T_c and a shell (surrounding the core) with a temperature of T_{sh} .

B. A three-layer model, after Tracy et al. (1980), that has been used to describe large lizards as essentially consisting of a core and shell, as in the two-layer model, and appendages with a temperature T_{ap} .

C. A four-layer model used here to describe pelycosaurs as essentially consisting of a core, shell, and appendages, plus a sail with temperature T_{sa} .

In all models, energy can enter the animals as absorbed radiation, Q_{abs} at the torso, appendages, and sail. These regions can also exchange energy as thermal radiation, convection, and evaporation, depending upon the temperatures and vapor density of the environment (T_r , the radiant tempera-

ture of the environment; T_a , the ambient air temperature; and ρ_a = ambient vapor density) and the surface temperatures of the animal (T_s = surface temperature of the torso). Energy can be generated via metabolism in the four layers (M = metabolic heat production) and stored in the tissues of the layers, according to the capacitances of the layers (C = the capacitance for heat storage, which is the product of the mass of the layer and the specific heat of the tissues in the layer).

Finally, the rate of heat transfer from the environment to the animal, or between layers of the animal, is governed by the physical processes of heat transfer. This is represented as a thermal resistance to heat transfer. Thus, r_{rad} is the resistance of thermal radiative heat transfer; r_{evap} is the resistance to evaporative heat loss; r_t is the resistance to conductive heat transfer through tissues; and r_b is the resistance due to blood flow between layers. (Actually blood flow is more easily thought of as facilitating heat transfer than of resisting it, but the electrical analogy forces representation as in this figure. Thus, when blood flow is very high, resistance to heat transfer is very low).

torso, and appendages). This model is converted to a "four-lumped" model to deal with energy exchange in sailed pelycosaurs (Fig. 2c). In this model, all surfaces of the body (torso surface, sh ; appendages, ap ; and sail, sa) exchange heat with the environment by radiation, convection, and evaporation. Each surface also exchanges heat with the core of the torso via blood flow and conduction between the core and skin.

Metabolic heat is generated in the torso surface (M_{sh}) and core (M_c), and in the appendages (M_{ap}) and sail (M_{sa}), although this source of energy is usually small in reptiles (Bennett and Dawson, 1976). Solar radiation is absorbed, Q_{abs} , by the skin of the torso, appendages, and sail.

Although our model treats the sail as an accessory appendage, heat exchange involving the sail differs from that involving the true appendages. An important difference is that the sail ordinarily sits well above ground where the ambient air temperature is often relatively low, and where the wind speed is relatively high. Thus, the sail is exposed to a different thermal environment from that of the rest of the body.

Model Simulations of Large Extant Lizards

The prediction, by biophysical models, of body temperatures of pelycosaurs obviously cannot be verified directly. Nevertheless, our confidence in such models is fortified by demonstrating that slightly simpler models (Fig. 2b) do accurately predict body temperatures of large extant reptiles.

We initially test the ability of the three-lump, transient-state model (Fig. 2b) to predict body temperatures of adult green iguanas (*Iguana iguana*) during heating and cooling in the laboratory. Parameters of the model are from Christian, Tracy, and Porter, 1983, except for the rates of blood flow to the periphery (skin of the torso and appendages), which are taken from Baker and White (1970). The simulation (Fig. 3) predicted that the ratio of the rates of cooling and of heating should be 0.70, which compares favorably with ratios calculated from data on living green iguanas of 0.70, by Baker and White (1970), and 0.72, by Turner (unpublished). Furthermore, the model accurately simulates the observed phenomenon (Turner and Tracy, 1983; Turner and Tracy, this volume) that blood flow to appendages accounts for most of the differences in rates of warming and cooling in reptiles (Fig. 3).

