Reports

Plates of the Dinosaur Stegosaurus: Forced Convection Heat Loss Fins?

Abstract. *It is suggested that the plates along the arched back and tail of* Stegosaurus *served an important thermoregulatory function as forced convection "fins." Wind tunnel experiments on finned models, internal heat conduction calculations, and direct observations of the morphology and internal structure of stegosaur plates support this hypothesis, demonstrating the comparative effectiveness of the plates as heat dissipaters, controllable through input blood flow rate, temperature, and body orientation (with respect to wind).*

Of all dinosaurs, perhaps the strangest in appearance is *Stegosaurus* (Fig. 1), which is characterized by a series of dermal bony plates along its back and tail. The morphology of the plates and their preserved arrangement (*1*) indicate that these structures stood upright near the dorsal midline of the animal, embedded in a thick hide. Furthermore, in contrast to the bilateral symmetry of most vertebrates, they were, except for the tail spikes, arranged in an alternating (staggered) pattern rather than paired.

Stegosaurus plates have been viewed as "armor" (*1*) or as anatomical structures that enhanced species-specific agonistic and sexual displays (*2*). Whatever the merits of these suggestions, the plate morphology and experimental and computational evidence assembled and discussed below suggest an important thermoregulatory function. We hope to demonstrate that their arrangement, size, shape, and probable vascularity ensured their value as convective heat loss fins, not unlike those currently used to enhance forced convective heat transfer in compact engineering devices (*3*). We first show, by heat transfer experiments with a model in a wind tunnel, that interrupted and staggered "fins" are particularly effectively deployed for augmenting convective heat loss, irrespective of horizontal wind direction. Then we consider heat transfer within each plate, showing, by specimen dissections and heat conduction computations, that their vascular structure and likely blood flow could render even the largest plates fully effective as heat dissipaters. Since the largest plates would be inefficient (≈ 4 percent efficient) in the absence of perfusion, control of blood flow would provide more than an order-of-magnitude change in fin heat dissipation, corresponding to an appreciable (≈ 50 percent) increase in overall convective heat loss at constant geometry, orientation, and wind speed. Physiologically interesting corollaries of these considerations, which strengthen the plausibility of our hypothesis, are pointed out where relevant.

Features deemed essential to our transient convective heat loss experiments (*4*) were (i) provision of a Reynolds number, Re, of at least 10^5 (*5*), (ii) addition of paired or staggered plates (interrupted fins) along the model's "back," with a plate/body surface area (A-) ratio comparable to that of *Stegosaurus*, (iii) thermal conductivity and plate thickness adequate to ensure negligible internal temperature gradients, and (iv) ability to examine both wind-aligned (head-on) and transverse orientations in the wind tunnel (*6*). The time dependence of the temperature difference T(model) − T(air) for model heating (*6*) and cooling was obtained on a recording potentiometer and ultimately computer-processed to obtain $\bar{h}$, the average convective heat transfer rate per unit area and temperature difference. Our pooled results for the total convective heat transfer ($\dot{Q} \propto \bar{h}A$; see Table 1) lead us to the following conclusions: (i) interrupted fins in the wind-aligned orientation are rather effectively deployed (a 28.3 percent increase in A leads to slightly more than a 35 percent increase in $\dot{Q}$ whether the fins are paired or staggered); (ii) only staggered fins are really effective in the transverse orientation (a 28.3 percent increase in A gives a 32.8 percent increase in $\dot{Q}$); (iii) in either orientation, continuous fins are far less effective than interrupted fins (individual plates); and (iv) interrupted staggered fins increase $\dot{Q}$ in the wind-aligned orientation (35.8 percent) somewhat more than $\dot{Q}$ in the transverse orientation (32.8 percent). In this connection, the benefits of interruption and staggering are well known in engineering forced convective heat exchangers (tube bundles, internal tube fins, and so forth) operating at near-transition Reynolds numbers (*3*); such "constructive interference" (by induced turbulence) would not exist if the fins were intended for radiative energy loss or gain (*7*). Similarly, while a double row, even of staggered plates (see Fig. 1), would be inefficient for radiative loss or gain [shadow effect (*8*)], we find them efficient for forced convection provided they are staggered. Observation (iv) has an interesting corollary: since a long unfinned body has markedly greater efficiency in the transverse than in the wind-aligned orientation (*9*) the $\dot{Q}$ of such a body with staggered plate fins added is less sensitive to horizontal wind direction than that of its unfinned counterpart, and this reduces (but may not entirely eliminate) its need to "behaviorally" modify body angle relative to the prevailing wind (*10*, *11*).

