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Brian K. McNab

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PHYLOGENY OF MAMMALS

BRIAN K. MCNAB

Department of Zoology, University of Florida, Gainesville, Florida 32611

Living mammals are distinguished from living reptiles in many ways, one of the most striking being in thermal behavior: The former are endothermic homoiotherms and the latter are ectothermic poikilotherms. Such dissimilar behavior reflects differences in the level of metabolism and the presence of a furred or scaled surface. Yet mammals evolved from reptiles, which raises the question of how (and when) the transition from ectothermy to endothermy occurred, assuming that the earliest reptiles, like contemporary species, were ectotherms.

There is an appreciable difference of opinion on the answer to this question. Many biologists, e.g., Martin (1903), Eisentraut (1960), Kayser (1961), and, to some extent, Cade (1964) and Dawson (1973), have suggested or implied that this transition occurred within the Mammalia, because they refer to the "poor" temperature regulation of many living mammals, such as monotremes, bats, sloths, etc., as being "primitive," or at least as occurring in "primitive" mammals. The implication is that in the phylogeny of these mammals no progenitor ever regulated its temperature better. However, others, e.g., Waring et al. (1966), McNab (1970, 1974b), and Kinnear and Shield (1975), have suggested that much of the variation in the temperature regulation of mammals is related to such factors as body size, food habits, and climate. This view implies that the poor temperature regulation of certain mammals is in fact adaptive and not a phylogenetic legacy.

It has been argued recently that the evolution of endothermy occurred in early reptiles, both in the phylogeny of mammals and in the phylogeny of dinosaurs and birds (Bakker 1971, 1972, 1975; de Ricqlès 1974). Bakker cites as evidence predator/prey ratios, posture, and (in agreement with de Ricqlès) bone structure. This view had lead to some polarization pro (Dodson 1974; Ostrom 1974) and con (Bennett and Dalzell 1973; Feduccia 1973; Thulborn 1973), but these papers have neither added evidence in favor of this hypothesis nor persuasively argued for an alternative.

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One of the crucial problems in the evolution of endothermy is the means by which it is accomplished, and with the exception of Cowles (1946, 1958) and Heath (1968), no authors have attempted to state how this transition might occur. In this paper I shall attempt to show how and, I hope, when the transition from ectothermy to endothermy occurred in the phylogeny of mammals.

METHODS AND DEFINITIONS

The proposed analysis depends upon the evolutionary sequence leading from reptiles to mammals. I will therefore rely upon the conclusions of Romer and Price (1940) for the evolution of pelycosaurs and of Hopson (1969) and Hopson and Crompton (1969) for the evolution of therapsids and the origin of mammals.

Body size is the one most important factor determining the level and precision of endothermy (McNab 1970, 1974b); obviously this factor cannot be ignored in a discussion of the evolution of endothermy. It is difficult to estimate body size, especially body mass, from fossils. It is thus necessary to use some indirect measure of body size, the most readily available being skull length. There are many difficulties in using skull length as a measure of body size. For example, reptiles generally have smaller skulls than mammals of the same mass, and in the transition from typical reptiles through mammal-like reptiles to typical mammals there will be a relative increase in skull size. This trend will detract from an estimated decrease in body size when skull length is used. Nevertheless, there is no practicable alternative to the use of the skull length, if some objective, quantitative measure of the change in size is desired. Skull lengths were derived from many original sources, but I depended mainly upon such secondary sources as Romer (1966) and Piveteau (1961). In a few cases the skull lengths of early Mesozoic mammals were estimated from jaw lengths.

Many biologists interested in the evolution of endothermy do not study temperature regulation per se, and therefore it will be of value to define several terms to insure clear communication. We are here concerned with two dichotomies: poikilothermy-homoiothermy and ectothermy-endothermy. The first deals with the constancy of body temperature. If body temperature varies appreciably during the course of a day, an animal is called a poikilotherm; if body temperature remains rather constant, it is called a homoiotherm. Naturally there is a gradation between these two extremes. The second dichotomy refers to the principal source of heat for the body. If it is external, an animal is called an ectotherm; if it is internal, an animal is called an endotherm. Again there is a graded series between these extremes, especially since an active ectotherm may produce heat at a rate equal to that in an inactive endotherm. Nevertheless, the basic question here relates to whether the rates of heat production are sufficient to permit an animal to maintain a body temperature appreciably above that of the environment. Actually, the ability of an animal to maintain such a temperature differential is given (approximately) by the ratio M/C, where M is the rate of metabolism and C is thermal conductance.

Thermal conductance is a measure of the ease with which heat moves from the animal to the environment and thus is a function of such surface properties of the animal as area, thickness of the integument, and peripheral circulation (McNab and Auffenberg 1976).

Many animals do not fit easily into this, or any other, simple classification of thermal behavior. Thus, most homoiotherms are endothermic, but animals that live in a thermally constant environment (like the sea) are trivially homoiothermic, even though they may be ectotherms. Other ectotherms, like basking lizards, are homoiothermic in the presence of the sun. Some endotherms periodically enter a poikilothermous-like state called torpor, but at other times most of these endotherms are capable of maintaining large temperature differentials with the environment.

An intermediate thermal state of considerable significance in the evolution of endothermy is found in large poikilotherms. They gain a degree of homoiothermy from a large mass and a small surface-to-volume ratio (McNab and Auffenberg 1976). The greater the mass, the greater the resistance to a change in temperature, i.e., the greater the thermal inertia. It can be argued that much, if not most, of the heat contained within such an animal of large size is derived from metabolism, and therefore it conceptually is an endotherm, even though it has a very low rate of metabolism. Normally, however, endotherms have high rates of metabolism and consequently maintain much larger differentials with the environment than do ectotherms, although this difference may disappear at large body masses (McNab and Auffenberg 1976).

There is another, fundamental difference existing between endotherms and ectotherms: As environmental temperature falls, the temperature differential maintained by an endotherm increases (because T_b remains constant), whereas the differential of an ectotherm remains constant or even decreases. The increase of ΔT in endotherms depends upon an increase in the rate of metabolism with a decrease in environmental temperature. Thus, at all temperatures and over all body masses, endotherms have higher rates of metabolism than ectotherms. It is therefore convenient to define an endotherm as an organism with a high rate of metabolism. Again, a very large animal may be homoiothermic by virtue of its large size, but it is not necessarily endothermic in the sense of having a high rate of metabolism or of raising its rate of metabolism with a fall in environmental temperature. We can more properly call such an animal an "inertial" homoiotherm (McNab and Auffenberg 1976).

In this paper I am interested in the origin of endothermy, but it shall turn out that one must be concerned with the origin of homoiothermy as well.

