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# The Metabolic and Thermoregulatory Status of Therapsids

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## Introduction

Endothermy, the internal production of heat, entails essentially constant high rates of metabolism that are costly in energy: birds and mammals typically consume at least ten times as much food as do ectothermic vertebrates. Independently attained in the mammalian and avian lineages, endothermy required quantitative and qualitative changes in nearly all systems related to energy utilization. Its acquisition involved major alterations in anatomy, physiology, behavior, and ecology. In view of its costs, the advantages of endothermy are not fully understood. Various authors have dealt with such desirable attributes as high body temperature (Heinrich, 1978), homeothermy (Crompton, Taylor, and Jagger, 1978), and expanded behavioral capacity (Bennett and Ruben, 1979); while others have noted that ectothermy has compensatory advantages of its own (e.g., Pough, 1980a). What is clear is that an early commitment to endothermy was made in two vertebrate lineages and that the subsequent radiations of those lineages have been very successful.

The question arises as to whether or not the reptilian ancestors of mammals and birds were also endothermic. There has been much recent debate about the existence of endothermy in dinosaurs (see Thomas and Olson, 1980), but it is the therapsid-mammalian lineage with which are concerned. An inquiry into the thermoregulatory status of therapsids is desirable not only because of its bearing on mammalian evolution, but also because of the significance of therapsids as a major faunal component in the late Paleozoic and early Mesozoic. The Therapsida com-

prise one of the largest and most diverse of the reptilian radiations, dominating vertebrate terrestrial communities from the mid-Permian through the Early Triassic. The diversity of body sizes and feeding types reflects occupation of a wide variety of environments and ecological niches. The cause of their decline is not known, but their direct descendents, the Mammalia, survived and comprise a still more diverse and successful group.

It is obviously difficult to ascertain physiological characters from dead animals. It is even more difficult to infer those characters from fossilized bones. There is consequently little agreement about the acceptability of various characteristics that have been advanced as evidence of thermoregulatory status, but, in contrast to the often acrimonious dissension about endothermy in dinosaurs, there is rather remarkable agreement that the advanced therapsids were in some degree endothermic. This view was first advanced by Brink (1956) in a paper that, while highly speculative, was influential in reorienting thought about the anatomical and physiological capacities of these animals. Others have also advocated some endothermic status for therapsids (Olson, 1959), 1971; Van Valen, 1960; Reed, 1960; Simpson, 1959; Parrington, 1967; Heath, 1968; Hopson, 1969, 1973; de Ricqlès, 1969b; Geist, 1972; McNab, 1978; Benton, 1979; Hotton, 1980; Baur and Friedel, 1980). In contrast, Crompton, Taylor, and Jagger (1978) maintain that endothermy was in fact a mammalian invention and that therapsids were ectothermic. Bakker has suggested that therapsids were essentially ectothermic (Bakker, 1971), that they were essentially endothermic (Bakker, 1975), and that they had a metabolic status intermediate between ectothermy and endothermy (Bakker, 1980). His work illustrates the elusiveness of the subject. As yet there has not been a concerted effort to reconcile different arguments. Here we review the assorted evidence and arrive at our own evaluation.

In order for an anatomical structure or other criterion to be diagnostic of a high metabolic rate or of endothermy, it must satisfy at least the following three conditions: it should have a clear and logical association with high rates of metabolism; it should not be explicable in terms unrelated to high levels of metabolism; and it should be absent in ectotherms. We have used these conditions to evaluate eight lines of reasoning that have been applied to the question of therapsid thermoregulation: the histological struc-

ture of therapsid bone; the pattern of posture and limb support; the presence of hair; brain size; other anatomical features, including the presence of a diaphragm, a turbinal complex within the nasal cavity, a bony secondary palate, and a parietal foramen; predatory/prey ratios of therapsid communities; biogeographic distribution of therapsids; and the comparative physiology of monotremes and therians.

