

The Evolution of Homeothermy: From Dinosaurs to Man

**David Robertshaw
Brody Memorial Lecture XVIII**

**Special Report 329
November, 1984**

**Agricultural Experiment Station
University of Missouri-Columbia**

The Board of Curators established the Samuel Brody Lectureship Fund in April, 1959. Lectures have been held as often as sufficient income from the endowment fund provided expenses and a small honorarium for a distinguished lecturer.

The committee will welcome additional contributions from any individual or group. Such funds will be applied to the principal or endowment fund of the Brody Memorial Lectureship Fund. Any increases in the endowment fund, of course, will allow lectures to be held more frequently.

The present Brody Memorial Lectureship Committee was appointed by Dean Roger Mitchell.

Dr. Harold D. Johnson, Brody Lecture Chairman

Dr. Ralph Anderson, Gamma Sigma Delta Representative

Dr. Richard P. Dowdy, Sigma Xi Representative.

The Evolution of Homeothermy: From Dinosaurs to Man

David Robertshaw
Department of Physiology and Biophysics
College of Veterinary Medicine and Biomedical Sciences
Colorado State University
Fort Collins, Colorado 80523

In honoring the memory of Samuel Brody it may seem somewhat tenuous that a topic such as this has any relevance to his work. However, great scientists frequently make single observations which open up new fields of scientific investigation. The observation I wish to develop is the paper published in 1952 by Kibler and Brody in one of the famous research bulletins of the Missouri Agricultural Experiment Station (#497) in which they revealed for the first time that cows sweat. Until that time it was assumed that cows were primarily panting animals who increased evaporative heat loss by increasing ventilation of the upper respiratory tract. Indeed, Brody himself made such a statement in his book *Bioenergetics and Growth*, published in 1945. The observation that sweating as an evaporative heat loss mechanism is not simply the prerogative of man or horses and the diversity of sweating mechanisms that have since been revealed now allows one to speculate on the different strategies for thermoregulation that have evolved in association with the appearance of homeothermy.

—D.R.

Homeotherms and Poikilotherms

The terms poikilotherm and homeotherm are supposed to describe the relationship between body temperature and the external environment in that the body temperature of poikilotherms is subject to environmental temperature changes whereas that of homeotherms is independent of such changes. However, many poikilotherms under natural conditions have a remarkably stable body temperature. This is achieved by behavioral means; when the habitat is reasonably stable in terms of its temperature, access to solar radiation or shade, a poikilotherm can maintain a very stable body temperature. However, the ecological niche is restricted to environments which remain relatively stable as exploitation of more adverse thermal environments, i.e. showing greater diurnal or seasonal variation, threatens the biochemical stability of the organism.

The advantages of a constant body temperature seem obvious. Nearly all the complex chemical reactions associated with life are tuned to operate at an optimal temperature. Any changes in body temperature alter the rates of various reactions differently and thereby disturb the system.

The basic difference between homeotherms and poikilotherms relates to their basal metabolic rate. A preferential terminology describes poikilotherms as ectotherms and homeotherms as endotherms. Both terms refer to the source of energy used to maintain body temperature; ectotherms rely primarily on external sources of energy such as solar radiation or conduction of heat from warm ground, whereas endotherms rely on their metabolic heat production. Thus, the rate of heat production in endotherms is 5 times greater than that of ectotherms.

This specific development, the transition from ectothermy to endothermy, carries a large bioenergetic price. The total energy budget of a population of endothermic birds or mammals is 10 to 30 times higher than that of an ectothermic population of the same size and weight. However, the price appears to be justified in that mammals and birds have developed more rapidly and have become dominant in the last 60 million years. This domination has been made possible by the sudden extinction of dinosaurs at the end of the cretaceous period. The endotherms that emerged, namely mammals and birds, may have had a common ancestor or they may have evolved endothermy independently of each other. Figure 1 presents one classification which suggests that endothermy has evolved separately in mammals and birds.

The Evolution of Endothermy

It must be remembered that evolution proceeds in slow steps. The change from an ectotherm to an endotherm would not have been sudden.