ANALYSIS

The Problem

Ectotherms are characterized by low rates of metabolism and high thermal conductances, endotherms by high rates of metabolism and low conductances. So the problem is, How can ectotherms be evolutionarily converted to endo-

therms in a manner such that intermediate stages are viable? This question assumes a greater importance when it is realized that the earliest mammals were very small. Thus, if they were homoiotherms, they must have had very high mass-specific rates of metabolism (i.e., they must have been endotherms).

It seems unlikely that small endotherms could evolve directly from small ectotherms because the low rates of metabolism and high conductances typical of ectotherms must be simultaneously converted to the very high rates and low conductances of small endotherms. Simultaneity is important because a small ectotherm with a low conductance is disenfranchized with respect to its heat source; equally, a small endotherm with a high rate of metabolism and "reptilian" conductance would squander heat in a hopeless attempt to maintain a constant body temperature. (The only small, naked mammal is *Heterocephalus glaber*, which lives underground in a closed, warm burrow [McNab 1966].)

It appears more likely that the evolution of small endotherms from small ectotherms took another, more indirect route whereby there could be a separation of the acquisition of high rates of metabolism from the acquisition of low thermal conductances. Cowles (1958) suggested that a decrease in thermal conductance evolutionarily preceded high rates of metabolism; this can be accomplished by an increase in mass. For example, reptiles weighing more than 10 kg have much lower conductances than those expected by extrapolation from lizards of small size (fig. 1). In fact, the conductances of reptiles are similar to those of mammals at masses between 30 and 100 kg. The low thermal conductances of large reptiles may result from a reduction in peripheral circulation and from a mechanical requirement for thick integuments in large animals. Large mammals, however, have much higher conductances than those expected from weight, apparently as a means of dissipating heat in animals with high rates of metabolism and small ratios of surface to volume.

Large living reptiles tend to be more homoiothermic (i.e., have more constant body temperatures) than small reptiles, due to low thermal conductances and high thermal inertias, even though they remain ectothermic in the sense that they are characterized by low rates of metabolism. But a large body size alone cannot guarantee a constant body temperature: Mackay (1964) showed that a Galapagos tortoise weighing 170 kg had a daily temperature variation of at least 3 or 4° C. Thermal stability can be further improved, of course, by adding insulation (in the form of fur or feathers) to the surface of large reptiles.

The scheme proposed for the evolution of small endothermic mammals from small ectothermic reptiles suggests, first of all, that the reptiles ancestral to mammals developed inertial homoiothermy at a body mass of 30–100 kg. A fur coat was then added, increasing the constancy of body temperature. Small endotherms subsequently were derived by (1) decreasing thermal conductance (i.e., sliding down the mammal curve in fig. 1), and (2) increasing the mass-specific rate of metabolism as body size decreased. Once inertial homoiothermy had been attained, all subsequent stages would have been homoiothermic. A
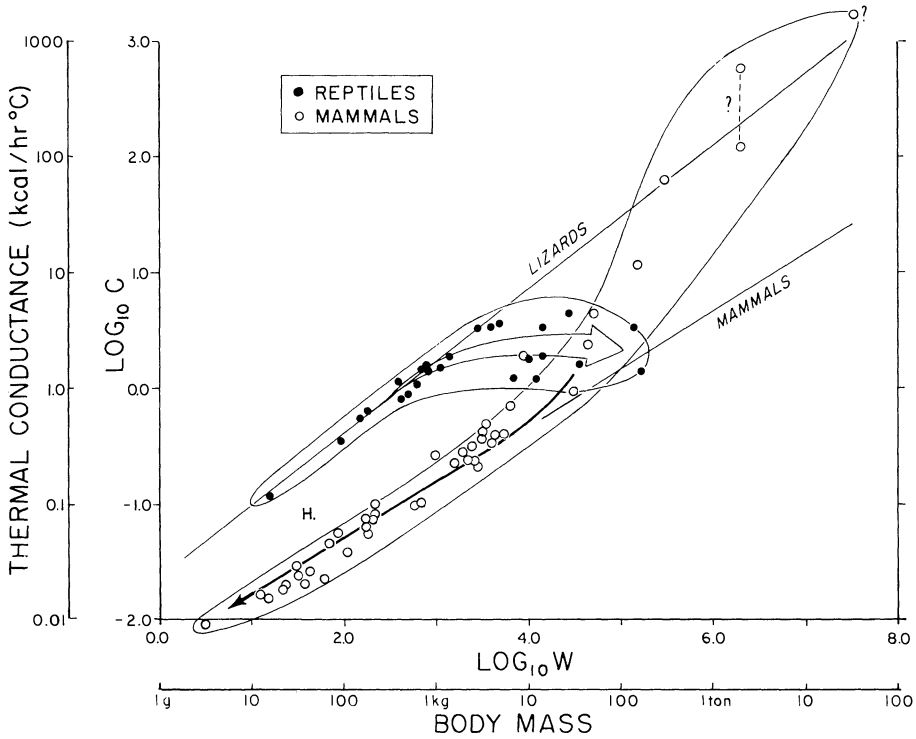
FIG. 1.—Total thermal conductance as a function of body mass in mammals and lizards (modified from McNab and Auffenberg 1976). Thermal conductance in the naked mole-rat, *Heterocephalus*, is indicated by *H*.

detailed examination of the phylogeny of mammals is now required to see whether in fact this pattern of body size occurred.

Phylogeny of Mammals

The phylogeny of mammals according to Romer and Price (1940), Hopson (1969), and Hopson and Crompton (1969) is shown in figure 2. In summary, the stem reptiles (cotylosaurs) gave rise to pelycosaurs, from whence came therapsids and in turn mammals. Unlike the earlier ideas of Simpson (1959) and Kermack (1967), recent information tends to favor a monophyletic origin of mammals (Hopson 1969; Hopson and Crompton 1969).

There are many detailed doubts about the phylogeny presented. The early therapsid interrelationships are not well understood, especially among the Theriodontia, Dinocephalia, and Anomodontia. The Ictidosauria, which are sometimes classified as mammals, but usually as therapsids, may have been derived either from scaloposaurid bauriamorphs or from early cynodonts; Hopson and Crompton (1969) believe the latter to be the case. Prototheria, which includes the living monotremes, has an uncertain origin. But these and

CENOZOIC

CRET.

JURA.