## Evidence for Endothermy in Therapsids

### *Histological structure of bone*

A great diversity of organizational types of bone is found in extant and extinct vertebrates. Two types of compact bone have been recognized, differing quantitatively in their fibral organization and degree of vascularization (Foote, 1916; Gross, 1934; de Ricqlès, 1969a). In one type, currently termed *lamellar-zonal*, compact bone is formed principally by periosteal deposition. Primary osteons are few. The bone has a layered appearance from which growth lines are sometimes adduced, and is poorly vascularized. In the other, termed *fibro-lamellar*, most of the matrix is deposited by numerous primary osteons, producing a woven fibrous appearance. Fibro-lamellar bone is well vascularized and is often reworked into extensive Haversian systems (secondary bones). However, there are numerous intermediate patterns that make clear distinctions difficult. Bone type varies with such factors as the aquatic, aerial, or terrestrial habits of the animal, body size, age of the individual, and area of bone examined (de Ricqlès, 1976b, 1977).

Differences in bone structure have been correlated with the taxonomic position of different vertebrate groups (de Ricqlès, 1969a, 1972a, b). Lamellar-zonal bone is found in most ectothermic vertebrates such as amphibians and extant reptiles. Fibro-lamellar bone is present in mammals and birds. Bone from most therapsids resembles that of modern mammals more closely than the bone of extant ectothermic reptiles. Pelycosaurians possessed typical lamellar-zonal bone (Enlow and Brown, 1956, 1957, 1958; Peabody, 1961; Enlow, 1969; de Ricqlès, 1974, 1978a). The diaphyses of their long bones show growth rings and are poorly vascularized. The only osseous tissue with a fibro-lamellar structure is found in the neural spines of some species. In contrast, the bony tissues of therapsids as a group show considerably more vascularity and different types of structural organization (Enlow and Brown, 1956, 1957, 1958; de Ricqlès, 1969b,

1972c, 1978a, b). There is, however, considerable diversity among therapsids. Bone from the eotheriodont *Biarmosuchus* is only slightly more vascular than that of pelycosaurs (de Ricqles, 1974), and the gorgonopsian(?) *Watongia* had typically lamellar-zonal bone (de Ricqles, 1976a). The anomodonts possessed several types of fibro-lamellar bone, each given its own designation. A common type has a very dense, thickened, and well-vascularized cortex, reminiscent of that of modern artiodactyls. Within some titanosuchids and dicynodonts, distinct growth rings are apparent. In the more advanced therapsids, and therocephalians, bauriamorphs, cynodonts, and tritylodonts, the bone has a more typically fibro-lamellar organization. Bone in these groups may be composed of very numerous and densely packed osteons and may show considerable Haversian substitution. Considerable differentiation is found among advanced therapsid groups.

Fibro-lamellar bone has been associated with endothermy and lamellar-zonal bone with ectothermy (de Ricqles, 1969a, 1972a, b). The relationship of bone histological structure to thermoregulatory status are not direct and are consequently controversial. As bone is not itself a thermogenic tissue, the presence of highly vascularized and metabolically active bone is not *a priori* evidence of endothermy. Nor is absence of vascularity necessarily indicative of ectothermy, since small mammals and birds (under 1 kg in body mass) lack fibro-lamellar bone. De Ricqles (1976a, 1978a, 1980) has maintained that fibro-lamellar bone is associated with rapid growth that requires rapid deposition and extensive reworking of primary bone tissue. He believes that such rapid growth is possible only in systems with the high metabolic rates associated with endothermy. Thus the primary correlation is held to be between growth rate and bone structure. It has also been suggested that with a higher rate of metabolism there is accelerated mobilization of calcium and phosphate salts from bone tissue. The high vascularization of fibro-lamellar bone, with its extensive Haversian network of vessels, might seem to permit more rapid release and deposition of these molecules (Bakker, 1975), but calcium can be released from bone very quickly even in ectotherms (Ruben and Bennett, 1981) and is probably rapid regardless of bone type. Diversity of bone types in therapsids may reflect a range of thermoregulatory strategies. De Ricqles (1978a) believes that the anomodonts were not stable endotherms, whereas the advanced therapsids were endothermic. These are reasonable