The three-lump model (Fig. 2b) also accurately

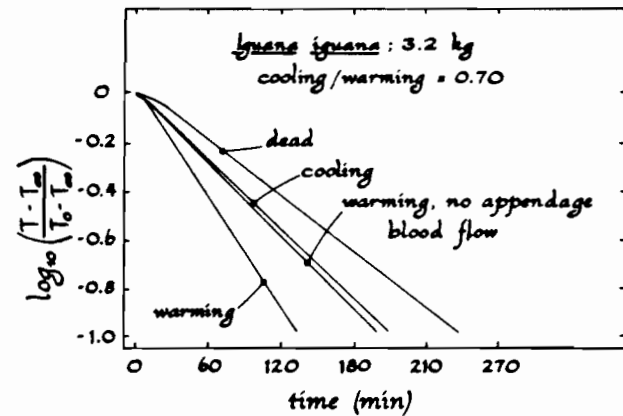


Figure 3. A computer simulation (using the model in Figure 2b) of temperature transients in a 3.2 kg green iguana (*Iguana iguana*). Simulations were for normal cooling and warming of a living lizard, cooling or warming of a dead lizard, and warming in a living lizard where blood flow between appendages and torso had been abrogate. Symbols are as in Figure 1.

predicts the body temperatures of large lizards during heating and cooling in nature. Christian and Tracy (unpublished) monitored the body temperatures of adult Galapagos land iguanas (*Conolophus pallidus*) that were tethered in full sun and later transferred to deep shade. Relevant meteorological data necessary for the model were recorded simultaneously (Christian, Tracy, and Porter, in press). Calculated and measured body temperatures were virtually identical during heating as well as cooling (Fig. 4).

Finally, Christian, Tracy, and Porter (1982) used the three-lump model to predict the maximum and minimum attainable body temperatures of Galapagos land iguanas in nature. Additionally, they used radio-telemetry to measure temperatures of free-ranging lizards. Measured temperatures were always bracketed by the predictions (Fig. 5). Lizards maintained a constant body temperature (homeothermy) during midday even when their thermal environment was changing dramatically.

Both the thermal environment and the temperatures selected by the Galapagos land iguanas change seasonally (Christian, Tracy, and Porter, 1982). Interestingly, the particular temperature selected during each season maximized the length of time during a day that a constant, high body temperature could be maintained. For example, the land iguana in Figure 5 would necessarily have shortened its period of homeothermy if it had selected either a higher or lower body temperature (see Christian, Tracy, and Porter, 1982).

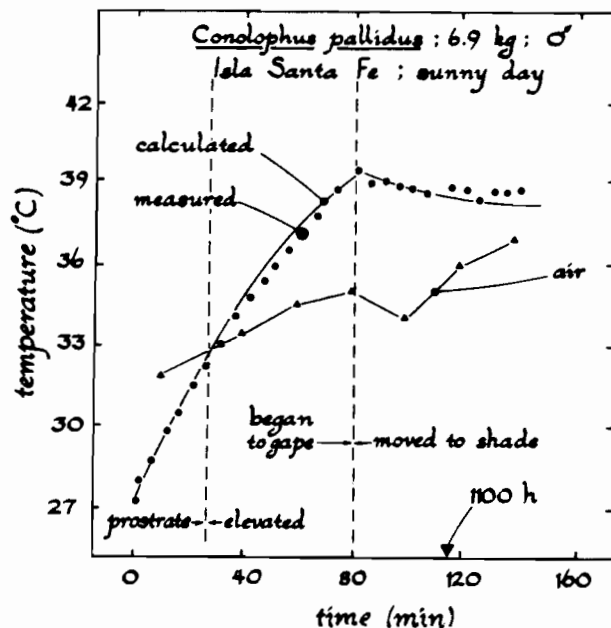


Figure 4. Measured and predicted body temperatures of a 6.9 kg Galapagos land iguana (*Conolophus pallidus*), tethered with a rope so that it had to remain in the microclimatic conditions of the experiment. Initially, the lizard was cool from overnight climatic conditions. At around 9:00 A.M., the lizard was tethered in full sunlight. The tethered lizard was not prevented from posturing or moving about, but it was prevented from moving to the shade. When the lizard reached a body temperature of around 39.5°C, it was moved to deep shade created by two layers of canvas tarp held 2 m above the ground surface with tent poles. Dots represent cloacal temperatures measured with a thermocouple held in place (approximately 6 cm into the cloaca) with tape. Model predictions of body temperature are represented with the solid line. Also presented are air temperature and notes of a change in behavior.