TRIASSIC

PERMIAN

CARBONIFEROUS

U

M

L

PROTOTHERIA

MULTITUBERCULATA

EUTHERIA   METATHERIA

SYMMETRODONTIA   PANTOTHERIA

TRICONODONTA

Peramus

DOCODONTA

Tritylodontidae   *Eozostrodon   Kuehneotherium*

ICTIDOSAURIA

Traversodontidae

MAMMALIA   Cynognathidae

Diademodontidae

Bauriidae

Galesauridae   Ericiolacertidae

Scaloposauridae

Procynosuchidae

BAURIAMORPHA   Whaitsiidae

CYNODONTIA   GORGONOPSIA

THEROCEPHALIA   DICYNODONTIA

TAPINOCEPHALIA

Pristerognathidae

TITANOSUCHIA

EOTITANOSUCHIA   VENYUKOVIAMORPHA

THERIODONTIA   DINOCEPHALIA

ANOMODONTIA

THERAPSIDA   *Dimetrodon*

Caseidae

Sphenacodontidae

Varanopsidae   Edaphosauridae

SPHENACODONTIA   Nitosauridae

EDAPHOSAURIA

OPHIACODONTIA

PELYCOSAURIA

COTYLOSAURIA

FIG. 2.—The phylogeny of pelycosaurs, therapsids, and mammals, according to the opinions of Romer and Price (1940), Hopson (1969), and Hopson and Crompton (1969).

other doubts to the side, more is known of the detailed origins of the Mammalia than of any other class of vertebrates.

An examination of the phylogeny of mammals shows that the sequence passed only through carnivorous lines: Cotylosauria—Sphenacodontia—Eotitanosuchia—Pristerognathidae—Procynosuchidae—Galesauridae—Mammalia (fig. 2). Herbivorous lines, such as Edaphosauria, Anomodontia, Dinocephalia, and presumably Tritylodontidae, although often elaborately developed, ultimately turned out to be evolutionary dead ends. Several lines of carnivorous

therapsids, such as Gorgonopsia, Therocephalia, and Cynognathidae, also left no descendants.

The question remains whether the sequence leading to mammals shows the pattern of an increase and then a marked decrease in body size, and whether such a pattern might give a clue to the origin of endothermy in mammals.

Variation of Size in the Phylogeny of Mammals

Body size, as measured by skull length, generally follows the expected pattern: cotylosaurs were small, pelycosaurs were at first medium-sized and then large, pristerognathids were large, procynosuchids were medium-sized, galesaurids were small, and the earliest Mesozoic mammals were very small (fig. 3). Romer and Price (1940) estimated that most pelycosaurs weighed between 20 and 100 kg. Eotitanosuchids and pristerognathids presumably had masses in the same range. These masses are within the range where the thermal conductances of large reptiles are similar to those of large mammals (fig. 1).

Skull length decreases from about 200 mm in pristerognathids to about 20 mm in the earliest mammals (fig. 3). If the body proportions of mammals were roughly similar to those of pristerognathids, the earliest mammals presumably had a mass of only about $(1/10)^3 = 1/1,000$ that of pristerognathids. That is, if the pristerognathids weighed about 20 kg, these mammals would have weighed about 20 g. However, if pristerognathids had smaller head-body proportions (i.e., if they were more "reptilian" in this character) than the earliest mammals, the fall in body mass would have been even greater. How can this marked fall in mass have contributed to the evolution of endothermy?

A Solution

The small size of cotylosaurs makes it reasonable to suggest that they were classic ectotherms with low rates of metabolism, high thermal conductances, and highly variable body temperatures. Of course, they may have shown behavioral temperature regulation. Moderate and, especially, large pelycosaurs may well have tended to be inertial homoiotherms, given the estimated masses for the large species, which ranged from 50 to 250 kg (Romer and Price 1940). But if the sail of *Dimetrodon* was used for behavioral temperature regulation, as suggested by Bramwell and Fellgett (1973), it may mean that these reptiles had some difficulty in maintaining a constant body temperature, even at a large size. This conclusion—the absence of a constant body temperature—is apparently also shown by bone histology (de Ricqlés 1974).