Birds may have evolved either from ancestors of the dinosaurs, the thecodonts, or from the dinosaurs themselves (Fig. 1). The earliest mammal-like reptiles, on the other hand, were the pelycosaurs. They, like the dinosaurs, were distinguished from their ancestors primarily in size. Many large species rapidly arose and, of course, the larger the animal, the greater the temperature stability. Table 1, which is taken from the work of Spotila et al. (1973), shows the relationship between temperature lability and body size in reptiles. By virtue of their thermal inertia, the larger species require no specific physiological mechanisms to maintain a relatively stable body temperature other than behavioral reactions to the thermal environment. Several groups of pelycosaurs developed a large dorsal sail which would allow both heat gain and heat loss through convection, assuming that blood supply to the structure could be varied. Likewise, many of the dinosaurs had large plate-like structures which histological examination suggests had a

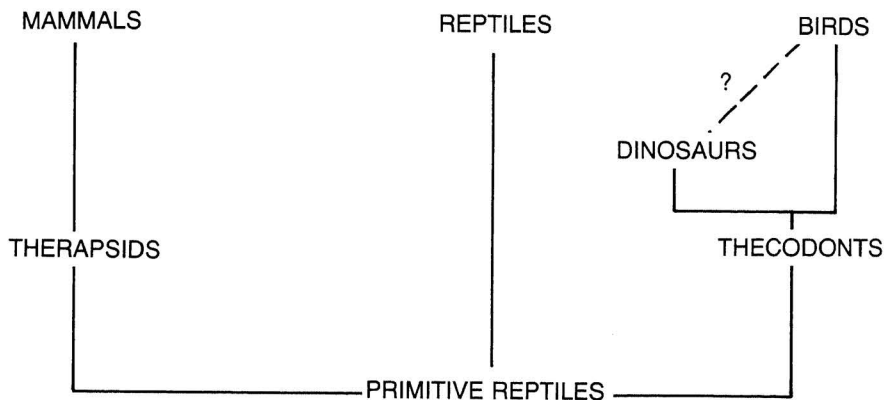
TABLE 1.
The calculated relationship between temperature lability and body size in reptiles

Body diameter (cm)	2	10	20	100	200
Time constant* (hr)	0.22	2.04	5.30	49.0	127

*The time constant is the period required for the body temperature to complete 63.7% of the change from one equilibrium temperature to a new equilibrium temperature when the external temperature changes (based on Spotila et al., 1973).

FIGURE 1.

One proposed classification that shows the origin of modern mammals, reptiles and birds.



good blood supply and which may have been a type of temperature regulatory control apparatus.

The pelycosaur was relatively successful in that they survived for 50 million years before becoming extinct 260 million years ago. They gave rise to the therapsids which ranged in size from rats to that of rhinos. Thereafter, these early mammal-like reptiles declined in size and their descendents, cynodonts, were small and probably insectivorous. In order to compete with the dinosaurs, they became nocturnal and, to survive the lower night temperatures, developed increased insulation by growing hair and by laying down a subcutaneous layer of fat. In addition, they probably increased their basal heat production. It is not clear if the ancestors of the cynodonts, the therapsids, already possessed these mammalian features.

However, some other features were developing in the therapsids which were probably important to their mammalian descendents in physiological