conclusions if indeed bone structure indicates a particular kind of thermoregulation. Some workers (Bouvier, 1977; Reid, 1981) dispute these correlations. There are indeed some disquieting discontinuities in these patterns, such as the absence of fibro-lamellar bone in small (and rapidly growing) endotherms and its presence in a labyrinthodont (Enlow, 1969). It is clear that the bone of therapsids is very different from that of their pelycosaurian ancestors and is more like that of their mammalian descendents. We believe that this line of evidence is suggestive of endothermy in advanced therapsids. However, because correlation between these characters and thermoregulatory status is not direct, and the bone of living endotherms and ectotherms does not separate into distinct and mutually exclusive types, we are inclined to regard this line of reasoning as inconclusive.

#### *Posture and limb support*

Limb suspension has been used as evidence both for and against endothermy in therapsids. Heath (1968) and Bakker (1971) agree that an erect posture, with limbs held vertically and directly under the body, is evidence for endothermy. Heath maintains that in contrast to the sprawling limb suspension characteristic of most modern reptiles, therapsids stood with a "fixed pillar stance." He argues that this fully erect stance is energetically more expensive because of increased muscle tonus, and is in fact a major source of heat production. Increased heat production from this source is seen as the cause of therapsid endothermy. Bakker, on the contrary, argues that therapsids had a sprawling, not an erect, limb suspension, and that in consequence they were ectothermic, being rather similar to modern monitor lizards in their thermoregulatory capacities. Bakker does not, however, maintain that there is a direct causal connection between posture and metabolic rate.

The purported associations between limb support and thermoregulatory pattern have been criticized elsewhere (Bennett and Dalzell, 1973; Feduccia, 1973). Contrary to Heath's opinion, mammalian endothermy does not depend primarily on heat production by skeletal muscle. Liver, kidney, brain, and heart metabolism account for the major portion of total resting rate of heat production. At rest, skeletal muscle tissue has a relatively low utilization of energy and a correspondingly small effect on total metabolic rate. It is doubtful that endothermy or a greatly increased metabolic rate could have been

achieved by muscular rearrangements alone. Without a causal connection, the associations of posture and thermoregulation are only correlations that are not distinct among modern animals. For instance, chameleons and crocodylians, strict ectotherms, possess a semi-erect stance, intermediate in condition between sprawling and fully erect posture (Bakker, 1971). So do modern monotremes, which are competent endotherms. Jenkins (1970, 1971) presents evidence that advanced therapsids (cynodonts) also had a semi-erect stance (contrary to both Bakker and Heath). Were they ectothermic as crocodylians are or endothermic as monotremes? Given the controversy concerning the actual form of limb suspension in therapsids and the tenuous associations between posture and thermoregulation, we believe that these arguments are also inconclusive.

### *Hair*

The discovery of therapsid hair would probably be the most unequivocal and decisive evidence for therapsid endothermy. The presence of hair is one of the most diagnostic mammalian traits and is clearly linked with thermoregulation. Such insulation would be primarily beneficial to an animal with an internal heat source in a cool environment. It might also serve as a shield against solar radiation and thus help prevent overheating. The most commonly cited evidence suggesting the presence of hair or hairlike structures are foramina on the facial portion of skulls of many theriocephalians, gorgonopsians, and cynodonts (see Van Valen, 1960, for references). These foramina have been interpreted as passages for nerves and blood vessels supplying rostral sensory vibrissae (Watson, 1931; Broili, 1941; Brink, 1956), which Broili and Brink contended would indicate hair on the rest of the body. However, rostral foramina do not necessarily indicate the presence of vibrissae. Similar foramina are present in the skulls of living ectotherms whose scaly skins lack both vibrissae and hair (Estes, 1961, 1964); in the lizard *Tupinambis*, rostral foramina are almost identical in shape, number, and distribution to those of the cynodont *Thrinaxodon*. Nor is it clear that sensory hairs on the snout indicate a pelage. We do not understand the origin of hair, but if its initial function were sensory, it is quite possible that vibrissae reflect the primitive condition and so could have appeared long before an insulative pelage had evolved.