Eotitanosuchids and pristerognathids may have been inertial homoiotherms. Such a conclusion can be derived with hesitancy from their large masses, but even more clearly from their nonlamellar bone structure (de Ricqlés 1974). Pristerognathids, especially, may have had a fur coat, which would have further contributed to a stable body temperature. However, there is no reason to believe that either group was endothermic in the sense of having a high rate of metabolism.
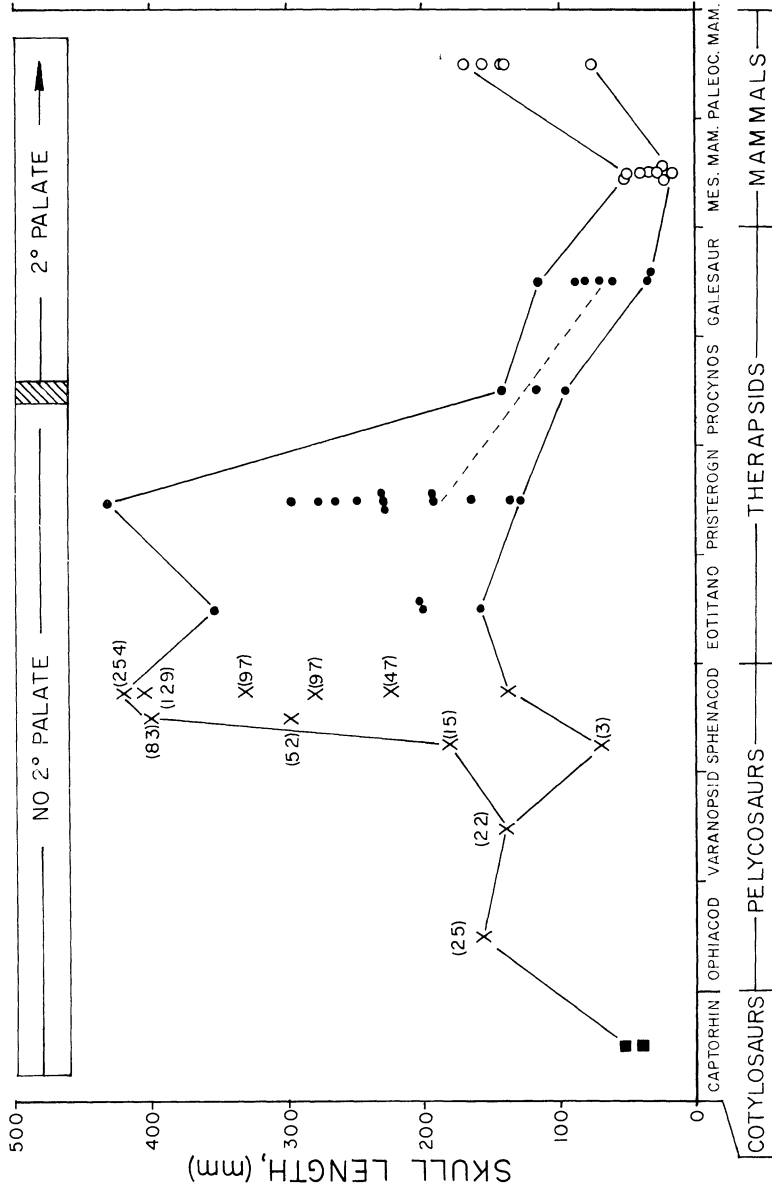
FIG. 3.—Skull length in the phylogeny of mammals. These data were taken from Romer and Price (1940), Romer (1966), and Piveteau (1961). The values in parentheses represent estimated masses in kilograms (Romer and Price 1940). The dashed curve represents the expected pattern of decrease in skull length, assuming that there was no decrease in total metabolism and that galesaurids were endotherms (see text).
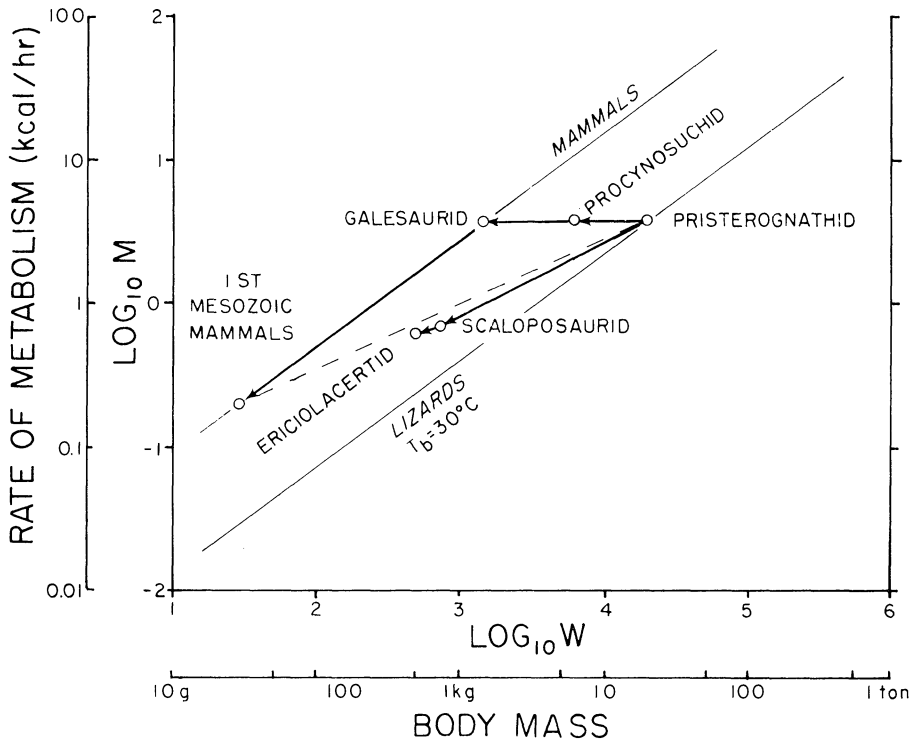
FIG. 4.—Basal rate of metabolism in mammals and standard rate (30° C) in lizards as a function of body mass. The curve for mammals is derived from Kleiber (1961) and that for lizards from Templeton (1970). The position of fossil reptiles and mammals were determined in the following manner. The mass of a pristerognathid ancestor to late cynodonts is assumed to weigh 20 kg and have a skull length of 200 mm. All masses of derived reptiles and mammals were then estimated from (skull length of animal ÷ 200)³ × 20,000. Pristerognathids were assumed to have rates of metabolism that fell on the lizard curve, and the deviations found in procynosuchids and scaloposaurids were assumed equal because of similar state of their secondary palates (see text). The earliest mammals were assumed to fall on the placental curve (see text).

The only way that the thermal independence of an inertial homoiotherm can be transferred to an animal with a small mass is to convert from ectothermy to endothermy. The means by which this conversion probably occurred can be demonstrated as follows. If the total rates of metabolism for both living mammals and lizards are plotted as functions of mass (fig. 4), it can be seen that at any given mass the rate is greater in mammals than it is in lizards. That is, a lizard will have the same total rate of metabolism as a mammal of smaller mass. So there is significance to the conversion of an ectotherm to an endotherm by means of a reduction in size, because the total rate need simply be kept constant. A reduction in mass with a constant total rate means, of course, that the mass-specific rate of metabolism increases, but there is some doubt as to the significance of mass-specific rates for ecological relations (see Kleiber 1970,

1975; McNab 1971). All mass-specific rates, including the exception of turnover rates cited by Kleiber (1975), can be represented as a ratio of $W^{0.75}/W^{1.00}$ $(= W^{-0.25})$, that is, as a total rate divided by a resource "pool." Furthermore, other biological parameters that appear to be inversely proportional to mass-specific rates of metabolism, such as time in torpor, can be fundamentally described as proportional to $W^{1.00}/W^{0.75}$ $(= W^{0.25})$ (see McNab 1974a). Therefore, mass-specific rates of metabolism, as convenient and as widely used as they are, have no unique biological significance. The fundamental way to represent metabolism is with total units, a conclusion that agrees with the intuitive observation that the rate of food consumption by animals increases, not decreases, with mass.

The minimal reduction in body mass required to convert an ectotherm to an endotherm can be estimated, assuming that the total rate of metabolism remains constant. Given the two equations represented in figure 4, one for mammals (Kleiber 1961) and the other for lizards (Templeton 1970), the mass must be reduced to 1/15 to make such a conversion. Thus, if a 20-kg pristerognathid had a rate of metabolism predicted by the lizard curve, a reduction in body mass to 1.3 kg would place its descendant on the mammal curve, if there had been no fall in total rate of metabolism. The minimal decrease in body size needed to make this conversion may actually be somewhat less if the earliest mammals had basal rates less than those found in placentals today. For example, if their rates were equal to those of contemporary marsupials, which is about 70% or 80% of placentals (MacMillen and Nelson 1969; Dawson and Hulbert 1970; McNab, personal observation), the minimal decrease in mass required for the conversion to endothermy is reduced to about 1/9. A fall in mass to 1/15 indicates a reduction in linear dimensions to $(1/15)^{1/3} = 1/2.5$.

The decrease in mass found in the evolution of cynodonts is clearly compatible with the minimal decrease in size required to convert an ectotherm to an endotherm. If it is assumed that galesaurids were endothermic, then their progenitors must have had a skull length approximately equal to $75 \times 2.5 = 188$ mm, which is within the range of skull lengths of pristerognathids (fig. 3). The continued decrease in mass from galesaurids to mammals (fig. 3) may mean that once endothermy was developed, the fall in the rate was proportional to $W^{0.75}$ (fig. 4).