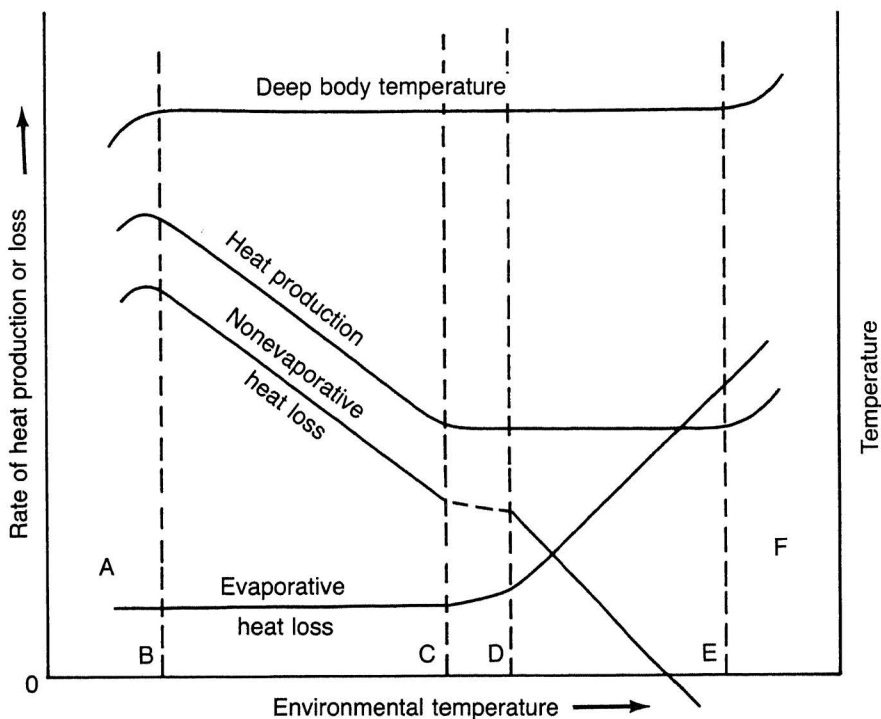
control of body temperature. The development of a bony palate separating the nasal from the oral cavity identifies the nasal cavity as the site for the humidification of inspired air. Additional casts of the brain show the development of a good sense of smell and the appearance of the vomeronasal organ known to be important in the detection of pheromones. Thus, social contact by smell was emerging which, together with maternal care and the evolution of family structure, required close olfactory contact. The glands necessary for the production of smell would probably be found in the skin. Since the animals already may have had hair, it is possible that these odor-producing glands were in close association with the hair follicles. Some of the specialized glands in the skin may also have become the primordial mammary glands. Thus, we can speculate on some of the features which, seventy million years ago at the end of the cretaceous period, became a significant part of the mammalian heritage.

The characteristics of the avian species as related to thermoregulation are somewhat different. They have evolved feathers, as opposed to hair, as an insulating mechanism. They possess little subcutaneous fat and no skin glands except the highly specialized preen glands. The question arises, did they descend from the dinosaurs or do they represent a separate group that separated from the dinosaur ancestry, survived and then flourished at the end of the cretaceous period? (Fig. 1) It is well established that Archaeopteryx had feathers, but it is not certain if Archaeopteryx was a dinosaur or from a separate line of thecodonts. If it was a dinosaur, were the dinosaurs then endotherms? As mentioned, large animal size brings with it a certain stability of body temperature and independence from the thermal fluctuations of the external environment. However, should the daily and seasonal temperature variation increase and should there be pronounced falls in environmental temperature, then dinosaurs, if they were ectotherms, would suffer decreases in body temperature to intolerably low levels. If the end of the cretaceous period was associated with an event which caused a sudden and prolonged fall in air temperature, the extinction of the dinosaurs would be explained; only those animals with some degree of insulation, such as the mammal-like reptiles and birds, could survive.

The survivors may not have had a resting heat metabolism as high as modern mammals. However, because of their insulation, they were able to maintain a constant body temperature at night. Their further success, however, depended on their ability to expand their nocturnal niche. This required the evolution of physiological, in addition to behavioral, mechanisms for the maintenance of constant body temperature which would allow them to exploit habitats with a wider diurnal and seasonal fluctuation. Figure 2 indicates the mechanisms that were developed to bring about this greater independence from the external environment.

FIGURE 2.

Diagram of relationship between heat-production, non-evaporative and evaporative heat-loss and deep body temperature in a homeothermic animal (from Ingram and Mount, 1975).



One physiological feature that was necessary, particularly for smaller animals to occupy the diurnal niche of hot environments, was the ability to maintain a body temperature greater than air temperature so that a continuous temperature gradient of nonevaporative heat loss could be maintained. Thus, body temperature began to be regulated at the higher level. This also necessitated an increase in the resting metabolic rate in order to maintain this elevated temperature during the night time hours. In some instances, this may have proved too costly in terms of energy because of fluctuating food availability occurring on either a daily or seasonal basis. An alternative strategy was to resort to a fall in metabolism and temperature at night (torpor) or a fall in metabolism and temperature in the colder months of the year (hibernation).

The other physiological mechanisms that have evolved are hypermetabolism due to shivering (or brown fat oxidation) and methods of increased evaporative heat loss.