These findings challenge our traditional view of thermoregulation. Most discussions of temperature regulation assume that ectotherms attempt to regulate to some "optimal" body temperature, the level of which is largely independent of the amount of time that the animal spends at that temperature. In contrast, land iguanas appear to select a body temperature that maximizes the amount of time (during the day) when body temperature can be held constant.

Hypotheses Concerning Thermoregulation in Pelycosaurs

With extant animals, one deduces patterns of temperature regulation by monitoring body temperatures in the field and laboratory and by analyzing the properties of the animal's natural en-

vironment (Fig. 5). Such patterns and properties serve as analogues with respect to extinct animals, and are then examined in terms of the peculiarities—such as body size and dorsal sail—of the extinct forms themselves. In this way, circumstantial evidence for or against a particular hypothesis is gathered. In this paper, we propose *a priori* hypotheses concerning thermoregulation in pelycosaurs and then use biophysical simulation to determine whether evolutionary trends in body size and elaboration of dorsal sail are consistent with these hypotheses. We start with alternative propositions:

1. Pelycosaurs were large enough to be "inertial homeotherms" (see Spotila, 1980). In the extreme, this hypothesis assumes that the sail has no significant thermoregulatory function (see below).
2. The sail of pelycosaurs facilitated regulation of body temperature by serving as a heat exchanger that could be used to expedite heat exchange with the environment (Bramwell and Fellgett, 1973). In this hypothesis, both body size

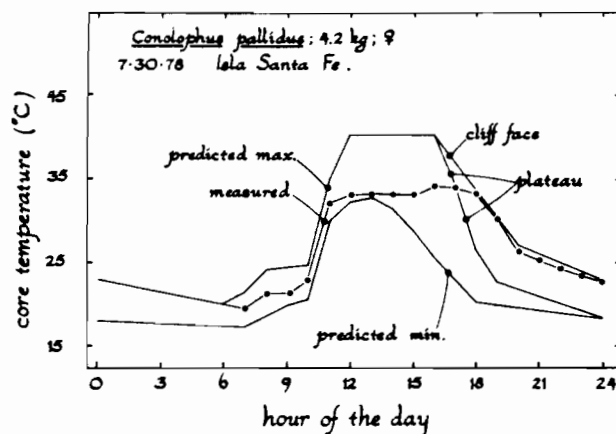


Figure 5. Predicted and measured body temperatures of the Galapagos land iguana (*Conolophus pallidus*) on Isla Santa Fe, Galapagos, in the cool season (July 30, 1978). Actual body temperatures were measured using radio telemetry. Predictions of body temperature were made using the model in Figure 2b (see Chrisitan, Tracy, and Porter, 1982). Predictions were made for the minimum attainable body temperature (that which would occur when the lizard was in deep shade, where the wind speed was greatest and air temperature lowest) and the maximum attainable body temperature (that which would occur when the lizard was in full sunlight and postured so that the maximum of its surface area would receive direct solar radiation). In addition, predictions of maximum attainable body temperature were made for the lizards found in two microhabitats: a plateau that received the full force of the prevailing winds at all times; and a cliff face that was shielded from the prevailing wind. During the cool season, the lizards all retreated to the warmer cliff face in afternoon.

and the sail jointly promote homeothermy (see below).

Both of these alternatives deal with the constraints that condition different ways of evolving homeothermy. thus, we are not directly asking "did homeothermy exist?" Instead, we are asking, "How will the use of a dorsal sail help an animal to maintain homeothermy?" and "Are the evolutionary trends in the evolution of body and sail size consistent with the best method of attaining homeothermy?"