It seems highly unlikely, however, that the total rate of metabolism would remain constant over an appreciable decrease in body mass. If the total rate of metabolism decreases with the fall in mass, the fall in mass (and therefore in linear dimensions) must be greater to complete the conversion to endothermy (fig. 4). The extent to which metabolism decreases will determine the factor by which mass must decrease. For example, if the total rate of metabolism falls 20%, the decrease in mass must be 20% greater than the decrease that assumes a fixed total rate of metabolism. If the pristerognathid weighed 20 kg, the expected decrease in mass would be to 1.1 kg. Or better, if endothermy was attained only with the reduction of body mass to that of the earliest mammals (ca. to 1/1,000), the total rate could have been reduced to only 5.3% of the original value! (This estimate compares with the predicted fall in metabolism

to 0.6% with a reduction in mass to 1/1,000, if metabolism remains proportional to $W^{0.75}$.) Therefore, the decrease in the total rate of metabolism most likely followed the dashed curve in figure 4 or, at least, along some curve between this curve and the one assuming the constancy of the total rate.

Irrespective of the curve that was actually followed, it can be concluded that the fall in mass during the evolution of the advanced cynodonts and early mammals is compatible with a shift from ectothermy to endothermy. This conclusion implies that procynosuchids had rates of metabolism intermediate between those of lizards and mammals (fig. 4).

Ventilation Rates and the Secondary Palate

In cynodonts a morphological confirmation of the shift to endothermy with a decrease in mass can be shown. The rate of ventilation increases with both a shift from ectothermy to endothermy and a decrease in mass (Stahl 1967; Bennett 1973; fig. 5). The evolution of endothermy by means of a reduction of mass in the phylogeny of mammals should consequently involve a large increase in the rate of ventilation (ca. 30 times). Such an increase implies that gas exchange must occur essentially without appreciable pause. It is noteworthy, therefore, that the development of a secondary palate in cynodonts occurs with a decrease in mass (fig. 3), even though a decrease in size alone is not sufficient to produce a secondary palate in lizards. In fact, the family Procynosuchidae represents a transitional stage in the development of a secondary palate (figs. 2 and 3), which probably indicates intermediate rates of ventilation produced by an intermediate level of metabolism (fig. 4) and an intermediate decrease in mass (fig. 3). It should be noted that the incomplete bony secondary palate may have been structurally completed in life by a cartilaginous shelf. This observation does not invalidate the intermediacy of the procynosuchids, but simply suggests that the midpoint of transition from low to high rates of metabolism may have occurred somewhat earlier.

The Endothermy of Late Cynodonts

The simplest conclusion based on this analysis is that the conversion to endothermy was complete with the Galesauridae. If this were the case, all descendants of the galesaurids probably were endotherms, including two lines that became extinct, the Diademodontidae-Traversodontidae-Tritylodontidae and the Cynognathidae, as well as the one that survived, the Mammalia themselves.

Another interpretation of the completion of endothermy is, of course, possible and even more likely. If the total rate of metabolism actually follows the dashed curve in figure 4, or at least a curve between this curve and the one assuming no change in the total rate of metabolism, the conversion to mammalian rates of metabolism was only completed with the decrease in size from galesaurids to mammals. Therefore, any line that increased in mass before
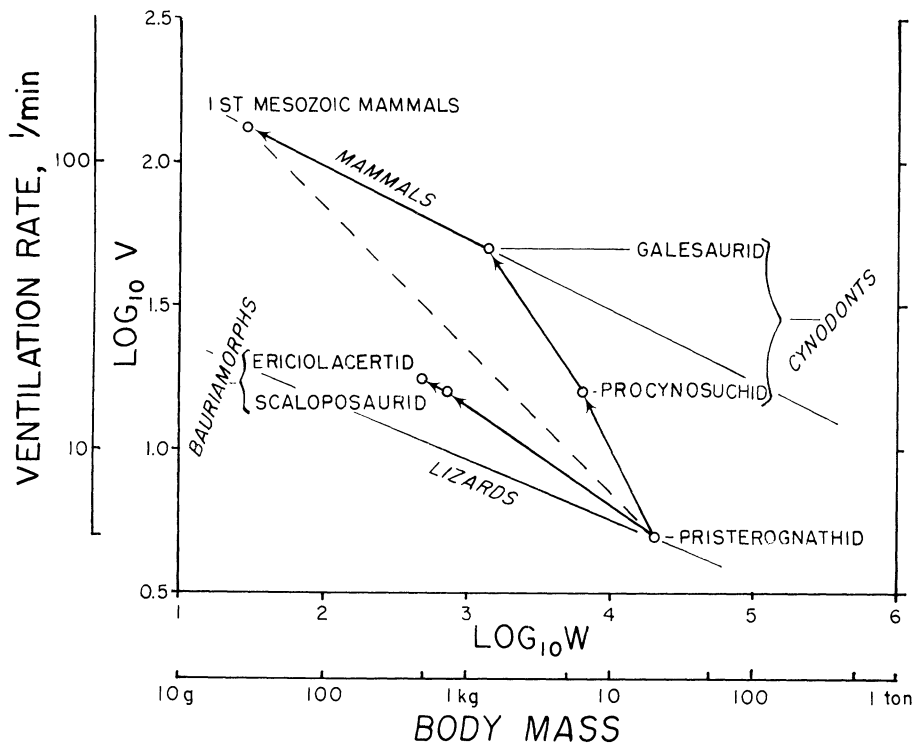
FIG. 5.—Ventilation rates in mammals and lizards as a function of body mass. Curves were taken from Stahl (1967) for mammals and (with modification) from Bennett (1973) for lizards. Bennett's curve was modified by removing the smallest species (for a detailed examination of its peculiarity, see Snyder [1971]) and a value of five breaths/min was added for a 13.7-kg *Varanus salvator* (Ross and Ellis, personal communication) to provide a greater mass range. The resulting curve ($V_{30} = 36.7 \ g^{-0.19}$) showed a significant negative correlation with mass ($r = -.675$, no.-16). Body masses of fossil reptiles and mammals were determined as in figure 4. Ventilation rates were assumed in a manner parallel to that used to determine rates of metabolism in figure 4.

attaining the small size of the earliest mammals must have had only inter-mediate (poor) endothermy. Such a condition may have been found in two lines of cynodonts that were derived from galesaurids and went extinct (fig. 6).

Bauriamorphs and Therocephalians

Two other suborders of therapsids are closely related to cynodonts: Bauria-morpha and Therocephalia. Bauriamorphs, like cynodonts, had a significant decrease in body size (fig. 7A) and a secondary palate, especially in the advanced families Ericiolacertidae and Bauriidae. (Ictidosauria may be a derivative of the Bauriamorpha or of the Cynodontia—in any case, they too had a complete secondary palate.)