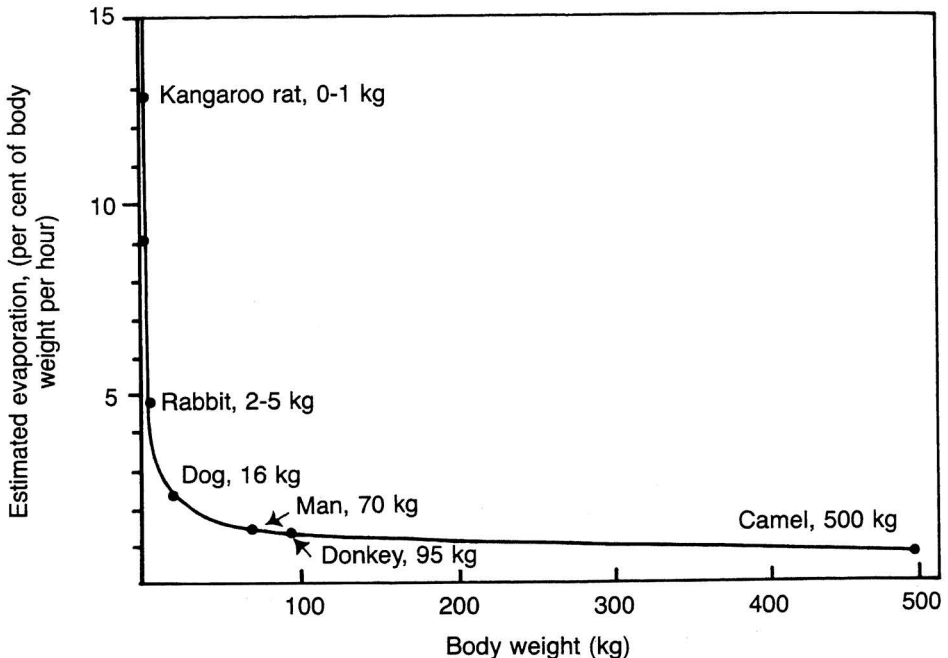
Evaporative Heat Loss Mechanisms

The need for an evaporative heat loss mechanism is probably size dependent. In small fossorial species there is probably no well developed evaporative heat loss mechanism since, as shown in Fig. 3, the quantity of water required for the maintenance of constant body temperature is proportionately very high. Likewise, the large terrestrial mammals such as elephants, do not appear to have any evaporative heat loss mechanisms, since their thermal inertia allows them to store heat during the day and dissipate it during the night (Hiley, 1975).

Of the evaporative heat loss mechanisms utilized by mammals and birds, panting and sweating have been described in mammals whereas in birds, panting (gular fluttering) appears to be their only evaporative heat loss mechanism.

FIGURE 3.

Estimated evaporation necessary to maintain a constant body temperature in a hot desert environment for mammals of various body sizes. The curve is calculated on the assumption that heat load is proportional to body surface (see text). It shows the rapid increase in the theoretical cost of heat regulation in small animals.



Since panting is such a widespread evaporative heat loss mechanism, and since it is also present in some reptiles (Schmidt-Nielsen, 1964), it has been proposed that this represents the primitive form of increasing heat loss by the vaporization of water. However, the magnitude of this increase in reptiles is not sufficient to allow them to maintain their body temperature more than a degree or two below ambient temperature, but would allow them time to escape to a cooler environment in the same way that panting from small mammals can only be of very short duration sufficient to allow time to find cooler conditions.

In addition, reptiles show that panting can selectively cool the brain by a specific vascular arrangement (Crawford, 1972). Such an arrangement, the rete mirabile, is also found in panting mammals and consists of a network of arteries supplying blood to the brain which penetrates the cavernous sinuses at the base of the brain. The cooled blood draining the nasal passage (where the evaporation takes place) thereby comes into close association with blood flowing in the opposite direction and supplying the brain (Baker and Haywood, 1968). Brain function is particularly sensitive to temperature and panting probably evolved to preserve brain temperature. Furthermore, panting is readily modulated by simply varying the level of ventilation of the upper respiratory tract.