Thus there is no good evidence that therapsids

possessed either vibrissae or pelage. On the contrary, a remarkable sample of fossilized skin from the dicynodont *Estemmenosuchus* shows neither hair impressions nor hair follicles (Chudinov, 1970). The epidermis of the skin was smooth and undifferentiated and lacked scales. The skin was well supplied with glands and was probably soft and pliable. No fossil traces of skin have been found in therapsid genera closer to the mammalian condition.

### *Brain Size*

In relation to body size, the brains of mammals and birds are approximately ten times greater in volume than those of extant reptiles (Jerison, 1973; Hopson, 1980). It has been suggested that the greater levels of activity associated with high metabolic rates require larger brain capacities than are found in modern reptiles (Feduccia, 1973), and that high metabolic heat production may be a precondition for neocortical elaboration (Bakker, 1980).

Cranial volume has been calculated for only about six cynodonts and one dicynodont (Jerison, 1973; Quiroga, 1979, 1980; Hopson, 1980). The encephalization coefficients (= ratio of observed value to a typical value for an advanced mammal of equal size) in these skulls are about 0.1–0.2, that is, ten to twenty percent of modern mammalian volumes. These cranial capacities are similar to encephalization coefficients of monitor and teiid lizards, which are known to be intelligent and active animals but are strictly ectothermic. Jerison (1973) believes that therapsids were largely still reptilian in their degree of brain evolution. Hopson agrees that their brains are more reptile-like than mammal-like (Hopson, 1969), but interprets their degree of brain development as indicating an intermediate status (Hopson, 1980).

Encephalization coefficients reported for Mesozoic mammals exceed 0.2, but are not substantially greater than those of therapsids (Jerison, 1973; E. Allen, personal communication.) Thus the attainment of mammalian status was not accompanied by a quantum jump in brain size. Comparison of brain size of therapsids and early mammals provide no evidence of thermoregulatory modes.

### *Other Anatomical Features*

Other anatomical features proposed as indicators of high metabolic rates and endothermy in therapsids include a muscular diaphragm, bony secondary palate, nasal turbinal complex, and loss

of the parietal foramen. The first three features are associated with ventilation and the provision of air to the lungs. It was on the basis of these structures that Brink (1956) originally claimed endothermy in therapsids. The oxygen extraction efficiencies (ratio of volume of oxygen removed to volume of air ventilated) of modern reptiles and mammals are quite similar (Bennett, 1973; Wood and Lenfant, 1976). Mammals must, therefore, exchange considerably more air to meet their metabolic requirements. The following alterations in ventilatory mechanisms within the mammalian ancestry might well have been associated with the attainment of endothermic metabolic rates.

#### DIAPHRAGM

The muscular diaphragm is the primary means of ventilation of mammalian lungs, and its presence in therapsids might signify increments in ventilation rates necessary to support higher metabolic rates. Brink (1956) inferred its presence from the reduction of the lumbar ribs among advanced theriodonts; in both cynodonts and bauriamorphs, the lumbar ribs become greatly shortened, and the rib cage assumes a more typically mammalian form.

The reduction of lumbar ribs give the skeletons of advanced therapsids a more mammal-like appearance, but it need not be associated with diaphragmatic breathing and endothermy. Rather, the reduction of lumbar ribs might be better correlated with locomotory refinements. Late theriodonts were developing capacities for greater activity and agility, which involved skeleto-muscular modifications related to rotation and flexion of the spinal column. Nor does the presence of a diaphragmlike mechanisms necessarily indicate endothermy. Several living reptiles, including crocodylians and some teiid lizards, possess diaphragmlike structures (for summary, see Goodrich, 1930, pp. 640–42). These structures are not homologous to the mammalian diaphragm, but they do function in ventilation although their possessors are clearly ectothermic.