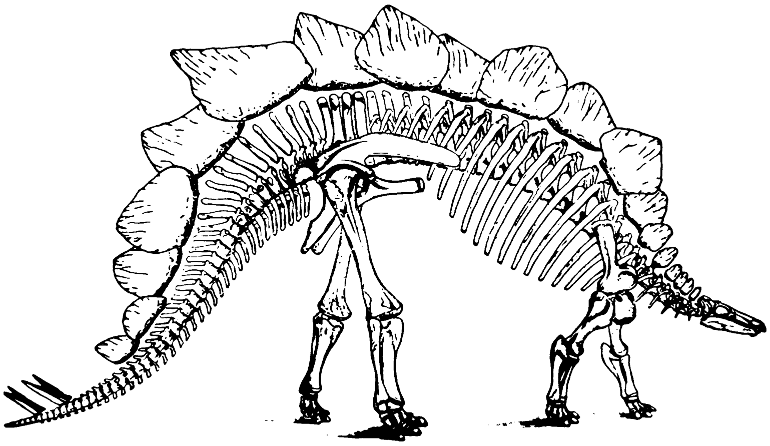
Table 1. Effect of fin deployment on experimental convective heat loss. For Re = 1 × 10^5 and no fins, $\bar{h}$ (wind aligned) = 1.2 × 10^{-2} watt cm^{-2} °K^{-1} and $\bar{h}$ (transverse) = 1.3 × 10^{-2} watt cm^{-2} °K^{-1} (*23*).

Fin type	Area increase (%)	Heat transfer increase (%)
Wind-aligned orientation		
Continuous, paired	44.5	35.4
Interrupted, paired	28.3*	35.4
Interrupted, staggered	28.3	35.8
Transverse orientation		
Continuous, paired	44.5	14.7
Interrupted, paired	28.3	27.3
Interrupted, staggered	28.3	32.8

*Comparable to the percentage area increase, 10^2 A(fin)/A(unfinned), for a living *Stegosaurus*.

For external fin area to be effectively utilized, internal heat transfer must also be adequate to maintain nearly uniform surface temperature (*12*) under the prevailing conditions of convective heat loss. The following heat conduction calculations and observations of actual plates reveal that while *Stegosaurus*'s plate geometry was probably fixed, the heat transfer effectiveness of the plate array could be controlled over a wide range by varying the flow or temperature of their blood supply.

We consider first the steady conduction of heat within an isolated fin of local thickness $2b(y)$, streamwise length distribution $l(y)$, and maximum height y_m, losing heat to a uniform air flow of velocity U. Assuming that (i) the effective plate thermal conductivity, λ, is constant and about that of quiescent H_2O (l);