Why then has sweating evolved as a heat loss mechanism? With the exception of man, all mammals that sweat also pant, so that although sweating has evolved, panting has been retained usually with diminished importance as sweating became more significant. Man, therefore, appears to be unique in that there is no evidence of thermoregulatory panting in man. It is difficult to speculate why this has occurred because some of the anthropoid primates, such as the chimpanzee, are closely related to man and show evidence of thermoregulatory panting (Hiley, 1976). One of the most likely explanations is that as the evolution of man progressed, the volume of the upper respiratory tract has diminished in size as the cranial vault expanded. A further possibility is that the loss of panting may be associated with the development of speech, a feature unique to man in the animal kingdom. One could envisage that these two functions, i.e. speech and panting, would be incompatible. We must, therefore, examine the role in sweating in species other than man in order to gain some clues as to the factors that precipitated its development.

Presumably, an additional evaporative heat loss mechanism would evolve if panting were insufficient to meet the demands for heat dissipation on account of either exposure to a greater heat load, or some characteristic which curtailed panting as an effective evaporative heat loss mechanism.

Evolution of Sweating

It appears that the primitive types of skin glands from which thermoregulatory sweat glands evolved consisted of either the apocrine or eccrine glands. The apocrine glands are associated with hair follicles and originally may have been involved in the production of smell. The sweat glands in the axillary region of man might be representative of the primitive form of apocrine sweat glands. The primitive form of the eccrine sweat glands are probably found on the hairless (glabrous) regions of the body such as the foot pads of the dog. The two types of skin glands are different, not only functionally but also physiologically; the eccrine glands are controlled by cholinergic nerve fibers whereas the apocrine glands are adrenergic. It is from these two types of glands that thermoregulatory sweating has evolved in man and animals.

Man and the Primates

If we examine sweat gland function in sub-human primates, we note that thermoregulatory sweating is the function of eccrine sweat glands only. As one progresses up the phylogenetic ladder to man, there is a gradual diminution in the number of apocrine sweat glands, which in the lower primates are found evenly distributed over the body and even in aggregates in certain parts of the body. In man, they are confined to the hairy regions of the axillary and pubic areas. The glands on the general body surface, therefore, are eccrine, similar to those on the palms and soles and possibly analogous to those of the foot pads of species such as the dog. Thus, in the process of evolution man has lost much of his fur covering and thereby many of the apocrine glands have disappeared and been replaced by eccrine glands that presumably were originally localized to the palms of the hands and the soles of the feet.

The eccrine glands on the frictional surfaces have been shown to be a means of enhancement of frictional contact (Adelman, Taylor and Heglund, 1975). This would be particularly important in primates adapted to an arboreal mode of existence. However, their function would not be thermoregulatory, but would be stimulated by the need to move rapidly from tree to tree, as for example, when being threatened by a predator. A vestige of this function is seen in man in that his glands are readily stimulated by emotional stimuli. However, they also respond to thermoregulatory stimuli and likewise, the sweat glands on the general body surface, whose prime function appears to be the maintenance of body temperature, will also respond to emotional stimulation (Ogawa, 1975). Thus, in the evolution of man, glands originally subservient to one function have developed an

additional function, namely thermoregulation, and they may represent an extension from a localized to a more generalized distribution.

Sweating in Species Other Than Man

The original observation by Kibler and Brody (1952) that cattle sweat led to investigations into the nature of this mechanism. Histologically, the glands appear to be similar to the odor-producing glands in the axilla of man. However, since Kibler and Brody (1952) clearly showed that the glands have a thermoregulatory function, it appeared that apocrine glands have evolved this function in a similar way to the eccrine glands of primates. Studies by Findlay and Robertshaw (1965) revealed that the glands are adrenergic in nature and that in cattle, each hair follicle has one sweat gland associated with it. Studies of other bovid species, such as the sheep and the goat, reveal that not all hair follicles have sweat glands associated with them, and only the larger hairs are thus endowed. The density of sweat glands in the skin of sheep and goats is therefore, much less than that of cattle.

In 1967, Bligh studied sweating from the skin of sheep and noted that heat exposure produced discrete discharges of moisture onto the surface of the skin and that each discharge was followed by a period during which the moisture evaporated. Furthermore, the magnitude of each discharge declined with time, an apparent "fatigue" effect. This is in contrast to the pattern of sweating observed by McLean (1963) in cattle, in which the discharges were relatively small and there is no decline in sweat output between the discharges, giving a stepwise appearance.

