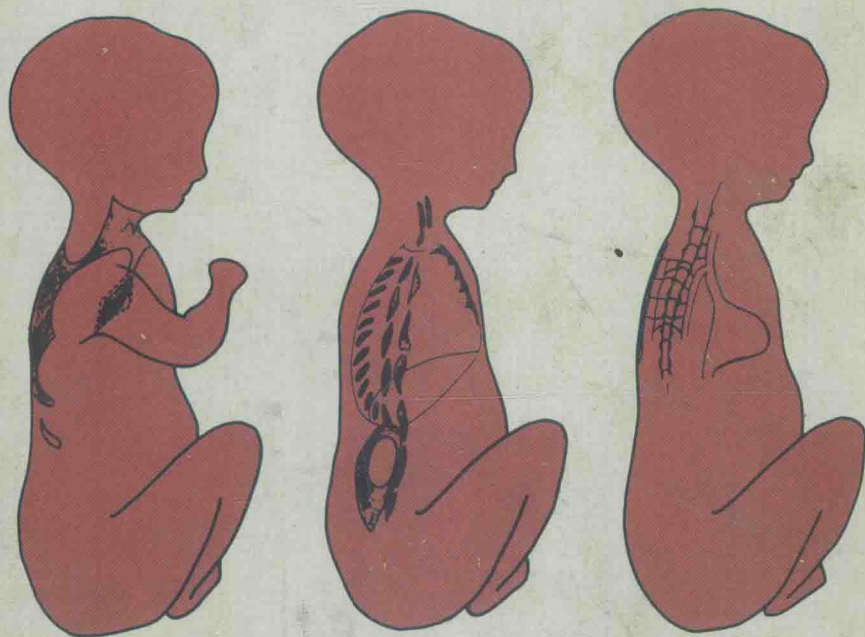


Comparative Physiology of Thermoregulation

VOLUME III

SPECIAL ASPECTS OF THERMOREGULATION

Edited by **G. CAUSEY WHITTOW**



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Comparative Physiology of Thermoregulation

Edited by G. CAUSEY WHITTOW

DEPARTMENT OF PHYSIOLOGY
SCHOOL OF MEDICINE
UNIVERSITY OF HAWAII
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Volume III

Special Aspects
of Thermoregulation



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COMPARATIVE PHYSIOLOGY
OF THERMOREGULATION

Volume III

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PREFACE

This third and final volume of "Comparative Physiology of Thermoregulation" attempts to do three things: It completes the taxonomic organization of the first two volumes, with a chapter on the "primitive" mammals. It deals with special aspects of thermoregulation. Aquatic mammals must be considered in this category because they are the only "warm-blooded" animals that live in a medium which has an enormous cooling power compared with that of air. Torpidity is a dramatic thermoregulatory phenomenon displayed by only certain groups of mammals, while the newborn mammal faces special problems in thermoregulation that distinguish it from the adult. Finally, the last chapter complements the arrangement of the first two volumes by its treatment of the evolution of thermoregulation from the standpoint of physiological systems rather than classes of animals.

It was initially hoped that this three-volume treatise would provide a useful reference work for the comparative physiologist. The reception accorded to the first two volumes suggests that this hope has been largely realized. However, it appears that the books have their greatest appeal to those engaged in the study of physiological ecology, and this lends to the work a currency which was not entirely anticipated at the time of its conception. In retrospect, its most appreciated feature would seem to be the comprehensive nature of the accounts of temperature regulation in different groups of animals, something that is rarely achieved by the published proceedings of symposia.

It is a pleasure to record my gratitude to Mrs. Jane Inouye and Miss Myrna Mew of the Department of Physiology, School of Medicine, University of Hawaii and to the staff of Academic Press for their great help and patience in the preparation of all the volumes.

G. CAUSEY WHITTOW

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I. Introduction

The relationship between the phylogeny of mammals and their homeo-thermic abilities has been an area of considerable speculation. This interest

dates from the latter part of the last century when various workers (de Miklouko-Maclay, 1883, 1884; Semon, 1894; Sutherland, 1897) reported that the body temperatures of monotremes, animals considered to be "placed lowest in the scale of mammals" (Sutherland, 1897), and marsupials were below and more variable than those found for other mammals. When the metabolic studies of Martin (1902) indicated that not only did these animals have lower body temperatures but also much lower rates of heat production than eutherians,* the idea that anatomically primitive mammals were primitive or inferior homeotherms became widely accepted. Subsequent studies on less advanced eutherians such as the edentates apparently confirmed that they also were endowed with only inferior temperature regulating abilities (Wislocki and Enders, 1935; Britton and Atkinson, 1938; Irving *et al.*, 1942) and the idea became established that a low and variable body temperature was generally indicative of a primitive level of homeothermism. Eisentraut (1960) classed mammals as higher or lower warm-blooded animals depending on whether their "activity" body temperature was above or below 36°C, phylogenetically old mammals being placed in the "lower" group.