Scaloposauridae represents a transitional stage in the development of the secondary palate in bauriamorphs and thus appears equivalent to the Procyno-
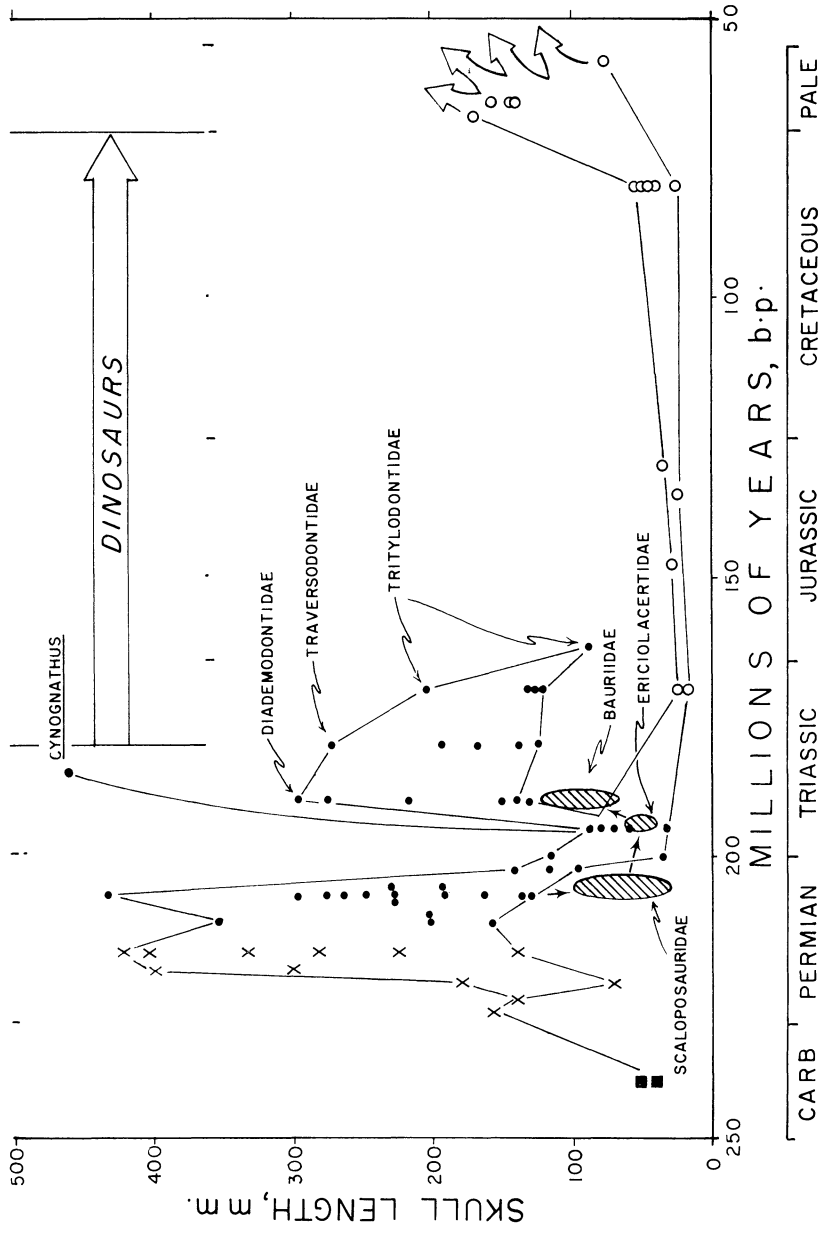
Fig. 6.—Skull length in the phylogeny of cynodonts and mammals as a function of time. The time span of dinosaurs is also indicated, but their skull size is not. Symbols for various groups as in figure 3, with the hatched areas representing the range of skull length in bauriamorphs.

suchidae amongst cynodonts (fig. 7A). Consequently, it is of interest to make a quantitative comparison between these two lines. The mean skull length in Procynosuchidae is about 120 mm and about 60 mm in Scaloposauridae. Therefore, in mass the procynosuchids were about $(120/60)^3$ = eight times larger than scaloposaurids. It can be concluded that these two groups of therapsids attained equivalent rates of ventilation (to produce an intermediate secondary palate) at appreciably different body masses. That is, the increase in rates of ventilation (from those values expected in pristerognathids) was mainly due to the maintenance of a high total rate of metabolism in procynosuchids and mainly due to a decrease in mass in scaloposaurids (figs. 4 and 5).

If bauriamorphs had appreciably lower rates of metabolism than cynodonts (fig. 4), the bauriamorphs of the same or smaller size would have been poorer temperature regulators. This conclusion leads to the following temporal observation: Bauriamorphs apparently arose from pristerognathids somewhat earlier than cynodonts (fig. 6) and attained a small body size earlier than cynodonts. Bauriamorphs thus appeared to have made an earlier attempt at endothermy, but with rates of metabolism between those of living mammals and lizards. Bauriamorphs were later replaced by cynodonts, possibly in part because of the better temperature regulation of cynodonts associated with higher rates of metabolism.

Therocephalians, at least as represented by the advanced family Whaitsiidae, had a body mass more or less equal to that of pristerognathids (fig. 7B). Some whaitsiids, such as *Whaitsia* itself, had a depressed palatal strip, which may have permitted gas exchange in a manner similar to an incomplete secondary palate (Watson and Romer 1956), but the separation of gas flow from the oral cavity, if it occurred, was never completed. There is no compelling evidence of endothermy in therocephalians; at best they were inertial homoiotherms with a fur coat.

Other Therapsids

The other lines of therapsid evolution, namely, the Anomodontia, Dinocephalia, and Gorgonopsia, tended to remain large. The few species that became small did so without the development of a secondary palate. The Dicynodontia, large and small, often had what appears to be a secondary palate formed of the premaxillaries, not of the maxillaries as is usually the case. Consequently, this structure is limited to the anterior tip of the skull and appears to be a means of structurally strengthening the peculiar beak that is found in many advanced species.