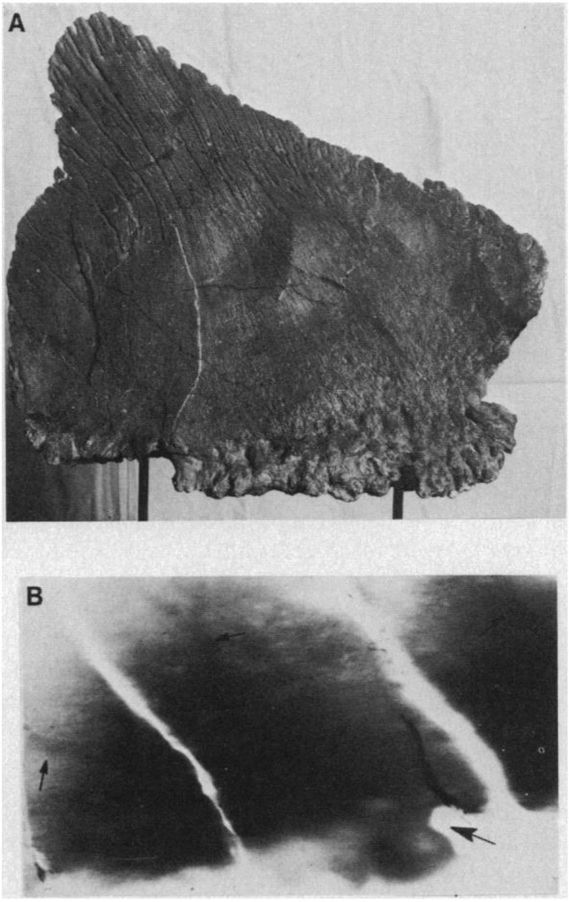


Fig. 1 (left). Reconstruction of *Stegosaurus* (*22*, modified after D. C. Marsh and C. G. Gilmore), length 6 to 7 m. Fig. 2 (right). (A) Large *Stegosaurus* dermal plate (U.S. National Museum specimen 4714), fore-aft length about 70 cm. (B) Mid-sagittal laminograph x-ray of *Stegosaurus* plate (Yale Peabody Museum specimen 1388), length of illustrated portion about 20 cm. The large arrow denotes a large foramen in the plate base. Smaller arrows indicate probable plate veins.

(ii) streamwise internal temperature gradients can be neglected compared to their longitudinal counterparts; (iii) the streamwise average air-side heat transfer coefficient $\bar{h}(y)$ is estimable by considering each element Δy of plate at height y to be an independent flat plate of length $l(y)$, one can calculate the fin effectiveness factor, η, defined as the ratio of the actual convective heat loss from a plate of specified geometry to that which would have occurred if the same plate had the root temperature T_0 everywhere.

Our calculations (*13*) reveal that in the absence of internal blood flow even small *Stegosaurus* plates would probably operate with $\eta \approx 0.2$, and for the largest known stegosaur plates η would be considerably less than unity [for example, $\eta \approx 0.04$ for a wind speed of 8.7 m/sec (20 miles per hour)]. But since longitudinal blood flow would increase the effective λ (*14*) enough to cause $\eta \approx 1$ even for the largest plates, blood perfusion would provide *Stegosaurus* with a simple means to significantly vary the heat loss effectiveness of all fins, especially the largest. Thus, despite their fixed geometry, and even at constant wind temperature, speed, and direction, *Stegosaurus* would have considerable control ($\approx$ 50 percent) over his total convective heat loss. Our observations of intact, cross-sectioned, and x-rayed stegosaur plates (*15*) (Fig. 2) provide strong evidence that the "living" plate must have indeed been capable of receiving a rich blood supply. External surfaces of stegosaur plates reveal branching grooves that, like the horn cores of horned vertebrates, are probably vascular channels. The bone interior is quite cancellous and reveals traces of large branching canals, which were probably venous drainages. While the mode of control of blood flow rate and temperature is unknown, three possible mechanisms or combinations thereof seem plausible: (i) vasomotor contraction and relaxation of the vessels supplying blood to the plates, (ii) countercurrent heat exchangers (situated near the bases of plates), and (iii) vascular shunts toward and away from the plates. All three mechanisms have ample precedent among living vertebrates (*11*, *16*).

Features of *Stegosaurus* deliberately not simulated in our model experiments are (i) plate size variation along the arched body (Fig. 1), (ii) plate planform shape (narrowed root, pointed tip), and (iii) plate roughness. However, these features further strengthen our forced convection hypothesis since (i) the largest plates are in the position of maximum wind exposure and speed near the highest point on the animals's arched back, and (ii) blade roots, immersed in the heated and retarded air boundary layer adjacent to the main body (*17*), would be comparatively ineffective. Hence, for the wind-aligned orientation, narrowing the streamwise length near the plate base would significantly reduce plate weight without too high a cost in reduced absolute heat loss or strength. Moreover, because of the longitudinal temperature gradients within the plate [local breakdown of assumption (ii) due to the streamwise nonuniformity of $\bar{h}$] and the increased $\bar{h}(y)$ in the transverse orientation, tip narrowing would be efficient for forced convection fins. Interestingly enough, while explanations (i) and (ii) are immediate corollaries of our forced convection hypothesis, they become problematic under rival hypotheses, such as the radiative fin hypothesis. Finally, while it is difficult to estimate for the plate of a living *Stegosaurus* (*18*), surface roughness would have had a beneficial effect on $\dot{Q}$ at these near-transition Reynolds numbers (*19*).

While more complete energy balance studies (*20*) on *Stegosaurus* and its unfinned contemporaries might shed valuable additional light on questions of their climatic tolerances and extinction, we now believe that *Stegosaurus*'s plates (Fig. 1), because of their evidently efficient deployment as forced convective heat loss fins, constituted a physiologically effective thermoregulatory adaptation (*21*).