Initial doubts were cast on the simplicity of this idea when several workers suggested that some marsupials had temperature regulating capabilities equal to those of eutherians (Bartholomew, 1956; Robinson and Morrison, 1957). The issue was still clouded, however, because licking, a supposedly primitive mechanism, was reported to be the principal form of heat dissipation at high temperatures. Recent studies (Dawson, 1969; Dawson *et al.*, 1969; Dawson and Bennett, 1971) have clarified the position of marsupials and shown that some species are excellent homeotherms which utilize similar mechanisms to maintain their body temperatures to those of advanced eutherians. Marsupials, however, do have lower body temperatures and a lower level of standard metabolism than the eutherians (Dawson and Hulbert, 1969, 1970; MacMillen and Nelson, 1969). The problem then is: What is primitive with respect to thermoregulation? There are two aspects to this question; first, the consideration of the level of body temperature under nonstressful conditions; and second, the problem of the stability of body temperature, together with the status of the different mechanisms which are involved in the maintenance of this stability over a wide range of environmental conditions.

"Primitiveness" in homeothermy has been attributed variously to animals with relatively low body temperatures, to those with unstable body temperatures, to those with low levels of metabolism, and to those with deficient

* In this review eutherian, rather than placental, is used as the general descriptive term for the nonmarsupial therian mammals; some marsupials have evolved a chorio-allantoic placenta.

mechanisms for heat loss. In this review these various aspects of thermoregulation are discussed as they apply to the more morphologically primitive groups of mammals. This has been done in order to see if there are patterns of similarity among these animals which enable them to be described, as a group, as primitive homeotherms.

II. Phylogeny of Primitive Mammals

Before going on to discuss thermoregulation and primitive mammals, it is necessary to make some general comments about these mammals and their relationships to each other. Table I contains many of the mammals which are regarded by most modern workers as possessing some basic primitive features (Anderson and Jones, 1967; Walker, 1968). Many of them are also highly specialized and discussion is possible about the applicability of the term primitive. This review, however, is not the place for an argument on semantics, and consequently these groups will be referred to as primitive mammals, but with the full understanding that many qualifications of this designation may apply.

Recent information indicates that the earliest mammals, in the Mesozoic, were much more closely related to one another than was previously thought (Hopson, 1969; Hopson and Crompton, 1969; Parrington, 1971). Contrary to theories of the polyphyletic origin of these mammals from different groups of therapsid reptiles (Kermack, 1967), the evidence now indicates that mammals were derived from a cynodont ancestor, probably within the family Galesauridae in the late Triassic over 200 million years ago. Of this early development and radiation of nontherian mammals there are survivors. These are the three genera of egg-laying monotremes from Australia, the echidnas or spiny anteaters (*Tachyglossus* and *Zaglossus*) and the platypus (*Ornithorhynchus*). The monotremes, in spite of their obvious specialization, have retained many of the features presumed to characterize the earliest mammals, and are therefore uniquely qualified among living tetrapod vertebrates to yield information about the physiology and anatomy of early mammals. There apparently was, however, a very early separation (about 200 million years ago) of the stock leading to the monotremes from that which gave rise to the living marsupials and eutherians, the therians (Hopson, 1969).

The last great radiation has been the radiation of the advanced or therian mammals, which include the marsupials or Metatheria and the placentals or Eutheria. Lillegraven (1969) in his review of the marsupial-eutherian dichotomy in mammalian evolution suggests that the marsupials and eutherians have been distinct for a long time, perhaps since the earliest Cretaceous about 130 million years ago. Another interesting point to come

TABLE I
MAMMALS USUALLY CONSIDERED PRIMITIVE

| | |
|--------------------------|-------------------------------------|
| Order Monotremata | |
| Family Tachyglossidae | Echidnas or spiny anteaters |
| Family Ornithorhynchidae | Platypus |
| Order Marsupialia | |
| Family Didelphidae | Opossums |
| Family Caenolestidae | Rat opossums |
| Family Dasyuridae | Carnivorous "mice" or "native cats" |
| Family Peramelidae | Bandicoots |
| Family Phalangeridae | Possums, Koala |
| Family Phascologyidae | Wombats |
| Family Macropodidae | Kangaroos and wallabies |
| Order Insectivora | |
| Family Erinaceidae | Hedgehogs |
| Family Talpidae | Moles |
| Family Tenrecidae | Tenrecs |
| Family Chrysochloridae | Golden moles |
| Family Solenodontidae | Solenodons |
| Family Soricidae | Shrews |
| Family Macroscelididae | Elephant shrews |
| Family Tupaiidae | Tree shrews |
| Order Dermoptera | |
| Family Cynocephalidae | Flying lemurs |
| Order Edentata | |
| Family Myrmecophagidae | Anteaters |
| Family Bradypodidae | Tree sloths |
| Family Dasypodidae | Armadillos |
| Order Pholidota | |
| Family Manidae | Pangolins |
| Order Tubulidentata | |
| Family Orycteropodidae | Aardvark |
| Order Hyracoidea | |
| Family Procaviidae | Hyrax |

out of Lillegraven's review was his conclusion that the common ancestor of both groups was probably much more "metatherian," i.e., marsupial-like, than eutherian. So while not on the direct line of descent, the more primitive marsupials, such as the smaller opossums and dasyurids, in their mode of life and many structural features, may give a picture of the Mesozoic forms from which the Tertiary mammals have come.