Evidence from bone histology (de Ricqlès 1974) suggests that early therapsids (e.g., eotheriodonts and titanosuchids) were intermediate in the conversion of poikilothermy to homoiothermy, while advanced therapsids, such as (large) dinocephalians, dicynodonts, and gorgonopsians, were (inertial) homoiotherms. These advanced therapsids may even have had a fur coat to increase their thermal independence. But there is no reason to believe that they were endotherms.
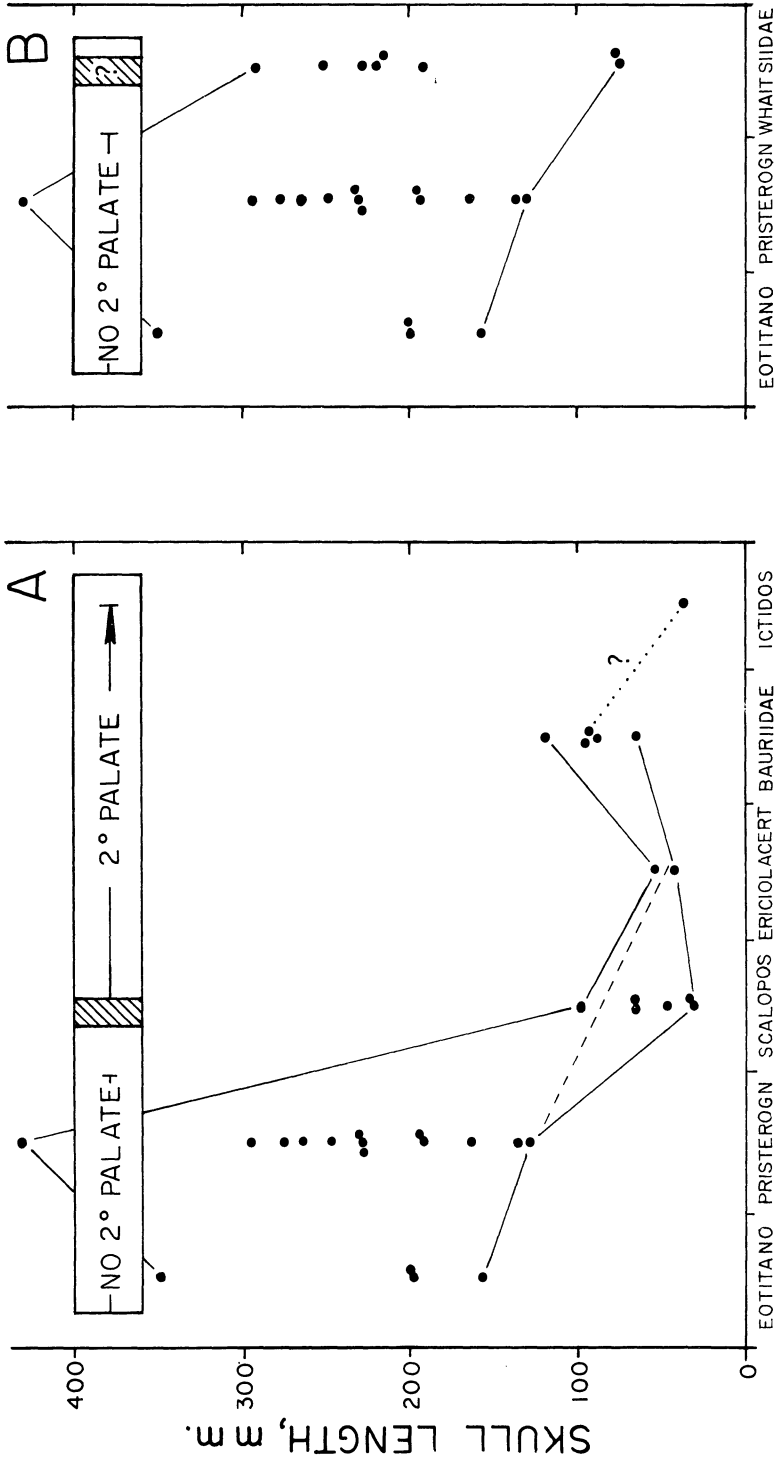
FIG. 7.—Skull length in the phylogeny of bauriamorphs (*A*) and therocephalians (*B*): data from Romer (1966), Piveteau (1961), and various other sources.

DISCUSSION

It is my conclusion that the evolution of endothermy in the phylogeny of mammals occurred first by increasing thermal independence from the environment through an increase in mass, then by modifying the thermal properties of the surface, and finally by decreasing body mass with only a moderate reduction in the total rate of metabolism. A secondary conclusion is that endothermy evolved independently at least three times in reptiles (cynodonts, bauriamorphs, and the line leading to birds). A marginal form of endothermy also evolved in pythons (Hutchison et al. 1966). Furthermore, if pterosaurs really had fur coats, as claimed by Brioli (1941) and Sharov (1971), they may represent an independent line of endothermy, given the small masses of early species. All therapsids other than cynodonts and bauriamorphs may have been homoiotherms (i.e., maintained a reasonably constant body temperature), but there is no compelling evidence that they were endothermic (i.e., had high rates of metabolism).

Bakker (1971, 1972, 1975) and de Ricqlès (1974) have concluded that all therapsids were endotherms. Bakker uses predator/prey ratios and posture as evidence of their endothermy and shares with de Ricqlès the belief that bone histology suggests endothermy in therapsids. Predator/prey ratios require many unproven assumptions on the ecological occurrences of predators and prey and on their comparative probabilities of fossilization. Furthermore, the estimate for food intake in large ectotherms derives from a loose extrapolation of data on *Varanus komodoensis* (see Thulborn 1973). The thermoregulatory significance of posture is unclear, especially as posture relates to the support of a large mass (see Bennett and Dalzell 1973). For example, it can be argued that the placement of the limbs under the body is a means of reducing the energy expenditure associated with the transport of a large mass, not evidence of the high rates of metabolism associated with endothermy, as suggested by Bakker.

De Ricqlès (1974) has an interesting discussion of the significance of Haversian canals in the structure of bone. He makes it clear that this structure is correlated with body size, growth rates, and age. If the presence of this secondary structure is in fact related to high rates of metabolism (endothermy), as de Ricqlès and Bakker suggest, it should be most highly developed in small mammals and in passerine birds, because these groups have the highest mass-specific rates of metabolism (which are the rates that de Ricqlès is concerned with). But de Ricqlès makes the following statement: "Again, an endotherm specialized in a very small body size, will not generally show in its skeletal histology any clear evidence of its very high metabolism because its overall growth rate will be low. This can be seen in bone structures of some mammals (shrews, small rodents) and birds (passerines). ... Only bones from medium-sized to large animals can show histological features pertaining to their pattern of thermal physiology and metabolic activity" (p. 60). Furthermore, in reference to ectotherms he states, "Only large sea turtles can sustain rather high rates of growth during early life ..., and they have an incipient endothermy probably caused by continuous muscular activity required for active swimming. ... It is indeed noteworthy that, among living reptiles, those

big turtles have the most elaborate bone tissues, with ... some Haversian substitution in old, large individuals. ... Tunas and swordfishes are among the largest teleosts, fast moving and possessing a kind of endothermy. ... Again, tunas show a ... rather extensive Haversian substitution ... in clear contrast to most other teleosts" (pp. 60–61).