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References and Notes

1. C. W. Gilmore, *Osteology of the Armored Dinosauria in the United States National Museum, with Special Reference to the Genus* Stegosaurus (U.S. National Museum Bulletin 89, Government Printing Office, Washington, D.C., 1914).
2. L. Davitashvili, *The Theory of Sexual Selection* (U.S.S.R. Academy of Sciences, Moscow, 1961), in Russian.
3. W. M. Kays and A. L. London, *Compact Heat Exchangers* (McGraw-Hill, New York, 1958).
4. This method of determining area-averaged heat transfer coefficients, $\bar{h}$, employs a high thermal conductivity model used as a transient calorimeter; for example, see W. H. Giedt, *Principles of Engineering Heat Transfer* (Van Nostrand, New York, 1957), p. 275.
5. This is within a factor of 5 of the value for a full-scale stegosaur exposed to a 4.5 m/sec (10 mile per hour) wind. *Stegosaurus* lived in an environment that experienced seasonal dryness [J. C. Dawson, "The sedimentology and stratigraphy of the Morrison Formation (Upper Jurassic) in northwestern Colorado and northeastern Utah," thesis, University of Wisconsin (1970)]. Coupled with the grazing pressure of large herbivores [R. T. Bakker, *Nature (London)* **229**, 172 (1971)], this probably resulted in a fairly open, parkland or savanna-like vegetation, where such a wind speed would not be unlikely. Forced convective heat transfer data for a small model are directly applicable to a full-scale animal or device exposed to the same fluid if the Reynolds number is the same for both the model and the full-scale animal. The Reynolds number is dimensionless and is given by $\mathrm{Re} \equiv \rho UL/\mu$, where ρ, U, and μ are, respectively, the fluid's density, velocity, and dynamic (Newtonian) viscosity, and L is the characteristic body dimension (for example, maximum body diameter); it may be regarded as the ratio of the characteristic linear momentum flux by convection, ρU^2, to the characteristic momentum flux (shear stress), $\mu U/L$, associated with molecular motion across streamlines. Since our tests (in air at 296°K and atmospheric pressure guarantee that μ/ρ is about the same for both model and full-scale device, we maintain the product UL as close as possible to that of the full-scale animal (this necessitates high wind speeds for small models).
6. These conditions were readily met, without resorting to a small-scale replica of dubious accuracy, by using a solid aluminum model composed of a cylinder 5.08 cm in diameter and 15.2 cm long capped with hemispheres and provided with either no fins, paired or staggered interrupted vertical fins (of rectangular shape, constant height, and 3.2-mm thickness) comprising 28.3 percent of the area of the unfinned model, or paired continuous fins of equal height comprising 44.5 percent of the unfinned body area. Two 125-watt cartridge heaters were embedded in the cylindrical portion of the model, along with a copper-constantan thermocouple to sense the model's temperature-time history following either the sudden onset or interruption of heating (at a continuous wind speed of 31.4 m/sec in a tunnel with a 30.4-cm-diameter test section). Five distinct heating rates between 68 and 100 percent of full heater power were employed. Even at maximum power, and hence for the largest value of $T(\text{model}) - T(\text{air})$ ($\approx$ 77°K), radiation and natural (buoyancy-driven) convection are negligible compared to convection in 31.4 m/sec air.
7. A number of fossil reptiles and amphibians sported elongations of the neural spines, probably connected by soft tissues to form a continuous ridge or sail-like structure. For some of these a thermoregulatory function (radiative) has been proposed [for example, see C. Bramwell and P. Fellgett, *Nature (London)* **242**, 302 (1973)]. However, while the plates of *Stegosaurus* would not be useless for radiative transfer (gain or loss) for all of the reasons discussed here, their efficiency as convectors would be far greater. Turning to interrupted surfaces, for forced convective heat transfer to or from deep tube bundles (more than six tubes in the streamwise direction) it is known that there is an optimum tube spacing ($\approx$ two diameters) to maximize the constructive interference at each Reynolds number (*3*). The optimum streamwise spacing for plates such as *Stegosaurus*'s, which would depend on such details as plate bluntness, alignment, roughness, and camber, has not been investigated here.