The relationships of the various primitive eutherians are still, to a large extent, unsettled (Szalay, 1968; McKenna, 1969). There appear to be two basic groups among the insectivores but their origins are clouded. The groups comprise on one hand the Erinaceidae, Talpidae, Tenrecidae, Solenodontidae, and Soricidae, and on the other the Macroscelididae and

Tupaiaidae. The Dermoptera are suggested to have affinities with the latter group of insectivores, while the Tubulidentata and Hyracoidea may be related to the condylarths, which were primitive ungulates. Very little is known about the affinities of the Edentata and Pholidota and their origins are uncertain.

Other groups which may be considered primitive are the bats, order Chiroptera, prosimian primates, and some members of other orders, such as the family Aplodontidae among the rodents. In general these groups will not be discussed since their degree of "primitiveness" is questionable. Bats have features which are presumed primitive (Jepsen, 1970) and there are indications that some aspects of their thermoregulation may also represent a less advanced position; they usually have lower metabolic rates than other eutherian mammals (Henshaw, 1970; Poczopko, 1971). However, because of the great diversity of thermoregulating patterns in this most specialized group it is difficult to effectively include them in a generalized discussion of primitive mammals. Several excellent reviews of the thermoregulatory capabilities of bats also have been recently published (McNab, 1969; Henshaw, 1970; Lyman, 1970) and consequently those with special interests in this group should consult these reviews.

III. Body Temperature under Nonstress Conditions

The obvious place to start a discussion of primitive mammals and temperature regulation is with body temperature itself, since this is the controlled variable, the end result of the overall process. Primitive mammals have been reported as having unusually variable body temperatures, in some cases being referred to as "approximately poikilothermic" (Britton and Atkinson, 1938); consequently there are difficulties associated with determining the "normal or desired" range of temperatures. These difficulties, most often, are related to the conditions under which measurements are made. In general, such problems apply to all measurements of body or core temperature (T_b) but become especially important when temperatures are sought for comparisons involving primitive groups. Valid comparisons appear possible when measurements have been made on animals resting in a thermoneutral environment. While these conditions may seem easily obtained this unfortunately is not so for measurements on many wild animals.

A. METHODOLOGICAL CONSIDERATIONS

Deep rectal or colonic temperature (T_{re}) is most routinely used to indicate core temperature. While this may not give an accurate assessment

of the thermal status of an animal under some conditions, no other easily measured single temperature is better. One of the main problems with this type of measurement is with the depth of insertion of the thermometer, thermocouple, etc. Schmidt-Nielsen *et al.* (1966) found that in the echidna (*Tachyglossus aculeatus*) the depth of insertion was very critical, particularly under cold conditions. In this regard the insertion depth of thermometers should be noted when considering some of the early studies which indicated very variable body temperatures in primitive species, e.g., Kredel (1928).

A knowledge of the thermoneutral conditions pertaining to a particular species is important when dealing with primitive animals. While many of the larger advanced mammals have a wide thermoneutral range and also maintain a relatively stable body temperature over a much wider range, the more primitive groups, with perhaps a lower metabolic rate, may have very restricted zones of thermoneutrality (see later discussion); this particularly applies to many of the smaller forms. Lower critical temperatures (T_{cl}) as high as 32°–33°C are possible and measurements made at ambient temperatures (T_a) in the vicinity of 20°C are consequently well outside thermally stress-free conditions. At the other end of the scale, care should be taken to ensure that ambient conditions for measurements are not too hot. While T_a of 30°C may be within the zone of thermoneutrality in many species it may be near the normal body temperature for some of the monotremes. Since these animals are deficient in their ability to prevent overheating, at this T_a their body temperatures rise markedly.

Perhaps the major difficulty which results in considerable problems of interpretation of body temperature measurements is the level of activity of the animals. Periods of intense activity may result in the production of heat at a rate much faster than it can be lost, resulting in a storage of heat and a consequent elevation of body temperature. There are two aspects to the problem: (1) How fast can the body temperature rise during struggling, and (2) how long does it take to return to a steady state after the activity has ceased? The rate of rise is usually more of a problem with smaller animals. Because the metabolism of mammals is related to $W^{0.75}$ (Kleiber, 1932, 1961; Dawson and Hulbert, 1969, 1970) the standard or minimal metabolism per unit weight is much greater in small animals than large animals; a 14-gm marsupial mouse has a standard heat production of 6.4 cal/gm hour while that of a 32.5-kg kangaroo is 0.83 cal/gm hour (Dawson and Hulbert, 1970). Maximal metabolism is likewise related to a similar function of weight (Jansky, 1965; Pasquis *et al.*, 1970). Consequently a burst of activity in a small mammal will produce a relatively larger increase in heat production per unit weight (i.e., volume), and a greater and more rapid rise in temperature, than would occur in a large