#### BONY SECONDARY PALATE

In animals with confluent nasal and buccal cavities, ventilation may be blocked when the mouth is full, which may be expected to embarrass the respiration of animals with high metabolic rates. It is argued that the separation of air and food passages by the bony secondary palate has obviated this problem for mammals, and

that the similar palate of advanced therapsids is therefore evidence of more continuous ventilation demanded by endothermic metabolic rates (Brink, 1956; McNab, 1978). However, living tetrapods other than mammals do not support this line of argument: a bony secondary palate is present in the ectothermic crocodylians and teiid lizards, but is lacking in the endothermic birds. Separation of the ventilatory stream is equally effective with a fleshy partition, which is present in many modern ectotherms. The primary function of the bony palate appears to be masticatory, as it serves as a platform for manipulation of the food by the tongue.

#### NASAL TURBINAL COMPLEX.

The nasal cavities of advanced therapsids approach a mammalian condition (Parsons, 1970). Casts of the nasal cavities of advanced theriodonts (*Diademodon*, Watson, 1931; *Nyctosaurus*, Hopson, 1969; *Thrinaxodon*, Brink, 1955) show clear points of attachment of extensive ethmo-turbinal bones or cartilages. Cynodont nasal cavities are more highly modified than those of other therapsids. The primary palate has been reduced, and the internal space is capacious enough to have permitted considerable elaboration of turbinal structures. Turbinals in modern mammals are covered with a moist epithelium and serve two primary functions, namely the conditioning of air incurrent to the lungs and the reclamation of water vapor from exhaled air. External air is warmed (or cooled) and humidified during its passage through the turbinal complex and is filtered by these structures so that dust and other debris does not enter the lung tissue. During exhalation, water is condensed on the turbinals as a result of cooling in the nasal cavity (Schmidt-Nielsen, Hainsworth, and Murrish, 1970), and is absorbed rather than being lost to the environment. Turbinals do not have any obvious function other than air conditioning. Their size is unrelated to the excellent olfaction of mammals, which is localized in rather small, nonturbinal areas of the nasal cavity. Turbinals are absent in living reptiles, which instead possess a series of conchae that are much less elaborate in form (Parsons, 1970).

Since the turbinals serve primarily to warm inspired air and to conserve water in living mammals, and since they are totally lacking in living ectotherms, we believe that the presence of complex turbinal structures constitutes the best anatomical evidence of endothermy in therapsids.



The parietal foramen lies on the midline of the skull between the parietal bones, and is the aperture through which the parietal eye gains access to the external environment. The parietal eye is part of the epiphyseal complex that includes the pineal body, which gives evidence of its presence in ancient fossils by distinctive sculpture on the ventral surfaces of the parietal bones near the foramen.

A parietal foramen, accompanied by a complete epiphyseal complex, is manifest in such conservative living reptiles as the rhynchocephalian *Sphenodon* and some lizards. The foramen and associated sculpture are present in all primitive tetrapods including captorhinomorphs, pelycosaurs, and most therapsids, which are therefore presumed to have had a complete epiphyseal complex. In the course of evolution, the external connection has declined and disappeared in all major lineages, but most living tetrapods retain an epiphysis or pineal body. The entire complex is lost only in a very few mammals and in the crocodylians as a group.

Experimental ablation of parts or all of the epiphyseal complex of living ectotherms and endotherms seems to affect thermoregulation or circadian rhythms. Roth and Roth (1980) have suggested that the original function of the complex was control of body temperature, when the chief basis of thermoregulation was behavioral. From this it is argued that progressive loss of the external connection of the epiphyseal complex indicates the advent of endothermy, in forms in which the pineal part of the complex is retained.

The difficulty with this line of reasoning is twofold. First, the function of pineal and parietal bodies remains poorly understood in detail. Second, although all living groups with a parietal foramen and complete epiphyseal complex are ectothermic, loss of foramen and parietal eye has taken place many times in tetrapod history, and the majority of living ectothermic tetrapods, as well as living endotherms, lack both foramen and eye. We therefore feel that it is premature to adduce definitive metabolic or thermoregulatory function from any particular epiphyseal configuration.

#### *Predator-prey ratios*

Because they must expend so much energy on thermoregulation, endotherms (mammals and birds) typically direct only from one to three percent of their assimilated energy to secondary productivity (tissue formation in reproduction

and growth; Golley, 1968). In ectothermic vertebrates, secondary productivity is often more than twenty percent of total assimilated energy, but there can be considerable overlap between the ranges of endotherms and ectotherms in this respect.