This approach also requires consideration of the possibility that pelycosaurs could have regulated their body temperatures at two alternative levels: at relatively low body temperature (ca. 30° C, Bakker, 1971); and a temperature that is higher than ambient air temperature (ca. 35° C).

Allometry of the Sail in Pelycosaurs

The dorsal sail appeared early in the history of two lines of pelycosaurs. The earliest members of the genus *Dimetrodon* were small (mass approximately 50 kg) and had proportionally smaller sails than did later and larger members of the genus (Fig. 6). Indeed, the allometric relationship between area of the sail, A_{sail} (m^2), and body mass, m (kg), for six species of *Dimetrodon* is:

$$A_{\text{sail}} = 0.005 m^{1.13}$$

(explained variance = 0.928). The pattern for *Edaphosaurus* was similar, but there are too few data to compute an allometric constant with confidence. These patterns imply that sail area did not evolve in direct relation to the area of the rest of the body, but rather it became proportionately much larger in large pelycosaurs (Fig. 6). A first guess, then, is that the sail was used as a heat exchanger to dissipate heat generated during exercise, but metabolic heat is generally proportional to $m^{0.75}$ (Schmidt-Nielsen, 1979; but see Heusner, 1982a, b), and the sail area is proportional to $m^{1.13}$.

Alternatively, the sail could have been important to large pelycosaurs while these animals were storing heat (during thermal transients), because the rate of storage of heat is proportional to $m^{1.0}$.

Modeling the Environment of Sailed Pelycosaurs

Dimetrodon and *Edaphosaurus* lived near the equator of the Lower Permian. *Dimetrodon*, which appears to have been primarily a predator

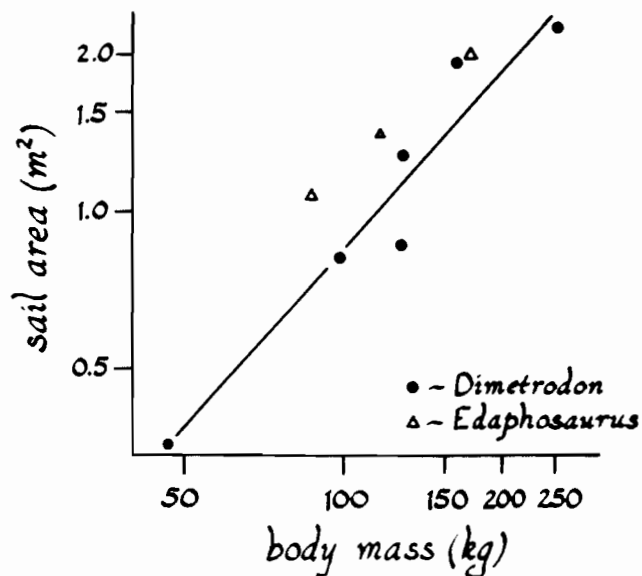
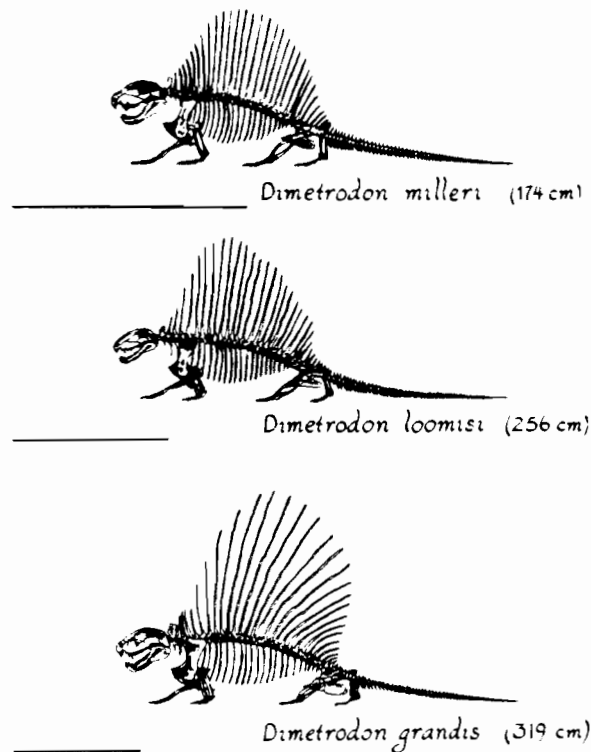