8. E. M. Sparrow and R. D. Cess, *Radiation Heat Transfer* (Brooks/Cole, Belmont, Calif., 1967).
9. The difference is about 6.6 percent for our present hemisphere-cylinder model; see legend of Table 1.
10. Lizards achieve and maintain high and fairly constant body temperatures by behaviorally changing the position of their bodies relative to the incident sunlight (*11*).
11. J. R. Templeton, in *Comparative Physiology of Thermoregulation*, vol. 1, *Invertebrates and Nonmammalian Vertebrates*, G. C. Whittow, Ed. (Academic Press, New York, 1970), pp. 167–221.
12. M. Jakob, *Heat Transfer* (Wiley, New York 1944), vol. 1, chap. 11.
13. Alternatively, because of internal heat transfer limitations, the effective external heat transfer area of a fixed geometry fin will differ from its true wetted area $A(\text{fin})$ by the factor η, which, for a given plate shape $[b(y)/b(0),\ l(y)/l(0)]$ and Reynolds number [based on $l_0 \equiv l(0)$] depends only on the dimensionless group $N \equiv y_m(\bar{h}_0/\lambda b_0)^{1/2}$, where $b_0 \equiv b(0)$. Numerical results for $\eta(N;\ \mathrm{Re}_0)$ were obtained by H. H. Feng, using a finite-difference method to approximate the steady-state $T(y)$ profile satisfying the one-dimensional heat conduction equation with split (two-point) boundary conditions. [The plate height y_m was divided into 20 equal segments and the shape functions $b(y)/b(0)$ and $l(y)/l(0)$ were obtained from measurements made on a petrographically sectioned plate with $y_m \equiv$ 0.38 m.]
14. Unidirectional blood flow would increase the effective λ by an amount proportional to the product of the blood flow per unit base area, blood heat capacity, and plate height [R. C. Seagrave, *Biomedical Applications of Heat and Mass Transfer* (Iowa State Univ. Press, Ames, 1971), p. 109]. Cutaneous blood flow in humans ranges from 0 to 0.25 ml cm^{-3} min^{-1} for a 70-kg human with a surface area of 2×10^4 cm^2 and a skin thickness of 0.3 cm (J. Stolwijk, personal communication). Assuming that the larger animal *Stegosaurus* could attain a maximum cutaneous flow of ≈ 0.2 ml cm^{-3} min^{-1} and taking an estimated total plate volume of 0.67×10^5 cm^3, maximum plate perfusion would have been about 1.1×10^4 ml/min, assuming the plates were not preferentially perfused. If this blood flow rate was distributed to the plates in accord with their individual masses (volumes) then the largest plates would receive ≈ 1.8 liter/min, enough to increase the effective λ more than 1000-fold, corresponding to fin effectiveness η of about 0.95. Even a blood flow rate of only 0.07 liter/min, corresponding to $\eta \simeq 0.5$, would provide more than a tenfold increase in η for the largest plates.
15. Cut and polished transverse and sagittal sections of *Stegosaurus* plates were made with the assistance of W. Phelps. Geologic interpretation of these sections was done with the assistance of T. Bultman and H. Dick. The spaces separating bone in the very cancellous plate interior are filled with sparry calcite that shows no signs of deformation (such as twinning of calcite crystals). Diagenetic distortion of the plate interior has thus been very slight. Biologic interpretation of the sections was done with the assistance of S. Saha and E. Crelin. R. Shapiro, N. Piscitelli, R. Brunetti, and P. Haughton assisted in the preparation and interpretation of laminograph x-rays of plates.
16. M. Brooks, *The Blood Supply of Bone: An Approach to Bone Biology* (Appleton-Century-Crofts, New York, 1971); W. W. Weathers and F. N. White, *Am. J. Physiol.* **221**, 704 (1971); L. A. Baker, W. W. Weathers, F. N. White, *J. Comp. Physiol.* **80**, 313 (1972); F. N. White, *Comp. Biochem. Physiol.* **45 A**, 503 (1973); E. N. Smith, *Physiol. Zool.* **48**, 177 (1975); T. M. McKenna and G. C. Packard, *Copeia* **1975**, 162 (1975); K. Schmidt-Nielsen, *How Animals Work* (Cambridge Univ. Press, New York, 1972); A. E. Greer, J. D. Lazell, R. M. Wright, *Nature (London)* **244**, 181 (1973); F. G. Carey and J. M. Teal, *Comp. Biochem. Physiol.* **28**, 199 (1969); *ibid.*, p. 205; I. Steen and J. B. Steen, *Acta Physiol. Scand.* **63**, 285 (1965); H. T. Hammel, *Annu. Rev. Physiol.* **30**, 641 (1968). A particularly important factor in determining the mode of control of plate perfusion in *Stegosaurus* would be the relative importance of peripheral compared to central nervous responses to skin, plate, and core temperature.