Bakker (1972, 1975, 1980) has proposed that these ratios are reflected in the standing crops of animal communities that are in steady state, and that they can be identified in fossil assemblages of predators and their prey. He argues that an assemblage in which the predators constituted only 2 to 3 percent of the animal biomass indicates endothermy in the predators, while a substantially greater ratio indicates ectothermic predators, the thermoregulatory status of the prey being irrelevant. Summaries of his analysis (Bakker, 1975, 1980) indicate that predaceous sphenacodont pelycosaurs constituted 35 to 60 percent of the biomass of their prey (mean ratio = 45% in 12 assemblages without predator concentrations). These ratios are interpreted as a typical ectothermic thermoregulatory pattern in sphenacodont predators. Ratios of 10 to 15 percent are reported for communities of therapsids, but the incision of a single "predator trapping" assemblage would increase the ratio to 24 percent (S.D. = 32.8, n = 6). Ratios of 0.8 and 3.4 percent, respectively, are reported as typical of communities of living and fossil mammals. Bakker (1980) therefore suggests that therapsids had metabolic levels intermediate between those of living endotherms and ectotherms, perhaps being endothermic but regulating body temperature at a lower level than that maintained by most extant birds and mammals.

Both the practicability of estimating community biomasses from fossil assemblages and the interpretation of such estimates have been criticized by Charig (1976), Tracy (1976), Béand and Russell (1980), Farlow (1980), and Hotton (1980), among others. Objections include the difficulty of determining what predators ate which prey; the dependence of biomass turnover on body size; and the questionable reliability of fossilization in preserving true community structure. Predator-prey ratios thus constitute one of the least reliable lines of evidence adduced for endothermy in fossil organisms, and we do not feel that they can be used to draw conclusions about thermoregulatory capacities of therapsids.

#### *Biogeographic Distribution*

Large reptiles are currently restricted to tropical and warm temperate areas, and it is generally assumed that only endotherms can occupy areas

with protracted cold seasons. Bakker (1975, 1980) argues that therapsids could never have dominated the Late Permian faunas of South Africa unless they had been endothermic, because Southern Gondwana lay at high southern latitudes during the Late Permian, and therefore had a very cold climate.

While it is true that South Africa was glaciated near the end of the Late Carboniferous, the ice sheets had disappeared by the beginning of the Early Permian. Many lines of evidence indicate a warm and generally equable climate by Late Permian time (Charig, 1976; Parrish, Parrish, and Ziegler, this volume; Hickey, personal communication, 1981). Marked seasonality is indicated by tree rings, but it was probably wet-dry rather than warm-cold. In addition to the dominant therapsids, the fauna included many large tetrapods that were doubtlessly ectothermic. Such large ectotherms among the Late Permian tetrapods in South Africa negate a cold climate of the time as evidence for therapsid endothermy.

#### *Comparative Physiology of Prototherian and Therian Mammals*

After attaining mammalian status, prototherians did not contribute to the evolutionary sequence leading to marsupials and placentals. Either they had arisen independently from therapsids (Olson, 1959; Simpson, 1959; Kermack, 1967; Mills, 1971), or they diverged from a common stock shortly after it arose from cynodonts in the Middle Triassic (Hopson and Crompton 1969; Crompton and Jenkins 1973, 1979). The traits common to prototherians and therians, therefore, must have either existed in common therapsid ancestors, evolved convergently, or evolved very quickly in concert during the short period before prototherian divergence (Carter, 1957; Hopson, 1969; Jenkins, 1970; Hulbert, 1981). If the number of features shared by prototherians and therians is large, the probability of convergence is small. Are the thermoregulatory mechanisms of extant monotremes similar to those of therians, or do they differ in numerous aspects?