In order to further understand differences in sweat gland function between various species of bovids, Robertshaw and Taylor (1969a) studied several species of wild East African bovid and showed that in the small species, sweating was similar to that previously described in the sheep and represented a relatively small amount of heat loss, panting being the major mode of evaporative heat loss, whereas in the larger species, sweating appeared to be the main means of evaporative heat loss, panting being relegated to a minor role. Thus, it appeared that, in the course of evolution, as animals became larger, sweating became more important as an evaporative heat loss mechanism and panting became less significant.

The explanation of this may be found in the observation of Crawford (1962) who demonstrated that the upper limit of panting is determined by the resonant frequency of the respiratory system. This would mean that as the species increase in size, the resonant frequency will decrease and thus, panting as a heat loss mechanism will be constrained by the physical properties of the respiratory system. The way in which this increase in cutaneous evaporation evolved, appears to be a function of the sweat gland

density in the skin. As shown in Table 2, individual glands of the Ayrshire cattle and British Saanen goats secrete at approximately the same rate.

Some studies carried out on the black bedouin goats indigenous to the Mediterranean areas indicated a further type of evolutionary process. These goats because of their color have a relatively high heat load which must be

TABLE 2.
The secretion rate of individual sweat glands
(nl/hr)* from different species

Species	Secretion Rate	Source
<i>Cattle</i>		
Ayrshire	11-16 (thorax)	Hales, Findlay and Robertshaw (1968)
Brahman	60 (scrotum)	Robertshaw and Vercoe (1980)
<i>Goat</i>		
British Saanen	13	Jenkinson and Robertshaw (1971)
Black Bedouin	66 (thorax)	Dmi'el, Robertshaw & Choshniak (1979)
<i>Monkey</i>		
Rhesus	100	Johnson and Elizondo (1974)
<i>Man</i>	450	Foster, Hey and Katz (1969)

*nanoliters/hour

dissipated by evaporative means. In contrast to the sheep studied by Bligh (1967), sweating is an important mode of evaporative loss for this species (Borut et al., 1979). When the secretory function of individual glands is examined, it is noted that the high, evaporative water loss is achieved by a greater secretory ability of each individual gland, although they fail to reach the secretory capability of the eccrine sweat glands of man. Thus, body size and heat load appear to have been selection factors in the evolution of sweating in bovid species.

Other large species, such as the camel, the horse, the rhinoceros and the giraffe (Robertshaw, 1980) also show thermoregulatory sweating. However, there does appear to be a further subdivision of the apocrine glands, in that the adrenergic controlled sweat glands of the bovidae appear to be mediated through alpha-receptors, whereas those of the equidae and camelidae have an adrenergic nerve supply which interacts with postsynaptic beta₂-receptors (Robertshaw, 1980).

It is not clear why different species should have such a fundamental difference as a type of postsynaptic receptors which activate sweat gland secretion. Presumably the ancestors of these different species had a primordial apocrine gland which is different from that of extant species. We

can only speculate as to what that function could have been. The presence of beta-receptors on the sweat glands suggests that originally they were stimulated only by circulating epinephrine, and therefore, sweat secretion was possibly only a feature of exercise, i.e. a condition where epinephrine levels would be elevated. Sweating may have only been relevant in emergency situations and evidence has been provided (Robertshaw and Taylor, 1969b) that exercise-induced sweating in the horse may have a dual component, part of the stimulation being derived by nerve stimulation and part by elevated levels of circulating epinephrine. Such a mechanism does not appear to be present in bovids (Dmi'el, Robertshaw and Chosniak, 1979). Thus, the original gland which may have had either a thermoregulatory or social function may have had no nerve supply and the beta-receptors of extant species may reflect that original type of gland.

Conclusion

A review of the fossil evidence for homeothermy together with an examination of the diversity of strategies for thermoregulation in extant species, particularly evaporative heat loss, provides a basis for an interesting speculation of the factors that may have influenced the development of specific physiological mechanisms for temperature regulation.