It seems perfectly clear that de Ricqlès (1974) is describing a condition in which Haversian substitution is correlated with thermal constancy (i.e., homoiothermy) and not with endothermy. This conclusion would explain why Haversian substitution is not characteristic of small endotherms, but is found in large ectotherms to some extent. This interpretation may also explain why dinosaurs had many secondary osteons: They were inertial homoiotherms. In fact, it can be argued (McNab and Auffenberg 1976) that dinosaurs had rates of metabolism lower than those extrapolated from lizards, because if dinosaurs had the high rates assumed by Bakker (1971, 1972) they would have run the risk of overheating. Note again that large animals tend to be naked, pre-sumably to reduce heat storage. Mammals may be limited to smaller masses than dinosaurs because of the commitment of mammals to high rates of metabolism.

The derivation of mammals from reptiles raises the question of how simul-taneous was the acquisition by mammals of the distinctive characteristics that today separate them from reptiles, namely, the squamosal-dentary jaw joint, fur coat, homoiothermy, endothermy, viviparity, and lactation. Some degree of homoiothermy has existed since at least the Middle Permian (early theriodonts and dinocephalians), based on the evidence of bone structure. The acquisition of a fur coat appeared at least in the early Triassic (galesaurids) but more likely in the Middle Permian (pristerognathids and late dinocephalians); it was probably associated with the attainment of effective inertial homoiothermy. The shift to endothermy probably occurred at the end of the Permian (procy-nosuchids and scaloposaurids) or the beginning of the Triassic. The mamma-lian jaw articulation—that is, the beginning of the taxon Mammalia—is first recorded in the late Triassic. Therefore, homoiothermy preceded mammals by as much as 40 million yr, a fur coat preceded mammals by as much as 35 million yr, and endothermy preceded mammals by as much as 25 million yr.

Hopson (1973) argued that the evolution of mammalian reproduction, as characterized by a small egg, altricial young, and elaborate parental care (but not necessarily viviparity), was the consequence of the evolution of a small body size and endothermy. A small body size requires a reduction in egg size, a reduction that is mainly accomplished by a reduced yolk mass, which in turn limits the degree of development possible in an embryo without a nutritional supplement. The shift from a reptilian form of reproduction to this early stage of mammalian reproduction apparently was not completed until late in the evolution of mammals, as is shown by the observation that late cynodonts, like living reptiles, were born with a functional dentition. The earliest mammals, however, show tooth replacement, indicating that their newborn young may have already depended upon lactation. This is essentially the stage presently occupied by monotremes and the one thought to be ancestral to marsupials and placentals. In fact, Lillegraven (1975) has suggested that therian ancestors

common to marsupials and placentals may have first evolved viviparity. Whatever the timing of the appearance of viviparity, Hopson (1973) suggests that it was a later, secondary consequence of the interaction among body size, endothermy, and the attainment of mammalian reproduction. The thesis of this paper, namely, that the evolution of endothermy was functionally connected with the reduction in body size, further emphasizes the tight interaction among these factors.

One of the most important questions that arises out of the view that the evolution of endothermy is associated with a decrease in size is, Why was there such a radical decrease in size? The decrease in cynodonts and bauriamorphs had an ecological, rather than physiological, cause. Prey size correlates positively with predator size among vertebrate carnivores (Rosenzweig 1966; Schoener 1967; Ashmole 1968; Erlinge 1969). It can be concluded that the evolution of a small body size in carnivorous therapsids was associated with, or produced by, a shift in food habits, at first from large to small vertebrates and, as the decrease continued, from small vertebrates to invertebrates, especially insects. This shift in prey selection may have issued from competition with the number of large, terrestrial carnivores (such as *Cynognathus*, therocephalians, gorgonopsids, and various thecodont derivatives, including ultimately the carnosaurs) and from a paucity of predators on small vertebrates and on invertebrates.

The question remains, however, why the evolution of a small body size lead to the evolution of endothermy in mammals but not in the evolution, say, of small lizards. This difference was due to at least two factors. One is that advanced therapsids were already committed homoiotherms, albeit a homoiothermy produced primarily by a large mass and a modified integument. The only way that homoiothermy can be maintained in a small mass is to convert to endothermic energetics. It may be that once a physiological commitment to homoiothermy is made, it is difficult, if not impossible, to reestablish true ectothermy. (Note that no living mammals are truly ectothermic, except possibly during periods of torpor, but even temperate bats arouse from torpor with disturbance or at unacceptably low ambient temperatures, a behavior well beyond the capacity of a frog or lizard.) The second factor of importance is that in the evolution of mammals there was a shift from diurnal to nocturnal habits (Jerison 1971), a conclusion partly based on the observation that mammals are the only major vertebrate group generally lacking color vision. Therefore, the combination of a commitment to homoiothermy, a reduction in body size, the switch to a mammalian form of reproduction, and a shift to nocturnal habits reinforced the trend to endothermy. Endothermy permitted mammals to exploit nocturnal prey well beyond the capacity of anurans and the (presumably) few nocturnal lizards. Most mammals remained small and nocturnal for about 100 million yr (fig. 6) when, with the extinction of the dinosaurs, they were now free to exploit the range of habits previously denied them.

SUMMARY

The evolution of the endothermy of mammals can be traced to the ectothermy of early reptiles. It is suggested that small endotherms cannot be

directly derived from small ectotherms because of the requirement for the simultaneous change in thermal conductance and the rate of metabolism. Instead, small ectotherms probably gave rise to large ectotherms (thereby increasing thermal inertia), a fur coat may have been added to increase thermal stability, and a decrease in size with only a modest decrease in the total rate of metabolism converted "inertial" homoiothermy to endothermy. Measurements of skull size in cynodont therapsids conform to this suggestion. A secondary palate is formed in cynodonts during the decrease in body size and is interpreted as a correlate of increased ventilation rates produced by a decrease in size and a conversion of ectothermy to endothermy.

A decrease in size and the formation of a secondary palate also occurred in bauriamorphs, which suggests that they too independently evolved endothermy, although it may not have been as effective as that developed in cynodonts. Other therapsids apparently were ectotherms, although a large body size may have contributed to an "inertial" homoiothermy.

It is concluded that many of the characteristics that distinguish mammals from reptiles, including endothermy, viviparity, and even lactation, may be related to the marked decrease in body size that occurred in the evolution of mammals from advanced therapsids. The reduction in body size combined with an appreciable temperature independence may have permitted cynodonts to exploit nocturnal insects as a food resource.

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