#### THERMOREGULATORY ASPECTS

The body temperature of echidnas and the platypus is maintained at 30°–32° C in their thermal neutral zones (Schmidt-Nielsen, Dawson, and Crawford, 1966; Dawson, 1973; Dawson and Grant, 1980). Although these temperatures are considerably below those of most advanced placentals (38 + ° C) and marsupials (~ 35° C), they

are similar to those reported for several insectivores and edentates (Dawson, 1973; Eisenberg, 1980). Echidnas and the platypus are good thermoregulators during acute cold exposure, maintaining temperature and increasing heat production to match heat loss down to, or below, freezing. However, during long-term exposure to cold, echidnas experience nocturnal decrements of as much as 10° C in body temperature (Augee, 1978). They become torpid when deprived of food. Monotremes are not tolerant of heat stress and become hyperthermic when ambient temperatures rise above 30° C. Standard metabolic rates are low in comparison to those of placentals and marsupials; however, a lower metabolic rate is to be expected as a result of their lower body temperatures. If metabolic rates of all mammals are adjusted to a common temperature, the metabolic levels of echidnas are 46–90 percent of those of advanced eutherians (Schmidt-Nielsen, Dawson, and Crawford, 1966; Augee, 1976; Dawson and Grant, 1980) and those of the platypus are 114 percent (Dawson and Grant, 1980). In comparison, mean values of metabolic levels (after similar thermal correction) of marsupials, edentates, and insectivores are, respectively, 90 percent, 80 percent, and 109 percent (Hulbert, 1980). In contrast, corrected metabolic values of reptiles are only 10–20 percent (Bennett and Dawson, 1976). Since there is considerably variability in metabolic level among different mammalian groups, there is little to differentiate the thermoregulatory ability or metabolic level of monotremes from that of “primitive” mammals in the marsupial-eutherian lineage (Griffiths, 1978). The comparatively low metabolic rates of monotremes seem to be largely a function of body temperature regulated at a low level. A large increment above reptilian metabolic levels has occurred in all mammalian groups, suggesting that this metabolic adjustment was already present in their common ancestors.

#### OXYGEN CONSUMPTION AND TRANSPORT

The levels of oxygen consumption required to support thermoregulation and activity in mammals are beyond the capacities of reptilian systems (Bennett and Ruben, 1979). The evolution of endothermy required an increase in capacities for oxygen delivery and utilization. The increments attained in monotremes are of the same order as in eutherians (summarized in Jenkins, 1970, and Griffiths, 1978). Monotremes possess typical mammalian lungs with intrapulmonary bronchi and alveolar sacs. These lungs are ventilated with a muscular diaphragm. The respira-

tory physiology of echidnas seems to conform to that of typical eutherians (Bently, Herreid, and Schmidt-Nielsen, 1967; Parer and Hodson, 1974). The hematological characteristics of monotremes are typically mammalian. Erythrocytes are non-nucleated, and hematocrits and blood oxygen capacities are equal to, or greater than, those of most eutherians (Johansen, Lenfant, and Griggs, 1966; Parer and Metcalfe, 1967a, b) and are substantially greater than those of reptiles (Pough, 1980b). The monotreme heart is four-chambered, although it retains a distinct sinus venosus (Rowlatt, 1968). Stroke volume and tissue oxygen extraction are similar in echidnas and eutherians (Parer and Metcalfe, 1967c). Heart rate is low in echidnas, in keeping with lower body temperature. Thus, in nearly all features of their oxygen delivery systems, monotremes are essentially similar to eutherians.

#### OTHER FEATURES

In contrast to their similarities in thermoregulatory and aerobic ability, monotremes differ from therians in other features of physiology and anatomy, which supports the idea of a long interval of independent evolution. These features include the neuroanatomical organization of the central nervous system, details of the immune and endocrine systems (e.g., the structure and function of the adrenal cortex), structure of the eye, and myological organization, among others (Jenkins, 1970). A particular feature of differentiation is the oviparous reproductive mode, accompanied by numerous differences in anatomy and physiology. It is noteworthy that these characters, which mark the uniqueness of monotremes, are largely dissociated from thermoregulatory ability and rate of energy utilization, whereas the characters that are shared by extant monotremes and therians involve oxygen transport and metabolic performance.