Figure 6. The relationship between the size of dorsal sails and the size of the body in some sailed pelycosaurs. Top: reconstructions of three members of *Dimetrodon* that differed greatly in size (the length of the bar in each case is 1m); and, graph, the relationship between the surface area of the dorsal sail and body mass in pelycosaurs of the genera *Dimetrodon* and *Edaphosaurus*.

of amphibians, would have spent much of its time near marshes and along streams. *Edaphosaures*, an herbivore, is most commonly found in deposits typically associated with standing water.

The environments of *Dimetrodon* and *Edaphosaurus* were, therefore, probably not heavily forested. The climate should have been warm, sunny, and without great daily or seasonal variation in temperature (Olson, this volume; Colbert, this volume; Parrish, this volume; Bakker, 1982). Additional support for the idea that sailed pelycosaurians lived in open habitats is suggested by the potential difficulties of maneuvering a large sail through a brushy or forested habitat.

We infer, therefore, that contemporary climates in open habitats in the tropics closely approximate conditions experienced by pelycosaurians during the Permian. Climate data from the Galapagos during the warm season (Christian, Tracy, and Porter, 1982) provide the basis of our simulations, but our conclusions are relatively insensitive to uncertainties in evaluating Permian climates.

Possible Thermoregulatory Significance of Size and Sails

Body size and sail area increase during the evolutionary history of sailed pelycosaurians. To evaluate the thermoregulatory significance of these trends, we examine a primitive and an advanced representative of this dynasty. The simulations for these forms suggest a scenario for the evolution of homeothermy at high body temperature in the Pelycosauria.

The earliest pelycosaurians were extremely small and had no sails (Reisz 1972). The earliest sailed forms, such as *Dimetrodon milleri*, were larger (ca. 50 kg). Nevertheless, they still could not have been inertial homeotherms because they were too small to dampen the effects of daily fluctuations in their thermal environments. Consequently, they could not have maintained a low body temperature (ca. 30° C) during the day (Fig. 7a). They could, however, have easily maintained homeothermy for much of the day by regulating at a high body temperature (ca 35° C). The sail of this reptile could have extended the period of daytime homeothermy at any temperature by perhaps as much as one hour (Fig. 7a), although its effectiveness would have been greater at high body temperatures.