17. At the relevant Reynolds numbers based on streamwise length (about 10^6) in the wind-aligned configuration, even an unseparated turbulent boundary layer at the location of the larger plates could have immersed some 10 to 20 percent of their height.
18. Of course, a keratinous sheath around each plate would have reduced the fin effectiveness η by an amount dependent on its thickness and thermal conductivity [J. A. Plamondon, *ASME Trans. (Ser. C)* **84**, 279 (1962)]. However, since goats and perhaps other bovids use sheathed horns to augment heat loss [C. R. Taylor, *Physiol Zool.* **39**, 127 (1966)], a similar sheath on *Stegosaurus* plates need not have been an insuperable $\dot{Q}$ barrier.
19. The forced convective heat transfer benefits of interrupted fins are passed up in many engineering applications because of the accompanying increase in momentum transfer, manifesting itself in high pressure drops (*3*) and aerodynamic drag. However, in the present context this penalty would be unimportant, since *Stegosaurus*'s "running" speed was probably not limited by aerodynamic drag.
20. See J. R. Spotila, P. W. Lommen, C. S. Bakken, D. M. Gates, *Am. Nat.* **107**, 391 (1973), R. C. Birkebak, *Int. Rev. Gen. Exp. Zool.* **2**, 269 (1966); W. P. Porter and D. M. Gates, *Ecol. Monogr.* **39**, 245 (1969); J. L. Monteith, *Principles of Environmental Physics* (American Elsevier, New York, 1973); D. M. Gates and R. B. Schmerl, *Perspectives of Biophysical Ecology* (Springer-Verlag, New York, 1975). The difficulty with attempting such an analysis to test the thermoregulatory significance of fins is that much information is needed about the animal's environment (temperature, radiation, humidity, and wind velocity regimes and amount and dispersion of plant cover), physiology (preferred body temperature, metabolic rates, activity level, thickness of superficial fat or keratin layers, rates of blood flow to superficial tissues (including fins), water economy, and even behavior (amount of time spent in or near water). While it is possible to make general statements about dinosaurian thermoregulation by the biophysical approach (Spotila *et al.*) consideration of the thermal strategies of specific dinosaurs may be beyond our present ability. Radiative or convective fins might be optimal for animals of a particular type under some environmental circumstances but not others. Thus, the fact that only a few dinosaurs sported plate or sail structures does not mean that these did not have a thermoregulatory function in the species where they did occur.
21. This does not preclude stegosaur plates being used to collect radiant energy to counteract occasional periods of low body temperature. However, for the reasons indicated in the text, this type of thermoregulatory function was probably of secondary importance. Use of the plates to increase body temperature through convective heat gain is unlikely. For this to occur, the air temperature would have had to be warmer than the animal's body temperature. Such additional heat would probably have been needed at night and in the early morning. However, air temperatures at such times are unlikely to have been warmer than a *Stegosaurus*'s body temperature (compare Spotila *et al.* (*20*). A heat-loss rather than a heat-gain function for the plates would also be more likely if dinosaurs were endotherms, as several authors have proposed [L. S. Russell, *J. Paleontol.* **39**, 497 (1965); J. H. Ostrom, *Proc. N. Am. Paleontol. Conv. Sect. D* (1969), p. 347; R. T. Bakker, *Evolution* **25**, 636 (1971); *Nature (London)* **238**, 81 (1972)].
22. A. S. Romer, *Vertebrate Paleontology* (Univ. of Chicago Press; Chicago, 1966).
23. The corresponding dimensionless heat transfer coefficients (Nusselt numbers) $\bar{h}L/\lambda$ (where λ is the fluid thermal conductivity) will be the same for both model and geometrically similar full-scale object.
24. We thank T. VanWinkle for his help with the continuous fin heat transfer experiment; W. Reifsnyder, F. G. Carey, and J. Stolwijk for their helpful discussions; and J. Ostrom, without whose encouragement and support this study would have been impossible. This report is dedicated to the memory of Dr. Ralph G. Nevins of the John B. Pierce Foundation (a Yale University affiliate) and Yale University Department of Engineering and Applied Sciences, whose death constituted an irreplaceable loss to the physiological heat transfer community and interrupted our fruitful interdisciplinary dialogue on physiological thermoregulation.

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