References

- Adelman, S., Taylor, C.R., and Heglund, M.C. "Sweating on paws and palms: What is its function?" *Am. J. Physiol.*, 229:1400 (1975).
- Baker, M.A., and Haywood, J.N. "The influence of the nasal mucosa and the carotid rete upon hypothalamic temperature in sheep." *J. Physiol.*, (Lond.) 198:561 (1968).
- Bligh, J. "A thesis concerning the process of secretion and discharge of sweat." *Environ. Res.*, 1:28 (1967).
- Borut, A., Dmi'el, R., and Shkolnik, A. "Heat balance of resting and walking goats: comparison of climatic chamber and exposure in the desert." *Physiol. Zool.*, 52:105 (1979).
- Brody, S. *Bioenergetics and growth*. New York: Reinhold Publ. Co., 1945.
- Crawford, E.C. "Mechanical aspects of panting in dogs." *J. Appl. Physiol.*, 17:249 (1962).
- _____. "Brain and body temperatures in a panting lizard." *Science*, 177:431 (1972).
- Dmi'el, R., Robertshaw, D., and Choshniak, I. "Sweat secretion in the black bedouin goat." *Physiol. Zool.*, 52:558 (1979).
- Findlay, J.D., and Robertshaw, D. "The role of the sympathoadrenal system in the control of sweating in the ox, *Bos taurus*." *J. Physiol.*, (Lond.) 179:285 (1965).
- Foster, K.G., Hey, E.N., and Katz, G. "The response of the sweat glands of the newborn baby to thermal stimuli and to intradermal acetylcholine." *J. Physiol.*, 203:13 (1969).
- Hales, J.R.S., Findlay, J.D., and Robertshaw, D. "Evaporative heat loss mechanisms of the newborn calf, *Bos taurus*." *Brit. Vet. J.*, 124:83 (1968).
- Hiley, P. "How the elephant keeps its cool." *Natural History*, 84:34 (1975).
- Hiley, D.A. "The thermoregulatory responses of the galago (*Galago crassicaudatus*), the baboon (*Papio cynocephalus*) and the chimpanzee (*Pan satyrus*) to heat stress." *J. Physiol.* (Lond.) 254:657 (1976).
- Ingram, D.L., and Mount, L.E. *Man and animals in hot environments*. Heidelberg: Springer-Verlag, 1975.
- Jenkinson, D. McE., and Robertshaw, D. "Studies on the nature of sweat gland 'fatigue' in the goat." *J. Physiol.* 212:455 (1971).
- Johnson, G.S., and Elizondo, R. "Eccrine sweat gland in *Macaca mulatta*: physiology, histochemistry and distribution." *J. Appl. Physiol.* 37:814 (1974).
- Kibler, H.H., and Brody, S. "Relative efficiency of surface evaporative, respiratory evaporative and non-evaporative cooling in relation to heat production in Jersey, Holstein, Brown Swiss and Brahman cattle 5° to 105°F." *Res. Bull. Mo. Agric. Exp. Sta.* #497. 1952.
- McLean, J.A. "The partition of insensible losses of body weight and heat from cattle under various climatic conditions." *J. Physiol.* 167:427 (1963).
- Ogawa, T. "Thermal influences on palmar sweating and mental influence on generalized sweating in man." *Jap. J. Physiol.* 25:525 (1975).
- Robertshaw, D. "Systemic pharmacology of adrenergic activators and inhibitors. Effects on sweat glands. *In Handbook of Experimental Pharmacology*. ed. L. Szekeres, Springer-Verlag, Berlin: 1980.

- _____, and Taylor, C.R. "A comparison of sweat gland activity in eight species of East African bovids." *J. Physiol. (Lond.)* 203:135 (1969a).
- _____. "Sweat gland function of the donkey (*Equus asinus*)." *J. Physiol. (Lond.)* 205:79 (1969b).
- _____, and Vercoe, J.E. "Scrotal thermoregulation in the bull (*Bos sp.*)." *Aust. J. Agric. Res.* 31:401 (1980).
- Schmidt-Nielsen, K. "Desert animals: physiological problems of heat and water." New York: Oxford Univ. Press, 1964.
- Spotila, J.R., Lommen, P.W., Bakken, G.S., and Gates, D.M. "A mathematical model for body temperatures of large reptiles: implications for dinosaur ecology." *Am. Nat.* 107:391 (1973).

The University of Missouri is an equal opportunity institution