The later sailed pelycosaurians (*D. grandis*) were

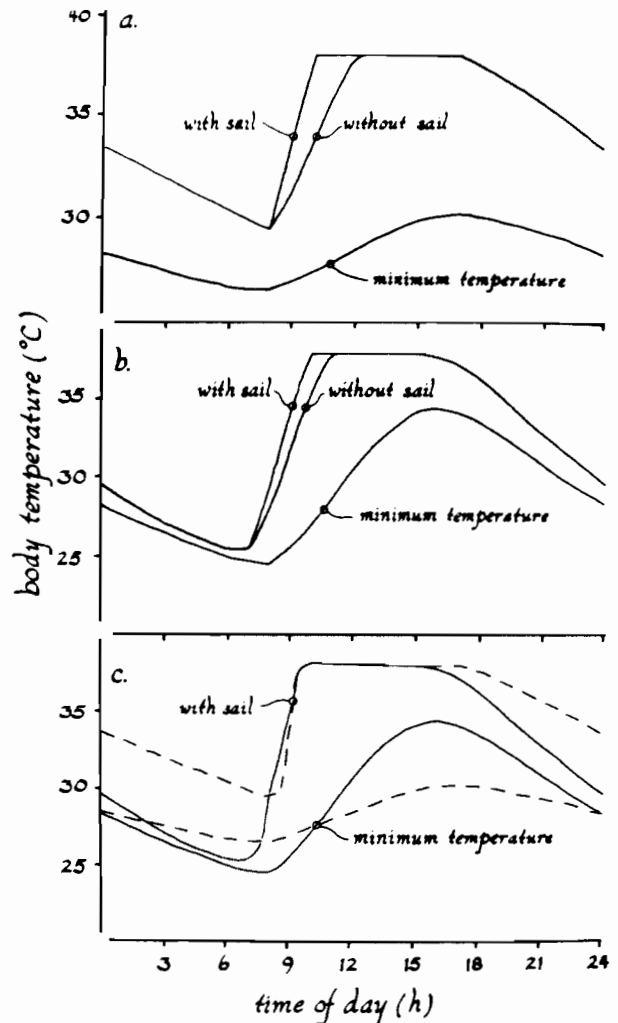


Figure 7. Computer simulations (using the model in Figure 2c) of the maximum and minimum attainable body temperatures of *Dimetrodon grandis* and *Dimetrodon milleri* in their presumed natural environments: A, body temperatures of *D. milleri* with and without benefit of a dorsal sail as an auxiliary heat exchanger; B, body temperatures of *D. grandis* with and without a dorsal sail; and C, body temperatures of *D. grandis* (solid line) and *D. milleri* (dashed line) superimposed for comparison. Both animals have benefit of their sails in this graph.

very large (250 kg), and as a result could have been inertial homeotherms at low body temperatures (ca. 30° C) for perhaps the entire day (Fig. 7b). In this case, the sail would have conferred no thermoregulatory advantage. This inference suggests a trend towards lower daytime body temperatures during the evolution of the sailed pelycosaurians, as *D. milleri* would have had a difficult time escaping high body temperatures at midday (Fig. 7a). Perhaps a more parsimonious interpretation is for the evolution of extended homeothermy at high body temperatures during

daylight hours, which would encompass evolutionary trends in both body size and in sail size. The large sail of advanced pelycosaurs would have enabled large reptiles to retain the ability to warm up quickly, an attribute otherwise restricted to very small animals (Fig. 7c), thereby increasing the period of homeothermy by more than one hour (Fig. 7b). Moreover, the large body size of late pelycosaurs should have further extended the period of homeothermy at high body temperatures. For example, large size alone could have enabled *D. grandis* to remain homeothermic at 35° C for three hours longer than *D. milleri* (Fig. 7c) once its body temperature had attained that level by virtue of the sail.

The simulations suggest that evolutionary trends in body size, sail size, and energy exchange with the environment in sailed pelycosaurs were related to promoting homeothermy at high body temperature. If this hypothesis is correct, it means that homeothermy at high body temperature occurred early in the history of the mammal-like reptiles. It must be noted, however, that therapsids did not arise from *Dimetrodon*, but rather from a more primitive, unsailed sphenacodont such as *Haptodus* (see Carroll, this volume). Thus, while our analysis does not imply that the predecessors of therapsids were homeothermic, it does suggest that advanced sailed pelycosaurs, and perhaps synapsids as a whole, had extensive potential to evolve sophisticated thermoregulatory adaptations.

Acknowledgments

This work was supported by a Guggenheim Fellowship, the National Science Foundation (DEB 8109667), the University of Washington Graduate School Research Fund, and the Department of Zoology and Entomology of Colorado State University. We appreciate the loan of a digitizer, used to measure sail areas of pelycosaurs, from R. T. Paine and M. Denny. We especially thank J. Lillegraven for enormously helpful comments on the manuscript. We owe particular thanks to Dr. Keith Christian whose work in the Galapagos was so important to the maturation of ideas expressed here.

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