If the latest common ancestry of monotremes and therians were ectothermic, it would be necessary to postulate independent evolution of a very great number of similar characters in the monotreme and therian lines. These include hair, sweat glands, a four-chambered heart, non-nucleated blood cells, high hematocrit and oxygen-carrying capacity of the blood, alveolar lungs, a diaphragm, and a greatly enhanced metabolic level. Moreover, these features would have had to evolve independently in a very short time, when little change was taking place except in jaw and brain morphology. Such an interpretation is less parsimonious than the view that

physiological and morphological systems associated with endothermy were inherited from advanced therapsids, at least at the level of cynodonts. The gross pattern of mammalian origin indicates that the common features present in the ancestral group were primarily thermoregulatory and energetic, and that modifications of the reproductive, endocrine, nervous, and skeleto-muscular systems (Jenkins, 1970) arose after divergence of prototherians and therians.

#### Conclusions

Our conclusions regarding the various lines of evidence adduced for therapsid endothermy are summarized in Table 1. Two lines of reasoning strongly support the attainment of endothermy in this group: the very large number of traits shared by monotremes and therians that relate to metabolic rate and oxygen transport; and the presence of nasal turbinals in advanced therapsids. We also believe that bone histology is somewhat suggestive of the existence of endothermy. There is clearly a major change that occurred early in therapsid evolution that made the structure of cortical bone more mammal-like. Other lines of evidence are either inconclusive or untenable.

It seems probable that at least the advanced theriodonts had high rates of metabolism and were endothermic. It is not clear, however, whether or not these therapsids were also homeothermic. Monotremes are not homeothermic, at least in continuing cold (Augee, 1978), and the temperatures of many "primitive" therians ap-

**Table 1.—Summary of features proposed to indicate high metabolic rates and endothermy in therapsids**

<i>Feature</i>	<i>Status as indicator</i>
Histological structure of bone	Suggestive
Posture and limb attitude	Inconclusive
Hair	Untenable
Brain size	Untenable
Other anatomical features	
Reduction of lumbar ribs	Untenable
Secondary palate	Untenable
Nasal turbinals	Very suggestive
Epiphyseal complex	Inconclusive
Predator-prey ratios	Inconclusive
Biogeographical distribution	Untenable
Comparative physiology of monotremes and therians	Very suggestive



pear to be rather labile, particularly during activity (Dawson, 1973; Crompton, Taylor, and Jagger, 1978; Dawson and Grant, 1980; Eisenberg, 1980). If therapsid thermoregulation were endothermic, body temperatures may have been low as in living monotremes. However, therapsid body temperatures could also have been as high as those of therians, or higher if the general environment were warmer than it is today, for regulation below ambient temperatures would probably be prohibitively expensive in water loss.

What more general adaptations would have favored the origin of endothermy among therapsids? Skeletal alterations suggestive of increased agility and a more active existence have long been noted as trends typical of advanced therapsids (Colbert, 1958; Olson, 1959, 1971; Van Valen, 1960; Parrington, 1967; Hopson, 1969; Geist, 1972). Limbs were lengthened and rotated under the body, girdles were lightened and re-oriented, and the spinal column became more regionally differentiated. These changes occurred in parallel in many independent phylogenetic lines (Olson, 1959). To the differentiation of skeletal features suggesting enhanced levels of activity, Olson (1959, 1971) related incipient endothermy or progressively more mammal-like thermoregulation.

Both enhanced activity and endothermy are linked to the expansion of aerobic ability (Bennett and Ruben, 1979). Modern reptiles have only very modest capacities for aerobically sustainable activity, and must utilize anaerobic metabolism for even limited levels of exertion beyond slow walking. Such anaerobically supported behavior cannot be sustained, and exhaustion ensues fairly rapidly. Expanded aerobic capacities, involving the enhancement of both resting and maximal rates of oxygen consumption, greatly enlarge the capacities of endotherms for routine activity, and give them a great range of endurance at near-maximum effort.

We believe that it was pressure for increased capacity for activity that selected for higher metabolic rates in this lineage. Increased activity may well have been more important than thermoregulatory considerations, if very warm and equable climates prevailed during the Early Triassic.

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